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Drawings of Scandinavian Plants 101–102

Epilobium L. Sect. Epilobium

Alf Oredsson and Sven Snogerup

OREDSSON, A. & SNOGERUP, S. 1975 07 08. Drawings of Scandinavian Plants 101—102. Epilobium L. sect. Epilobium. — Bot. Notiser 128: 1—7. Lund. ISSN 0006-8195.

Drawings and descriptions are given for *E. hirsutum* L. and *E. parviflorum* SCHREBER.

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In Scandinavia, *Epilobium* L. sect. *Epilobium* is represented by nearly twenty species, sect. *Chamaenerion* TAUSCH by *E. angustifolium* L. (not treated) only. For practical reasons the species can be divided into four groups: (1) native southern; (2) native northern; (3) naturalized North American species; (4) escapes originating from New Zealand. Except for *E. montanum* L. and *E. collinum* C. C. GMELIN the species grow mainly in wet places, but many of them are also found in waste places where the most deviating forms are often found.

Self-pollination dominates in the section but various intermediates are none the less known. They are easily recognized by the more or less reduced seed-setting often in combination with a long period of flowering. Such stands, which are probably of hybrid origin, are found primarily in fens.

Hybrids that have been reported are mentioned, but the current survey concentrates upon the pure species. The descriptions have been prepared on the basis of material from the Scandinavian Herbarium of Lund and observations made in nature. Morphological terms are according to STEARN (1966). Measurements refer to the normal range of variation, as well as extreme values (in brackets). The drawings should be regarded merely as examples, showing characters otherwise difficult to visualize.

According to RAVEN (1968) the chromosome number is 2n=36 in all species of the section, as far as investigated. The standard work by HULTÉN (1971) accounts for most of the distributional records. In two recent papers by SKVORTSOV and RUSANOVITCH (1974) and BERGGREN (1974) the structure of the seed surface is discussed on the basis of scanning electron microscopy. Scanning photomicrographs of seeds will be presented in our final contribution to the current series, as will also a complete list of the literature gone through and a key to the species.

OREDSSON is responsible for the drawings, SNOGERUP for the text.

101. **Epilobium hirsutum** L. 1753

Perennial herb, (30—)70—150(—180) cm high. Stem usually richly branched in middle and upper part, producing several usually 5—20-flowered inflorescences. Stolons hypogean, fleshy, white to reddish or brownish, usually 2—4 mm thick, 5—50 cm long, with opposite, scale-like leaves of varying shape, at end rosuliferous or those produced late in autumn ending in a ± swollen turion.

Stem terete or almost so, near the base 4—10 mm thick, often with short, in-

Fig. 101.

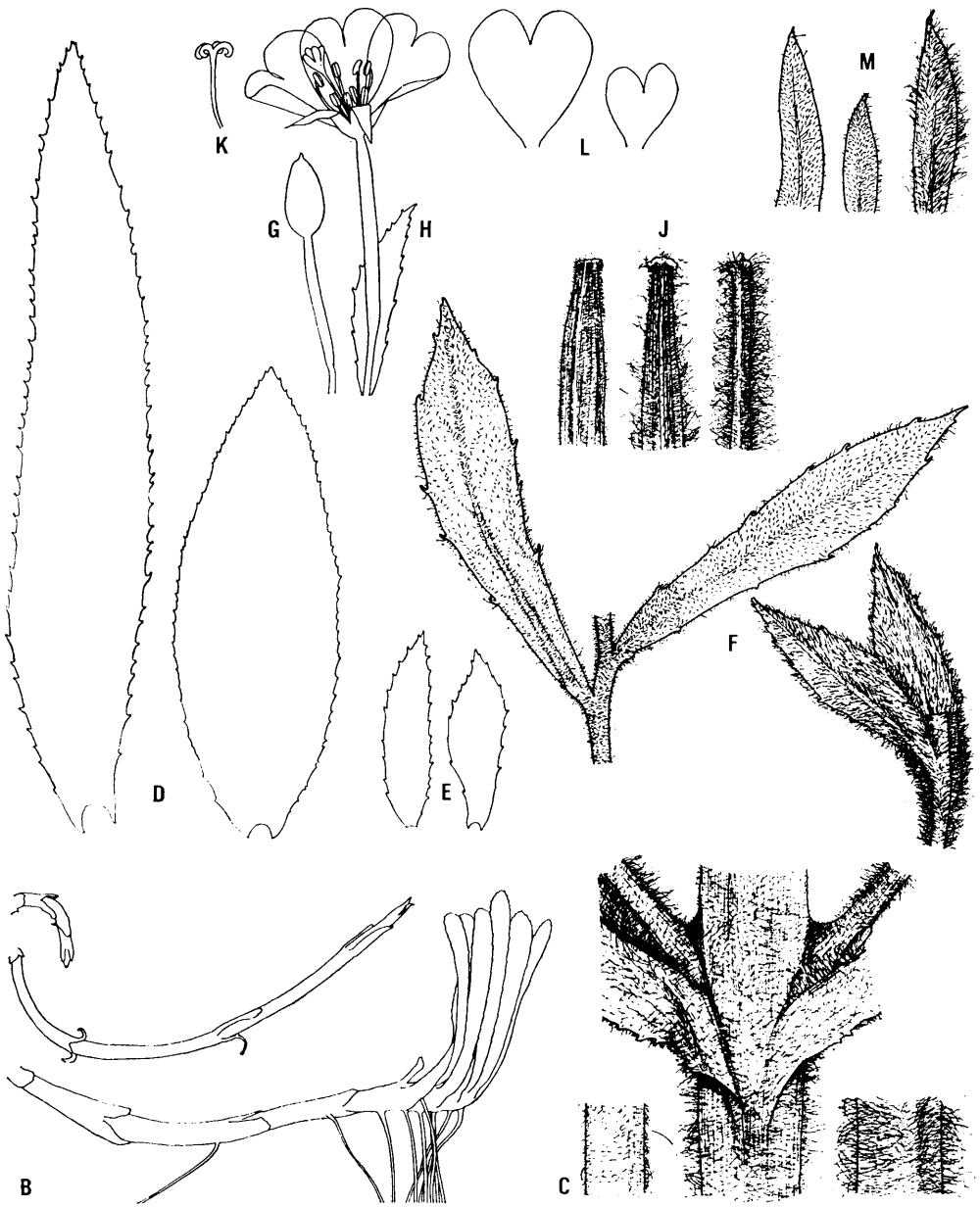

Fig. 101. *Epilobium hirsutum* L. — A: Habit, ×1/3. — B: Stolons, ×1/2. — C: Stem node and stem parts with deviating types of indumentum, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem part and leaves, ×2.5. — G: Bud, ×1. — H: Flower, ×1. — J: Apical parts of capsules, ×2.5. — K: Style, ×1. — L: Petals, ×1. — M: Sepals, ×2.5.

conspicuous raised lines below the midrib of the leaves. Usually densely glandular-pubescent and with numerous patent, evenly distributed often slightly crispulate hairs, rarely the glandular hairs almost lacking and replaced by a dense covering of eglandular hairs; glandular hairs 0.15—0.30 mm, eglandular hairs 1.50—2.50 mm; falling off from older parts of the stem.

Leaves usually all opposite, rarely a few upper ones alternate, all non-petiolate. Basal leaves soon withering; spathulate to lanceolate or ovate. Middle cauline leaves (40—)60—120(—150) mm long, (10—)15—30(—40) mm broad, narrowly ovate or rarely lanceolate, semiamplexicaul and decurrent up to 10 mm, acute to apiculate, serrate with usually unequal, incurved teeth up to 1.5 mm long, serration weaker in the basal part of the margin. Upper leaves smaller, more lanceolate in form. Indumentum of leaves patent to semi-patent, hairs both glandular and eglandular, usually slightly shorter than those on the stem, usually denser on the abaxial side of the midrib.

Bracts large, leafy. Pedicels in bud erect, in flower and fruit erecto-patent. Buds ellipsoidal, mucronate. Sepals 8—13 mm, connate to 1.5—2.5 mm at base, narrowly ovate, apiculate, green with ± reddish veins and margins, usually with glandular hairs only, rarely with ± dense eglandular hairs as well. Petals (10—)15—20(—22) mm, shallowly notched, purplish-red or rarely more reddish-violet. Anthers 1.8—3.0 mm, long filaments 6—9 mm, short filaments 2.5—5.0 mm, usually c. 1/2 as long as the long ones. Style longer than the stamens, stigma 4-lobed, lobes 3—5 mm long, usually recurved in flower, rarely remaining erecto-patent.

Capsule stalk (6—)10—15(—20) mm. Capsule (60—)75—85(—90) mm, either glandular-hairy only or also with ± dense eglandular hairs up to 2 mm long. Seeds ± obliquely ovoidal, flattened on one side, 1.0—1.3 mm long, 0.5—0.6 mm broad, acute at base, neck inconspicuous, surface with c. 30 papillose longitudinal ridges, chalazal hairs c. 50—60, 8—12 mm long. Flower normally protandrous.

E. hirsutum occurs spontaneously along ditches and the margins of streams and ponds as well as in some rich fens in S. Scandinavia, but is also commonly introduced on different types of disturbed ground. It has a wide distribution in Europe, Asia, N. and S. Africa, and is widely spread as a casual established in N. America.

In Scandinavia *E. hirsutum* is common in Denmark and in Skåne, Sweden. There are many localities along the coasts and in the lowlands of Västergötland, Östergötland, Södermanland and Uppland, and it has been locally introduced in Norway, Sweden and Finland as far north as c. 62°N.

Known hybrids: with *E. lamyi, montanum, parviflorum, roseum* and *palustre.*

102. **Epilobium parviflorum** SCHREBER 1771

Perennial herb, (15—)35—90(—120) cm high. Stem in small specimens often simple with a single apical inflorescence, larger ones sparsely to richly branched especially in the upper part, producing several 3—20-flowered inflorescences. Basal rosettes either sessile or especially in the autumn on epigean stolons 0—3(—5) cm long, 0.5—3.0 mm thick, herbaceous but reddish to reddish-violet, rarely pale, with opposite, scale-like, often spathulate leaves. Rosette leaves spathulate, often reddish, subglabrous.

Fig. 102. *Epilobium parviflorum* SCHREBER. — A: Habit, ×1/3. — B: Basal rosettes, ×1/2. — C: Stem node and stem part with other type of indumentum, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem part with leaves, ×2.5. — G: Buds, ×1. — H: Flower, ×1. — J: Apical parts of capsules, ×2.5. — K: Style, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.

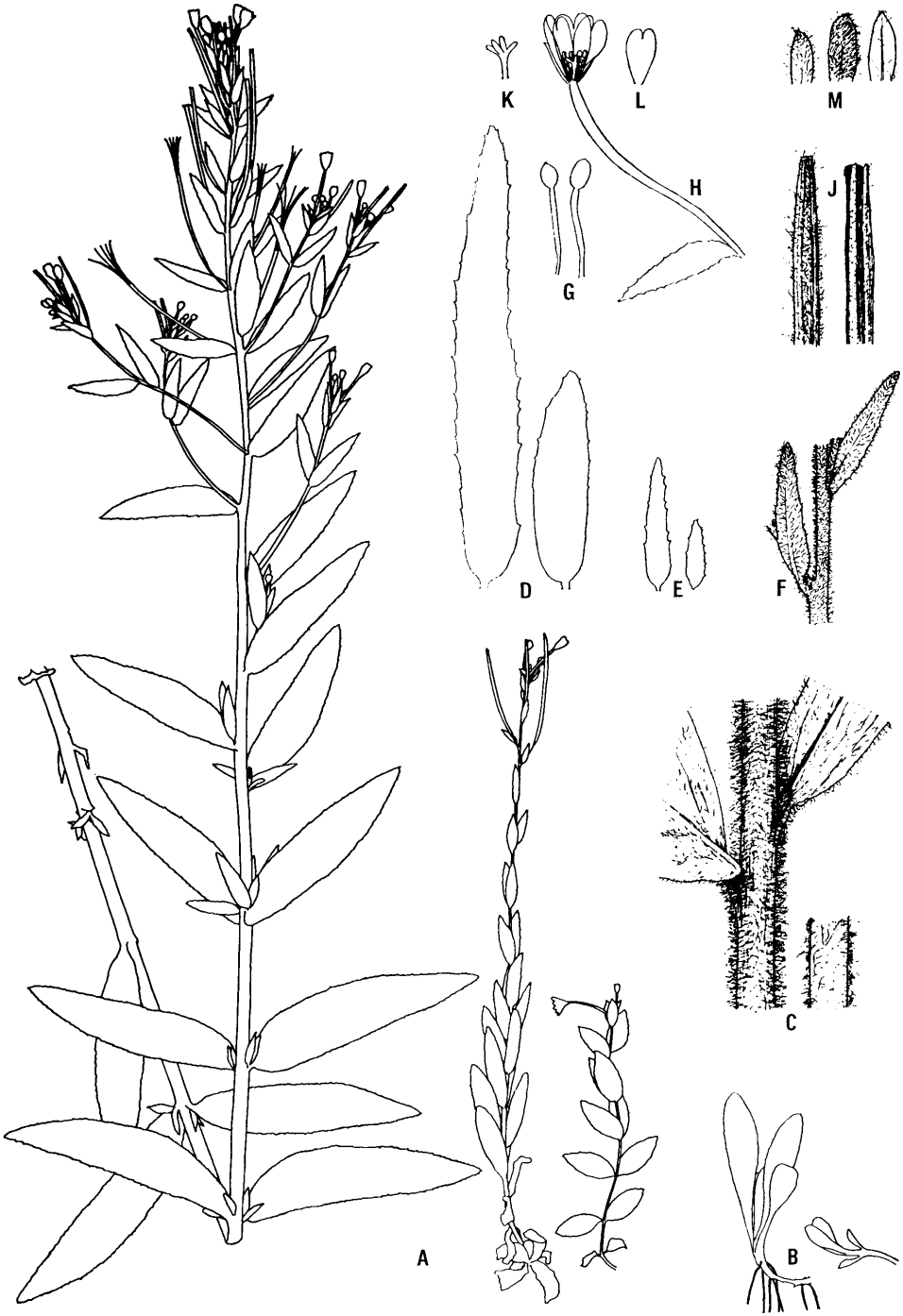

Fig. 102.

Stem terete or almost so, near the base 1—8 mm thick, often with short, inconspicuous raised lines below the midrib of the leaves, with a usually dense indumentum of eglandular, patent but ± crispulate hairs 0.6—1.2 mm long and in the upper part also glandular hairs 0.2—0.3 mm long, indumentum persistent on older parts of the stem though less dense.

Leaves usually opposite in basal and middle parts, alternate above, rarely all ± markedly alternate. Basal leaves soon withering, spathulate to narrowly ovate, rarely elliptical to ovate, usually only 10—15 mm long, entire to sparsely serrate, usually obtuse; petiole up to 15 mm long. Middle cauline leaves (20—)40—120(—140) mm long, (7—)10—20(—30) mm broad, usually narrowly ovate, rarely very narrowly ovate, ovate or lanceolate, acute to apiculate, serrate with usually unequal, patent or ± incurved teeth up to 1.3 mm long, serration weaker towards the base; never decurrent, petiole 1—3(—5) mm long. Upper leaves gradually becoming smaller with longer petioles. Indumentum lacking or sparse on the basal leaves, on the middle cauline leaves consisting mainly of evenly and ± dense eglandular, patent to semi-patent, ± crispulate hairs usually 0.2—0.5 mm long, on the upper leaves fewer eglandular hairs but also ± dense glandular hairs.

Bracts large, leafy. Pedicels in bud erect, in flower erect to erecto-patent, in fruit erecto-patent. Buds ellipsoidal, obtuse, short-mucronate. Sepals (3.5—)5.0—7.0(—7.5) mm, connate to 1.2—2.0(—3.0) mm at base, ovate to narrowly ovate or rarely lanceolate, acute to apiculate, green with ± reddish margins and veins, usually with eglandular hairs only, more densely hairy towards apex. Petals (5—)7—9(—11) mm, with a sharp, 1.5—2.5 mm deep notch, purplish-pink to reddish-violet. Anthers 0.6—1.0 mm, long filaments 3—6 mm, short filaments 1.8—4.0 mm, usually c. 2/3 as long as the long ones. Style about equal in length to the long stamens, stigma 4-lobed, lobes 1.5—2.0 mm, flat, usually remaining erecto-patent in flower.

Capsule stalk (7—)12—15(—25) mm. Capsule (40—)50—60(—75) mm long, either with glandular hairs only or with both glandular hairs 0.1—0.2 mm long, and eglandular 0.5—1.5 mm long, rarely with eglandular hairs only or subglabrous. Seeds obliquely obovoidal to almost ellipsoidal, flattened on one side, 0.9—1.2 mm long, 0.45—0.55 mm broad, obtuse at base, neck inconspicuous, surface densely papillose, but papillae not in visible lines, chalazal hairs c. 35—50, (5—)6—7(—8) mm long. Flower homogamous.

E. parviflorum occurs along ditches, banks of streams and shores of ponds and lakes as well as in some rich fens and on open ground, wet fields and different types of disturbed ground, mainly on rich soils. Its spontaneous distribution includes Europe, W. and SW. Asia and N. Africa, but it has also been reported as a casual in other areas and as naturalized in N. America.

In Scandinavia *E. parviflorum* is common in Denmark, in the Swedish provinces of Skåne, Öland, Gotland and eastern Södermanland and Uppland and on Åland. In other parts of C. and S. Sweden the species is scattered. It does not occur spontaneously north of 61°N. It has only been reported from isolated localities on the mainland of Finland and in the Oslo area of Norway.

Known hybrids: with *E. hirsutum, roseum, palustre, obscurum, lamyi, adnatum, adenocaulon* and *glandulosum*.

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Revision of the Genus Cardamine L. (Cruciferae) in South and Central America

Bo Sjöstedt

SJÖSTEDT, B. 1975 07 08. Revision of the genus Cardamine L. (Cruciferae) in South and Central America. — Bot. Notiser 128: 8—19. Lund. ISSN 0006-8195.

From South and Central America and the West Indies 97 species of *Cardamine* have been described. The following taxa are recognized: *C. africana* L., *C. bonariensis* JUSS. ssp. *bonariensis* and ssp. *eremita* (STAND. & STEYER.) BO SJÖSTEDT comb. nov., *C. chenopodiifolia* PERS., *C. geraniifolia* (POIR.) DC. and *C. glacialis* (FORST.) DC. *C. chenopodiifolia* and *C. geraniifolia* show a narrow amplitude of variation, while the others are more complex. Other names of species are reduced to synonymy.

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The name *Cardamine* appeared for the first time in literature in 1549 in Liber II by JAKOB COUPYLO. LINNAEUS established the genera *Cardamine* and *Dentaria* (1753). CRANTZ (1769) united these two genera under the name of *Cardamine* L. For more detailed studies of the history of the genus *Cardamine* up to 1903 see SCHULZ (1903 pp. 280—624). He considered this genus to have 117 species distributed in all the continents.

In South and Central America SCHULZ distinguished 27 species of *Cardamine* which he considered to belong to the sections *Cardamine, Paphyrophyllum* and *Macrocarpus.* Three of these species he had described himself. At the same time he gave 41 other species of this genus the rank of subspecies or form. E. GILG and R. MUSCHLER (1909) reported 23 new species of *Cardamine* from this area. But these authors drew attention to the fact that only eleven of those species had been defined. Since 1903 ten other species of *Cardamine* from South and Central America and the West Indies have been described. Up to now 37 species of this genus have been held to exist in this area.

The author, who has carried out a detailed examination of extensive material (850 specimens), distinguishes five different species, *C. africana* L., *C. bonariensis* JUSS. ex. PERS., *C. chenopodiifolia* PERS. and *C. glacialis* (FORST.) DC. which belong to the section *Cardamine* and *C. geraniifolia* (POIR.) DC. which belongs to the section *Macrocarpus.* According to SCHULZ species of section *Cardamine* have short siliquae and thin placentae while the section *Macrocarpus* O. E. SCH. is distinguished by long siliquae and thick placentae.

The Herbaria cited are abbreviated according to HOLMGREN & KEUKEN, Index Herbariorum (1974). A list with localities of specimens can be ordered from the author.

KEY TO THE CARDAMINE SPECIES IN SOUTH AND CENTRAL AMERICA AND THE WEST INDIES

1. Species with fruits under and above soil ..... *C. chenopodiifolia*
1. Species with fruits above soil only 2

2. Leaves doubly or simply pinnate, deeply incised. Seeds 3.0—3.2 mm long . *C. geraniifolia*
2. Leaves simply pinnate 3
3. All leaflets alike ..... *C. bonariensis* ssp. *eremita*
3. Lateral and terminal leaflets different 4
4. Seeds always longer than 2.0 mm. Siliquae 16—65 mm long. Petals white—purple, 2—14 mm long. Leaflets triangular—ovate—linear. Leaf margins serrate—dentate—crenate. Leaflets often mucronate ..... *C. africana*
4. Seeds 1.8 mm or shorter. Siliquae 7—35 mm long. Petals always white, 2.5—10 mm long. Leaflets rounded—elliptic—linear. Leaf margins crenate—undulate—entire. Leaflets seldom mucronate 5
5. With bracts. Seeds 0.8—1.2 mm long ..... *C. bonariensis* ssp. *bonariensis*
5. Without bracts. Seeds 1.4—1.8 mm long. ..... *C. glacialis*

1. **C. africana** L.

LINNAEUS (1753) Spec. plant. ed. 1, II p. 655. — Lectotype: HERMANN (1698) Paradisus Batavus Fig. p. 202.

ICONS: PLUKENET (1696) Phytographia p. 252. — P. HERMANN (1698) Paradisus Batavus p. 202. — S.n. *C. borbonica* PERS., WIGHT (1843—45) Ic. Pl. Ind. Or. III t. 941. — S.n. *C. corymbosa* HOOK. FIL., HOOKER, Ic. Pl. Ind. Or. VII t. 686. — S.n. *C. borbonica* PERS., WIGHT (1846) Spicil. Neilgher I t. 9. — S.n. *C. picta* HOOK., HOOKER (1847) London Journ. Bot. VI t. 12. — S.n. *C. Jamesonii* HOOK., ENGLER (1903) bot. Jahrb. XXXXII t. 7 Fig. 52. — S.n. *C. Johnstonii* OLIV., ENGLER (1903) bot. Jahrb. XXXII t. 6 Fig. 37. — S.n. *C. chilensis* DC., ENGLER (1903) bot. Jahrb. XXXXI t. 9 Fig. 4. — KOORDERS (1912) Exkursionsfl. II p. 289. — FYSON (1915) Nilgiri et Pulney Hilltope II 13. — L. BOLUS (1923) Nature Notes Wild. Fl. Prot. Soc. S. Africa No. 2. — S.n. *C. ovata* BENTH., ROLLINS (1945) Annals of the Missouri Bot. Garden 35 p. 100.

SYNONYMS: *C. borbonica* PERS. (1807) Syn. II p. 195. — *C. anteniquana* BURCH. (1821) apud DC. Syst. Nat. II p. 252, nomen falsum. — *C. ternata* BORY. (1821) apud DC. Syst. Nat. II p. 252, nomen nudum. — *C. rubifolia* SMITH (1821) apud DC. Syst. Nat. II p. 252, nomen nudum. — *C. chilensis* DC. (1821) Syst. Nat. II p. 254. Holotype: RUIZ et PAVON n. 1104 (BM)! — *C. Burchelli* SPRENGEL (1825) Syst. vet. p. 886. — *C. Wightiana* WALLISH (1828) Catal. n. 4780, nomen nudum. — *C. allevia* COMMERS. (1832) apud DC. Syst. Nat. II p. 252, nomen nudum. — *C. ovata* BENTH. (1845) Plant. Hartweg. p. 158. Holotype: HARTWEG n. 881 (K)! — *C. obliqua* HOCHST. (1847) apud A. RICHARD, Tent. Fl. Abyss. p. 196. — *C. picta* HOOK. (1847) Journal of Arn. Arb. Lond. Jour. Bot. VI p. 292 Tab. 12. Holotype: PURDIE coll. 1846. — *C. Jamesonii* HOOK. (1847) Lond. Jour. Bot. VI p. 293. Holotype: JAMESSON n. 88 (NY)! Isotype: (BM)! — *C. armoracioides* TURCZ. (1854) Bull. Soc. Imp. Nat. Moscou XXVII p. 293. Holotype: LINDÉN n. 1416 (Charkow). Isotypes: (BM, K)! — *C. nevadensis* TURCZ. (1854) Bull. Soc. Imp. Nat. Moscou XXVII p. 295. Holotype: FUNCK & SCHLIM n. 1542 (P)! — *C. punicea* TURCZ. (1854) Bull. Soc. Imp. Nat. Moscou XXVII 2: 295. Holotype: FUNCK et SCHLIM n. 1542 (G). — *C. tolimensis* PL. & LIND. (1862) Ann. Sci. Nat. Ser. IV: 17 p. 59. Holotype: GOUDOT (P)! — *C. ibaguensis* TR. & PL. (1862) in Ann. Sci. Nat. Ser. IV 17 p. 60. — *C. pulchra* LIND. & PLANCH Pl. Coulomb 12. — *C. javanica* MIQ. (1873) Illustr. Fl. Archip. Ind. 17 Tab. 10. — *C. Johnstonii* OLIVER (1887) Transact. Linn. Soc. Lond. Ser. 2 p. 328. Holotype: JOHNSTON ex. coll. in Kilimandjaro 1884 (K)! — *C. speciosa* BRITTON (1889) Bull. Torr. Bot. Club. 16 p. 16. Holotype: RUSBY n. 1199 (NY)! — *C. Lehmanni* HIERON. (1895) Engl. bot. Jahrb. 20 Beiblatt 49 p. 16. Holotype: LEHMANN n. 4759 (B). Isotypes: (K, S)! — *C. ecuadorensis* HIERON. (1895) Engl. bot. Jahrb. 20 Beiblatt 49 p. 19. Holotype: LEHMANN n. 4826 (B)! — *C. fulcrata* GREENE (1897) Pittonia III p. 155. Holotype: PALMER n. 4989 (B). Isotypes: (BM, C, K, P, S)! — *C. Aschersoniana* O. E. SCH. (1903) Engl. bot. Jahrb. 32 p. 410. Holotype: GOLLMAR n. 369 (B). — *C. innovans* O. E. SCH. (1903) Engl. bot. Jahrb. 32 p. 417. — *C. Bradei* O. E. SCH. (1923) Notizblatt VIII p. 328. Holotype: A. C. BRADE n. 2305 (B). — *C. porphyrophylla* EKMAN (1925) Fedde's Repertorium 21: 62. Holotype: EKMAN n. 18502 (S)! — *C. Albertii* O. E. SCHULZ (1927) Notizblatt Berlin p. 342. Holotype: KILLIP et SMITH n. 15595 (B). Isotype (K)! — *C. ocoana* O. E. SCHULZ (1933) Fedde's Repertorium 32 p. 84. Holotype: EKMAN n. 11702 (S)! — *C. rhizomata* ROLLINS (1940) Journ. Arn. 21 p. 392. Holotype: C. V. PENLAND et R. H. SUMMERS n. 870 (GH)! — *C. jejuna* STANDL. & STEYERM. (1944) Field. Mus. Bot. 23 p. 54. Holotype: STANDLEY n. 50569 (F)! — *C. balneriana* STANDL. & STEYERM. (1944) Field. Mus. Bot. 23 p. 157. Holotype: STANDLEY n. 83332 (F)!

Perennial herb with a suffruticose root up to 6 mm thick. Stolons sometimes occur. The whole plant glabrous or more or less covered with hairs. Stem more or less branched, mostly pale green or very seldom purple at the base, 2—9 dm high. Leaves pale to dark green, sometimes purple below, pinnate, 3—13 leaflets on each leaf. Lower leaves petiolate. Upper leaves mostly sessile. Leaflets lanceolate—triangulate—ovate—elliptic, apex obtuse or mucronate. Terminal leaflets always petiolate, cuneate—truncate, seldom rounded at base, 2—14 cm long, 1—4 cm broad. Margins of the leaflets serrate—dentate—crenate.

Inflorescence racemose, with or without bracts. Sepals green to purple, with transparent margins, oblong—elliptic, glabrous or very seldom hairy, 2—6 mm long. Petals white—pinkish—purple, short-petiolate, oblong—spathulate, 2—14 mm long. Peduncles 2—23 mm long. Ripe siliquae 16—65 mm long, 1—3 mm broad. Pedicels 8—37 mm long. Styles 1—6 mm long. Seeds reticulate, elliptic, 2—3 mm long, 1—2 mm broad.

LINNAEUS (1753) described *C. africana,* but as early as 1696 this species had been made known through PLUKENET. He gave the following description: "Nasturtium Africanum floribus albis spicatis et foliis ternis Christophorianus facie." In Phytographia there is also a picture of *C. africana* L. but this is rather indistinct. PLUKENET had collected the reproduced specimen in Hortus Reg. Hampton. PAULUS HERMANN (1698) gave a detailed description of this species and furthermore made an excellent picture of *C. africana* L. in Paradisus Batavus, chosen here as lectotype. LINNAEUS in his description referred to HERMANN's picture.

DE CANDOLLE (1821) described *C. chilensis* and emphasized that the species had hairy leaflets with crenate margins, while *C. africana* L. had glabrous leaflets with serrate margins. But in his description LINNAEUS did not mention whether the leaves of *C. africana* L. were hairy or not (cf. Fig. 1). BENTHAM (1845) studied specimens of *Cardamine* from Colombia and on the basis of that material described *C. ovata.* He pointed out that the margins of the leaflets of that species were incisedly dentated as opposed to those of *C. africana* L. which were dentate. BENTHAM said further: "Raceme seldom is furnished with leaves." In spite of this statement SCHULZ distinguished between *C. ovata* BENTH. and *C. africana* L. by saying that the former always had bracts, the latter never.

TURCZANINOV (1854) described *C. nevadensis* TURCZ. on the basis of a specimen with white flowers from the state of Merida in Venezuela. In the same year he studied another specimen of *Cardamine* from Merida, but this had violet flowers, and he considered it to be a new species: *C. punicea* TURCZ. (cf. further discussion). Furthermore TURCZANINOV said in his description: "due to the fact that the flowers are violet to purple coloured it is allied to *C. picta* HOOK.". He consequently realized that *C. punicea* TURCZ. and *C. picta* HOOK. were closely related, but did not consider them to be the same species. HIERONYMUS (1895) described *C. Lehmanni* HIERON. based on a specimen from the province of Cauca in Colombia. He said that it was allied to *C. ovata* BENTH., *C. angulata* HOOK. and *C. fulcrata* GREENE, which indicates that earlier delimitations of the species within *C. africana* L. have been to narrow.

SCHULZ (1903) described *C. innovans* O. E. SCH. He also argued that it was allied to *C. fulcrata* GREENE but that it differed in its leafless raceme (cf. *C. ovata* BENTH.). In 1928 SCHULZ described *C. albertii* O. E. SCH. based on a specimen from the province of Santander in Colombia. He argued that the species was closely allied to *C. Jamesonii* HOOK. from which it differed in having 1—2 pairs of leaflets and smaller flowers. The latter has up to 4 pairs of leaflets on each leaf. In

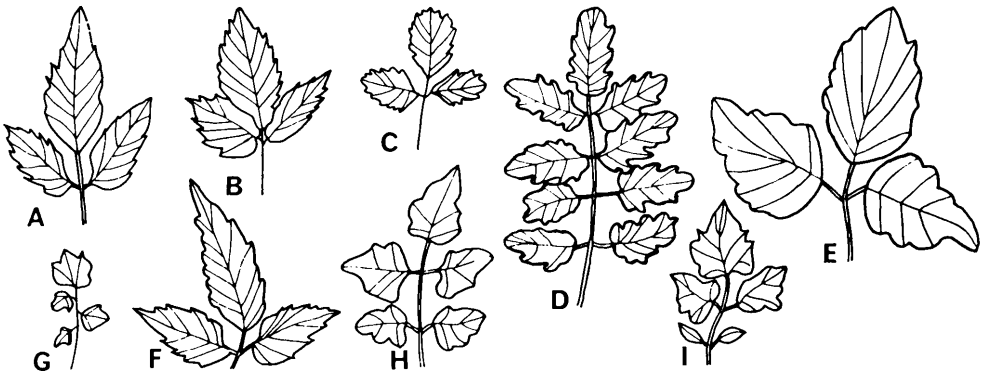

Fig. 1. Leaves of South and Central American specimens of *Cardamine africana*. — A: EKMAN n. 5431. — B: BUCHTIEN n. 455 (as *C. ovata*). — C: ASPIUND n. 7554 (as *C. ovata*). — D: VON SNEIDERN n. 1781, (as *C. Jamesonii*). — E: MOSÉN n. 395. — F: VON TÜRCKHEIM n. 3030. — G: EKMAN n. 11702 (as *C. ocoana*). — H: EKMAN n. 10110 (as *C. Jamesonii*). — I: EKMAN n. 10054 (as *C. Jamesonii*). — All ×0.5.

my opinion *C. Albertii* O. E. SCHULZ is more closely related to *C. ovata* BENTH. than to *C. Jamesonii* HOOK. SCHULZ (1933) studied specimens of *Cardamine* from Haiti and on the basis of these described a new species, *C. ocoana* O. E. SCHULZ. Among other things he pointed out that this species often produced rosette leaves from stolons. He considered this species to be allied to *C. Jamesonii* HOOK., differing from the former in having larger lateral leaflets distinctly lobed and with long petioles. STANDLEY and STEYERMARK (1944) described *C. balneriana* STAND. & STEYER. on the basis of a specimen collected in Guatemala. They said, among

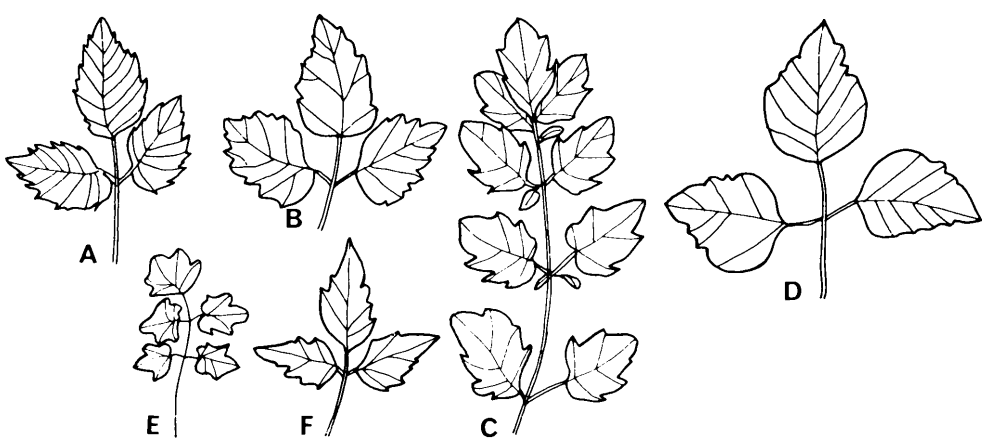

Fig. 2. Leaves of African specimens of *Cardamine africana*. — A: HAFSTRÖM n. 511. — B: O. HEDBERG n. 1531. — C: FRIES & FRIES n. 1179 (as *C. Johnstonii*). — D: EKBLOM n. 106. — E: E. SCHELPE n. 2718 (as *C. Johnstonii*). — F: Y. SJÖSTEDT (as *C. Holtziana*). — All ×0.5.

other things, that it was an unusually distinctly separate species, without doubt related to *C. fulcrata* GREENE and *C. innovans* O. E. SCHULZ, but differing from both in the great number of leaflets.

DISCUSSION BASED ON HERBARIUM MATERIAL. *C. africana* L. shows very broad amplitudes of variation in both floral and vegetative characters.

Stem. The length of the stem varies as a rule between 20 and 90 cm. But on one label is written: "Herba caule tenuiprolonga 15-pedali subvolubili." (On Chimborazo in Ecuador.)

Leaves. The lower side of the leaves is usually green, rarely purple as in the case of the specimen EKMAN n. 18502. EKMAN considered this divergence to be so important that he described the new species *C. porphyrophylla* EKMAN on the basis of that specimen. But it was a modification (growing on cliffs). Corresponding changes of colour have been observed by me on plants of *C. chenopodiifolia* PERS. and *C. hirsuta* L., which I have grown in sand exposed to sun. Both DE CANDOLLE and BENTHAM tried to separate species of *Cardamine* on the basis of the fact that the margins of the leaflets could be serrate or dentate, but I have found both types of serration on one and the same specimen in three cases, viz. HOLM et ILTIS n. 5444 (P), ASPLUND n. 20302 (S) and HEYDE et LUXE n. 2993 (B, K).

Petals. The length of the petals also shows considerable variation, 2.5—14 mm. The colour varies from white to pink or violet. (note LEHMANN n. 4825 collected in Loja, Ecuador: "Blüten weiss oft rosa." Shorter petals are usually white, while a violet colour is more frequent in longer ones. Specimens with 3 or 5 leaflets on each leaf often have shorter (2.5—9 mm) petals than those with seven or more (4—14 mm), but there is a great amount of overlapping (Fig. 3).

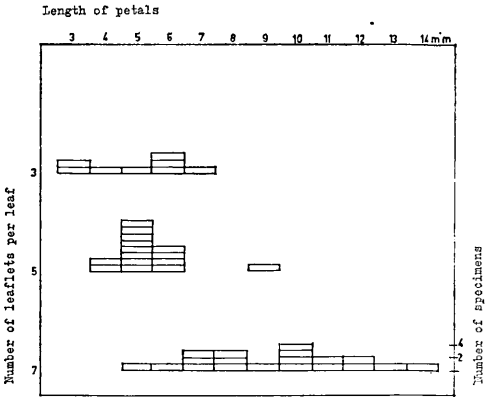

Fig. 3. Length of petals of specimens of *Cardamine africana* with varying number of leaflets on lowest stem-leaf).

C. africana L. has a continuous variation as regards the shape and size of petals and leaves, and I therefore consider this species to be a complex.

DISTRIBUTION. *C. africana* L. is a pantropical species. It also occurs in Mexico, Africa, India and the East Indies. It is striking that *C. africana* L. in Africa and the East Indies is very similar to those occurring in South America (cf. Figs. 1 and 2).

2. **C. bonariensis** JUSSIEU ex PERS.

PERSOON (1807) Syn. II p. 185. — Holotype: in JUSSIEU's herb. (P!).

ICONS: O. E. SCHULZ (1903) Engler bot. Jahrb. t. 10 Fig. 2. s.n. *C. flaccida* CHAM. & SCHL.

SYNONYMS: *C. flaccida* CHAM. & SCHL. (1826) Linnaea I p. 21. — *C. nasturtoides* BERTERO (1829) Merc. Chil. p. 600, nomen nudum. — *C. Berro* STEUD. (1840) Nomencl. Bot. 2 ed. I p. 280, nomen nudum. — *C. nasturtifolia* STEUD. (1840) l.c., nomen nudum. — *C. hirsuta* HOOK. & ARN. (1841) Bot. Beecheys Voy. non L. — *C. laxa* BENTH. (1845) Pl. Hartweg. p. 158. Holotype: HARTWEG n. 880 (BM)! — *C. ramosissima* STEUDEL (1856) Flora XXXIX p. 409. — *C. minima* STEUDEL (1856) Flora XXXIX p. 410. Holotype: LECHLER n. 1811 (K)! — *C. alsophila*

PH. (1859—60) Linnaea XXX p. 186. — *C. demissa* PL. & TR. (1862) Anal. Sc. Nat. ser. XVII p. 60. — *C. axillaris* WEDD. (1864) Anal. Sc. Nat. 5 ser. I p. 291. Holotype: in SGO! — *C. marginata* PH. (1865) Anal. Univ. Chil. XXVII p. 324. Holotype: SGO n. 49376 (SGO)! — *C. andicola* PH. (1891) Verzeich. Pfl. Prov. Antofagasta. Holotype: in SGO! — *C. bracteata* PH. (1893) Anal. Univ. Chil. LXXXI p. 85. Holotype: in SGO! — *C. micropetala* PH. (1893) Anal. Univ. Chil. LXXXI p. 76. Holotype: SGO n. 49306. — *C. caespitosa* PH. (1893) Anal. Univ. Chil. LXXXI p. 79. Holotype: in SGO! — *C. tridens* PH. (1893) Anal. Univ. Chil. LXXXI p. 79. Holotype: SGO n. 63882 (SGO)! — *C. Killipii* O. E. SCHULZ (1927—28) Notizblatt Bot. Gart. Berlin 341. Holotype: n. 15596 E. P. KILLIP et C. SMITH (NY)!

Nasturtium turfosum KUNZE apud WALP. (1843) Nov. Act. Acad. Caes. Leop.-Carol. XIX 1 Suppl. 247. — *Nasturtium radicans* WALP. l.c.

C. bonariensis JUSS. ex PERS. consists of two subspecies, viz. ssp. *bonariensis* and ssp. *eremita* (STANDL. & STEYER.) BO SJÖSTEDT. Common to the two taxa is that they are perennial herbs, that they have spathulate petals (overlapping lengths) and petiolate leaves.

DIAGNOSTIC CHARACTERS OF C. BONARIENSIS SSP. BONARIENSIS AND SSP. EREMITA

ssp. *bonariensis*	ssp. *eremita*
Perennial herb.	Perennial herb.
Stem ± hairy, 4—60 cm high, weak, usually creeping.	Stem glabrous, 3—20 cm high, not creeping.
Leaves petiolate, leaf stalk up to 4 cm long.	Leaves petiolate, leaf stalk up to 1.5 cm long.
3 to 9 leaflets on each leaf.	5 to 7 leaflets on each leaf.
Leaflets petiolate, linear—ovate, cuneate—truncate at base, apex obtuse—mucronate.	Leaflets sessile, linear—lanceolate, cuneate at base, apex obtuse—mucronate.
Leaf margins dentate—lobate—entire.	Leaf margins entire.
Terminal and lateral leaflets not alike. Terminal ones cuneate—truncate at base, 5—20 mm×4—19 mm. Lateral ones cuneate—oblique at base, 2—13 mm× 1.5—10 mm.	All leaflets alike, 3—7 mm×1—2.5 mm.
Inflorescence with bracts, raceme.	Inflorescence without bracts, raceme.
Sepals pale green, oblong—elliptic, 1.3—2.2 mm long.	Sepals pale green with white margins with a purple tinge, oblong, 2.5 mm long.
Petals white, oblong—spathulate, 2.5—5.0 mm long.	Petals white, spathulate, 5—6 mm long.
Siliquae 7—22 mm×0.8 mm.	Siliquae 20—27 mm×10 mm.
Style 0.8—1.7 mm long.	Style 1—1.8 mm long.
Seeds flat, ellipsoid, reticulate, 0.8—1.2 mm× 0.6—0.9 mm.	Ripe seeds not seen.

The greatest difference between the two taxa is that in *C. bonariensis* JUSS. ex PERS. the lateral and terminal leaflets differ, while all leaflets of *C. eremita* STANDL. & STEYER. are alike. I consider this difference to be too unimportant to distinguish between two species, but on the other hand I consider them to belong to different subspecies. The former always grows in damp places such as along brooks and in moist meadows, while the latter grows on cliffs.

C. bonariensis JUSS. ex PERS. ssp. **bonariensis**

DISCUSSION BASED MAINLY ON DESCRIPTIONS. PERSOON and JUSSIEU (1807) described *C. bonariensis* JUSS. ex

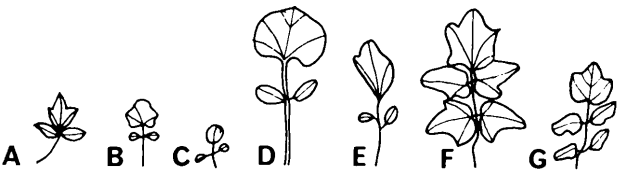

Fig. 4. Leaves of *Cardamine bonariensis*. — A: SKOTTSBERG n. 251 (as *C. flaccida*). — B: FAGERLIND n. 2040. — C: HAMMARLUND n. 156 (as *C. flaccida*). — D: SPARRE n. 348 (as *C. flaccida*). — E: FAGERLIND n. 972. — F: SKOTTSBERG n. 435 (as *C. flaccida*). — G: SPARRE n. 2260 (as *C. flaccida*). — All ×0.5.

PERS. on the basis of a specimen in JUSSIEU's herbarium collected in Buenos Aires. I wish to point out the following information in the description: "lower leaves 3-foliate, leaflets almost rounded, upper leaves obtuse, trilobate, flowers axillar." O. E. SCHULZ looked upon *C. bonariensis* JUSS. ex PERS. as a subspecies of *C. flaccida* CHAM. & SCHL., but this species was not described until 1826. According to present rules of nomenclature *C. bonariensis* JUSS. ex PERS. is the correct name of this species. In the diagnosis for *C. flaccida* CHAM. & SCHL. the following should be noted: "Raceme always with axillar leaves at the base." The leaflets are irregularily crenate and 3—7, but the authors added that the leaflets are very variable (cf. Fig. 4). BENTHAM (1845) studied *Cardamine* specimens from the province of Cauca in Columbia and on the basis of these described *C. laxa* BENTH. The description said among other things: "Leaflets 3—7, petiolate, reniform—ovate —oblong", so the number of leaflets is the same as in *C. flaccida* CHAM. & SCHL., while some leaflets are almost round as in *C. bonariensis* s.str. STEUDEL (1856) described *C. ramosissima* STEUDEL (from Chile). This species had 3—5 leaflets on each leaf and they are crenate or entire. STEUDEL (1856) also distinguished *C. minima* STEUD. as a new species. This species also has 3 or 5 leaflets on each leaf. They were almost round with entire leaf margins.

DISCUSSION BASED ON HERBARIUM MATERIAL. The number of leaflets on each leaf varies from 3—9 on the lowest leaves. The inflorescence always has bracts. The length of the petals varies from 2.5 to 5.0 mm. The length of the siliquae shows a wide amplitude of variation (7—30 mm).

DISTRIBUTION. *C. bonariensis* ssp. *bonariensis* occurs from El Salvador in the north to Chile in the south and in Brazil, Uruguay and Argentina. It grows along brooks or in damp meadows from 50 to 4,500 m.

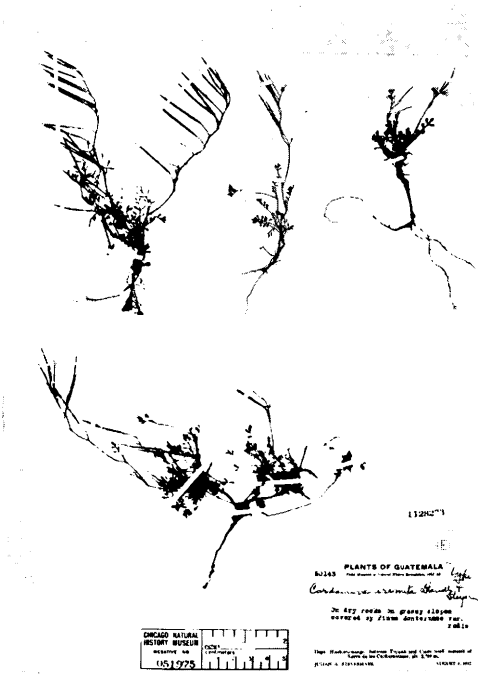

Fig. 5. *Cardamine bonariensis* ssp. *eremita* (holotype, F).

C. bonariensis JUSS. ex PERS. ssp. **eremita** (STANDL. & STEYER.) BO SJÖSTEDT

C. eremita STANDLEY & STEYERMARK (1944) Field. Mus. Pub. Bot. 25: 53 1944. — Holotype: J. A. STEYERMARK n. 50143 (F)!

DISTRIBUTION. This subspecies has only been found in the mountains of Cuchumatanes in the central parts of Guatemala at 3,300—3,700 m. on cliffs in a pine forest.

Guatemala: STEYERMARK n. 50143, 51975 s.n. *C. eremita* STANDL. & STEYERM. Dept. Huehuetenango: between Tojquia and Caxin bluff, summit of Sierra de los Cuchumananes, alt. 3,700 m. On dry rocks and grassy slopes covered by *Pinus Montezumae* var. *rudis* 6 VIII 1942. (F).

3. **C. chenopodiifolia** PERS.

PERSOON (1807) Syn. II p. 195. — Holotype: COMERSSON (P)!

SYNONYMS: *Heterocarpus fernandeziana* PHILIPPI (1856) in Bot. Zeit. XIV p. 641 et Anal. Univ. Chil. p. 164. Phototype in SGO! — *C. argentina* SPEGAZZINI (1896) Contribution al estudio de la flora Minist. de Orb. Publ. de la prov. de Buenos Aires. Holotype: SPEGAZZINI n. 829 (SI).

ICONS: ST. HILAIRE (1829) Fl. Bras. Merid II t. 106. — ENGLER-PRANTL. (1891) Nat. Pflanzenfam. III: 2 Tab. 119. — O. E. SCHULZ (1903) Engler Jahrb. XXXII t. 7 Figs. 1—5, 22—30, 50. — VALENOVSKY (1910) Vergl. Morphol. Pfl. III p. 1074. — HEGI (1903) Fl. Mittel-Eur. IV p. 69. — PHYSIS (1916) p. 249. — MASSART et al. (1922—23) Mission Biol. Belge au Brazil I Fig. 89.

Annual herb. The whole plant more or less densely covered with hairs. Stem 5—48 cm long. Basal leaves petiolate, pedicels up to 5 mm long. Upper leaves sessile. Leaves elliptic—obovate, apex rounded, leaves dentate—undulate—entire (cf. Fig. 6), cuneate at base, 2—11 cm long, 0.8—4.5 cm broad. Peduncles without bracts. Inflorescence a raceme. Sepals pale to dark green, oblong. Petals white, spathulate, 3—4 mm long. Seeds flat, ellipsoid, winged, normal seeds 2.0—2.6 mm long, 1.5—1.8 mm broad. Geocarp seeds 3.0—3.2 mm long, 2.6—3.0 mm broad.

MORPHOLOGY. *C. chenopodiifolia* PERS. displays a very narrow amplitude of variation. The margin of the leaves varies from entire to dentate, but all the specimens I cultivated show a tendency to form leaflets. The most interesting thing about this species is that it has geocarpous fruits (with only two seeds).

DISTRIBUTION. *C. chenopodiifolia* PERS. occurs in Bolivia, Brazil, Paraguay, Argentina and Chile. It grows in pasture and in shady woods.

CULTIVATION EXPERIMENT. An experiment was carried out in the garden "Bergianska trädgården" in Stockholm to find out the possibility of modification. The seeds were sown in pots filled with sand or soil. When the plants were some centimeters high they were repotted. Half of the pots were shaded by some open stakes. The other pots were not shaded. Most of the plants showed little modification, but the unshaded plants in sand showed a marked difference in height, 3.5 cm as compared with about 20 cm. Only one "dwarf" plant developed flowers and only one siliqua (4 mm long) was formed. On the others the length of the siliquae varied from 20 to 26 mm. The leaves were larger on plants growing in shade. The leaves showed a variation

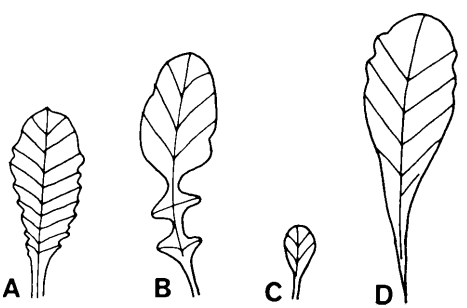

Fig. 6. Leaves of *Cardamine chenopodiifolia*. — A: LINDMAN n. 339. — B: Specimen cultivated in the garden "Bergianska Trädgården" in Stockholm. — C: HERTER n. 62. — D: PEDERSEN n. 790. — All ×0.5.

from dentate to crenate, i.e. leaves at different levels had different types of leaf margins (cf. *C. africana* L.).

	length of siliqua	length of style
soil, sun	21—23 mm	0.5 mm
soil, shade	20—26 mm	0.4—0.5 mm
sand, shade	20—22 mm	0.2—0.3 mm
sand, sun	4 mm	0.1 mm

The material comprised 17 plants. The experiment shows that the length of the plant, siliqua and style can be highly modified by the environment.

4. **C. glacialis** (FORST.) DC.

DE CANDOLLE (1821) Syst. Nat. II p. 265. — Holotype: I. G. FORSTER s.n. *Sisymbrium glaciale* FORST. (BM)!

SYNONYMS: *Sisymbrium glaciale* FORST. (1789) Comment. Soc. Reg. Sc... Gotting. IX pp. 36—37. — *Sisymbrium grandiflorum* MOLINIA SAGGIO (1810) Stor. Nat. Chil. ed. 2 p. 292. — *C. tuberosa* DC. (1821) Syst. Nat. II p. 254. Holotype: RUIZ & PAVON s.n. *Erysimum* DOMB. (BM)! — *Erysimum tuberosum* DOMB. (1821) apud DC. Syst. Nat. II p. 254, nomen nudum. — *Sisymbrium tuberosum* LAG. (1821) apud DC. Syst. Nat. II p. 254, nomen nudum. — *C. antiscorbutica* BANKS. & SOLAND. (1821) apud DC. Syst. Nat. II p. 265, nomen nudum. — *C. nivalis* GILL. (1833) Hook. Bot. Miscell. p. 136. — *C. affinis* HOOK. & ARN. (1833) Bot. Michell. p. 137. Holotype: BRIDGES, Valparaiso (E)! — *C. tenuirostris* HOOK. & ARN. (1830) Capt. Beechy's voyage p. 6. — *C. cordata* BARN. (1845) GAY Fl. Chil. I p. 109. Holotype: GAY (K)! Isotype: in SGO! — *C. decumbens* BARN. (1845) GAY Fl. Chil. I p. 109. Holotype: GAY n. 329 (P)! Isotype in SGO! — *C. rostrata* GRISEBACH (1856) Abhandl. Kgl. Gesellsch. Göttingen IV p. 115. Type material: LECHLER n. 841 (K, P)! — *C. gongylodes* PH. (1856) Linnaea XXVIII p. 664. Holotype: FUNCK SGO n. 49417 (SGO)! — *C. vulgaris* PH. (1856) Linnaea 28 p. 665. Holotype: PHILIPPI n. 110 (K)! — *C. Lechleriana* STEUDEL (1856) Flora XXXIX p. 409. Holotype: LECHLER n. 2249 (B). Isotypes: (K, SGO)! — *C. intermedia* STEUDEL (1856) Flora XXXIX p. 410. Holotype: BERTERO n. 1793 (P)! — *C. strictula* STEUD. (1856) Flora XXXIX p. 410. Holotype: LECHLER n. 1116 (B). — *C. pusilla* PH. (1856) Linnaea XXVII p. 665. Holotype: SGO n. 49308 (SGO)! — *C. litoralis* PH. (1865) Anal. Univ. Chil. XXVII p. 313. Holotype: SGO n. 63893 (SGO)! — *C. Solisii* PH. (1865) Ibid. XXVII p. 325. Holotype: SGO n. 63895 (SGO)! — *C. variabilis* PH. (1864—65) Linnaea XXXIII p. 5. Holotype: PHILIPPI SGO n. 49329 (SGO)!, isotype: (K)! — *C. pentaphylla* PH. (1864—65) Linnaea XXXIII p. 6. Holotype: PHILIPPI SGO n. 49337 (SGO)! — *C. calbucana* PH. (1872) Anal. Univ. Chil. XLI p. 668. — *C. andina* PH. (1893) Anal. Univ. Chil. LXXXI p. 71. Holotype: in SGO. — *C. integrifolia* PH. (1893) Ibid. p. 71. Holotype: SGO n. 63907 (SGO)! — *C. monticola* PH. (1893) Ibid. LXXXI p. 72. Holotype: SGO n. 49321 (SGO)! — *C. triphylla* PH. (1893) Ibid. p. 72. Holotype: SGO n. 49342 (SGO)! — *C. macrostachya* PH. (1893) Ibid. p. 75. Holotype: SGO n. 49419 (SGO)! — *C. stricta* PH. (1893) Ibid. p. 77. Holotype: SGO n. 71638 (SGO)! — *C. ovata* PH. (1893) Ibid. p. 69. Holotype: SGO n. 71452 (SGO)! — *C. hispidula* PH. (1893) Ibid. p. 79. — *C. Palenae* PH. (1893) Ibid. p. 79. Holotype: SGO n. 71618 (SGO)! — *C. Grandjotii* O. E. SCHULZ (1934) Notizblatt Berlin pp. 39—40. Holotype: GRANDJOT n. 1 (B). Isotypes: (S, SGO)!

Perennial herb, sometimes with tuberous roots. The whole plant glabrous or more or less densely covered with hairs. Usually one stem, sometimes several, 3—45 cm. Leaves with 3—13 leaflets. Basal and stem leaves petiolate, leaf stalks up to 12 cm long, upper leaves sessile. Leaflets rounded, obovate, lanceolate—linear, apex rounded—mucronate, leaf margins dentate —crenate—undulate. Terminal leaflets usually petiolate, cordate—cuneate at the base, 3—40 mm long, 1—45 mm broad. Lateral leaflets cuneate—oblique at base, 1—20 mm long, 0.5—7 mm broad. Peduncles always without bracts.

Inflorescence a raceme. Sepals white, sometimes with a tinge of violet, oblong—elliptic, 2—4.2 mm long. Petals white with short stalks, oblong—elliptic, spathulate, 4—10 mm long. Peduncles 2—7 mm long. Ripe siliquae 18—35 mm long, 10—16 mm broad. Pedicels 3—22 mm long, style 1.3—3 mm long. Seeds flat, ellipsoid, the surface reticulate, 1.4—1.8 mm long, 0.7—1.0 mm broad.

DISCUSSION MAINLY BASED ON DESCRIPTIONS. FORSTER (1789) described *C. glacialis* (FORST.) DC. under the name of *Sisymbrium glaciale* FORST. In 1821 DE CANDOLLE revised the genus *Cardamine* and placed this species in the genus *Cardamine*. FORSTER stressed the fact that the roots of this species had white fibrous secondary roots. In the same year DE CANDOLLE described *C. tuberosa* DC., wich he considered to be different from FORSTER's species because of its tubers. HOOKER and ARNOTT (1830) received specimens of *Cardamine* from Concepcion in Chile. On the basis of these specimens they described *C. tenuirostris* HOOK. & ARN. The name of the species stresses the fact that the pistil of this species has a long narrow style, but the length of the style varies continuously within *C. glacialis* (FORST.) DC. (cf. cultivation experiments with *C. chenopodifolia* PERS.). GRISEBACH (1856) also considered the appearance of the style to be an important character and described *C. rostrata* GRISEBACH. HOOKER and ARNOTT also described *C. affinis* HOOK. & ARN. on the basis of a specimen, which BRIDGES had collected in Valparaiso in Chile. Among other things they said about this species: "This species stands in the same relation to *C. tenuirostris* H. & A. as *C. hirsuta* L. does to *C. parviflora* L. and is only different in the relative breadth of the leaflets, in particular in the terminal leaflets." BARNEOUD (1845) described *C. cordata* BARN. He considered this species to be characterized by its "fleshy" leaves. This is probably a modification. PHILIPPI (1856—97) described 27 species of *Cardamine* which I consider to belong to *C. glacialis* (FORST.) DC. SCHULZ (1934) described *C. Grandjotii* O. E. SCHULZ. In a note he pointed out: "This new species is different from all others described up to now in the respect that the stamens are longer than the petals." But I have examined the type collection and have found that in fact this applies to some of the flowers only.

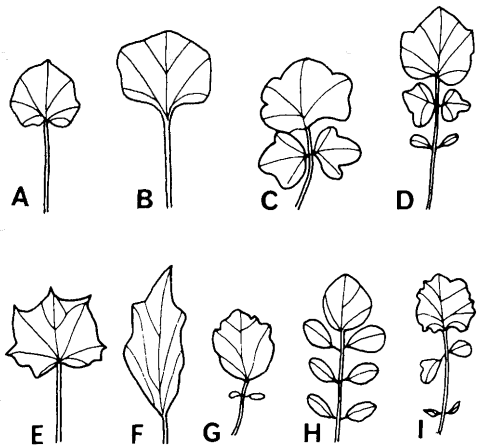

Fig. 7. Leaves of *Cardamine glacialis*. — A: C. and I. SKOTTSBERG (as *C. tuberosa* DC.). — B: WERDEMANN n. 1313 (as *C. cordata* BARN.). — C: C. GRANDJOT (as *C. tuberosa* DC.). — D: VALENTIN n. 187. — E: SPARRE n. 4887 (as *C. cordata* BARN.). — F: BUCHTIEN n. 170 (as *C. variabilis* PH.). — H: SPARRE n. 1558 (as *C. andina* GILL.). — I: GRANDJOT (as *C. Grandjoti*). — All ×0.5.

DISCUSSION BASED ON HERBARIUM MATERIAL. *Leaves.* The shape of the leaflets shows a wide variation. The sepals are as rule white, with sometimes a tinge of purple. Petals are always white, 4—10 mm long. There is no connection between the length of the leaflets and the number of leaflets on each leaf (cf. Fig. 8).

Fruits. Siliquae 18—35 mm long. Style 1.3—3.0 mm long. Seeds 1.4—1.8 mm long. As a rule there is only one row of seeds in each valve, which is considered to be characteristic of *Cardamine*. Of interest is that on the type collection of *C. cordata* BARN. there are siliquae with an incomplete second row of seeds. But the seeds in that row are only 1 mm long.

DISTRIBUTION. *C. glacialis* (FORST.) DC. has a very wide distribution: Chile, Argentina, the Falkland Islands, Tristan da Cunha, Kerguelen, Campbell Island, southwestern Australia and New Zealand. Specimens from Australia and New Zea-

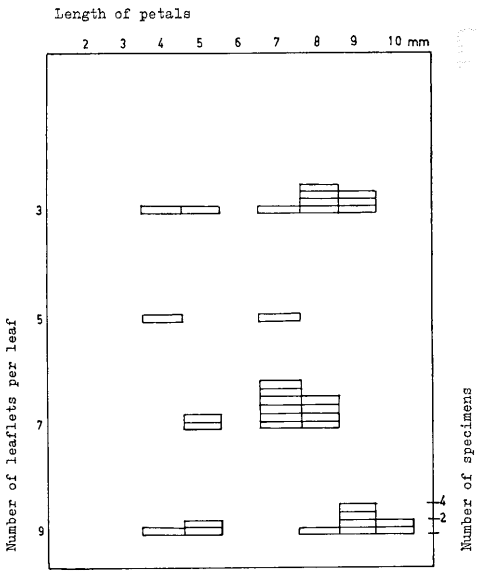

Fig. 8. Length of petals of specimens of *Cardamine glacialis* with varying number of leaflets on lowest stem-leaf.

land are very similar to *C. glacialis* s. str. The greatest variations within this species are to be found in Chile. *C. glacialis* (FORST.) DC. usually occurs in damp localities such as in bogs and near glaciers.

5. **C. geraniifolia** (POIR.) DC.

DE CANDOLLE (1821) Syst. Nat. II. — Holotype: 1162 LECHLER (SGO)!

SYNONYMS: *Sisymbrium geraniifolium* POIRET (1806) Encycl. Bot. VII p. 218. — *Dentaria geraniifolia* REICHE (1896) Fl. Chil. I p. 104.

ICONS: J. D. HOOKER (1844—47) Fl. Antarct. tab. 88.

Perennial herb, more or less hairy. Stem strong, upright, up to 55 cm high. Root up to 6 mm thick. Leaves petiolate, leaf stalk up to 10.5 cm long, 7—11 leaflets on each leaf, leaflets deeply incised—bipinnate. Terminal leaflets cuneate at the base, 2—4 cm long, 0.6—3.5 broad.

Inflorescence a raceme. Peduncles 6—16 mm long. Sepals pale green, oblong, 5—6 mm long. Petals white, spathulate, 12—17 mm long. Ripe siliquae 7.0—8.5 cm long, 2.0—3.0 cm broad, pedicels 18—22 mm long, style 4—6 mm long. Seeds ellipsoid, the surface reticulate, 3.0—3.2 mm long, 1.4—1.5 cm broad.

C. geraniifolia (POIR.) DC. shows a rather narrow amplitude of variation. Of interest is that on some specimens the margins of some leaflets are so deeply incised that they become bipinnate (cf. Fig. 9).

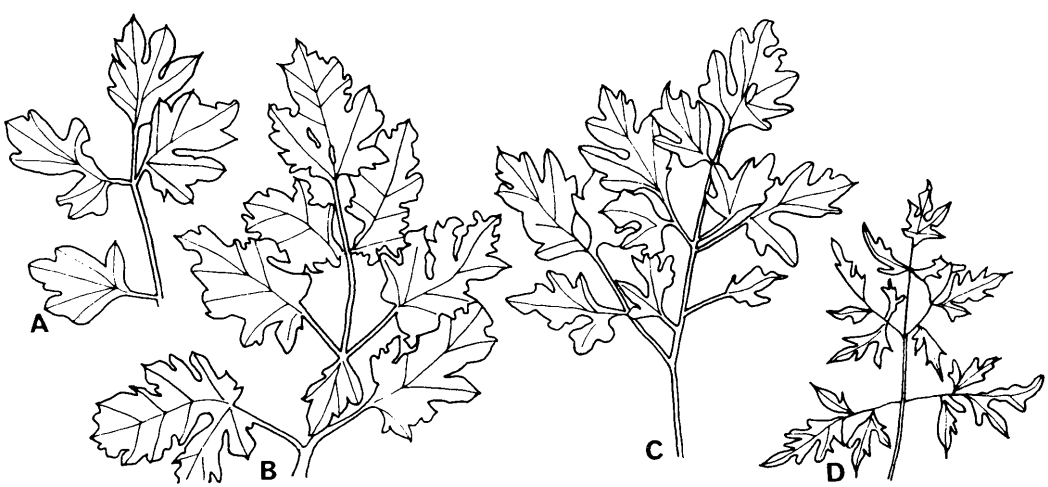

Fig. 9. Leaves of *Cardamine geraniifolia*. — A: LECHLER n. 1162. — B: DUSÉN n. 107. — C: ANDERSSON n. 318. — D: SKOTTSBERG n. 194. — All ×0.5.

DISTRIBUTION. *C. geraniifolia* (POIR.) DC. occurs in Chile and Argentina, from Rio Negro to Tierra del Fuego. It grows on shores and in shady forests.

ACKNOWLEDGEMENTS

I wish to express my sincere thanks to the Directors and the Curators of various Herbaria for allowing me to study specimens. Sincere thanks are due especially to Dr ALICIA LOURTEIG, Dr OSVALDO BOELCKE (Buenos Aires), Dr D. SUCRE (Rio de Janeiro), Professor A. BURKHART (San Isidro BA), Professor CARLOS MUNOZ (Santiago de Chile) and Dr RAMON FERRYERA (Lima).

For help in my work I owe sincere thanks to Professor FOLKE FAGERLIND, Professor TYCHO NORLINDH (especially as regards morphology) and the Curator BENKT SPARRE (taxonomical problems and geographical data).

APPENDIX

List of synonyms. 1: *Cardamine africana* L.; 2: *C. bonariensis* JUSS. ssp. *bonariensis*; 3: *C. bonariensis* JUSS. ssp. *eremita* (STAND. & STEYER.) BO SJÖSTEDT; 4: *C. chenopodiifolia* PERS.; 5: *C. geraniifolia* (POIR.) DC.; 6: *C. glacialis* (FORST.) DC.

Cardamine affinis H. & A.=6
C. Albertii O. E. SCH.=1
C. alsophila PHIL.=2
C. andicola PHIL.=2
C. andina PHIL.=6
C. antiscorbutica BANKS.=6
C. argentina SPEG.=4
C. armoracioides TURCZ.=1
C. Aschersoniana O. E. SCH.=1
C. axillaris WEDD.=2
C. balneriana STAND. et STEYER.=1
C. borbonica PERS.=1
C. bracteata PH.=2
C. bradei O. E. SCH.=1
C. Burchelli SPR.=1
C. caespitosa PHIL.=2
C. calbucana PHIL.=6
C. chilensis DC.=1
C. cordata BARN.=6
C. corymbosa HOOK. FIL.=1
C. decumbens BARN.=6
C. demissa TRIANA & PL.=2
C. ecuadorensis HIER.=1
C. eremita STAND. & STEYER.=3
C. flaccida CH. & SCHL.=2
C. fulcrata GREENE=1
C. gongylodes PH.=6
C. Grandjoti O. E. SCHULZ=6
C. hirsuta H. & A. non L.=2
C. ibaguensis TR. & PL.=1
C. innovans O. E. SCHULZ=1
C. integrifolia PH.=6
C. intermedia HOOK.=6
C. Jamesonii HOOK.=1
C. jejuna STAND. & STEYER.=1
C. Johnstonii OLIVER=1
C. Kilippi O. E. SCHULZ=2
C. laxa BENTH.=2
C. Lechleriana STEUDEL=6
C. Lehmanni HIERON.=1
C. litoralis PH.=6
C. macrostschya PH.=6
C. magellanica PH.=6
C. marginata PH.=2
C. micropetala PH.=2
C. minima STEUD.=2
C. monticola PH.=6
C. nasturtioides BERTERO=2
C. nevadensis TURCZ.=1
C. nivalis GILL.=6
C. obliqua HOCHST.=1
C. ocoana O. E. SCH.=1
C. ovata BENTH.=1
C. palenae PH.=6
C. pectinata KZ.=6
C. pentaphylla PH.=6
C. peteroana PHIL.=6
C. picta HOOK.=1
C. porphyrophylla EKMAN=1
C. pubescens PH.=6
C. pulchra LIND. & PLANCH.=6
C. punicea TURCZ.=1
C. pusilla PH.=6
C. ramosissima STEUD.=2
C. reniformis PH.=6
C. rhizomata ROLLINS=1
C. rostrata GRISEB.=6
C. Solisii PH.=6
C. speciosa BRITTON=1
C. stricta PH.=6
C. strictula STEUD.=6
C. tenuirostris H. & A.=6
C. tolimensis PL. & LIND.=1
C. tridens PH.=2
C. triphylla PH.=6
C. variabilis PH.=6
C. vulgaris PH.=6
Dentaria geraniifolia REICHE=5
Heterocarpus fernandeziana PH.=4
Nasturtium radicans WALPERS.=2
Nasturtium turfosum KUNZ.=2
Sisymbrium glaciale FORST.=6
Sisymbrium geraniifolium POIR.=5
Sisymbrium grandiflora MOLINIA=6

Lepidium L. (Cruciferae) in Tropical Africa

A Morphological, Taxonomical and Phytogeographical Study

Bengt Jonsell

JONSELL, B. 1975 07 08. Lepidium L. (Cruciferae). A morphological, taxonomical and phytogeographical study. — Bot. Notiser 128: 20—46. Lund. ISSN 0006-8195.

The morphology of the *Lepidium* species growing in tropical Africa is studied with special emphasis on seed structure. The variation in the palisade layer of the testa is of special interest from a taxonomic point of view, as is also the external structure, when seen under the scanning electron microscope. All the taxa have highly reduced flowers and are probably strongly autogamous. On this basis the taxonomic principles pertinent to the present problem are discussed, and the taxonomy of the tropical African taxa is revised. Nine species are found to occur within the area, among them *L. sativum* L., which is not formally treated here. Two of the remaining species are introduced, *L. bonariense* L. and *L. virginicum* L. *L. africanum* (BURM. FIL.) DC. has the widest distribution (Sudan—S. Africa) and is variable. A part of the S. African population is recognized as subsp. *divaricatum* (AIT.) JONSELL comb. nov. Four species are local endemics, viz. *L. suluense* MARAIS, and *L. angolense* JONSELL, *L. inyangense* JONSELL and *L. keniense* JONSELL, which are here described as new species. Most of the species belong to a group with S. African affinities, while *L. armoracia* FISCH. & MEY. is a member of a Mediterranean element. For *L. africanum* subsp. *africanum* and *L. bonariense* the chromosome numbers 2n=16 and 2n=64, respectively, are reported. Both are first reports for the species.

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The present study is a revision of *Lepidium* in tropical Africa, an area from which very little material was available for THELLUNG's fundamental monograph of the genus (THELLUNG 1906 b), and for which all that has accumulated since has been only tentatively determined. Special emphasis will be laid on the fine structure of the seeds, which has been little studied in the genus and not previously employed for its taxonomy.

Lepidium contains more than 140 species, all over the world, and only a very small fraction of the taxa is treated here. The subdivision of the genus presented by THELLUNG (1906 b p. 56), based on silicula shape, is admittedly largely artificial. One African species, the well-known *L. sativum* L. forms a monotypic section, *Cardamon* DC, and indeed takes an isolated position. It is frequent in Ethiopia, where probable wild or primitive cultivated forms occur. SCHWANITZ (1967) considered it to have gene centres in the Ethiopian, as well as in the Mediterranean, Near East and Central Asian regions, and its true geographical origin cannot be decided. It will not be formally treated here, only included in the key and its morphology briefly discussed. This paper will thus become confined to sect. *Lepidium* (=sect. *Nasturtioides* (MEDIK.) THELL.), which is by far the largest in the genus.

The area surveyed is Africa south of the Sahara southwards to the northern

(eastern) borders of Namibia, Botswana, S. Africa and Swaziland. For this area a revision by MARAIS (1966, 1970) supplies a firm basis. Detailed descriptions will be presented for the six species indigenous in tropical Africa, and condensed ones for the two aliens.

MATERIAL AND METHODS

The study is based upon the tropical African herbarium material of the genus, ca. 160 collections (excluding *L. sativum*), distributed on ca. 250 sheets available in B, BM, BR, COI, EA, FI, K, LISC, LISU, M, P, S, STU, UPS, WAG, Z (abbreviations follow HOLMGREN & KEUKEN 1974). For special purposes also collections in G, LE, PRE and W were consulted. A great number of collections from outside tropical Africa were also studied. A few living plants of *L. africanum, L. armoracia* and *L. bonariense* were investigated in cultivation in the greenhouse. A list of the collections revised is deposited in UPS and copies can be obtained on request.

Seeds were mainly cut on a freezing microtome at 20 μ and stained in safranine. A number of sections were also made from seeds embedded in paraffine. All available tropical African collections with ripe seeds were investigated and in addition a number of South African and Extra-African specimens were included. Sections from a total of ca. 150 collections were studied.

The chromosomes were observed in root-tips fixed in chrome-acetic formalin, embedded in paraffine, sectioned at 14 μ, and stained in gentian violet. Voucher specimens are deposited at UPS.

TAXONOMIC PRINCIPLES

In the tropical African *Lepidia* variation can be observed in a long array of features, but how this variation should be estimated for taxonomic purposes imposes special problems. THELLUNG (1906 b pp. 52—55) discussed at some length the characters which could be used for taxonomy at species level. He emphasized the fact that in different parts of the genus different kinds of characters showed constancy within the species. What is in one group a good key character varies in another seemingly at random. The certainly very widespread autogamy of this genus helps to preserve the deviating character combinations that may appear. To this difficulty is added another, in that similar stages in e.g. floral reductions, so common in this genus, have certainly been achieved along a number of different lines. There are for example in montane parts of both S. America and Central Asia species highly reminiscent of some of those treated here, but certain features such as the pubescence indicate that the similarity is quite superficial. On the other hand groups of closely allied species with similar, reduced flowers of course exist (e.g. the *L. africanum*-group). Furthermore, as MARAIS (1970 p. 84) pointed out, intraindividual variation in floral and fruit characters is unusually great, which means that a quantitative treatment of them can hardly be recommended.

This leads on to the difficult problem of what would be reasonable to recognize as species in an inbreeding group of plants as this, and what criteria we should use to define the taxa. It is superfluous here to cite anew the classical examples of the problem, which can be found referred to, among others, in for example STEBBINS (1950) and DAVIS & HEYWOOD (1963). I will only point to the fact that distinct minor forms, which it would be reasonable to interpret as the result of inbreeding, may, if opportunity for outcrossing arises, turn out to be either occasional combinations easily broken down, or constant forms genetically isolated from their most similar relatives. GRANT (1964) showed in *Gilia* that even the latter kind of inbreeders may grow mosaically intermingled in an area, and constitute sibling, but neither geographically nor ecologically vicarious "biological" species. Indeed a mosaic situation might promote the development of sterility barriers.

For the present problem the information provided by the herbarium material must be almost exclusively relied upon. It will be more the combination of certain

characters that makes it possible not only to define but also to determine a species, since single key characters are rarely infallable. Geographical aspects are also relevant. In principle phytogeography should be founded on solid taxonomy, but not necessarily on those taxa where we are in special difficulties. Here an established phytogeographical pattern may instead serve as a guide. The tropical African species have been distinguished with these principles in mind. They imply that within the widespread *L. africanum,* with its large-scale, partly mosaical variation, no taxonomic subdivision apart from the regional subsp. *divaricatum* is accomplished (p. 36). We do not know anything at all about the genetical isolation between these forms, and cannot presuppose anything either. The various forms of *L. africanum* may be well isolated genetically, or they may be poorly isolated; the same is true of the forms of the low-growing perennials (*L. angolense, L. inyangense, L. keniense*), whose considerable spatial isolation is an additional reason to regard them as separate species. The alternative would be a collective species including as well a number of S. African taxa, but this would probably end up in a long chain of forms, unwieldy to keep together and at variance with traditional species concepts in the genus.

Our species concept in *Lepidium* is mainly influenced by THELLUNG (1906 b) whose major work has become the frame within which later, regional accounts have been set. Whether THELLUNG's species concept was too wide or narrow cannot of course be answered in a simple way, but his infraspecific taxa, of which there are many in some of his more variable species, are not consistent with our present views. It is true that some of them, in the light of recent collections, have been raised to specific rank, but many are deviations such as we regard as commonplace within inbreeders. The range from cosmopolitan weeds to extremely local endemics met with in the genus adds further problems to the concepts of the taxa.

GROSS MORPHOLOGY

LONGEVITY. No clear distinction can be made between annual, biennial and perennial taxa. The indigenous species without apophytic tendencies seem to be long-lived perennials with thick woody roots and stem-bases in older plants. They are virtually subshrubs. The species which grow partially or exclusively as weeds are much more variable. In cultivation some strains of *L. africanum* always flowered and died within a few months (e.g. RYMAN 173 (UPS)), while others produced new shoots from the base and basal parts of the stems, which did not die off (e.g. JONSELL 2972 (UPS)). In one strain from Ethiopia (from seeds of DE WILDE 4550 (WAG)) the leaf-rosette lasted more than a year before flowering. The introduced *L. bonariense* seems to comprise strains with various properties. The Tanzanian JONSELL 2138, repeatedly sown in the greenhouse, was consistently a short-lived annual, while RYMAN 151 (from Kenya) only formed a rosette the first year. All the species seem to be in principle pollacanthic, although some strains are reduced to strict annual status.

LEAVES. The shape of leaves (Fig. 1), especially whether undivided or pinnatifid to pinnatipartite constitutes a quite useful specific character provided that leaves of corresponding position and kind (cf. below) are compared. Nevertheless individuals (populations?) with more or less pinnate leaves may occur in species with normally undivided leaves, e.g. in some *L. africanum*-collections from Ethiopia. From Mozambique there is a large collection (MENDONÇA 2797, 2797 a, BM, BR, LISC, WAG) with transitions from simple to pinnate leaves. This collection gives, however, the impression of being intermediate between *L. africanum* and *L. su-*

luense, which might explain the inconsistency. Since in many cases only the evanescent rosette and lowest cauline leaves were found to be divided, this character, even when constant, can be difficult to use in practice.

In perennial strains the primary cauline leaves are often deciduous and replaced by the leaf-rosettes of axillary shoots, which may not develop further. In *L. africanum,* where this is most evident, the "primary" leaves are linear to oblanceolate, and the "secondary" ones markedly spathulate in outline and more serrate. In some specimens of *L. suluense* the primary cauline leaves are undivided, the secondary ones pinnate (Fig. 1 H). Plants with only one or the other leaf-type present may therefore appear very different from each other.

PUBESCENCE. In most of the species there is considerable variation as to pubescence, from strongly puberulous to practically glabrous specimens. In the latter hairs usually remain on the adaxial side of the pedicels. The type and direction of hairs are good characters but deviating individuals occur (cf. p. 57). The hairs are always unicellular and unbranched, but may be cylindrical, subulate or clavate, and straight, falcate or retrorse. Within any one specimen the hair-type is highly constant with respect to these characters, but size may vary quite a lot.

FLOWERS. All species treated here give the impression of being highly autogamous, but this was confirmed in cultivation only for *L. africanum* and *L. bonariense*. The flowers bear many signs of autogamy, especially the reduction of petals and stamens, which often dehisce in bud. There is, however, a clear difference between plants with comparatively well-developed petals and those with very reduced ones. The former is true for *L. armoracia* and *L. sativum,* which have petals at least equalling the sepals in length and with conspicuous, widened

Fig. 1. Drawings of leaves. — A: *L. armoracia,* Ethiopia, DE WILDE 7026 (WAG), middle cauline leaf. — B—E: *L. africanum* subsp. *africanum,* all from Ethiopia. — B: TERRACIANO & PAPPI 971 (FI), upper primary cauline leaf. — C: TERRACIANO & PAPPI 997 (FI), middle secondary, cauline leaf. — D: TERRACIANO & PAPPI 971 (FI), basal cauline leaf. — E: DE WILDE 4550 (WAG), middle primary cauline leaf. — F—G: *L. keniense,* VERDCOURT 3820 (BR). — F: involute upper cauline leaf. — G: basal cauline leaf. — H: *L. suluense,* GRANDVAUX BARBOSA 7772 (LISC), middle cauline leaf (one primary with two axillary secondary ones). — I—J: *L. angolense,* WELWITSCH 1190 (BM). — I: upper cauline leaf. — J: basal cauline leaf. — K: *L. bonariense,* Ethiopia, DE WILDE 6951 (WAG), upper cauline leaf. — L—M: *L. inyangense,* ROBINSON 1969 (LISC). — L: upper cauline leaf. — M: basal cauline leaf. — N: *L. virginicum,* Mozambique, MARQUES 2195 (COI), middle cauline leaf.

blades. The other species all have oblanceolate—linear petals shorter than the sepals, and in each of them, even within one individual, they may vary from being almost the same length as the

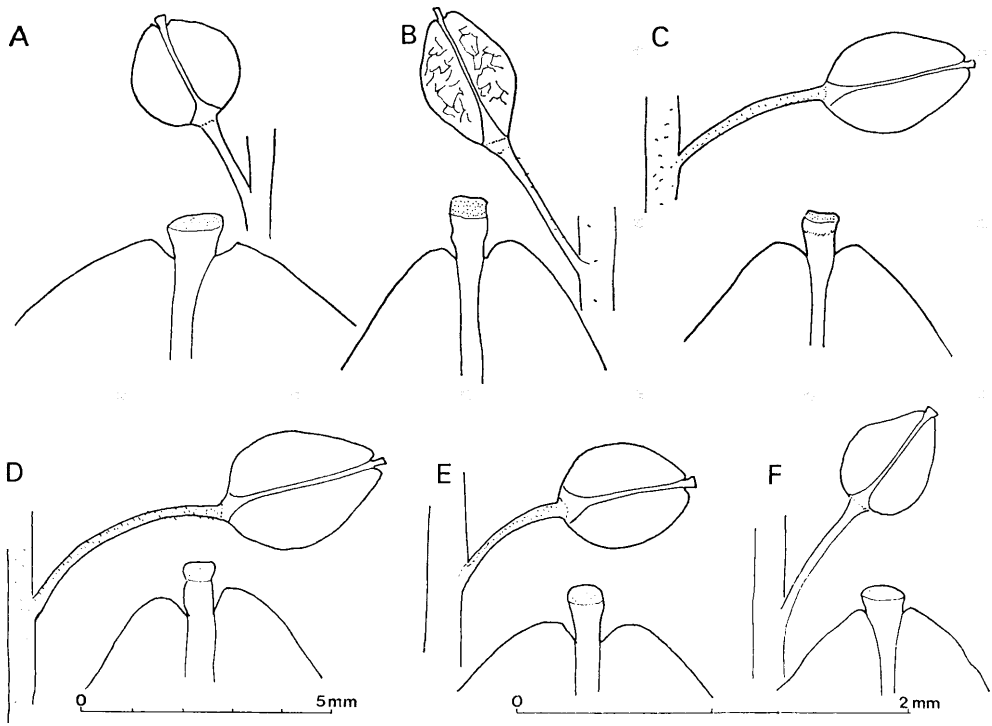

Fig. 2. Drawings of siliculae with pedicels, and apices of siliculae of the *L. armoracia*-group. — A—E: *L. armoracia*. — A: SCHIMPER II: 741 (P), type of "subsp. *abyssinicum*". — B: Tanzania, NEWBOULD 6300 (EA). — C: Ethiopia, DE WILDE 7026 (WAG). — D: QUARTIN-DILLON & PETIT s.n. (P), type of "subsp. *intermedium*". — E: PETIT s.n. (P), type of "subsp. *alpigenum*". — F: *L. graminifolium*, Italy, CESATI 8 (UPS). — The 5 mm scale refers to the siliculae with pedicels, the 2 mm scale to the apices.

sepals to absent. Flowers of median position in the racemes are usually the best developed ones. Only in the introduced *L. virginicum* among the species treated here, can forms with well-developed as well as forms with reduced petals be found, in tropical Africa only the latter.

Staminal reductions run parallel to those in petals. *L. sativum* has the full number, 6, while *L. armoracia* has 4 or 2 with intra-individual variation. The reductions may take place in various ways, as the four are either all median (fide THELLUNG 1906 a) or two lateral and two median. If only two are present they may be lateral or median. The species with very reduced petals consistently have only two median stamens left.

The nectarial tissue is visible as glands, in *L. sativum* as many as 6, one between each of the stamens. As a rule there are only four, placed at either side of the filament bases of each pair of stamens or, more usually, of the solitary median stamen. These glands, which in some S. African species are distinctively shaped (MARAIS 1970), are in the tropical African ones on the whole of a common, broadly conical type and diagnostically rather unimportant.

SILICULAE. Variation in siliculae (Figs. 2 and 3) comprises size, shape in outline, venation of the valves, style length and the size of the apical sinus. Apart from *L. sativum*, which is outstanding in its large

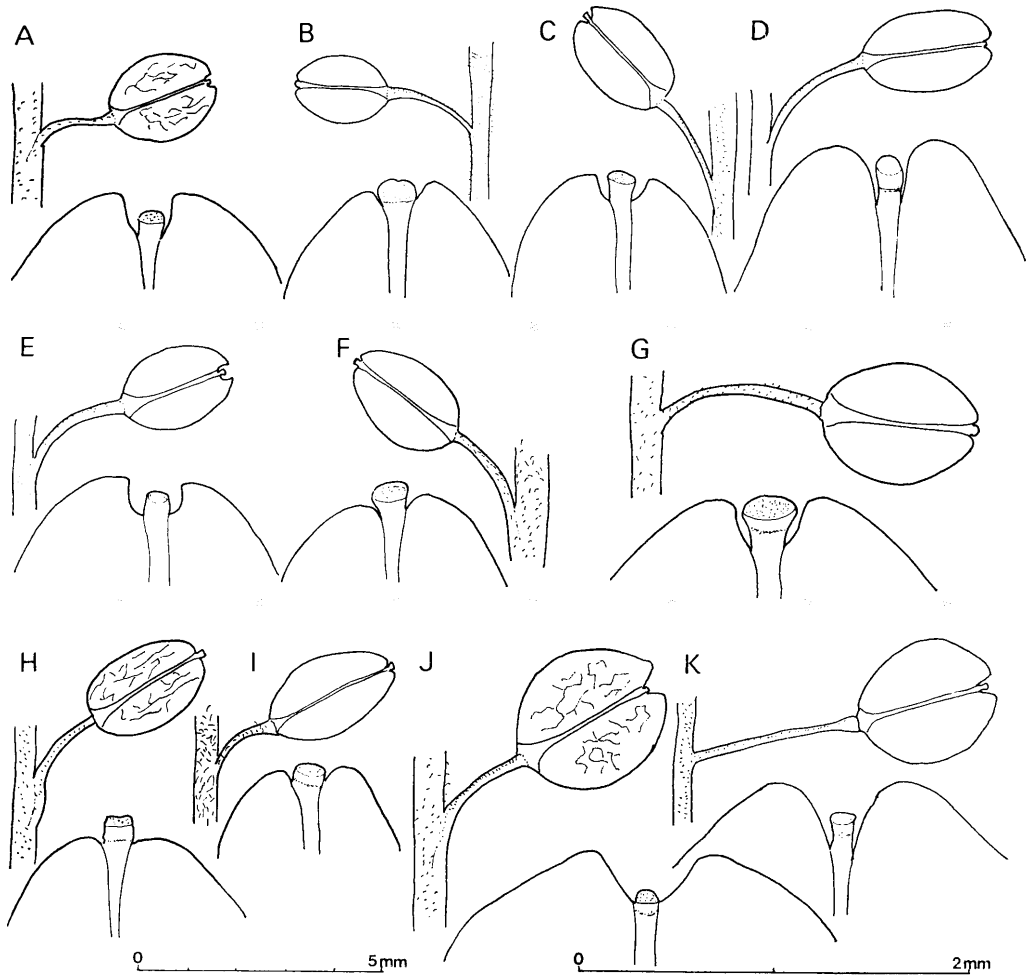

Fig. 3. Drawings of siliculae with pedicels, and apices of siliculae of the *L. africanum*-group and of the introduced species. — A—D: *L. africanum* subsp. *africanum*. — A: Ethiopia, DE WILDE 4550 (WAG). — B: Kenya, FRIES & FRIES 875 (UPS). — C: Uganda, LYE 6917 (EA). — D: Rhodesia, DRUMMOND 4933 (BR). — E: *L. suluense*, GOMES & SOUSA 3654 (COI). — F—G: *L. keniense*. — F: Kenya, VERDCOURT 3820 (BR). — G: Ethiopia, GILLETT 14365 (EA). — H: *L. angolense*, WELWITSCH 1190 (BM). — I: *L. inyangense*, ROBINSON 1969 (LISC). — J: *L. bonariense*, Ethiopia, DE WILDE 6951 (WAG). — K: *L. virginicum*, Mozambique, MARQUES 2195 (COI). — The 5 mm scale refers to the siliculae with pedicels, the 2 mm scale to the apices.

and winged siliculae, the two last mentioned characters are the most important. The lateral wings, best visible at the distal margin of each loculus, are in all the other species indistinct or absent. Their presence is best indicated by the more or less corresponding apical sinus, at the base of which the style is inserted. This sinus varies from being a deep and wide emargination (e.g. in *L. africanum* and *L. bonariense*, Fig. 3 A, J) to only faintly retuse in *L. armoracia* (Fig. 2 A—E).

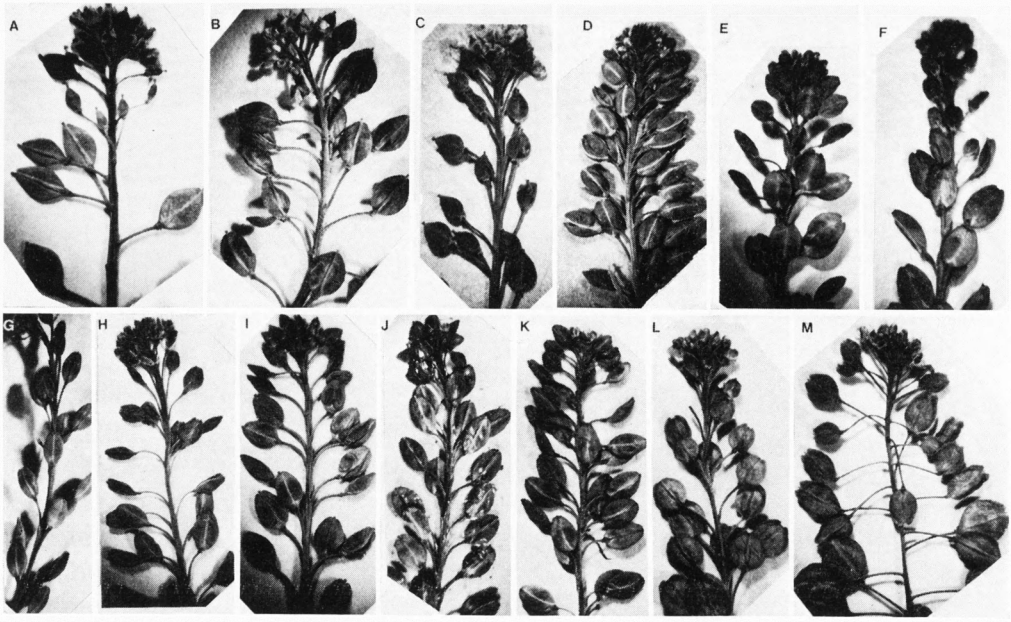

Fig. 4. Racemes with ripe fruits. — A—B: *L. armoracia*. — A: Tanzania, NEWBOULD 6300 (EA). — B: Ethiopia, DE WILDE 7026 (WAG). — C: *L. graminifolium*, O.S. 12.VII.1854 (UPS). — D—E: *L. africanum* subsp. *africanum*. — D: Kenya, FRIES & FRIES 875 (S). — E: Ethiopia, DE WILDE 4550 (WAG). — F: *L. africanum* subsp. *divaricatum*, S. Africa, LEISTNER 2432 (K). — G: *L. trifurcum*, S. Africa, FLANAGAN 1560 (PRE). — H: *L. suluense*, GOMES & SOUSA 3654 (COI). — I: *L. keniense*, GLOVER et al. 821 (K). — J: *L. angolense*, WELWITSCH 1190 (COI). — K: *L. inyangense*, ROBINSON 1969 (K). — L: *L. bonariense*, Ethiopia, DE WILDE 6951 (WAG). — M: *L. virginicum*, Mozambique, MARQUES 2194 (COI). — All ca. ×2.1.

Independently the style length varies, which means that in distinctly emarginate siliculae, the stigma may be contained within or be outside the sinus margin, while it in only slightly retuse ones is of course always outside. Most specimens are easy to assess by means of these characters but a few collections deviate enough to cause overlap between species, especially in *L. africanum*, while extremes such as *L. bonariense* and *L. armoracia* are always clearcut. The deviating specimens always fall in other characters within the range of the species concerned and are hence of more practical than theoretical difficulty. Deviations may also occur within one raceme, and, moreover, unripe siliculae have often proportionately longer styles than fully ripe ones.

Size and shape of siliculae are of some diagnostic value, but absolute measurements mean little. *L. armoracia* has sometimes, as in Tanzania, markedly rhombic—ovate siliculae (Fig. 2 B), while most material from Ethiopia has elliptic ones (Fig. 2 C, E).

PEDICELS. The direction of the pedicels (Figs. 2—4), whether straight (Fig. 2 B), curved (Fig. 3 H) or arcuate (Fig. 3 D) and erecto-patent (Fig. 2 A), patent (Fig. 3 J) or divaricate (Fig. 3 K) is of considerable taxonomic importance. In this respect too, *L. armoracia* shows un-

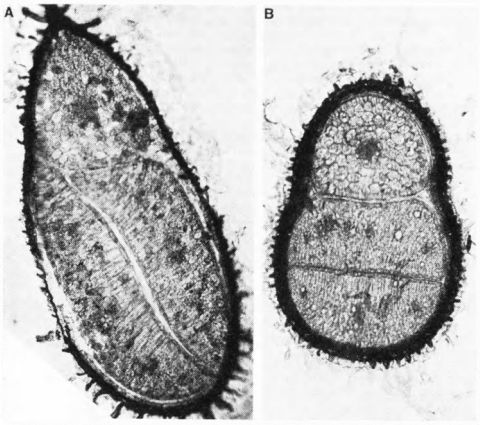

Fig. 5. Cross-sections of seeds. — A: Obliquely accumbent cotyledons, *L. virginicum*, MARQUES 2195 (LISC). — B: Incumbent cotyledons, *L. africanum*, LYE 6197 (EA). — Both ca. ×50.

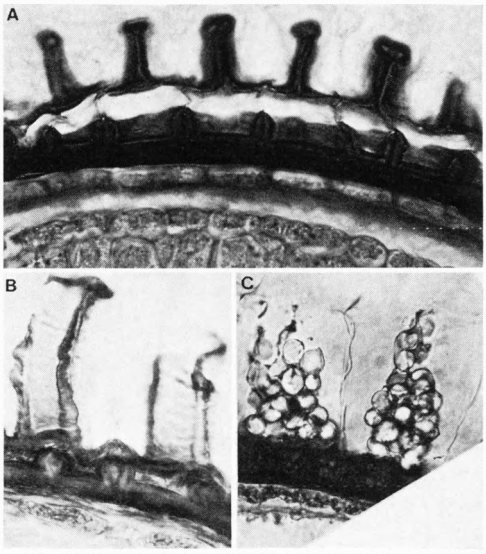

Fig. 6. Cross-sections of testa showing columns of the epidermis. — A: *L. suluense*, MENDONÇA 2797 (BR), ca. ×385. — B: *L. bonariense*, Tanzania, SHABANI 810 (EA), ca. ×385. — C: *L. virginicum*, Switzerland, SAMUELSSON 25.VI.1921 (UPS), ca. ×250.

usual variation with the Tanzanian and some other forms having straight, erecto-patent pedicels, contrasting both with most plants of this species and with the species with very reduced petals, which all have curved to arcuate pedicels. The latter feature discriminates well e.g. towards *L. ruderale* L., erroneously reported from tropical Africa (cf. p. 38). Pedicel length is on the whole an unreliable character, often varying greatly within one and the same raceme.

SEED STRUCTURE

Seed structures are increasingly being used in taxonomic studies in Cruciferae, especially the anatomy and external structure of the testa. The basic earlier studies, summarized by NETOLITZKY (1926), have in more recent years been complemented by surveys of the seeds in a great number of genera and species (ČERNOHORSKÝ 1947, VAUGHAN & WHITEHOUSE 1971 and, concerning external structure only, MURLEY 1951).

The position in the embryo of the cotyledons in relation to the radicle, and the degree of folding of the former, are characters that have long been used to help to define suprageneric groups within the family (DE CANDOLLE 1824, SCHULZ 1936). Such characters have turned out to be less constant within genera than was once believed, and in *Lepidium* incumbent (the majority of species) as well as obliquely accumbent (e.g. *L. virginicum*) cotyledons are known (Fig. 5).

Immediately inside the testa and closely associated with it there is in *Lepidium*, as in nearly all Cruciferae, the one-cell thick aleurone layer (Figs. 6 A, 7), which is the remains of the nucellus. As far known it does not show any variation of taxonomic interest.

The testa proper of Cruciferae seeds consists of layers formed by both integuments, but as a rule those generally considered to emanate from the inner integument (cf. e.g. STORK 1971 p. 285; further references in VAUGHAN & WHITEHOUSE

1971) do not differentiate in the maturing testa. This layer has been variously referred to as "colour cells" (GRAM 1894), "Pigmentschichte" (NETOLITZKY 1926) owing to its often dark colour, "épiderme interne" (ČERNOHORSKÝ 1947) and "inner parenchyma" (VAUGHAN & WHITEHOUSE 1971). In *Lepidium* it is sometimes seen as a cellular membrane but is in most cases compressed and without cellular structure (Figs. 6 A, 7, 8). This variation is intraspecific or even intraindividual.

The following layer, generally called the palisade layer (Figs. 7, 8), is the innermost one derived from the outer integument. It is one cell thick and nearly always well developed in Cruciferae seeds. The cell-walls are often thickened and the various ways in which these thickenings are accomplished offer, together with cell shape, variation of taxonomic interest. VAUGHAN & WHITEHOUSE (1971) discerned eight main types of palisade cell layers, which in many cases showed constancy within genera or even groups of higher rank, although the fairly small number of species surveyed did not, as the authors admitted, permit far-reaching conclusions. Four *Lepidium*-species were included in their study and all were found to have the inner tangential and the whole radial cell walls thickened. They differed in cell shape, one of them (*L. campestre* (L.) R. BR.) having the cells radially elongated, and the others (among which was *L. sativum* L.) tangentially elongated. They were therefore referred to different main types, "F" and "E", respectively. But for the discovery of both types in *L. sativum* ("F" e.g. in SCHIMPER 7 (P), from Ethiopia), the species investigated here have their cells tangentially elongated throughout but as a rule only the lower halves of the radial cell walls thickened (Fig. 8 A, B, D—G), which corresponds to type "D" of VAUGHAN & WHITEHOUSE (1971). In many cases the layer is, however, compressed, so that the outer tangential wall rests upon the radial thickenings with the thin part of the radial walls folded inbetween (Fig. 8 C, H). Within *Lepidium* the variation between at least groups "D" and "E" seems of no taxonomic significance.

For the species investigated here the shape of the radial cell-wall thickenings was found to be of considerable interest. The thickenings are of several, on the whole distinct types when seen in transverse section. In "type I" the thickenings taper gradually outwards, forming with that of the adjacent cell a structure spire-like in outline (Figs. 7 A, 8 A—C). *L. armoracia, L. graminifolium,* and *L. inyangense* showed this type. In "type II" the thickenings are parallel-sided and only distally contracted so as to form with that of the adjacent cell a triangular tip; sometimes the thickening is rather convexly rounded (Figs. 7 B, 8 D—G). The bases of the thickenings are in type II broader (0.06—0.11 μ when measured over two adjacent thickenings), against 0.04—0.05 μ in type I. Only in cells where only the lowermost part of the radial cell-wall is thickened can it be difficult to distinguish between types I and II, but this does not seem to occur with any constancy within any one individual. Type II is present in all the rest of the indigenous tropical African taxa (*L. africanum* subsp. *africanum, L. angolense, L. keniense, L. suluense*) as well as in the S. African ones studied (*L. africanum* subsp. *divaricatum, L. capense, L. ecklonii, L. trifurcum*) and in the introduced *L. virginicum*. In "type III" the thickenings are of the same size as in type II, but not distally tapered, the end being flat in section (Figs. 7 C, 8 H). Type III was observed only in the introduced *L. bonariense*. In *L. ruderale,* finally, the ends of the radial thickenings in sections appear as notched around the mid-lamella (Fig. 8 I). (For the material investigated see p. 21.)

The structures described show remarkable constancy within the species studied and therefore mean an addition to the characters of taxonomic value in the

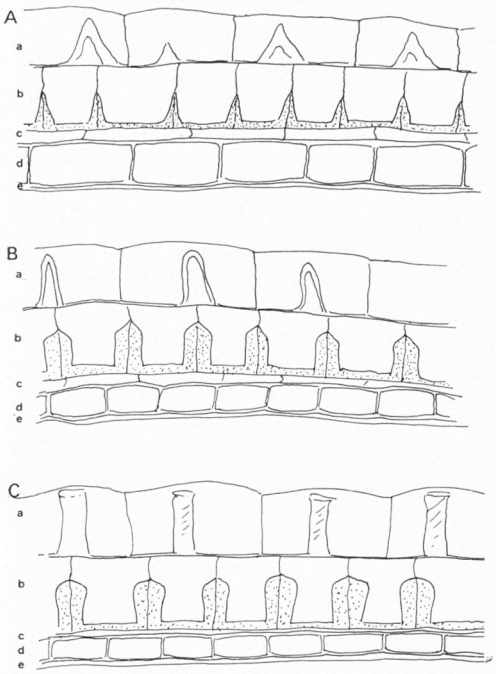

Fig. 7. Schematic drawings of testa in cross-section (a=epidermis; b=palisade layer; c=inner parenchyma; d=aleurone layer; e=hyaline layer; terminology according to VAUGHAN & WHITEHOUSE 1971, cf. text). — A: Palisade layer, Type I. — B: Ditto, Type II. — C: Ditto, Type III. — See further in text. — Ca. ×500.

genus. In the African taxa it on the whole divides what would for other reasons be reasonable to keep apart, and joins species that make a general impression of being closely allied. But taxa with similar structure need not of course be closely allied — *L. virginicum* and the *L. africanum*-group, both with "type II", certainly do not belong together. The general constancy of these characters at species level makes the few exceptions worth detailed study to decide whether their taxonomic position should be reconsidered

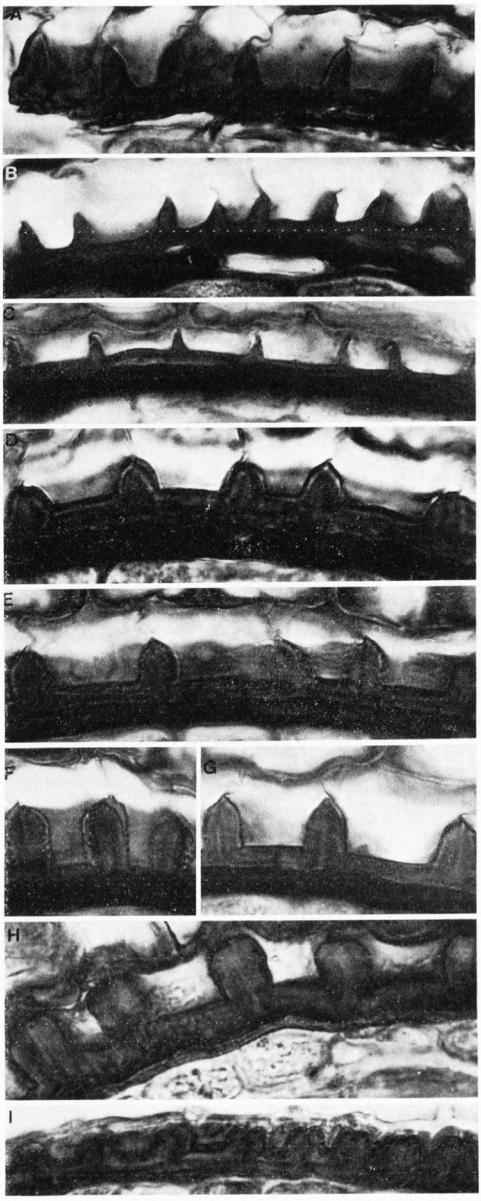

Fig. 8. Cross-sections of testa, palisade layer. — A—C: Type I. — A: *L. armoracia,* Tanzania, NEWBOULD 6300 (EA). — B: *L. armoracia,* Ethiopia, SOLLEGGIO 19 (FI). — C: *L. inyangense,* ROBINSON 1969 (K). — D—G: Type II. — D: *L. africanum,* Uganda, PURSEGLOVE 3620 (EA). — E, F: *L. suluense,* MENDONÇA 2797 and 2797 a (BR), resp. — G: *L. africanum,* Kenya, RYMAN 173 (UPS). — H: Type III. *L. bonariense,* Kenya, NJUKU 2 (EA). — I: *L. ruderale,* Czechoslovakia, JEDLIČKA 1312 (UPS). — All ca. ×510.

or their seed anatomy regarded as exceptional (cf. *L. inyangense* p. 35). It remains to be proved whether these structures are of any use for *Lepidium* taxonomy in general. The situation described may reflect the fact that the African *Lepidium* species belong to disparate phytogeographical elements (cf. p. 39). When the genus is surveyed as a whole it may well be impossible to draw limits between the different types referred to here.

In some Cruciferae a subepidermis is developed outside the palisade layer. It was illustrated for *L. campestre* as a compressed non-cellular layer by ČERNOHORSKÝ (1947 Fig. 62, p. 57) but it has otherwise not been observed in the genus (cf. Figs. 6 A, 7; VAUGHAN & WHITEHOUSE 1971 Fig. 8 B).

The outermost cell layer (testa epidermis acc. to VAUGHAN & WHITEHOUSE 1971, often also called "outer epidermis", "épiderme externe") is well developed in the species of *Lepidium* studied here (Figs. 6 A, 7). The epidermis cells are rich in mucilage, which in contact with water swells considerably and breaks through the cell walls. The ultrastructure and chemical nature of this mucilage was studied in *L. sativum* by MÜHLETHALER (1950) and KALAČ & ZEMANOVÁ (1959), respectively. In all the species studied here there is a large more or less hollow column left on the inner tangential cell wall after the swelling and rupture of the cell. The shapes of the columns in the African species are on the whole intermediate between those described for *L. sativum* and some other species by VAUGHAN & WHITEHOUSE (1971), i.e. they have a hollow centre, which is rather wide especially distally. More recently the shapes of the columns of mucilaginous seed epidermis have been found to be of great taxonomic value at species and genus level (STORK 1971, 1972 concerning *Malcolmia* and related genera), but in *Lepidium* the structures do not seem to be elaborate enough to permit accurate distinctions to be made. A tendency for the columns of *L. armoracia* to be narrower with narrower and upwardly more abruptly widened lacunae was noticed. In *L. virginicum* some collections were found to have columns with a granular structure (Fig. 6 C), while others (e.g. MARQUES 2195 (LISC) from Mozambique) were quite normal. No other means of distinguishing between these plants was found, but the case may merit further study.

In *Lepidium* in contrast to for example *Rorippa* (JONSELL 1968), the size and shape of the epidermis cells were not found to be of taxonomic importance. The testa surface is extremely finely sculptured and its details cannot usually be observed with confidence under the stereomicroscope for differences to be discerned. MURLEY (1951) reported tuberculate, alveolate, areolate and reticulate seeds in various species, but found some of the species impossible to distinguish on external seed characters. In all the species treated here the testa looks minutely reticulate, and only the seeds of *L. bonariense* and *L. virginicum* are possible to keep apart from the rest because of their size and wings.

The scanning electron microscope revealed in the indigenous African species a fine reticulum (the material studied is listed in the Appendix). Bulges from which striae radiate are in most cases visible in the middle of the areoles and seem to correspond to the above-mentioned columns, around which the outer cell wall seems to be more or less depressed. The reticulum is in all species except one very thin and low (sometimes even rather dissolved, Fig. 9 G), and especially in *L. armoracia* very regularly built (Fig. 9 A, B, J). Only *L. keniense,* a species partly defined by its testa surface structure (cf. p. 35), has a considerably coarser and more raised reticulum (Fig. 9 E, F, L) which is, however, in some specimens rather irregular. It is possible that *Lepidium* seed surfaces when observed at a proper magnification

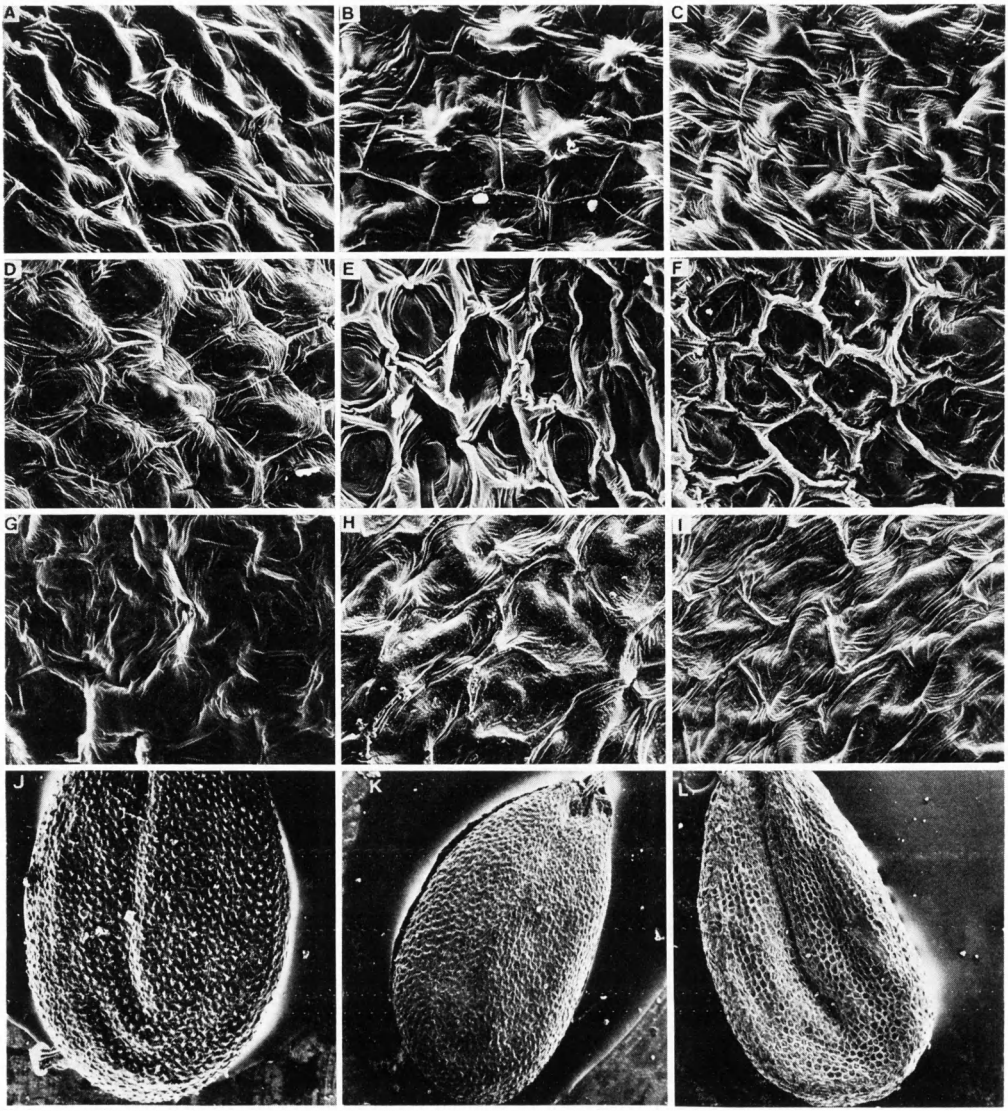

Fig. 9. Scanning electron photomicrographs of testa surface. — A—B: *L. armoracia*. — A: Tanzania, GREENWAY 9919 (K). — B: Ethiopia, FIORI 1033 (FI). — C—D: *L. africanum*. — C: Kenya, RYMAN 173 (UPS). — D: Ethiopia, PAPPI 2951 (FI). — E—F: *L. keniense*. — E: Kenya, VERDCOURT 3820 (BR). — F: Ethiopia, GILLETT 14365 (K). — G: *L. suluense*, GRANDVAUX BARBOSA 7772 (COI). — H: *L. angolense*, WELWITSCH 1190 (K). — I: *L. inyangense*, ROBINSON 1969 (K). — J: *L. armoracia*, FIORI 1033 (FI). — K: *L. africanum*, RYMAN 173 (UPS). — L: *L. keniense*, VERDCOURT 3820 (BR). — A—I ca. ×480, J—L ca. ×40.

will turn out to be of a taxonomic importance comparable to that in other genera of Cruciferae (cf. e.g. BERGGREN 1962 (*Brassica*), JONSELL 1971, 1973 (*Rorippa*)).

TAXONOMIC DISCUSSION

L. armoracia. THELLUNG (1906 a, b) recorded this species from Ethiopia and the Yemen. He united with it three species described by RICHARD (1847; cf. synonymy) to which he gave subspecific or varietal rank. Nevertheless CUFODONTIS (1954 pp. 140—141) again listed these three entities as separate species. One of these, *L. abyssinica,* was based on the collection SCHIMPER 741, most probably the same that supplied seeds for the type of *L. armoracia* (cf. synonymy; THELLUNG 1906 b p. 172).

L. armoracia was again revised by FRANCHETTI (1958). She made some rearrangements of the infraspecific taxa (cf. synonymy) but maintained THELLUNG's circumscription of the species. She gave a distribution map based on most of the herbarium material available from Ethiopia, which shows the species to be restricted to Eritrea and Tigre, except for one erroneous locality in S. Ethiopia (Mega; GILLETT 14365, cf. p. 36 and Appendix). I have found no evidence for its occurrence in the extra-Ethiopian regions listed by FRANCHETTI (1958), viz. Kenya, S. Africa, Tibet; these records certainly follow as a result of earlier misconceptions. The Kenya record (also in CUFODONTIS 1954) can be traced back to SCHULZ (1927), who determined two FRIES collections of *L. africanum* (FRIES & FRIES 875 (K, S, UPS) and 1034 (UPS)) as *L. armoracia.*

FRANCHETTI's subdivision of *L. armoracia* was based upon the shape of siliculae and pedicels (cf. description). The type variety with straight pedicels and rhombic siliculae was known only from the few old SCHIMPER collections. The others, which as circumscribed by FRANCHETTI show indistinct differences from each other in pedicel shape and more striking ones in plant size, have ecological preferences corresponding to the latter feature, one (var. *intermedium*) growing often in river-beds at lower altitudes, the other (var. *alpigenum*) in drier places higher up. These facts and the fact that gatherings are from very irregularly distributed localities, which are often in close proximity to each other suggest that infraspecific taxa should not, at least not at present, be recognized in *L. armoracia.* The plants from the Yemen described with hesitation by THELLUNG (1906 a, b) as *L. schweinfurthii* undoubtedly belong to *L. armoracia.* But for that slight incongruity my circumscription of the species is in accordance with that of THELLUNG and FRANCHETTI. The simple, slightly serrate, somewhat firm leaves (Fig. 1 A), the well developed petals and the retuse long-styled siliculae (Fig. 2 A—E) constitute the best characters and makes it outstanding among the tropical African species. This impression is reinforced by its testa anatomy (cf. p. 28).

Within this framework fall some recent collections from N. Tanzania (Serengeti region (BAUM 378 (EA, WAG), GREENWAY XII 1956 (EA), and 9919 (EA,K), NEWBOULD 6300 (EA, K)). Both gross morphological features and testa anatomy point clearly to their inclusion in *L. armoracia.* They have rather rhombic siliculae, straight pedicels, and are glabrous except for some scattered very short hairs along the stem, rhachis and pedicels. They are accordingly rather similar to the type material of *L. armoracia* (THELLUNG's subsp. *abyssinicum,* FRANCHETTI's var. *armoracia*). The specimens were collected within an area of ca. 30×30 km and there is no variation of importance within the material. They look completely perennial, the localities are described as open to closed grassland on tuff soil, and there seems to be no reasons to doubt that they are indigenous.

The African distribution of *L. armo-*

racia is thus clearly disjunct with an interval of ca. 1,800 km (Fig. 10 A). It may in the future become partly filled by new gatherings in Ethiopia but less probably in the now comparatively well-known upland Kenya. *Minuartia filifolia* (FORSK.) MATTF. shows a similar distribution; it is found in the mountains of Ethiopia (incl. Eritrea) and adjacent parts of Sudan and Somalia, and also in the N. Tanzanian Mt. Hanang at ca. 3,600 m alt., which is about 180 km south of the *L. armoracia* localities (cf. TURRILL 1956). It is thus more montane than *L. armoracia*. Although a fairly conspicuous plant, this *Minuartia* has so far not been discovered in the Kenyan mountains.

Closest to *L. armoracia* is *L. graminifolium*, a chiefly Mediterranean species (Fig. 10 A). Its thinner leaves, acutely ovate, non-retuse siliculae (Fig. 2 F), always straight pedicels, and practically always six stamens are the major differentiating features. Of all the variants of *L. armoracia*, the type and the SCHIMPER collections (cf. above) and the Tanzanian specimens are closest to *L. graminifolium* (cf. characters above). The two taxa form a well-defined "superspecies" and are similar enough for their treatment as subspecies to be defensible. Their ranking as species is, however, in accordance with the taxonomic concepts in *Lepidium*, and they also turn out to be phytogeographically natural entities. Rather closely related to this species pair is probably the *L. lyratum*-complex with several species in Central Asia and Persia.

The *L. africanum*-group. The rest of the native *Lepidium* species form a group of apparently closely related species, here referred to as the *L. africanum*-group. All have flowers with reduced petals and only two stamens; other uniting characters are the curved to arcuate pedicels, somewhat notched siliculae (Fig. 3 A—I), usually more or less reflexed hairs and the testa palisade cell walls of type II (with the notable exception of *L. inyangense*). Leaf-shape varies quite a lot (Fig. 1 B—J, L, M) as does longevity and various details of the silicula. The determination of such plants show in the herbaria much confusion, and some of the few published accounts are equally confused (SCHULZ 1927, GONÇALVES 1961, ROBYNS & BOUTIQUE 1951, EXELL 1973). It is clear that taxa very close to and partly conspecific with the tropical African species occur in S. Africa, and for that area a great deal of the taxonomic and nomenclatural confusion was resolved by MARAIS (1966, 1970). The present revision must largely be concerned with the similarities between the tropical and South African forms, which latter I have found it superfluous to revise anew.

Particularly problematic from a taxonomic point of view are a number of perennials with a thick, strongly lignified root giving rise to numerous basally more or less lignified shoots, so that they are often practically subshrubs. The leaves are undivided and the siliculae are retuse, not emarginate, and nearly always with projecting stigma. Practically every collection has its distinctive minor features, not unexpected for autogamous plants that may have been isolated for a long time. Plants of this general habit occur in Mega in S. Ethiopia, a few places in the Kenya uplands, the Inyanga area in Rhodesia, Huila area in Angola, as well as in S. Africa. The few collections are in many cases rich in specimens. The taxonomic treatment of this material presents problems owing to the vagueness of available characters (p. 22) and the suspicion that much remains to be discovered about these inconspicuous plants. According to the present species concept of the genus (cf. p. 22) their character combinations indicate that they constitute more than one species.

Of the tropical African collections only the one from Angola (WELWITSCH 1190) has been previously described, viz. as var. *aethiopicum* of *L. ruderale* (HIERN 1896). It was placed by THELLUNG (1906 a) as a

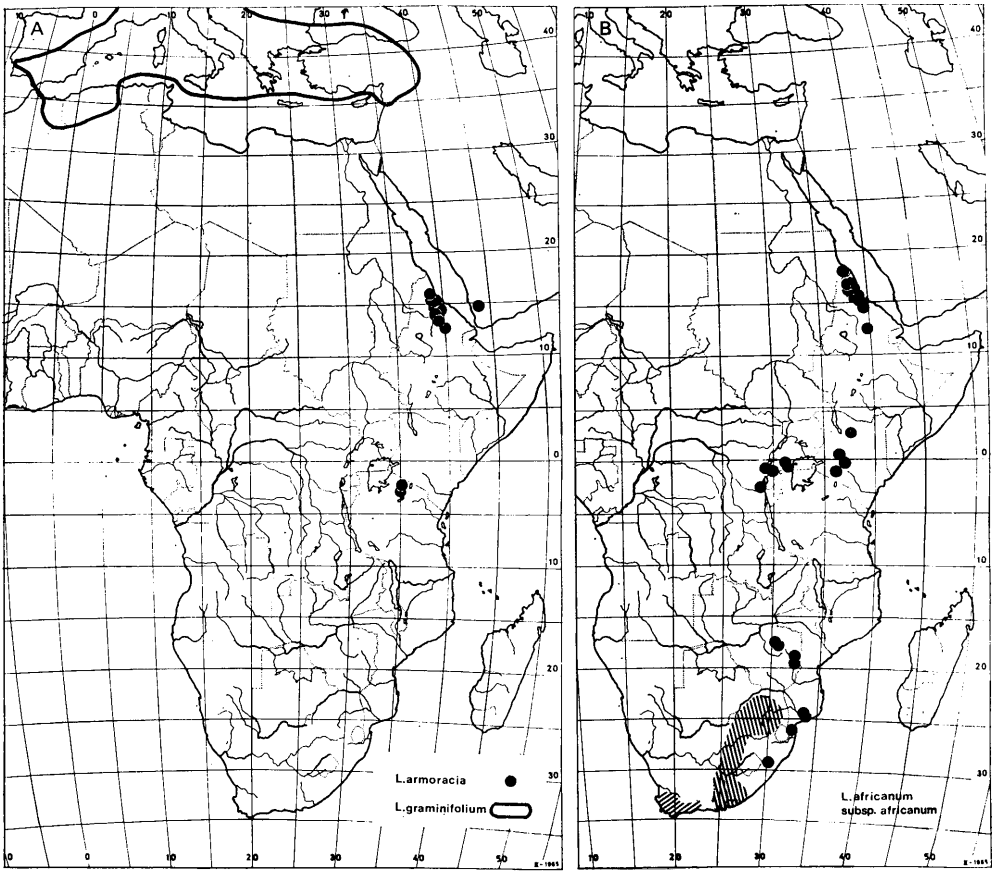

Fig. 10. A: Total distribution of *L. armoracia* and approximate distribution of *L. graminifolium* (arrow points at occurrence in the Crimea). — B: Total distribution of *L. africanum* subsp. *africanum* (within hatched areas approximate). — C: Total distributions of *L. angolense, L. inyangense, L. keniense* and *L. suluense.* — Each symbol represents one or more herbarium collections.

variety of *L. africanum,* a name used by him for what is here called *L. capense* THUNB. (cf. synonymy). A query indicates, however, that THELLUNG was uncertain of its proper position, and it is a quite distinct plant. The rather narrow siliculae with distinctly veined valves, only a minute emargination and prominently projecting style (Fig. 3 H) make it distinct both from the other tropical African collections and from *L. capense,* which, however, also has a projecting style. Other important features of the Angolan plant are the undivided leaves (in *L. capense* the basal ones are usually pinnatifid), the curved pedicels, which are set at an angle of only ca. 45° (Figs. 3 H, 4 J) (in *L. capense* and the tropical African collections they divaricate to 60—90°).

Morphologically as well as geographically (Fig. 10 C), the Angola plant occupies a very isolated position. It cannot with any justification be united with any other known species, nor does it bridge a gap between other species in such a way that might suggest the uniting of such species.

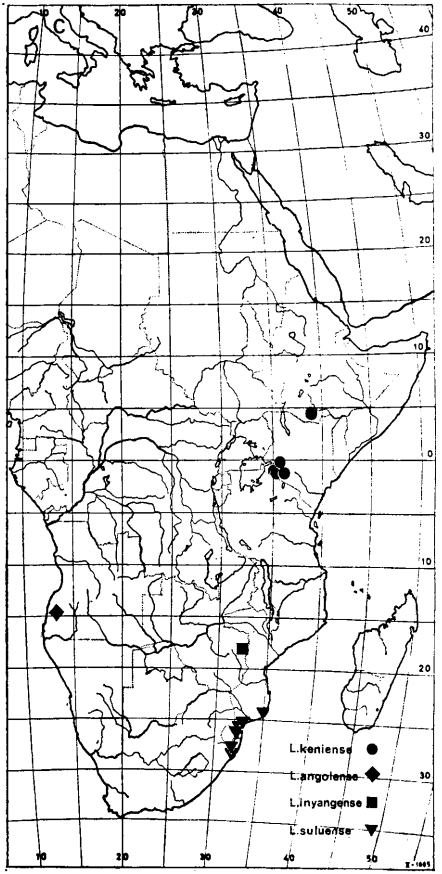

Fig. 10 C.

Therefore, in spite of the existence of only one collection, I find it necessary to describe it as a new species, *L. angolense* (see p. 43). Fortunately the material is copious and in good condition.

The isolated collection from the Inyanga area in E. Rhodesia (ROBINSON 1969; cf. Fig. 10 C) was attributed to "*L. africanum* var. *aethiopicum*" (=*L. angolense*) by EXELL (1960), and it has the minute emargination of the silicula (Fig. 3 I) in common with *L. angolense*. The cauline leaves (Fig. 1 L, M), which are especially apically acutely serrate and densely pubescent in part, agree on the other hand with the S. African *L. ecklonii* SCHRAD., the siliculae of which are, however, distinctly emarginate. Moreover the Rhodesian plant is outstanding in the nature of its pubescence, which is very dense and consisting of narrow, falcate, often ca. 0.3 mm long hairs, while those of *L. ecklonii* are only 0.1—0.2 mm long and more subulate. The testa palisade layer is of type I (Fig. 8 C), not otherwise seen in this group of species. The profile of the wall thickenings is here still more pointed and narrower than in *L. armoracia,* and thus very clearly different from type II. With respect to the general constancy of the palisade layer structure this feature confirms the impression of taxonomic isolation of the Rhodesian plant. It will therefore be described (p. 43) as a separate species, *L. inyangense,* the resemblance of which to the species mentioned above may be only rather superficial.

The seven Kenyan—S. Ethiopian collections (cf. Appendix) have a number of features in common. The siliculae are slightly but distinctly retuse, usually with projecting style, they are rather broad in relation to the length, and the valves have no or only indistinct nervature (Fig. 3 F—G). The stem and rhachis are less pubescent than in *L. angolense* and especially *L. inyangense,* with only reflexed hairs ca. 0.1 mm long. The primary leaf rosette was not present, but the cauline leaves are all lanceolate to linear (Fig. 1 F—G), seem rather coriaceous and bear short hairs only along the midveins. The amount of pubescence varies, however, between the collections. This character combination distinguishes it from the two above-mentioned species as well as from any of the S. African ones, of which *L. capense* undoubtedly is the most similar. The latter species has, however, more or less pinnatifid lower cauline leaves, while they are practically entire in the East African specimens that are possible to study in this respect (e.g. NAPIER 555). Moreover the seeds of all collections have a coarse testa reticulum (cf. p. 30 and Fig. 9 E, F,

L) not met with in the rest of the tropical African material, nor in *L. capense* and the other S. African species studied. (One collection of *L. keniense,* BALLY 8430, could not be studied in this respect because of failed seed-setting.) These East African collections have thus so much in common and can be so clearly distinguished from other species that I regard them too as a separate species, *L. keniense* described on p. 42 (cf. Fig. 10 C). The collection from S. Ethiopia is somewhat deviating by its shorter style, divaricate pedicels and broader siliculae (Fig. 3 G). In herbaria this species has hitherto usually passed as "*L. africanum* var. *aethiopicum*". The collection cited by AGNEW (1974) as an example of *L. africanum* (NAPIER "1525"=N. 553 and 555) is in fact this species.

Within the *L. africanum*-group besides the three species described collections are found with longer stems with straighter branches, which may arise from the whole length of the stem or only from its upper part. These plants seem usually to be erect and 3—5 dm long, but may become much longer with straggling, much-branched stems. Such plants are usually lignified below and definitely perennial, but very thick roots and stem-bases were not observed. The long and straggling plants often form axillary leaf-rosettes with spathulate leaves (cf. p. 23). Short-lived forms also occur, and are in some areas perhaps more common (cf. p. 22).

Collections of this general habit occur in rather large numbers from Sudan and Eritrea southwards through certain upland areas of eastern tropical Africa down to southern Africa. The apparently perennial forms are mainly from Ethiopia and N. Kenya, while most material from other tropical regions seems to be short-lived and to have partly grown as weeds.

Among the probably short-lived plants are some collections from Mozambique with pinnate or pinnatifid cauline leaves (cf. also p. 22 and Fig. 1 H) and rather deep and narrow emargination of the silicula, the lobes of which usually converge (Fig. 3 E). Such plants were described by MARAIS (1966) as *L. suluense,* which also occurs in Natal (Fig. 10 C). There are, however, specimens combining the silicula type of *L. suluense* with the type of undivided leaves found in *L. africanum* (e.g. MENDONÇA 2797 a, cf. p. 22 and below), and the species may be impossible to delimit sharply. In spite of such morphological intermediates, the nature of which cannot now be decided, I recognize this species, especially because no collections with the typical *L. suluense* features were seen from outside a limited area.

The great majority of collections, which are all attributable to *L. africanum,* have undivided or somewhat pinnatifid leaves, and distinct but comparatively broad emarginations, from which the style projects only slightly or not at all. *L. africanum* will as a result of the inclusion of all these forms become variable, not least as regards longevity. This means a partial contradiction of the way it was circumscribed by MARAIS (1966, 1970), who included in *L. africanum* only short-lived forms, mostly occurring as weeds. The S. African perennials of close affinity were regarded by him as a separate species, *L. divaricatum* AIT., divided into two subspecies. The rarer of these, subsp. *trifurcum* (SOND.) MARAIS, is outstanding in several features (cf. below). The more widespread subsp. *divaricatum,* occurring both in S. Africa and Namibia, is indeed very similar to certain forms of *L. africanum,* especially the perennial ones of N.E. tropical Africa, and to some collections from Rhodesia. The differentiating features of subsp. *divaricatum* include leaf-shape, size of siliculae and seeds and degree of pubescence (cf. p. 42). Undivided as well as pinnatifid cauline leaves seem to exist in both *L. africanum* s.str. and subsp. *divaricatum* (cf. MARAIS 1970 p. 90). The siliculae of subsp. *divaricatum* are as a rule both longer and broader (Fig. 4 F, cf. p. 42), but the dif-

ferences from *L. africanum* are not absolute. In subsp. *divaricatum* the rhachis is glabrous or bears scattered, short hairs, while *L. africanum* is in tropical Africa usually moderately to densely puberulent. Two Rhodesian collections from Umtali (CHASE 4572 (K, LISC, SRGH); PHIPPS 2174 (BR, EA)) and two from Marsabit in N. Kenya (BALLY 5476 (EA, K), FADEN 68/602 (EA)) come in this respect very near to subsp. *divaricatum*; were it not for their smaller siliculae and seeds they would fall within its limits. The N. Ethiopian perennials, which are very uniform, differ from subsp. *divaricatum* mainly in their dense rhachis pubescence and the clearly smaller average size of their siliculae and seeds.

In Namibia from which rather a lot of subsp. *divaricatum* has recently been collected, it appears variable and approaches the Ethiopian plant even in pubescence (e.g. MERXMÜLLER & GIESS 3404 (M)). Others from Namibia deviate in their compact fruiting racemes and densely appressed cauline leaves (MERXMÜLLER & GIESS 2835 (M), URSCHLER s.n. (M)). (The specimen SEYDEL 3457, cited by MERXMÜLLER (1966) as *L. divaricatum* does not belong to this taxon but is probably an undescribed species.)

I find the features by which *L. divaricatum* subsp. *divaricatum* differs from *L. africanum* so vague when considered over its whole range that I cannot but regard them as conspecific. I retain subsp. *divaricatum* as a subspecies under *L. africanum* (cf. p. 41).

On the other hand subsp. *trifurcum* deviates so much that I prefer to restore it to specific status as *L. trifurcum* SOND., (but circumscribed according to MARAIS 1966, not THELLUNG 1906 a, b) instead of recognizing it as a subspecies under *L. africanum* s. lat. It is completely glabrous, even along the adaxial side of the pedicels, which are erecto-patent and only slightly curved, never spreading to reflexed as in *L. africanum*, and the siliculae are remarkably narrow and usually ovate (Fig. 4 G). This characteristic plant occurs within a restricted area in N.E. South Africa (cf. MARAIS 1970).

L. africanum subsp. *africanum* would thus comprise short-lived S. African and all the tropical African material of the species. A short-lived weed type grows in Rhodesia (e.g. DRUMMOND 4933 (BR, K, S)) and in tropical East Africa (e.g. PURSEGLOVE 3620 (BR, EA, K) from Uganda, HENDRICKX 7836 (BR) from Kivu in Zaïre). Plants collected near Mt. Kenya (FRIES & FRIES 875 and 1034 (cf. p. 32), and JONSELL 2972 (UPS), which grew as a weed) comprise a local form deviating in unusually long and straight hairs. Another local, native form is certainly the one from Marsabit in N. Kenya (cf. above), which is obviously perennial; it is outstanding in being nearly completely glabrous, and in having a very shallow emargination from which the style projects distinctly. It can be questioned whether this form is not deviating enough to be recognized as a separate taxon. A final local, uniform variant is the one from N. Ethiopia, already frequently referred to, which extends northwards to the Red Sea Hills in Sudan (JACKSON 2883 (K)). The fact that local forms are easy to discern makes it probable that *L. africanum* as a weed is an apophyte, indigenous in the areas where it now occurs (cf. Fig. 10 B). (A curious collection from S. Mozambique, TORRE 7510 (EA, LISC), is a subshrub, which is tentatively attributed to *L. africanum* s. lat.)

The plant here called *L. africanum* has until recently passed as *L. divaricatum*. The tropical African and the short-lived S. African plants were usually called *L. divaricatum* AIT. subsp. *linoides* (THUNB.) THELL. (based on *L. linoides* THUNB.) or even identified with a var. *subdentatum* (BURCH. ex DC.) THELL. of this taxon, as in FRANCHETTI (1958) for the Ethiopian form. All these names are

typified by collections from S. Africa, and those of the latter were included by MARAIS (1966) in subsp. *divaricatum*. As MARAIS (1966) demonstrated the name *L. africanum* has been misapplied by DE CANDOLLE (1821) and THELLUNG (1906 a, b), as the BURMAN (1768) type and description of *L. africanum* turned out to fall within the limits of what had passed as *L. divaricatum*. The type of *L. divaricatum* AIT. was regarded by MARAIS (1966 p. 107) as belonging to another species than *L. africanum* and the name *L. divaricatum* was thus retained in this sense. This taxon is, however, recognized by me only as a subspecies of *L. africanum* (cf. p. 41). For the species earlier (e.g. by THELLUNG 1906 a, b) called *L. africanum, L. capense* THUNBERG (1800) became the correct name. This species, frequently referred to above, is restricted to the Cape Peninsula.

The introduced species. *L. bonariense,* native in central S. America (Argentina, Uruguay, Brazil, Paraguay, Chile *fide* HITCHCOCK 1945), has become introduced in many parts of the world. It is widespread in S. Africa (MARAIS 1970) and apparently extending its range in parts of tropical Africa, from where the first specimens date from the 1950s. It seems invariably connected with cultivation there and has not become really naturalized. It is easy to distinguish from the native African species by its leaves (Fig. 1 K), siliculae (Fig. 3 J) and seeds (cf. key and description). In S. America it is somewhat variable and its delimitation from some other species is debatable (THELLUNG 1914, HITCHCOCK 1945, BOELCKE 1964). The only variation of importance in Africa concerns its longevity, about which the literature reports are contradictory (THELLUNG 1906 b considered it a perennial, BOELCKE (1967) an annual; cf. p. 22).

Another introduced species, *L. virginicum* L. has, however, been confused with *L. bonariense*. *L. virginicum,* which grows as an introduction in S. Africa (MARAIS 1970), is in tropical Africa known only from one rather comprehensive collection from Mozambique (MARQUES 2194—2195 (COI, LISC)), which was taken for *L. bonariense* by EXELL & GONÇALVES (1973). The leaves, which in *L. virginicum* are undivided except for those of the primary rosette (cf. p. 44) constitute the most striking difference. It is true that some S. American forms of *L. bonariense* have undivided leaves (THELLUNG 1914, HITCHCOCK 1945, BOELCKE 1967), but the pedicel direction and the shape of the silicula emargination, prominent in both species, are also distinctive. The latter is in *L. virginicum* rather narrow, and the stigma is carried on a short but distinct style (Fig. 3 K); in *L. bonariense* it is broadly widened and with a practically sessile stigma (Fig. 3 J). On this point the descriptions of the two species in Flora Europaea (1964) are rather misleading, nor do the differences in petal length stated in its key hold good (cf. p. 44). Specimens of *L. virginicum* from Mozambique have petals as reduced as *L. bonariense*. Obliquely accumbent cotyledons were observed in its embryos (Fig. 5 A), as well as in the eight other collections studied, from various parts of the world. In *L. bonariense* only incumbent cotyledons were seen. *L. virginicum* is a native of N. America, and has become widespread in for example large parts of Europe. To a still higher degree than for *L. bonariense* it seems reasonable to suspect that the introductions to Africa have taken place via Europe.

L. ruderale L. was reported from tropical Africa in many older flora works (cf. synonymies). This is simply due to confusion with the superficially similar species of the *L. africanum*-complex, from which it is distinguished by the straight pedicels, the short, neither curved nor reflexed hairs, and anatomical features of the seed (cf. p. 28).

PHYTOGEOGRAPHY

L. armoracia, the closest relative of which is *L. graminifolium* (cf. p. 23 and Fig. 2 F), belongs to the Mediterranean genetical element (cf. WHITE in CLAPHAM & WHITE 1970 p. 55 for a discussion of this term) of the upland tropical East African flora (map Fig. 10 A). The role of this element has been assessed only for the Afro-alpine flora (HEDBERG 1965 p. 524), and it is only sparsely represented here. The distribution of *L. armoracia* was commented upon above (p. 33).

The remaining indigenous species, which are in my opinion closely allied, belong to a South African genetical element. This statement is based upon the following considerations. Southern Africa is an important centre of diversity for *Lepidium* with about 15 native species. Some undescribed ones are probably to be added, especially from Namibia. The S. African species seem to fall into various groups of affinities, but their relationships in detail have still to be clarified. As emphasized above a number of species restricted to S. Africa are most certainly the closest relatives of the group of tropical African species. Such relatives are found both in the Cape (*L. capense*) and the Karroo-Namib phytogeographical regions as well as in the S. African parts of the Sudano-Zambesian regions (cf. WHITE 1972 as to phytogeographical division). It seems therefore appropriate to regard these tropical species as belonging to the S. African element of the tropical African upland flora; no further definition of their phytogeographical affinity is possible at present.

The S. African genetical flora element of tropical Africa has been elucidated for the Afro-alpine flora and to some extent for the taxonomically far less well known Afro-montane flora (HEDBERG 1965, 1970, WEIMARCK 1941, NORDENSTAM 1969 among others). The tropical African *Lepidium* species are on the whole montane and usually confined to low-montane areas. WHITE (1965), who discerned the Afro-montane Region as one of the principal phytogeographical entities in Africa, tries (in CHAPMAN & WHITE 1970 pp. 64—65) to define the lower limit of this Region with special reference to Malawi. It is found there somewhere between 1,065 and 1,525 m. The *L. africanum* group in tropical Africa proper reaches no lower than 1,100 m and then perhaps only as weeds. They usually grow between 1,400 and 1,800 m, and may reach 2,200 (Mega in S. Ethiopia). In N. Ethiopia their altitudinal range is larger, but they are still montane. They would therefore belong to the Afro-montane phytogeographical element. Only in southernmost Mozambique do some species grow at low altitudes, near the coast, viz. *L. africanum* (sporadically and perhaps as an introduced weed) and *L. suluense*, which is endemic to this coastal strip and to its prolongation into Natal (cf. p. 36).

The only widespread species, *L. africanum,* shows the wide disjunctions (Fig. 10 B) characteristic of many S. African and Cape elements in tropical Africa (cf. e.g. WEIMARCK 1941, NORDENSTAM 1969 pp. 56 and 59, GRAU 1973). The restricted endemics, *L. keniense, L. inyangense* and *L. angolense* are all from Afro-montane areas that are regarded as centres of endemism (WEIMARCK 1941).

The S. African element is poorly represented among tropical African Cruciferae. None of the genera endemic to southern Africa, of which *Heliophila* is by far the most important, reach tropical Africa proper. The best example besides *Lepidium* is *Rorippa nudiuscula* THELL., which grows in S. Africa—Rhodesia and has an outlying group of localities in montane East Africa.

TAXONOMY

KEY TO THE LEPIDIUM SPECIES IN TROPICAL AFRICA

1. Siliculae longer than 4 mm; wings prominent ..... *L. sativum*
1. Siliculae shorter than 4 mm; wings absent or indistinct 2
2. Petals longer than or equalling sepals 3
2. Petals shorter than sepals or absent 4
3. Siliculae slightly retuse with distinctly projecting style ..... *L. armoracia*
3. Siliculae deeply emarginate with style wholly within the sinus ..... *L. virginicum*
4. Siliculae suborbicular. Seeds narrowly winged 5
4. Siliculae elliptic, oblong or ovate. Seeds not winged 6
5. Cauline leaves pinnatifid to pinnate ..... *L. bonariense*
5. Cauline leaves ± deeply serrate ..... *L. virginicum*
6. Siliculae distinctly emarginate; stigma within, or rarely only just projecting beyond the sinus. Stems mostly branched only in upper parts. Stems and branches ± straight. Annuals or short-lived perennials 7
6. Siliculae only retuse; stigma projecting beyond the sinus (rarely just at its margin). Stems branched ± equally along their whole length. Stems and branches curved. Perennials, often sub-shrubs 8
7. Emargination narrow and rather deep with margins distally converging. Cauline leaves usually pinnate ..... *L. suluense*
7. Emargination broader with margins not converging distally. Cauline leaves undivided to pinnatifid ..... *L. africanum* subsp. *africanum*
8. Most parts of plant densely pubescent with mostly thin, ± falcate hairs, ca. 0.3 mm long. Leaves markedly oblanceolate and apically serrate ..... *L. inyangense*
8. Moderately to sparsely puberulent with retrorse hairs, ca. 0.1 mm long. Leaves linear to oblanceolate, entire or distantly serrate 9
9. Silicula valves with prominent veins. Silicula narrower than 1.9 mm ..... *L. angolense*
9. Silicula valves without or with very indistinct veins. Siliculae nearly always broader than 1.9 mm ..... *L. keniense*

Lepidium armoracia FISCH. & MEY.

FISCHER & MEYER 1842: 77. — Orig. coll.: Specim. cult. in horto bot. petropolit. e sem. coll. SCHIMPER in Ethiopia (LE holotypus!).

L. abyssinicum A. RICHARD 1847: 21. *L. armoracia* FISCH. & MEY. subsp. *abyssinicum* (A. RICH.) THELLUNG 1906 a: 176. — Orig. coll.: Ethiopia, Tigre, SCHIMPER II: 741 (P holotypus!).

L. alpigenum A. RICHARD 1847: 22. *L. ruderale* L. var. *alpigenum* (A. RICH.) OLIVER 1868: 69. *L. armoracia* FISCH. & MEY. subsp. *intermedium* (A. RICH.) THELL. var. *alpigenum* (A. RICH.) THELLUNG 1906 a: 177. *L. armoracia* FISCH. & MEY. var. *alpigenum* (A. RICH.) THELL.; FRANCHETTI 1958: 170. — Orig. coll.: Ethiopia, Ouodgerate, PETIT s.n. (P holotypus!).

L. intermedium A. RICHARD 1847: 21. *L. armoracia* FISCH. & MEY. subsp. *intermedium* (A. RICH.) THELLUNG 1906 a: 176. *L. armoracia* FISCH. & MEY. var. *intermedium* (A. RICH.) FRANCHETTI 1958: 169. — Orig. coll.: Ethiopia, Tchélikote, QUARTIN-DILLON & PETIT s.n. (P holotypus!).

L. ruderale sensu OLIVER 1868: 69 p.p., ENGLER 1892: 223 p.p., DURAND & SCHINZ 1898: 137 p.p., non L.

L. graminifolium sensu DURAND & SCHINZ 1898: 136 p.p., non L.

L. schweinfurthii THELLUNG 1906 a: 178. — Orig. coll.: Yemen, Menacha (Manakha), 16. II.1889, SCHWEINFURTH 1392 (G holotypus!).

Perennial herb or subshrub with a thick woody taproot. Stems several from the base, woody at base or often even to quite high up, 20—50 cm high, ascending to erect, richly branched. Basal leaves evanescent, petioled, oblanceolate, undivided or with a few basal lobes, serrate towards the apex. Cauline leaves indistinctly petioled, rather firm, up to 4 cm long, lanceolate, oblanceolate or linear, acute, attenuate at base, sparsely serrate to entire; apices and teeth ± cartilaginous. Racemes terminal, rather lax in fruit (Fig. 4 A—B), up to 25 cm long. Pedicels 3.0—4.5 mm long, straight and erecto-patent or arcuately patent (Fig. 2 A—E). Stems, leaves, rhachis and pedicels sparsely puberulent with very short, patent to recurved, sometimes scabridulous hairs, or glabrous. Sepals ovate to oblong, green with prominent membranous margins and often tinged

with violet, 0.8—1.2 mm long. Petals white, equalling or longer than sepals, 1.2—1.8 mm long, spathulate to clawed. Stamens 4 or 2 (median and/or lateral). Nectaries broadly cylindrical to obtusely conical. Siliculae orbicular, elliptic, rhombically elliptic or ovate, retuse, 2.5—3.8×2.0—2.5 mm; style prominent, distinctly projecting beyond the sinus (Fig. 2 A—E). Seeds wingless, bright red-brown, 1.3—1.7×ca. 0.8 mm, with a faint, very fine, regular reticulum (Fig. 9 A—B, J). Palisade layer of testa of type I (Fig. 8 A—B). Cotyledons incumbent in embryo.

ECOLOGY: open dry grassland, dry riverbeds, rocky ground, "kopjes". Alt. ca. 1,500—2,800 m.

DISTRIBUTION: Yemen, N. Ethiopia, N. Tanzania (Fig. 10 A).

Lepidium africanum (BURM. FIL.) DC.

Lepidium africanum (BURM. FIL.) DC. subsp. **africanum**

DE CANDOLLE 1821: 552 quoad synon., non quoad descr. et auct. nonn.

Thlaspi africanum BURMAN FIL. 1768: 17. — Orig. coll.: S. Africa, Cape Province, BURMAN FIL. s.n. (G holotypus!).

L. ruderale sensu OLIVER 1868: 69 p.p. et auct. sqq., non L.

L. divaricatum AIT. subsp. *linoides* sensu EXELL 1960: 192, GONÇALVES 1961: 63, EXELL & GONÇALVES 1973: 8 p.p., non *L. divaricatum* AIT., nec subsp. *linoides* (THUNB.) THELL. s.str.

L. divaricatum AIT. subsp. *subdentatum* (BURCH. ex DC.) ENGLER 1915: 262 quoad basion., non quoad specim., CUFODONTIS 1954: 141, non DC.

L. divaricatum AIT. subsp. *linoides* (THUNB.) THELL. var. *subdentatum* sensu ROBYNS & BOUTIQUE 1951: 526, FRANCHETTI 1958: 172, non var. *subdentatum* (BURCH. ex DC.) THELL. s.str.

L. armoracia sensu SCHULZ 1927: 1103, non FISCH. & MEY.

Annual—perennial herb (sometimes nearly a subshrub) with rather slender taproot. Stems one to many from the base, sometimes woody in basal parts, 20—75 cm high, erect or straggling, usually branching only from above the middle. Basal leaves in a short-lived rosette, oblanceolate. Cauline leaves not distinctly petioled, thin, up to 6 cm long, acute, attenuate; the primary ones lanceolate—oblanceolate, distantly serrulate or, in lower leaves pinnatifid; the secondary ones more pronouncedly oblanceolate and serrulate. Racemes terminal and axillary, rather dense in fruit (Fig. 4 D—E), up to 15 cm long. Pedicels 2.5—3.7 mm long, curved or arcuately patent (Fig. 3 A—D). Stem, leaves, rhachis and pedicels sparsely to rather densely puberulent with very short retrorse, rarely straight hairs. Sepals ovate, green, with membranous margins and often a tinge of violet, 0.6—0.8 mm long. Petals absent or up to 0.5 mm long, narrowly spathulate or linear. Stamens 2 (median). Nectaries ± conical. Siliculae elliptic to ovate (usually 1.5—1.8 times as long as broad), shallowly but distinctly emarginate 1.8—3.2×1.4—2.1 mm; style with its stigma usually not projecting beyond the sinus, or rarely reaching just beyond it (Fig. 3 A—D). Seeds wing-less, red-brown to brown, 1.1—1.4×ca. 0.7 mm with a faint, very fine reticulum (Fig. 9 C, D, K). Palisade layer of testa of type II (Fig. 8 D, G). Cotyledons incumbent in embryo (Fig. 5 B). Chromosome number 2n=16 (cf. Appendix).

ECOLOGY: open dry grassland, arable fields, roadsides. Alt. (100—)1,100—2,600 m.

DISTRIBUTION: Sudan (Red Sea Hills), N. Ethiopia, Kenya uplands, montane areas of Uganda and eastern Zaïre, eastern Rhodesia, south Mozambique and large parts of S. Africa (Fig. 10 B).

Lepidium africanum (BURM. FIL.) DC. subsp. **divaricatum** (AIT.) JONSELL comb. nov.

L. divaricatum AITON 1789: 375. — Orig. coll.: Specim. cult. "L. divaricatum Banks' ex Hort. Kew." (G). For synonymy cf. MARAIS 1966: 107 under *L. divaricatum* AIT. subsp. *divaricatum*.

Differs from subsp. *africanum* in its always perennial habit in combination with branching along the whole length of the stem, usually very sparse pubescence, larger siliculae (2.5—3.7×1.8—2.3 mm) and larger seeds (ca. 1.4×0.8 mm). Testa reticulum faint, very fine; palisade layer of type II. Cotyledons incumbent in embryo.

DISTRIBUTION: confined to Namibia and South Africa (Cape Prov. and Orange Free State).

Lepidium suluense MARAIS

MARAIS 1966: 109. — Orig. coll.: S. Africa, Natal, Hlabisa Distr., WARD 4577 (PRE holotypus!).

L. divaricatum AIT. subsp. *eu-divaricatum* THELL. var. *dissectum* THELLUNG 1906 a: 167. — Orig. coll.: Mozambique, Delagoa Bay, Khocène, XI. 1890, JUNOD 314 (Z holotypus!).

L. divaricatum subsp. *divaricatum* sensu EXELL 1960: 192, GONÇALVES 1961: 63 saltem p.p., EXELL & GONÇALVES 1973: 8 saltem p.p., non AIT.

L. africanum var. *aethiopicum* sensu EXELL 1960: 190 p.p., EXELL & GONÇALVES 1973: 7, non *L. africanum* (BURM. FIL.) DC., nec var. *aethiopicum* (HIERN) THELL.

Probably short-lived perennial (perhaps also annual) with rather slender taproot. Stems usually solitary, sometimes woody in basal parts, 30—60 cm high, erect with long, straight branches along their whole length. (Basal leaves not seen.) Cauline leaves usually petiolate, thin, up to 5 cm long, ± lanceolate to elliptic in outline; the lower ones subpinnatifid to acutely serrate; the upper and in particular the secondary ones pinnatisect with narrow, linear lobes (rarely undivided and distantly serrate). Racemes terminal, rather dense in fruit (Fig. 4 H) and up to 25 cm long. Pedicels 2.0—3.5 mm long, arcuate. Stem and rhachis sparsely, and pedicels more densely, puberulent with very short retrorse hairs; leaves practically glabrous. Sepals oblong, green with membranous margins, 0.7—0.8 mm long. Petals absent or up to 0.3 mm long, almost linear. Stamens 2 (median). Nectaries triangular. Siliculae elliptic, 2.2—3.0×1.7—1.9 mm, rather deeply and narrowly emarginate with the lobes ± converging towards the mouth of the sinus; style with its stigma not projecting beyond the sinus (Fig. 3 E). Seeds wingless, red-brown, 1.1—1.4×0.6—0.7 mm with a faint ± dissolved, very fine reticulum (Fig. 9 G). Palisade layer of testa of type II (Fig. 8 E—F). Cotyledons incumbent in embryo.

ECOLOGY: open sandy ground. Alt. 0—250 m.

DISTRIBUTION: southernmost Mozambique and northern Natal (Fig. 10 C).

Lepidium keniense JONSELL sp. nov.

Herba perennis vel suffrutex, e basi valde ramosa, pilis minutis retrorsis sparsim induta. Caules ascendentes vel decumbentes, ramosi, 10—30 cm longi. Folia caulium vix petiolata, subcoriacea, lanceolata, integra vel serrulata. Racemi fructiferi subdensi pedicellis arcuate patentibus. Petala sepalis breviora, alba, linearia. Stamina duo. Siliculae ellipticae, retusae, valvis non venatis. Stylus distinctus; stigma huius ex sinu protrudens. Semina non alata, inconspicue sed subgrosse reticulata.

Orig. coll.: Kenya, Masai Distr., Narok, 11.XII.1963, VERDCOURT 3820 (EA holotypus! BR, K isotypi!).

L. africanum sensu AGNEW 1974: 95 p.p., non (BURM. FIL.) DC.

Perennial herb to subshrub with a thick woody taproot. Stems many—numerous from the base, woody at base or often even to quite high up, 10—30 cm long, ascending or decumbent, richly branched along their whole length. Basal leaves evanescent, oblanceolate, entire to sparsely serrate. Cauline leaves indistinctly petioled, rather firm and often involute, up to 5 cm long, lanceolate to nearly linear, acute, attenuate, entire to distantly serrulate; apices and teeth ± cartilaginous. Racemes mostly terminal, dense in fruit (Fig. 4 I), up to 12 cm long. Pedicels 3.0—4.5 mm long, arcuately patent (Fig. 3 F—G). Stem

leaves, rhachis and pedicels finely and usually sparsely puberulent with very short retrorse hairs. Sepals ovate, green with membranous margins, occasionally with a tinge of violet, 0.8—1.3 mm long. Petals white, always shorter than sepals, nearly linear, up to 0.8 mm long. Stamens 2 (median). Nectaries triangular to cylindrical. Siliculae elliptic (1.3—1.6 times as long as broad), retuse, 2.5—4.0× 1.7—3.0 mm; valves not or very indistinctly veined; style distinct, its stigma usually projecting beyond the sinus (Fig. 3 F—G). Seeds wingless, red-brown, 1.2—1.6×ca. 0.8 mm with a faint but rather coarse reticulum (Fig. 9 E, F, L). Palisade layer of testa of type II. Cotyledons incumbent in embryo.

ECOLOGY: open, dry sometimes rocky grassland. Alt. ca. 1,850—2,400 m.

DISTRIBUTION: S. Ethiopia (Mega) and S.W. Kenya (Fig. 10 C).

Lepidium angolense JONSELL sp. nov.

Suffrutex, e basi valde ramosus, pilis tenuibus retrorsis parce indutus. Caules decumbentes, ramosi, ad 25 cm longi. Folia caulium inferiora petiolata, superiora sessilia, subcoriacea, lanceolata ad oblanceolata, serrata. Racemi fructiferi densi, pedicellis erecto-patentibus curvatis. Petala sepalis breviora, sublinearia. Stamina duo. Siliculae ellipticae, retusae, valvis distincte venatis. Stylus distinctus ex sinu protrudens. Semina non alata, inconspicue et tenue reticulata.

Orig. coll.: Angola, Huíla, inter Humpata et Serra de Uiahoia, 23.IV.1860, WELWITSCH 1190 (K holotypus! BM, COI, G, LISU, P isotypi!).

L. ruderale L. var. *aethiopicum* HIERN 1896: 25. *L. africanum* (BURM. FIL.) DC. var. (?) *aethiopicum* (HIERN.) THELLUNG 1906 a: 187. Typus: vide supra.

Perennial subshrub with a thick woody taproot. Stems numerous from the base, woody to rather high up, ca. 25 cm long, decumbent, richly branched along the whole length. (Basal leaves not seen.) Leaves petiolate or (upwards) sessile, rather firm and ± involute, with lamina up to 15 mm long, narrowly lanceolate—oblanceolate, acute, attenuate, acutely serrate especially towards the apex; apices and teeth somewhat cartilaginous. Racemes terminal, dense in fruit (Fig. 4 J), up to 12 cm long. Pedicels ca. 2.5 mm long, erecto-patent, curved (Fig. 3 H). Stem, leaves, rhachis and pedicels moderately puberulent with thin retrorse hairs. Sepals oblong, greenish, ca. 0.8 mm long. Petals white, nearly linear, ca. 0.5 mm long. Stamens 2 (median). Nectaries rectangular. Siliculae elliptic, retuse, 2.7—2.9×1.7—1.8 mm; valves with prominent veins; style distinct, projecting beyond the sinus (Fig. 3 H). Seeds wingless, red-brown, ca. 1.2×0.7 mm with a faint and very fine reticulum (Fig. 9 H). Palisade layer of testa of type II. Cotyledons incumbent in embryo.

ECOLOGY: in rather dry, abandoned fields. Alt. ca. 1,600 m.

DISTRIBUTION: Angola, Huila Distr. (only known from type collection; Fig. 10 C).

Lepidium inyangense JONSELL sp. nov.

Suffrutex humilis, e basi ramosus, pilis falcatis dense indutus. Caules decumbentes, parum ramosi, 6—10 cm longi. Folia caulium sessilia, subcoriacea, oblanceolata, ad apicem acute incisa, Racemi fructiferi densi, pedicellis arcuate patentibus. Petala sepalis breviora, late linearia. Stamina duo. Siliculae ellipticae, retusae, valvis indistincte venatis. Stylus distinctus, stigma huius ex sinu protrudens. Semina non alata, inconspicue et tenue reticulata.

Orig. coll.: Rhodesia, Inyanga, Gairesi Ranch, 20.XI.1957, ROBINSON 1969 (K holotypus! LISC, SRGH isotypi!).

L. africanum (BURM. FIL.) DC. var. *aethiopicum* sensu EXELL 1960: 190 p.p., non (HIERN) THELL.

Perennial subshrub with rather thick woody taproot. Stems several from the base, woody to rather high up, 6—10 cm long, decumbent, with rather few branches. (Basal leaves not seen.) Leaves practically sessile, rather firm, up to 15

mm long, oblanceolate, acute, attenuate, in the distal part serrate with few but prominent incisions; apices and teeth slightly cartilaginous. Racemes terminal, dense in fruit (Fig. 4 K), up to 7 cm long. Pedicels ca. 2.0 mm long, arcuately patent (Fig. 3 I). Stem, leaves (especially on basal and central parts), rhachis and pedicels densely pubescent with thin, comparatively long, falcate hairs. Sepals ovate, green, with white margins, 0.8—1.0 mm long. Petals white, broadly linear, ca. 0.4 mm long. Stamens 2 (median). Nectaries narrowly triangular. Siliculae elliptic, retuse, 2.5—2.7×1.4—1.6 mm; valves without distinct veins; style distinct but short, projecting beyond the sinus (Fig. 3 I). Seeds wingless, dull red-brown, ca. 1.3×0.7 mm with a faint and very fine reticulum (Fig. 9 I). Palisade layer of testa of type I (Fig. 8 C). Cotyledons incumbent in embryo.

ECOLOGY: "Bare ground by riverside". Alt. ca. 1,800 m.

DISTRIBUTION: Eastern Rhodesia, Inyanga area (only known from the type collection; Fig. 10 C).

Lepidium bonariense L.

LINNAEUS 1753: 645. — Orig. coll.: planta ex America austr. illustr. DILLENII 1742: 318, Tab. 286, Fig. 370.

Annual to perennial herb with one to many stems, erect—ascending, 20—70 cm high, branching above, puberulent with thin, straight or retrorse hairs. Leaves pinnatifid to tripinnatipartite, with ± lanceolate, serrate lobes. Racemes dense in fruit (Fig. 4 L). Pedicels 2.5—5.5 mm, ± patent, arcuate (Fig. 3 J). Sepals greenish, ca. 1 mm long. Petals usually 0.5—0.8 mm long or absent. Stamens 2 (median). Nectaries triangular. Siliculae suborbicular, 2.8—4.0×2.5—3.0 mm, widely and deeply emarginate; style very short with stigma completely contained within the sinus, usually close to its base (Fig. 3 J). Seeds narrowly winged, light red-brown, 1.4—1.8×ca. 0.9 mm. Palisade layer of testa of type III (Fig. 8 H). Cotyledons incumbent in embryo. Chromosome number 2n=64 (cf. Appendix).

ECOLOGY: weed of cultivation, roadsides etc., mostly in upland areas.

DISTRIBUTION: native of S. America. Almost cosmopolitan weed. African specimens seen from Ethiopia, Kenya, Uganda, Tanzania, Mozambique, Rhodesia and S. Africa.

Lepidium virginicum L.

LINNAEUS 1753: 645. — Orig. coll.: specim. in horto bot. upsal. cultum, Herb. Linnaei No. 824: 18 (LINN, lectotypus!).

L. bonariense sensu EXELL & GONÇALVES 1973: 7 p.p., non L.

Annual (or slightly perennial) herb with one to few stems, erect—ascending, 20—80 cm high, branching above, puberulent with thin falcate hairs. Leaves oblanceolate (lowest ones sometimes pinnatifid), acutely serrate. Racemes rather dense in fruit (Fig. 4 M). Pedicels 3.5—5.5 mm, divaricate, straight (Fig. 3 K). Sepals greenish, ca. 1 mm long. Petals white, longer or shorter than sepals. Stamens 2 (median). Nectaries triangular. Siliculae suborbicular, 3.0—3.5×2.7—3.5 mm, rather widely and deeply emarginate; style short with stigma completely contained within the sinus (Fig. 3 K). Seeds narrowly winged, red-brown, ca. 1.5×0.9 mm. Palisade layer of testa of type II. Cotyledons obliquely accumbent in embryo (Fig. 5 A).

ECOLOGY: weed of cultivation, etc.

DISTRIBUTION: native of N. America. Widespread as a weed. African specimens seen from Mozambique and S. Africa.

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APPENDIX

List of specimens, for which the chromosome number was determined and/or whose seeds were studied in the scanning electron microscope (SEM).

L. africanum subsp. *africanum:* Ethiopia, PAPPI 2951 (FI), SEM. Kenya, BALLY 5476 (EA), SEM, RYMAN 173 (UPS), 2n=16, SEM. — *L. africanum* subsp. *divaricatum:* Namibia, VOLK 12698 (M), SEM. S. Africa, LEISTNER 2432 (K), SEM. — *L. angolense:* Angola, WELWITSCH 1190 (K), SEM. — *L. armoracia:* Ethiopia, FIORI 1033 (FI), SEM. Tanzania, GREENWAY 9919 (K), SEM. — *L. bonariense:* Kenya, RYMAN 151 (UPS) and 164 (UPS), both 2n=64; v. HOFSTEN 504 (UPS), 505 (UPS) and 530 (UPS), all 2n=ca. 64. Tanzania, JONSELL 2138 (UPS), 2n=ca. 64. — *L. capense:* S. Africa, DOD 2889 (K), SEM. — *L. ecklonii:* S. Africa, ACOCKS 9314 (K), SEM, MARAIS 423 (K), SEM. — *L. inyangense:* Rhodesia, ROBINSON 1969 (K), SEM. — *L. keniense:* Ethiopia, GILLETT 14365 (K), SEM. Kenya, BOGDAN 1041 (K), SEM; GLOVER et al. 821 (K), SEM, NAPIER 553 (EA) and 555 (K), SEM; VERDCOURT 1157 (K) and 3820 (BR), SEM. — *L. suluense:* Mozambique, GRANDVAUX BARBOSA 7772 (COI), SEM. — *L. trifurcum:* S. Africa, POTS 793 (PRE), SEM.

Factors Possibly Influencing the Range of Shrubby Rubus Species in Sweden

I. Severity of Winter

Alf Oredsson

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In 1973, earliness of autumn colouring and leaf fall was recorded for wild raspberry, dewberry and eighteen blackberry species native to Sweden. Using four species as standards one of which at least was to occur in each of the 35 localities investigated, all the twenty species could be compared, in principle as if growing under uniform conditions.

A correlation between earliness and size of distributional area in Sweden was established.

Divided into five groups of earliness the combined area of distribution of the species corresponds relatively well with severity of winter, so that late species are restricted to areas where extreme winter conditions are of short duration, whereas species with early autumn colouring and early leaf fall also occur where there are extreme winter conditions for a comparatively long period of time.

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The northern boundary of some twenty European blackberry species traverses southern Sweden. Three main patterns of distribution can be observed with considerable variation in frequency and range. None the less, preference for a coastal habitat is common to all (OREDSSON 1973, 1974).

Along the coasts of southern Sweden there is a zone with a maritime climate stretching 30—40 km inland (ÅNGSTRÖM 1968 pp. 120 ff.). Compared with the interior the number of days when frost occurs during the vegetative period is low (WALLÉN 1965), winters are shorter and less severe (ÅNGSTRÖM 1953).

Since shrubby *Rubus* species do not flower until the second year the canes must survive the first winter to set fruit. Variation in size of distributional area in the species native to Sweden could conceivably be due to hereditary differences in hardiness. The purpose of the present paper is to test this hypothesis.

As regards trees, hardiness is initiated with decreasing day-length in late summer (EVERT 1968). The same applies to raspberries (WILLIAMS & HUDSON 1956). Whether or not this is true of all shrubby *Rubi,* the fact remains that during the critical period day-length is approximately uniform over the entire area of investigation (LINDHOLM 1965).

Hardiness increases with the fall of temperature. There is a threshold temperature of hardening (usually 5° to 10°C), above which the tissue again becomes sensitive (LEVITT 1956). Raspberry canes may become dormant and shed their leaves when exposed to temperatures no lower than 2° to 4°C (WILLIAMS & HUDSON 1956). In Germany, however, most of the

blackberry species retain their leaves until the following spring, unless the are ". . . spells of unusually severe frost" during the winter (WARMING & GRAEBNER 1933 p. 318; author's translation). Considering how much climate also varies locally, the accumulated hardening effect of temperature at a given time must generally differ even between adjacent localities. Since the canes examined in the present study where taken from an apparently uniform area within each locality, differences should be at their least.

In higher plants, abscission ". . . is the result of organ maturity, senescence, or injury" (CARNS 1966 p. 309). In raspberries, primocane maturity is largely governed by day-length and temperature (WILLIAMS & HUDSON 1956). Along the canes of raspberry as well as blackberry ". . . leaf-fall always proceeds from the base in acropetal succession" (LIEGEL 1961 p. 42; author's translation), probably a manifestation of senescence.

Having studied more than twenty genera of trees and shrubs cultivated in Sweden, ANDERSSON and SYLVÉN (1936 p. 611) conclude: ". . . within a genus, the earlier a species becomes decolorized or loses its leaves the more cold resistant it is" (author's translation). In raspberry varieties grown in Norway ". . . a close relationship was found between hardiness and length of the rest period" (THORSRUD & HJELTNES 1963 p. 116). After a severe occurrence of cane death in Scottish raspberry plantations JENNINGS et al. (1964 p. 65) report: ". . . the varieties and seedlings which habitually shed their leaves late in the first year of growth were more prone to damage than those which shed them early". Early leaf abscission was ". . . directly related to winterhardiness" in raspberry cultivars during a four-year period in Canada (VAN ADRICHEM 1970 p. 187). When growing foreign blackberries in southern Sweden, TAMÁS (1962 p. 45) found ". . . a good correlation between hardiness and the degree of leaf decoloration in the autumn".

Thus, it is highly probable that under natural conditions autumn colouring and leaf fall constitute an adequate measure of hardiness for the *Rubus* species under consideration. Other methods of assessment are also available, one of these being based on the electrical conductivity of cell-sap (see NYBOM et al. 1962).

MATERIAL AND METHODS

In 35 localities, principally along the coast of southern Sweden (Appendix), all with at least one of the *Rubus* species *corylifolius, plicatus, nessensis* and *idaeus* (the four standard species), autumn colouring and leaf fall was recorded for wild raspberry (*idaeus*), dewberry (*caesius*) and eighteen blackberry species.

Each locality was visited once, either in October or late in November 1973 (three of the October localities were revisited). At least two species were recorded at a time. I tried to find a homogeneous area covering most of the occurrence from which three primocanes (first-year growth) per species were taken by random sampling.

Beginning at the node of the leaf to unfold last (keeping to the main stem if the cane was branched) and ending at the fourth node from below, each leaf on the canes chosen was subjectively classified according to this scale:

1 green
2 partly autumn-coloured
3 autumn colours predominant
4 withered
5 shed, petiole persisting
6 shed, petiole absent

The number of classified leaves varies from 3 to 44 per cane (average 18.4). Three hundred canes in all were examined, five of these being completely naked. Of the remainder none were entirely green.

Locality mean shows how far autumn colouring and leaf fall had advanced in each separate species when the locality concerned was visited. It is based directly on the sum of the leaves classified.

Locality difference is the difference in locality means of any two species recorded at one time.

Table 1 shows data collected in the form of locality means.

Table 1. Locality means. The higher the value the more advanced the autumn colouring and leaf fall. For positions of localities see Appendix.

Locality	Date	*idaeus*	*caesius*	*scissus*	*nessensis*	*sulcatus*	*plicatus*	*thyrsanthus*	*nitidus*	*corylifolius*	*taeniarum*	*bellardii*	*insularis*	*hartmanii*	*lindebergii*	*radula*	*scheutzii*	*axillaris*	*fuscus*	*vestitus*	*sprengelii*
1	Oct. 5	4.74	.	.	.	.	2.62	2.45	.	.	.	.	.	.	.	.	.	.	.	.	.
2	6	3.86	.	.	.	2.45	.	.	.	.	.	.	.	.	.	.	2.27	.	.	.	.
3		.	.	.	.	.	.	.	.	2.52	.	.	.	.	.	.	1.63	.	.	.	.
4		.	.	.	.	.	.	2.97	.	.	.	2.72	.	.	.	.	.	.	.	.	.
5		4.08	.	.	.	4.42	.	.	.	.	.	3.10	.	.	.	.	.	.	.	.	.
6	7	4.27	.	.	.	.	.	.	.	3.26	.	.	.	.	.	.	.	.	2.61	.	.
7		.	.	.	.	.	.	.	.	3.45	.	.	.	.	.	.	.	.	2.49	.	.
8		.	.	.	.	.	.	.	.	3.20	.	.	.	2.75	.	.	.	.	.	.	.
9		4.04	.	.	.	.	.	.	.	.	.	.	.	2.58	.	.	.	.	.	.	.
10		4.29	.	.	4.11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
11	13	4.79	.	4.66	4.17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
12		.	.	.	.	.	.	.	.	3.56	.	.	.	.	2.63	2.82	.	.	.	.	.
13		.	.	.	4.65	.	3.90	.	.	.	.	.	.	.	.	.	.	.	.	.	2.49
14		.	.	.	.	.	.	.	.	3.94	.	.	3.58	.	.	.	.	.	.	.	.
15	14	5.37	.	.	4.26	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
16		5.10	.	.	4.13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
17	15	.	.	.	3.67	.	.	.	.	.	2.73	.	.	.	.	.	.	.	.	.	.
18		.	.	.	.	.	4.07	.	.	3.56	3.89	.	.	.	.	.	.	.	.	.	.
19		.	.	.	.	.	3.05	.	.	3.15	.	.	.	.	.	.	.	.	.	.	2.08
20		3.95	.	5.29	4.29	.	3.63	.	.	.	.	.	.	.	.	.	.	.	.	.	.
21	20	.	4.09	.	.	.	3.42	.	3.76	.	.	.	3.09	.	3.25	.	.	3.27	.	.	.
22		.	.	.	.	.	3.12	.	3.25	.	.	.	.	.	.	.	.	.	.	.	.
23	21	.	.	.	.	.	4.35	.	.	.	.	.	.	.	3.31	.	.	.	.	3.08	.
24		.	.	.	4.83	.	4.47	.	.	.	.	.	.	.	.	3.49	.	3.70	.	.	.
25		3.81	.	.	3.81	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1.89	.
31	Nov. 24	.	.	.	.	.	4.57	.	.	4.36	.	.	.	.	.	3.25	.	.	.	.	.
32	24, 25*	.	.	.	.	4.87	.	.	.	5.20*	.	.	.	.	.	.	.	.	.	.	.
33	25	.	.	.	.	.	.	.	.	4.96	.	.	.	.	.	.	3.24	.	.	.	.
34		.	.	.	.	.	.	4.07	.	4.24	.	3.00	.	.	.	.	.	.	.	.	.
35		.	.	.	.	.	.	.	.	5.09	.	.	.	.	.	.	.	.	3.21	.	.
36		.	.	.	.	.	.	.	.	4.93	.	.	.	3.39	.	.	.	.	.	.	.
37	26	.	.	.	.	.	5.50	.	.	.	4.55	.	.	.	.	.	.	.	.	.	.
38		.	.	.	5.80	.	4.92	.	.	.	.	.	.	.	.	.	.	.	.	.	.
39	27	.	.	5.36	5.90	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
40		.	.	.	.	.	.	.	4.72	.	.	.	.	.	3.97	.	.	.	.	.	.
41		.	.	.	.	.	5.80	.	.	.	.	.	4.61	.	.	.	.	3.43	.	.	.
42	28	.	.	.	.	.	5.39	.	.	.	.	.	.	.	4.09	.	.	.	.	3.70	.
43		.	.	.	.	.	5.53	.	.	5.44	.	.	.	.	.	.	.	.	.	.	3.77

RESULTS

Earliness of the Species Compared

The point in keeping to localities where at least one of the four wide-spread standard species occurs was to make it possible to compare the twenty species as if all were growing in one locality. This was achieved in two steps, as follows: (1) The relative positions of the standard species were established, (2) The locality means of all species investigated were related to the fixed positions of the standard species.

(1) To illustrate how the relative positions of the standard species have been established *corylifolius* and *plicatus* will be taken as examples. In four localities (nos. 18, 19, 31 and 43) both species were found, the locality difference between them being −0.51, +0.10, −0.21 and −0.09. In other localities four other species have been recorded either together with *corylifolius* or with *plicatus*. One of these four is *lindebergii*. In one of its localities (no. 12), *corylifolius* was also recorded, but not *plicatus*. The reverse was true of two other localities (nos. 21 and 23). Note: Observations made during the same month only have been considered. The locality difference calculated between *corylifolius* and *lindebergii* was +0.93 and between *plicatus* and *lindebergii* +0.17 and +1.04 (average +0.61). An indirect difference could thus be calculated for *corylifolius* as compared with *plicatus* using *lindebergii* and was found to be (+0.93−+0.61=) +0.32. Corresponding values were also derived using *idaeus* (+0.21), *radula* (−0.24) and *insularis* (+0.03). These four indirect differences were added to the four locality differences and the sum divided by eight, the result (−0.05) being an estimate of the actual difference between *corylifolius* and *plicatus*.

Estimates have only been made for pairs of standard species that are both found in one locality at least. If *plicatus* is given the value of zero, the estimates of the actual differences between the standard species are as below. (As *idaeus* is found together with all the other three species, the average of the three separate estimates is given here.)

−0.05 *corylifolius*
0.00 *plicatus*
+0.80 *nessensis*
+1.08 *idaeus*

(2) To illustrate how the locality means were related to the fixed positions of the standard species *scheutzii* from locality no. 3 may serve as an example. The locality difference between *scheutzii* and *corylifolius* is −0.89. As the fixed value of *corylifolius* is −0.05 this value must be added to get the relative value for *scheutzii*, which thus is −0.94.

In a locality where more than one standard species occurred *plicatus*, if present, was used as the standard, otherwise *corylifolius*, *nessensis* or *idaeus* in that order. By mistake, no standard species were recorded for locality no. 4 (*thyrsanthus* and *bellardii*) nor for no. 40 (*lindebergii* and *nitidus*). Except for *lindebergii* relative values for these species have been calculated by indirect methods. Unless recorded together with other standard species relative values of the standard species themselves were not calculated.

Finally, the blackberry species were ranked according to earliness of autumn colouring and leaf fall.

As the actual differences may not be the same in October and November the following adjustment has been made. As regards the fourteen species that were recorded in three localities only (two in October, one in November), the rank was determined from the average of the three relative values. For the remaining four species means have been calculated for each of the two months. The sum of the November mean and twice the October mean have then been divided by three.

In Fig. 1 the relative values of the species are shown. The plotted values for both October and November are found to lie along an approximately straight line with roughly the same angle of ascent for both months. This demonstrates an actual difference in earliness between species. Unfortunately, there is considerable intraspecific variation so that the relative order of closely ranked species is not clear.

Some idea of the extent of this variation may be gained from the October values for the fourteen species recorded twice that month. If the intraspecific variation is measured against the range of variation of the fourteen species (from +1.66, *scissus* to −1.41, *sprengelii*, see Fig. 1) the results are found to lie between 1 and 57 % (average 13 %).

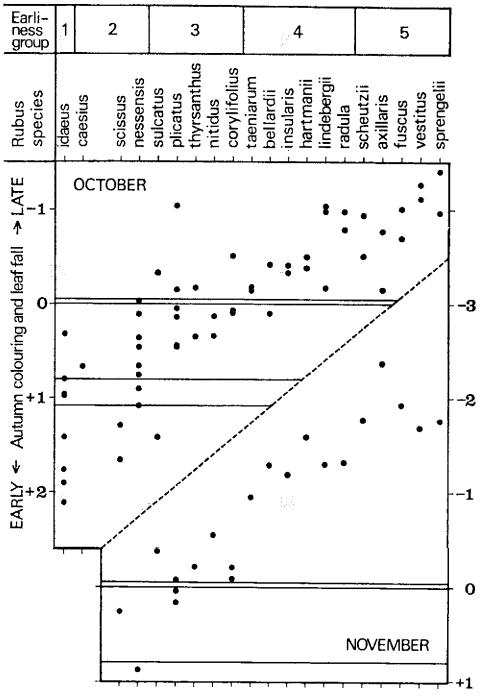

Fig. 1. Relative earliness with respect to autumn colouring and leaf fall (dots). Fixed values for the relative positions of the four (for November, three) standard species (lines).

Table 2. The blackberries ranked according to (a) earliness of autumn colouring and leaf fall, (b) size of distributional area within Sweden.

Rubus species	a	b
scissus	1	7
nessensis	2	1
sulcatus	3	8
plicatus	4	2
thyrsanthus	5	4
nitidus	6	17.5
corylifolius	7	3
taeniarum	8	10.5
bellardii	9	9
insularis	10	10.5
hartmanii	11	13
lindebergii	12	5
radula	13	6
scheutzii	14	14
axillaris	15	12
fuscus	16	15.5
vestitus	17	17.5
sprengelii	18	15.5

Correlation between Earliness and Range

In Table 2 the ranks of the blackberry species with respect to earliness of autumn colouring and leaf fall are compared with the ranks with respect to size of distributional area within Sweden (OREDSSON 1974, Table 3 c, Number of Squares). Spearman's coefficient of rank correlation test (SOKAL & ROHLF 1969 pp. 538—540) applied to these two variables gives +0.647, significant at the 1 % level.

There are two distinct centres of distribution for blackberries in Sweden (OREDSSON 1974 pp. 61—65, subgroups 1 and 7), one covering the coastal parts of Östergötland and NE Småland, the other comprising NW Skåne. The former includes *sulcatus, thyrsanthus, bellardii, hartmanii, scheutzii* and *fuscus*. For both earliness of autumn colouring and leaf fall and size of distributional area the order is the same, except for the first two species, which are interchanged. The order is also the same for three of the four species found in the other centre of distribution, viz. *lindebergii, axillaris* and *vestitus,* whereas *nitidus* is conspicuous as a comparatively early species with an exceedingly limited area of distribution.

Length of Extreme Winter Compared with Range

To facilitate the comparison of length of extreme winter and size of distributional area the species (including *idaeus* and *caesius*) were divided into five groups with respect to earliness of autumn colouring and leaf fall (Fig. 1). Average number of days with mean temperature −10°C or lower calculated over a 30-year period (1901—30) is the measure denoting length of extreme winter.

GROUP 1. With the exception of the islands of Öland and Gotland, *idaeus* is

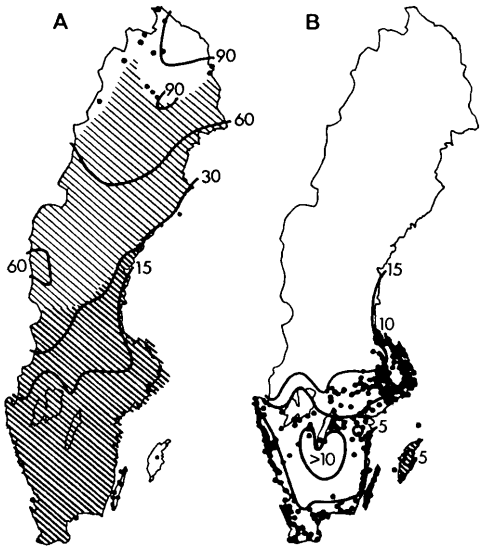

Fig. 2. Distribution of A: wild raspberry and B: dewberry in Sweden. Very common—common occurrence (thick lines), fairly common—less common (fine lines), isolated finds (dots). After HULTÉN (1971). — Length of extreme winter (p. 51) indicated by isochrones for 5—90 days. After ÅNGSTRÖM (1953).

common over the whole of southern Sweden up to the isochrone for 30 days with extreme winter conditions. Though becoming less frequent going northwards, the species is widespread up to the 60-day isochrone. Farthest north, where extreme winter lasts for 90 days or more, wild raspberry is not found (Fig. 2 A).

GROUP 2. Dewberry (*caesius*) is common on Gotland only and does not occur at all in the uplands of southern Sweden. In the east the northern limit of distribution agrees fairly well with the 15-day isochrone (Fig. 2 B). In the west the same applies to the northern limit for *nessensis* (Fig. 3 A). The third member of this group, *scissus,* is a strictly south-western species, the range of which coincides completely with part of that of *nessensis.*

GROUP 3. Two species, viz. *plicatus* and *corylifolius,* together account for the entire range of this group, with the exception of a small area NE of Stockholm, where *thyrsanthus* is the only species found. None of the five species in this group occur where extreme winter lasts for more than 10 days (Fig. 3 B).

GROUP 4. All the six species of this group contribute to its range which is mainly restricted to areas where extreme winter lasts less than 5 days (Fig. 3 C).

GROUP 5. The distribution of the five species in this group is discrete. While the combined area of distribution corresponds substantially with that of group 4, the actual area covered is considerably less (Fig. 3 D). In the east of Sweden, species of both group 4 and group 5 are found even where extreme winter lasts for more than five days.

CONCLUSIONS

In the main, the later the incipience of autumn colouring and leaf fall, the less widespread the species. If the species are considered groupwise, the general distribution is the same but the area covered becomes more limited with tardiness of autumn colouring and leaf fall. The contours of these areas tend to lie parallel to the isochrones for number of days with extreme winter conditions.

Thus it seems as if severity of winter sets the ultimate limit to the occurrence of shrubby *Rubus* species in Sweden, a limit that varies with the hardiness of the individual species, a character apparently reflected in earliness of autumn colouring and leaf fall.

Other factors of interest in this respect will be discussed in forthcoming papers.

ACKNOWLEDGEMENT

I wish to thank Mr BJÖRN MARKLÉN for his assistance in the field irrespective of temperature.

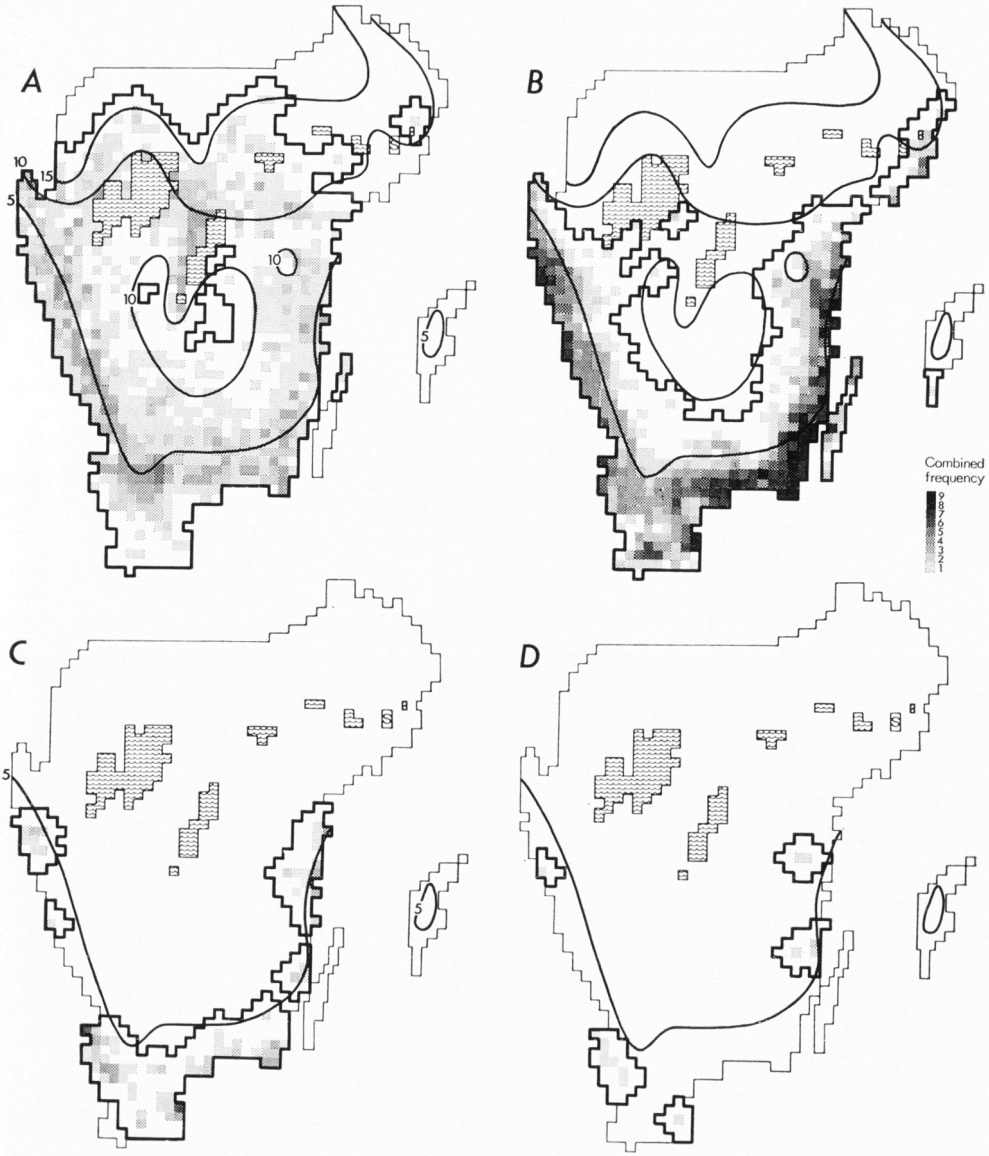

Fig. 3. Distribution of blackberry species in Sweden. Separate maps for earliness groups (see Fig. 1). — A: Group 2 (*caesius* excluded), two species. — B: Group 3, five species. — C: Group 4, six species. — D: Group 5, five species. Range (thick zigzag line) and Combined frequency (scale inset), the latter based on the levels of frequency, maximum four per species (see ORedsson 1974). — Isochrones for 5—15 days with extreme winter conditions.

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APPENDIX

List of localities. Originally found when the author carried out his own frequency mapping of blackberry species in Sweden, 1959—63. Roadsides, except for no. 22 (pasture). Maps available at the University Library of Lund.

No.	Province	Distance from the nearest church
1	Blekinge	Backaryd, 1,800 m ENE
2	Småland	Döderhult, 200 m SE
3		Oskarshamn, 2,300 m SSE
4		Västervik, 3,500 m E the southern church
5		Lofta, 7,100 m ESE
6		Ukna, 5,800 m WSW
7		Ukna, 2,700 m WSW
8	Östergötland	S:t Anna, 7,900 m SE
9		S:t Anna, 10,700 m SE
10		Börrum, 4,300 m SSW
11	Skåne	N. Åkarp, 4,700 m NNE
12	Blekinge	Mjällby, 3,900 m S
13	Skåne	Fågeltofta, 2,400 m ESE
14		Sövde, 5,000 m SSW
15	Småland	Ljungarum, 3,600 m ENE
16	Västergötland	Tvärred, 1,900 m NW
17	Bohuslän	Högås, 3,200 m SSW
18		Stala, 1,100 m S
19		Marstrand, 3,700 m ENE
20	Halland	Svartrå, 4,200 m W
21	Skåne	Jonstorp, 3,500 m NW
22		Förslöv, 1,400 m NNE (Grevie, 2,400 m ESE)
23		Ask, 2,000 m SSE
24		Stenestad, 4,100 m SE
25		Stenestad, 7,200 m E
31	Småland	Ålem, 4,100 m SW
32		Oskarshamn, 1,600 m N
33		Oskarshamn, 2,200 m S
34		Västervik, 6,300 m NNW the northern church
35		See No. 7
36	Östergötland	Gryt, 900 m NNE
37	Bohuslän	Stala, 4,000 m SSE
38		Stala, 5,600 m SSE
39	Halland	Våxtorp, 5,900 m S
40	Skåne	See No. 22
41		Välinge, 2,400 m NNW
42		See No. 23
43		S:t Olof, 2,700 m WSW

A Morphological Analysis of Phenotypes in Populations of Quercus (Fagaceae) in Sweden

Ulf Olsson

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Quercus petraea (MATTUSCHKA) LIEBL. and *Q. robur* L. are indigenous to Sweden. This study shows that they hybridize within the whole range of *Q. petraea* in southern Sweden. Six types of oak apart from the specific ones are described. A hybrid or introgressive origin for these interspecific phenotypes is suggested on the basis of the information derived from population analyses by means of pictorial scatter diagrams, and on the basis of pollen stainability. The special problem of mixed oak woods, i. e. the occurrence of both specific phenotypes and interspecific types within a relatively small area is discussed. Four hypotheses about the causes of the unexpectedly great variability in peduncle length in *robur* oaks are presented. The study contributes to the species concept of *Q. petraea* and *Q. robur* in giving the amplitudes of some diagnostic characters for trees with high male fertility (pollen stainability). However, because of the common occurrence of intercrossing the specific status of the oak taxa should be revised.

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There are two species of native oaks in Sweden, the common or pedunculate oak (*Quercus robur* L., syn. *Q. pedunculata* EHRH.) and durmast or sessile oak (*Q. petraea* (MATTUSCHKA) LIEBL., syn. *Q. sessiliflora* SALISB., *Q. sessilis* EHRH.). They belong to the subgenus *Quercus* (Subgenus *Lepidobalanus* (ENDL.) OERSTED) which has eighteen European representatives (SCHWARZ 1964). Most of these oaks are deciduous but semi-evergreen species are also indigenous within the distribution range of sessile and pedunculate oak in Europe. The evergreen oaks of subgen. *Sclerophyllodrys* O. SCHWARZ have a mainly Mediterranean distribution. The morphological and phenological characteristics of the evergreen and deciduous oaks point to a tropical or subtropical origin (SCHARFETTER 1953). There is reason to believe that *Q. petraea* and *Q. robur* retreated to the Mediterranean region or the Middle East during a glacial period. The pedunculate oaks reached western Sweden about 6500 B. C., the sessile oaks not until c. 2000 B. C. (LINDNER 1935). In historical times these oaks have more than any other kind of tree been associated with the activities of man. *Q. robur* in particular has been widely planted for hundreds of years. This together with the possibility of a common ancestor and the great number of intermediate oaks gives rise to difficulties of identification. Some surveys of the literature on the problems of the specific status of sessile and pedunculate oaks have recently been published (KRAHL-URBAN 1959, JONES 1959, GARDINER 1970).

Both *Q. petraea* and *Q. robur* are protandrous and cross-pollinated (IRGENS-MÖLLER 1955). The variation in the taxa

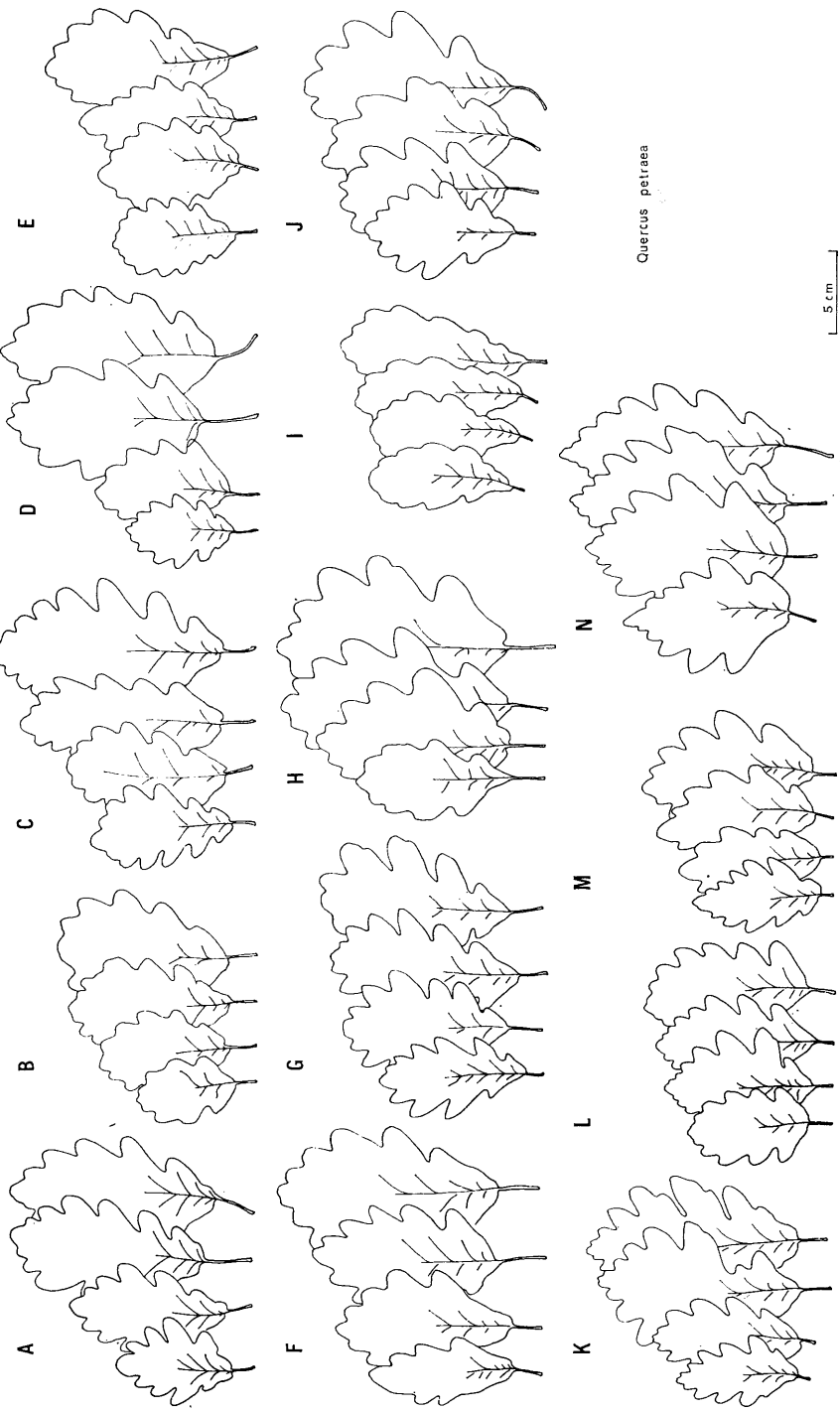

Fig. 1. Q. *petraea*. Variation in leaf shape and size within a population of sessile oak. Of each tree (A—N) four leaves of different size are taken from S—SW exposed twigs.

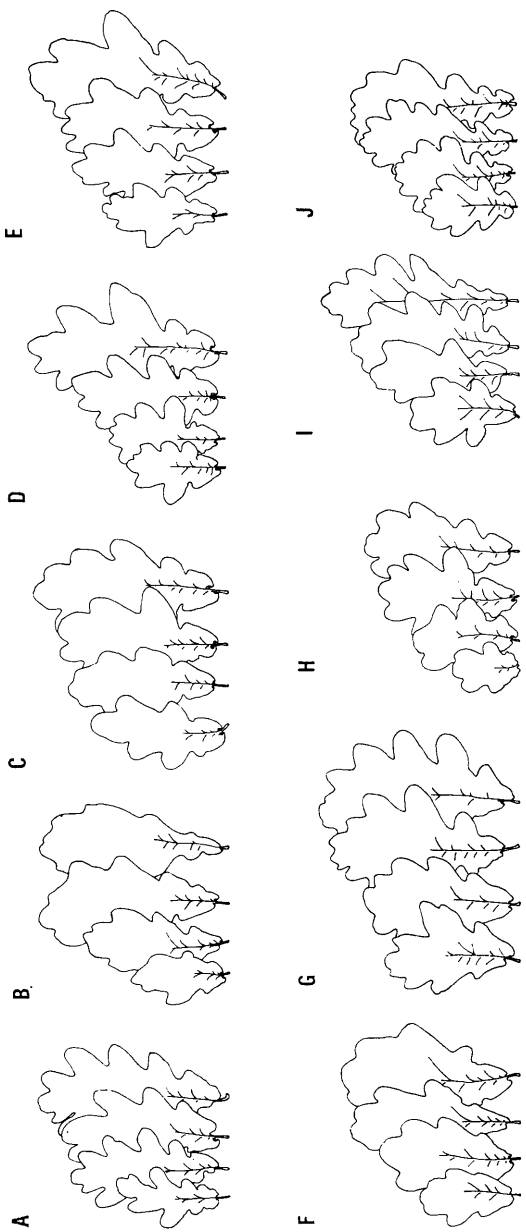

Fig. 2. *Q. robur*. Variation in leaf shape and size within a population of pedunculate oak. Of each tree (A—N) four leaves of different size are taken from S—SW exposed twigs.

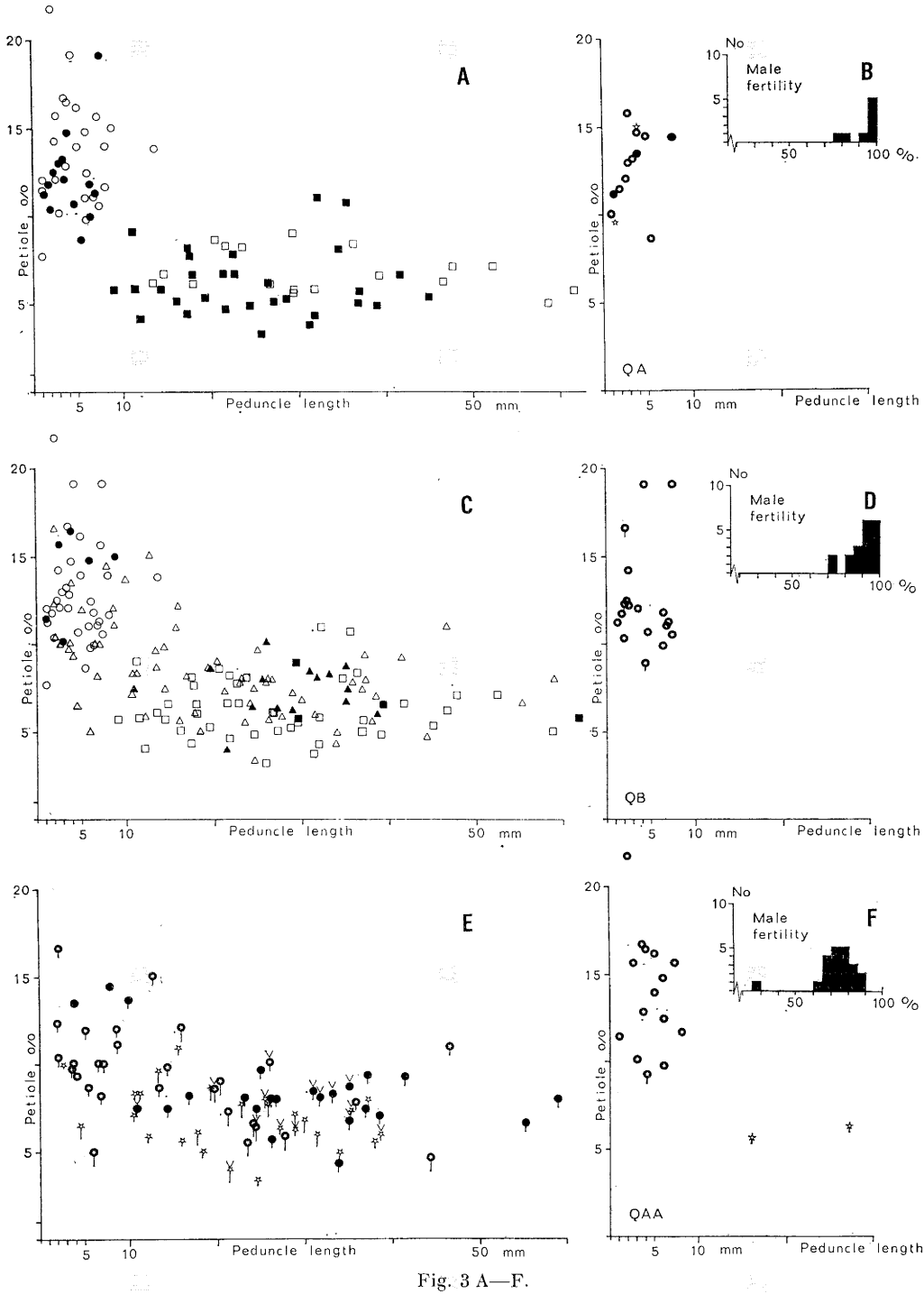
A
B
C
D
E
F
Petiole, o/o
Peduncle length
mm
No
Male fertility
%
QA
QB
QAA

Fig. 3 A—F.

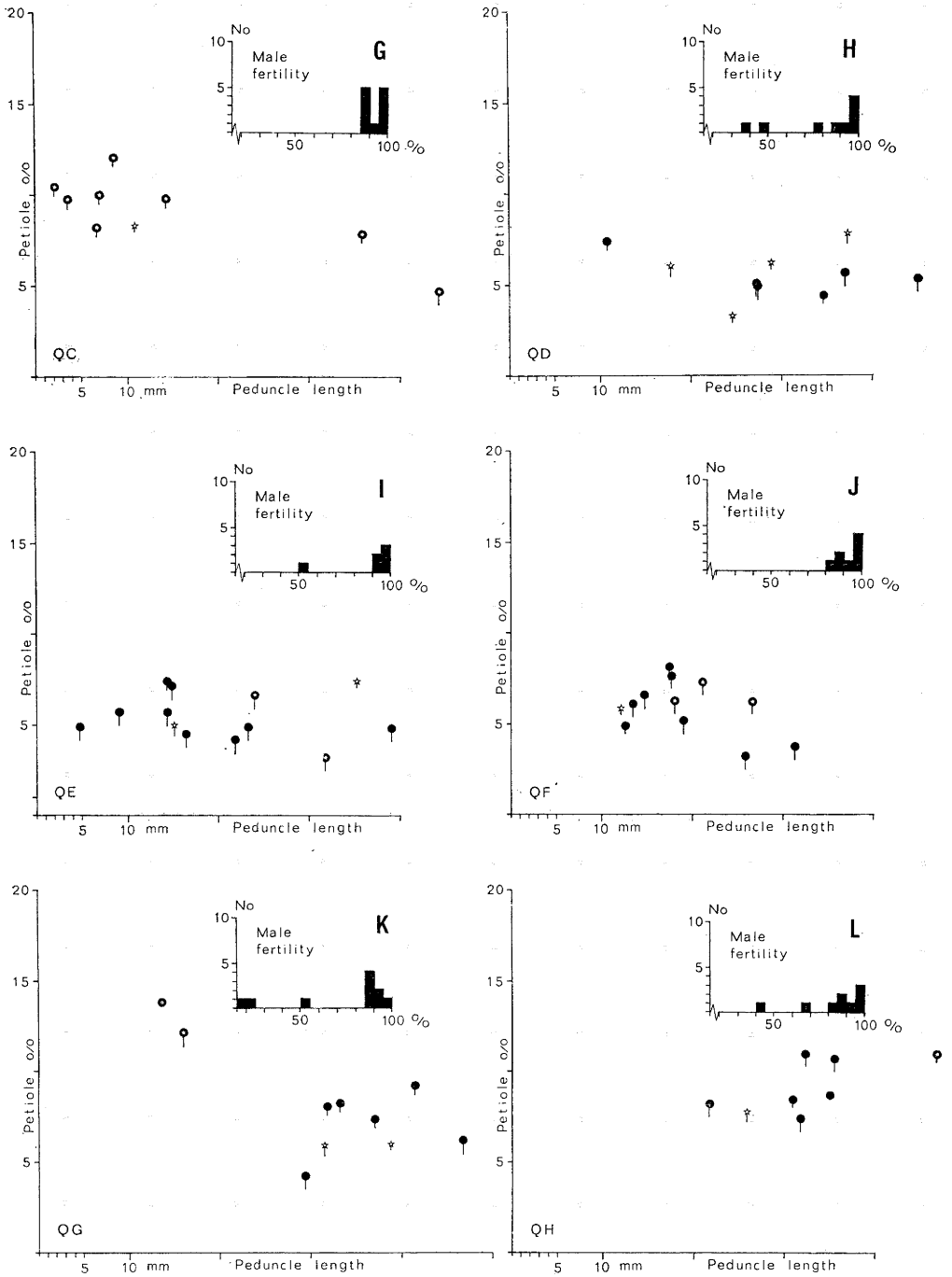
G
No
Male fertility
50
100 %
QC
Petiole, o/o
Peduncle length
5
10 mm
H
QD
I
QE
J
QF
K
QG
L
QH

Fig. 3 G—L.

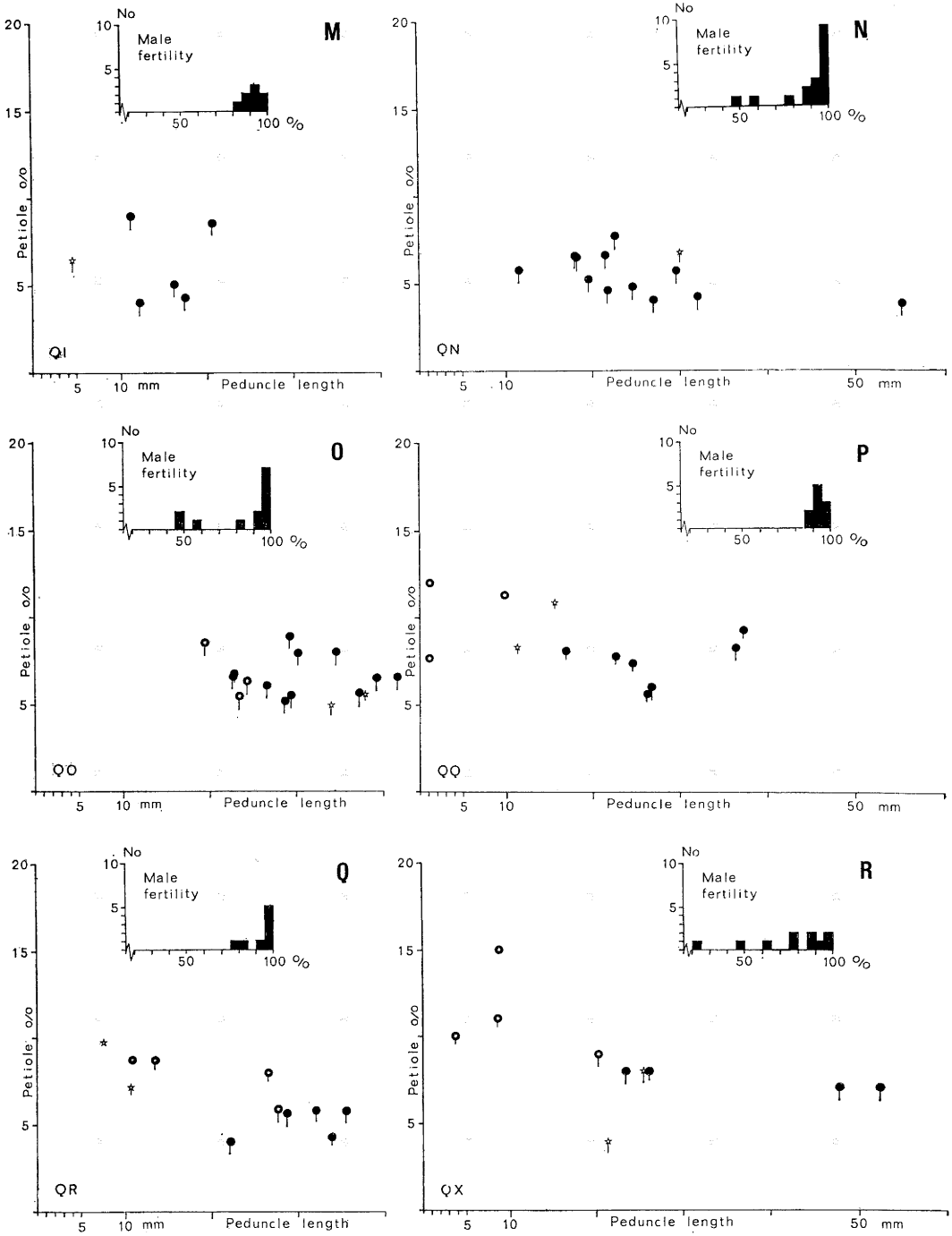
M
No
Male fertility
Petiole, o/o
Peduncle length
mm
QI
N
QN
O
QO
P
QQ
Q
QR
R
QX

Fig. 3 M—R.

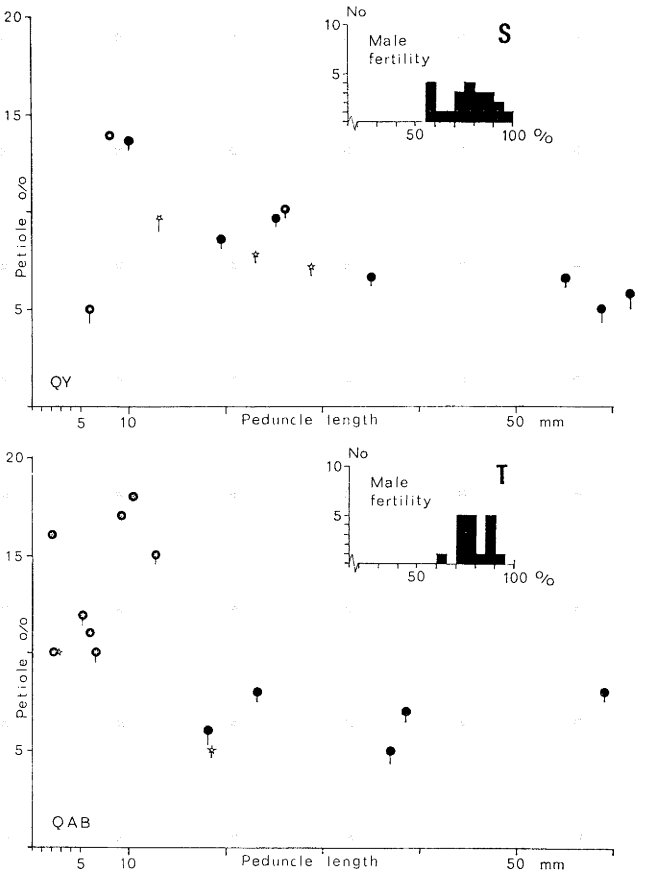

Fig. 3. Combined petiole % and peduncle length. — A: Scatter diagram for all individuals classified as theoretical species types (phenotypes *petraea (a)* and *robur (i)* respectively). Circles: individual values for "petraea"-oaks; squares: individual values for "robur"-oaks. Solid symbols represent individuals with a pollen stainability exceeding 90 per cent. — C: Scatter diagram as in A. Values for all individuals of indeterminate origin (interspecific phenotypes *b*—*h*) are added (triangles). Solid symbols represent individuals with a pollen stainability below 70 per cent. — E: Scatter diagram for the interspecific phenotypes *b*—*h* as in C, but each type is designated by symbols (see Fig. 4) of combined secondary characters as shown in Table 1. Oaks with a pollen stainability below 70 per cent are indicated by V. — B, D, F—T: Pictorialized scatter diagrams for all trees examined in 17 populations of oak in southern Sweden. The frequency distribution of pollen stainability values for the individuals of a population is added each figure in a separate diagram. The symbols used of combined secondary characters are shown in Fig. 4. Their diagnoses are given in Table 2.

is shown in the individuality of general leaf shape as exhibited in the survey of oak-leaf types presented in Figs. 1 and 2. Spontaneous self-fertilization in *Q. petraea* has been reported (WETTSTEIN-WESTERHEIM 1935). PYATNITSKII (1934) and KOLESNIKOV (1933) tried selfing oaks and found pronounced differences in degree of variability between the selfed progeny and normal plants. However, an increase in the heterozygosity, with subsequent variation caused by spontaneous

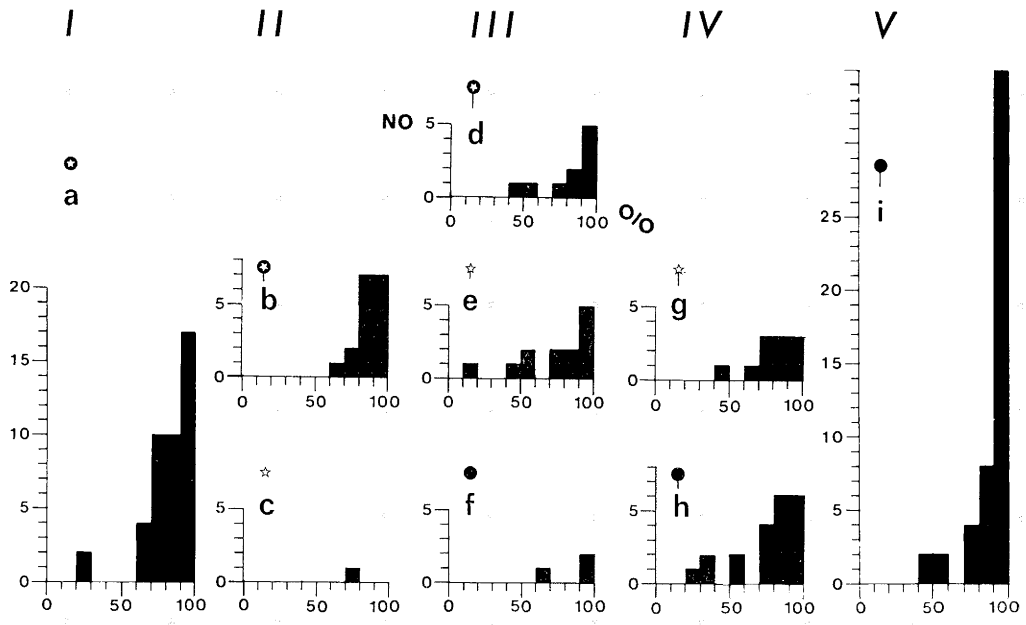

Fig. 4. Histograms showing the frequency distribution of nine phenotypes of oak in different classes of pollen stainability. The phenotypes are designated by symbols and arranged in five groups (I—V) according to Table 2.

intraspecific crossing between different local races or provenances, is of greater importance. This tendency is accelerated by the planting of oaks all over northern Europe. It has also been suggested that *Q. petraea* and *Q. robur* had hybridized and back-crossed to produce trees with intermediate morphology. As regards sessile and pedunculate oaks in Sweden, similar conclusions concerning introgression have been reached by JOHNSSON (1952) from the study of progeny tests, and by KRAHL-URBAN (1951) who compared the gross morphology of oaks in Sweden and in the rest of Europe.

The aim of this study is not primarily to solve any specific taxonomic problems, but to assess the degree of morphological heterogeneity of natural oak populations within the range of sessile oak in southern Sweden. The possibility of introgression is discussed on the basis of the occurrence of provisional species types as represented by the most homogeneous "sessile" or "pedunculate" populations studied. An attempt has also been made to determine the taxonomic position of individuals and populations of oak. The investigation has been influenced by similar studies carried out in Britain by COUSENS (1962, 1963, 1965) and CARLISLE & BROWN (1965). Unlike these authors I have presented the distribution of gametic fertility within the oak populations as the percentage of pollen stainable in cotton blue, and used it as an important factor in population analysis.

MATERIAL AND METHODS

Sampling and Collecting Techniques

All natural oak populations investigated have been taken as being representative of the variation in oaks within parts of the

Table 1. The diagnostic ranges for secondary characters with symbols.

Character	Diagnosis — Range	Symbol	
1. Abaxial stellate pubescence	2—4-branched, trichomes abundant	*(petraea)*	✪
	Only up to 2-branched trichomes or all types very sparse	(indeterminate)	☆
	Branched trichomes absent	*(robur)*	●
2. Auricle type	Lobes weak or nil; lamina not sharply reflexed	*(petraea)*	·
	Medium lobes not reaching the petiole; lamina sharply reflexed	(indeterminate)	¡
	Lobes well developed reaching the petiole on at least one leaf; lamina sharply reflexed	(robur)	¡
	Theoretical *petraea* type *(a)*		✪
	Theoretical *robur* type *(i)*		● ¡

distributional range of *Q. petraea,* viz. in Skåne, Blekinge and Bohuslän (cf. HULTÉN 1950). To confirm whether or not the species were indigenous inquiries were made of the owner of the forest (where known) as to the origin of the oak stand. In other cases the relative age of the oaks and the characteristics of the site have been studied to determine whether the trees had been planted or whether the wood was indigenous. A preliminary trial using a table of random sampling numbers to get the combined coordinates for localities on economic maps and satellite photos (ERTS; Kullaberg region) was performed. Owing to the low frequency of indigenous oak stands in the regions investigated, statistical randomization of the oak populations was found to be impracticable. However, the populations primarily chosen were not later refused unless their indigenous nature was disputed.

The individuals of a sample were taken from a limited area with a maximum diameter of c. 80 m because of the limited range of pollen dispersal under "normal" conditions within an oak forest (SEMERIKOV & GLOTOV 1971). A maximum sample of about 20 trees was chosen from a relatively large oak stand along an arbitrary line (60—100 m). In some cases of smaller populations the sample chosen represents all older oaks within the restricted range. A tree was chosen and labelled independent of its flowering or fruiting state.

All trees were labelled with aluminium plates on which is indicated the population (QA, QB etc. and QAA, QAB etc.) and the individual trees (01, 02 etc.).

For four years (1971—1974) the localities of oak stands that had been marked were visited twice a year to collect samples of leaves and of flowering and fruiting twigs. Because of phenological differences between populations in particular in time of flowering and in fruit-yield from year to year, the collections were not completed until 1974. To induce anthesis in male flowers, small twigs were placed in a greenhouse at the Botanical Gardens, Lund, during February and March (1973) and kept under identical microclimatic conditions. The dormancy of fertile buds was broken in 72 per cent of the oaks, leading to anthesis. Only this pollen (n=200) was used for calculating male fertility. (Note: The diagrams in Figs. 3 A, 3 C, 3 E, 4 showing the distribution of oaks of known male fertility do thus not represent the total number of all oaks investigated as represented in Table 2.) Twigs with fruiting peduncles only were collected from September to October to study the characteristics of leaves and fruits.

Differences in petiole length expressed as per cent of total leaf length (mean values, n=25—44) from samples of leaves taken in W, N, E and S parts of an oak crown have been observed. Examples: *Q. robur* isolated in an open field: 4.2 % (W), 4.1 (N), 4.9 (E), 4.7 (S); *Q. petraea* in a closed stand: 15.9 (W), 15.3 (N), 12.9 (E), 12.3 (S); introgressive oak in a closed stand: 7.4 (W), 8.4 (N), 7.1 (E), 6.0 (S). To minimize variation in diagnostic characters due to position on the tree,

twigs were always taken from south sides of the crown, using a pole-cutter, at a maximum heigth of c. 4.5 m. Lammas shoots and epicormics were avoided as being known to be aberrant or modified in relation to the annual shoot.

Method of Population Analysis

Of the various graphical techniques devised by ANDERSON (1949), the pictorial scatter diagram has been used by COUSENS (1962, 1963, 1965) and by CARLISLE & BROWN (1965) who compared the methods of hybrid index (HI) and pictorial scatter diagrams (PSD) applied to the study of British oaks. They argued that PSD provides better information on hybridization and introgression. This method has also been used by the author analysing the variation pattern of Swedish oak populations. The pattern of the scatter is interpreted in terms of degree of hybridization and introgression. Four main diagnostic characters are used. Two of these, viz. the length of the petiole expressed as percentage of total leaf length, and the length of the peduncle to the first flower bract or first bract scar are recorded as continuous variables according to COUSENS, and designated primary characters. The other two are secondary characters: abaxial leaf pubescence and auricle type. The latter is also defined according to COUSENS (1962) and is based on the development of the basal lobes which in the extreme *robur* shape overlap the petiole, and the amount of reflexion of the lamina where it joins the petiole (see Diagnosis, Table 1). The indumentum character is classified in a slightly different manner from that suggested by COUSENS (1963). No distinction is made between small and large erect trichomes. The stellate pubescence is recorded separately for bifurcate trichomes only, and 2—4-branched trichomes (cf. OLSSON 1974).

Table 1 shows the diagnostic ranges and the symbols for secondary characters. Each of them have a *petraea* (phenotype *a*), indeterminate and *robur* (phenotype *i*) range giving nine possible combinations or phenotypes, classified according to their degree of divergence from either theoretical species type (Table 2: *a, i*). The degrees of divergence (0—4) are calculated from the scores (0, 1, 2 or reverse order) of the three ranges of a secondary character, and may attain a maximum value of 4 for the difference between two specific phenotypes.

The population sampled is designated by the most represented class of phenotypes. The general categories obtained are presented in Table 2. The heterogeneity index of a population is obtained from the sum of relative degrees of divergence from either "species type" (see above) for the phenotypes observed, and is applied to species or aff. species dominating woods only (cf. COUSENS 1965).

POPULATION ANALYSIS

Phenotypes

The frequency distribution of phenotypes observed (Table 2) gives a general picture of the variability of combined secondary characters in the oak populations. No one population consists of one phenotype only. The types that are commonest have been assumed to be the specific types. Thus 23 per cent of all the oaks investigated have the combination characteristic of phenotype *a (petraea)* which is dominant in three populations from Skåne and Bohuslän. In the same provinces seven populations representative of woods dominated by *robur* are found. The *robur (i)*-phenotype comprises 31 per cent of the oaks. Of the intermediate types those of an indeterminate position, viz. *d, e,* and *f* (Table 2, class III) may be of special interest as suggesting F_1 hybrids. No one population is dominated by this intermediate group of phenotypes but they are present in all other categories of woods and only three populations in all lack these types: one *petraea*-dominated and two *robur*-dominated populations. The *b, c* and *g, h* phenotypes show close affinities with the respective specific types and may in some cases belong to the normal variational range of the species. This may partly explain the rather high frequencies of *b* and *h* phenotypes in some of the populations dominated by *petraea (a)* and *robur (i)*.

All theoretically possible phenotypes are represented in the material (Fig. 3, QA, QB etc.) The phenotype with the lowest frequency is a "sessile" oak *(c)* which either lacks stellate 3—8-branched tri-

Table 2. Classification of secondary character combinations and their frequencies. The population samples are classified in general categories on their component sec. combination classes. Heterogeneity index is compiled from the degrees of difference from either "specific" phenotype for the individuals of a population.

General category	Population sampled	Code	Phenotypes observed—no. of oaks Sec. character combination classes									Total	Heterogeneity index
			I	II		III			IV		V		
			a	b	c	d	e	f	g	h	i		
Phenotype *a* or *petraea*-dominated	Hjärås, Sk.	QA	9	—	2	—	—	3	—	—	—	14	0.57 (*a*)
	Sundsvik, Boh.	QB	17	3	—	—	—	—	—	—	—	20	0.15
	Kullaberg, Sk.	QAA	17	1	—	—	2	—	—	—	—	20	0.25
Aff. *petraea*-dominated	Nedre Dal, Boh.	QC	—	9	—	2	1	—	—	—	—	12	1.25 (*a*)
Intermediates dominating	—		—	—	—	—	—	—	—	—	—	—	—
Aff. *robur*-dominated	Sännås, Boh.	QG	1	—	—	2	1	—	1	4	2	11	1.36 (*i*)
Phenotype *i* or *robur*-dominated woods	Skredsvik, Boh.	QD	—	—	—	—	2	—	2	2	5	11	0.72 (*i*)
	Åby, Boh.	QE	—	—	—	2	1	—	1	1	8	13	0.62
	Hamburgö, Boh.	QF	—	—	—	3	1	—	—	1	7	12	0.75
	Resö, Boh.	QH	—	1	—	—	1	1	1	1	6	11	0.82
	Skärje, Boh.	QI	—	1	—	—	—	—	1	—	7	9	0.44
	Hemlinge, Sk.	QN	1	3	—	—	—	—	1	—	15	20	0.70
	Veberöd, Sk.	QO	—	—	—	3	1	—	1	1	10	16	0.63
Mixed woods	Lönsboda, Sk.	QQ	3	—	—	—	2	—	—	4	3	12	—
	Åbrolla, Sk.	QR	1	4	1	1	1	—	—	1	5	14	—
	Tjurkö, Bl.	QX	1	2	—	1	—	—	2	1	3	10	—
	Verkö, Bl.	QY	1	3	—	1	2	—	1	8	2	18	—
	Skogdala, Bl.	QAB	5	3	1	—	1	1	—	3	2	16	—
	Totals		56	30	4	15	16	5	11	27	75	239	—
	Per cent		23	13	2	6	7	2	5	11	31	100	—
Degrees (0—4) of difference from either theoretically specific phenotype according to the sec. character combination classes (I—V)			0	1	1	2	2	2	3	3	4	(*a*)	—
			4	3	3	2	2	2	1	1	0	(*i*)	—

chomes, or may have sparse trichomes of any of these types. The three classes of phenotypes displaying more or less interspecific characteristics were found to be equally common, viz. II: 15 %, III: 15 %, IV: 16 % (Table 2). This uniform distribution suggests that the diagnostic secondary characters used are under polygenic control. This is discussed below, under Gametic Fertility and Population Structure.

Mixed Oak Woods

The occurrence of mixed oak woods, i. e. with both specific phenotypes and interspecific forms within a rather limited and sometimes isolated area of the presumably uniform biotope, is a problem of great interest when studying the formation of a population and its evolution. This category of oak woods is relatively common in southern Sweden. About one third of the populations sampled in loca-

lities primarily in NE Skåne and in Blekinge are of this type.

The development of conditions necessary for interspecific cross-pollination is appreciably increased by the fact that both species have been planted. As regards Sweden attention can be called to the fact that King Charles XII in about 1700 ordered the extensive planting of oaks to supply timber for the future Swedish fleet. This may be in particular true of the oak woods of Blekinge in the vicinity of the naval base at Karlskrona (cf. QX, QY in Table 2). Recent natural mixed oak populations of a limited range within the sympatric woods of the species, as represented by this study, may in part be the result of the activity of jays which fly away with acorns and bury them in another part of the wood. No information is available on the relative importance of, and the relative frequency of, the long-distance dispersal of acorns by birds or other animals as compared with local regeneration of a population by the seedlings from acorns that have dropped from the trees. Owing to the combination of the non-randomizing effect of planting by man and of fruit dispersal by birds, precautions must be taken when analyzing isolated cases of mixed oak samples by methods based upon the assumtion of randomized cross-pollination and dispersal of diaspores.

To test the specific nature of all oaks of the phenotypes *a* (*petraea*) and *i* (*robur*), the degree of differentiation of the continuous secondary characters was assessed by using them as coordinates of scatter diagrams. Fig 3 A shows that the theoretical species types (*petraea,* circles; *robur,* squares) are not entirely discretely differentiated entities although they do not overlap. The continuous secondary characters of *i (robur)* have a very wide range of variation. If each coordinate is considered independently (petiole length in percentage of leaf length and peduncle length respectively) there is an overlapping of the two species. The variation of biotopes increases the number of ecotypes found and the degree of heterogeneity of the gene pool of oaks in Sweden as represented in this investigation, so the scatter is wider as could be expected. This could well explain the wide variation in peduncle length.

A second possibility is that the extreme values represent introgressive types formed by backcrossing towards either species.

A third hypothesis is that the primary characters are under polygene control as is also the case with secondary characters. The majority of oaks of *petraea (a)* or *robur (i)* types in a single *petraea-* or a single *robur*-dominated population respectively are scattered within a relatively narrow zone on the diagram (Figs. 3 D - QB, 3 N - QN, etc.). A similar observation was made by COUSENS (1963) when studying isolated Scottish oak populations. Owing to the possible polygenic nature of the character peduncle length there is reason to believe that within the specific range of this character provenances or ecotypes of different types are formed.

Fourthly, the variability of peduncle length for the "provisional" *robur* type may be the result of isolated occurrences of inbreeding. This could produce individuals displaying greater variability in the character in question than that found in the mother trees, presumably as a result of some homozygous effect on the balanced polygenic system.

Gametic Fertility and Population Structure

Fertility tests, i. e. the determination of male fertility as the percentage pollen grains stainable with cotton blue, have long been used as an indication of hybridity. Fig. 4 shows the frequency distribution of individuals of known pollen stainability within samples of nine phenotypes divided into five classes (I—V). As regards the total sample of the specific phenotypes of *a* (I) and *i* (V) discussed above, Fig. 4 shows that 8 per cent only

of *i* has a pollen stainability of less than 70 per cent, the corresponding value for the *petraea (a)* phenotypes being 14 per cent. The relative frequency of the interspecific phenotypes with low pollen stainability is 19 per cent. As seen in the scatter diagram for petiole %/peduncle length values (Fig. 3 C), the interspecific oaks with low pollen stainability (solid triangles) have a distribution limited to the range of the *robur* type (squares). This may indicate a gene flow in the direction of *robur*.

The next step in the analysis is to compare the percentages of oaks with low pollen stainability (< 70 %) within each group of non-specific phenotypes and their distribution in the scatter diagram (Fig. 3 E). The types are designated by the symbols *b*—*h* (see Fig. 4) which are symbols of combined secondary characters as shown in Table 1. Oaks with a pollen stainability below 70 % are indicated by ∨. Their distribution in classes (II—IV) of ascending degrees of divergence from the theoretical *petraea* species type is as follows: II: 5 %; III: 27 %; IV: 29 %. Of these, class IV *(g, h)* is distributed in a rather narrow zone with a centre at about the coordinates 8/30 of petiole %/peduncle length (Fig. 3 E). Phenotypes *i* with high pollen stainability (> 90 %) are considered to represent "good" specific *robur* oaks. Their distribution is shown in Fig. 3 A (solid squares). One can observe that some *g* and *h* oaks with low pollen stainability (Fig. 3 E) have a position outside the centre of concentration of *robur* oaks and may constitute introgressive products towards *Q. robur*.

The intermediate (s. str.) phenotypes (III) with low fertility do not have the expected intermediate position in the diagram of combined primary characters (Fig. 3 E). In the group as a whole, however, including oaks with normal pollen stainability, there is a zone of concentration which is more or less intermediate, indicating that, to a great extent, assumed F_1 hybrids have an unexpectedly high percentage of pollen stainability. SNOGERUP (1967) has discussed the causes of a similar distribution in filial generations of *Erysimum*. He also mentioned other cases of "cryptic structural hybridity", as it was termed by STEBBINS (1945), which implies that structural heterozygosity displayed as minor translocations and inversions may cause slight reductions only in fertility of F_1. The F_2 individuals of *Erysimum* were reported to show greater variation in pollen stainability than in first generation hybrids and the values were on the average lower.

If the gametic lethality of spontaneous *Quercus* hybrids is also mainly due to meiotic disturbances and cryptic structural hybridity, the distribution of *g* and *h* (Figs. 3 E, 4: IV) phenotypes of low stainability is explainable.

Apart from the material presented in this investigation the author has investigated oak populations that have been reported as "*Q. petraea* woods". (They are not included here as being non-randomly chosen). Two examples: at Sibbarp, Osby (Skåne) a population was found to consist of isolated trees of *Q. petraea* mixed with *Q. robur* and introgressive individuals. In one particular wood in Håverud (Dalsland; SYLVÉN 1945) *Q. petraea* is represented in greater numbers but the introgressives are predominant. It is my opinion that isolated homogeneous stands of *Q. petraea* are very rare.

CONCLUSIONS

The distribution in scatter diagrams (petiole %/peduncle length, Fig. 3 A) of *petraea* and *robur* oaks with a high pollen stainability (> 90 %) agrees reasonably well with the distribution presented by COUSENS (1963) for oaks in Scotland. It may also be true that *Q. petraea* and *Q. robur* in Sweden and Scotland and regions of NW Europe are of the same origin and have evolved along similar lines. Theoretical species types *(a, i)* as described

and discussed above probably therefore belong to *Q. petraea* (MATTUSCHKA) Liebl. and *Q. robur* L. However, because of the general occurrence of intercrossing the specific status of *petraea* and *robur* needs to be examined, a task that is outside the scope of this investigation.

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Mallomonas trummensis Nov. Spec. (Chrysophyceae) Studied by Means of Scanning and Transmission Electron Microscopy

Gertrud Cronberg

CRONBERG, G. 1975 07 08. Mallomonas trummensis nov. spec. (Chrysophyceae) studied by means of scanning and transmission electron microscopy. — Bot. Notiser 128: 69—72. Lund. ISSN 0006-8195.

Mallomonas trummensis nov. spec. is described from the formerly polluted lake, Trummen, in central southern Sweden. The ultrastructure of the cell, scales and bristles was investigated by means of scanning and transmission electron microscopy. *M. trummensis* belongs to the *Tripartitae*. Of the *Mallomonas* species previously described it most closely resembles *M. portae-ferreae* PÉTERFI & ASMUND.

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Mallomonas trummensis was found in the lake, Trummen, in southern Sweden. This formerly polluted lake has now been restored (ANDERSSON et al. 1973). The chemical and physical conditions have been investigated since 1968 (BENGTSSON et al. 1974).

M. trummensis was found in samples taken from the lake from February to April 1971, the lake being covered with ice for part of this time. During this period the pH was 7.0—7.7 and the temperature 0.5—2.8° C. The dominating phytoplankton species then was *M. eoa* TAKAHASHI (CRONBERG 1973).

Plankton was collected with a water sampler and fixed with Lugol's solution. The sample was washed with distilled water.

For purposes of scanning electron microscopy a drop of the sample was placed on a round cover glass which was then glued onto a specimen stub. After the drop had dried the stub was covered with a layer of gold (60 %) and palladium (40 %) under vacuum. The microscope used was a Cambridge Stereoscan Mark II A.

For examination by transmission electron microscopy a drop of the sample was placed on formvar-coated grids and dried. It was then studied directly under a Philips transmission electron microscope.

The description of *M. trummensis* is based on the scanning electron microscopic investigations. The measurements of cells, scales and bristles are made on the electron micrographs. Under the light microscope *M. trummensis* could not be distinguished from *M. eoa* TAKAHASHI or *M. coronifera* MATVIENKO that was also found in the lake during this period.

Mallomonas trummensis CRONBERG nov. spec.

Cellula elongate ovoïdes, 20—25 μm longa, 5—6 μm lata, squamis rhombicis dimorphis tecta, anticis appendices setiformes duorum generum cuique unam gerentibus, posterioribus nullas setas exhibentibus.

Species inter Tripartitas referenda. Squamae apicales 3×4 μm magnae, quaque tholo et crista V-formi ornata, posteriores 2×4 μm magnae, cristas sed nullos tholos exhibentes. Area media crista V-formi limitata transverse costata, inter costas dense punctulata.

Setae solum in parte antica cellulae formatae, squamis apicalibus laxe affixae, aliae 9—10 μm longae, denticulatae, circiter 10 aliae 20—25 μm longae, nullis dentibus armatae, sensim attenuatae, retro directae.

Cystae non visae.

Planta in lacu Trummen Sueciae Meridionalis inventa.

TYPUS: Fig. 1 in this paper.

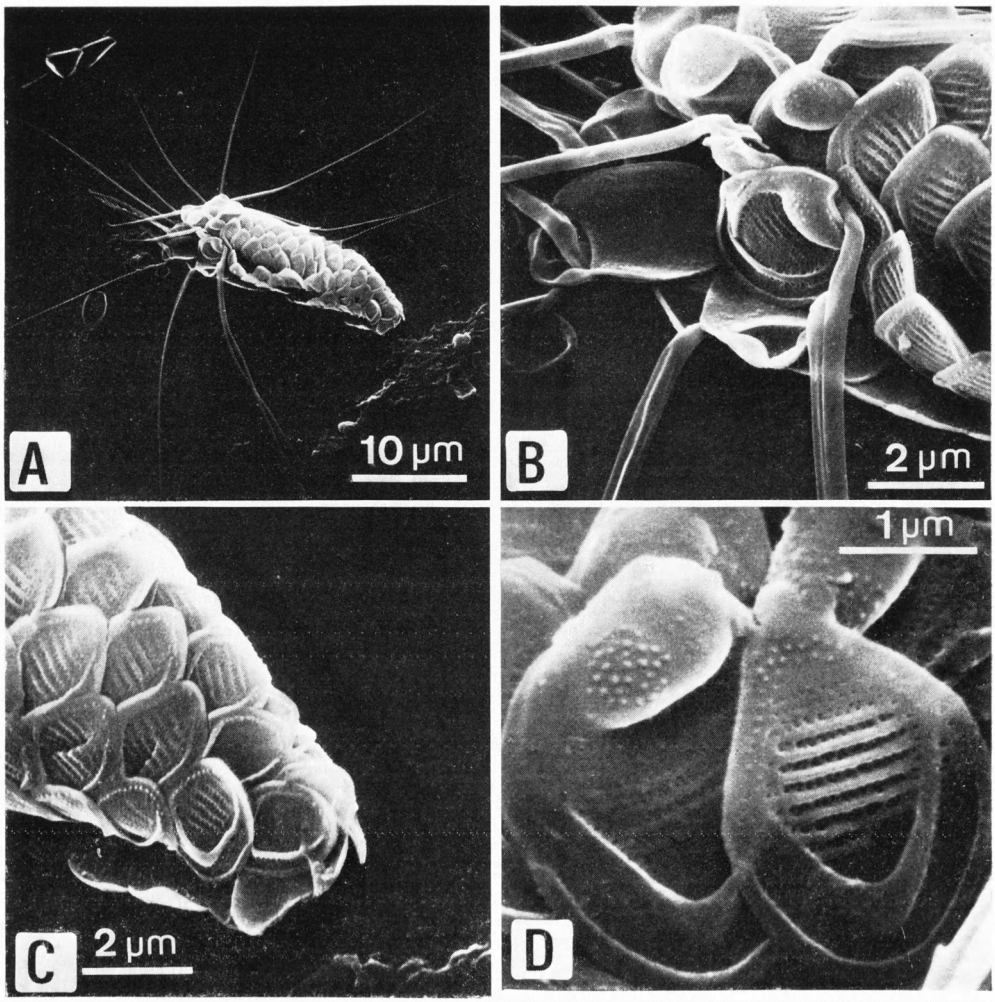

Fig. 1. *Mallomonas trummensis*.— A: A complete cell showing the apical part with short serrate bristles and long thin bristles to the left of the cell seen under the scanning electron microscope (SEM). — B: Anterior part of cell showing scales with dome and bristles loosely fastened to dome (SEM). — C: Posterior part of cell showing scales without dome and bristles (SEM). — D: Two scales, to the left apical scale with dome, to the right a body scale without dome (SEM).

The cell is narrowly elliptic, the cell length being 20—25 µm and the cell breadth 5—6 µm. The cell has two types of scales and two types of bristles. Only the apical part of the cell carries bristles (Fig. 1 A). The scales that carry bristles are *Tripartitae* scales with dome, shield and flange (HARRIS & BRADLEY 1960), whereas the other scales lack the dome (Figs. 1 D, 2 C). The scales are rhomboid. The shield has 6—7 transverse ribs and between these there is a fine network (Figs. 1 B, 2 A, B). On the dome are small round raised dots. On the prolongation of the V-rib against

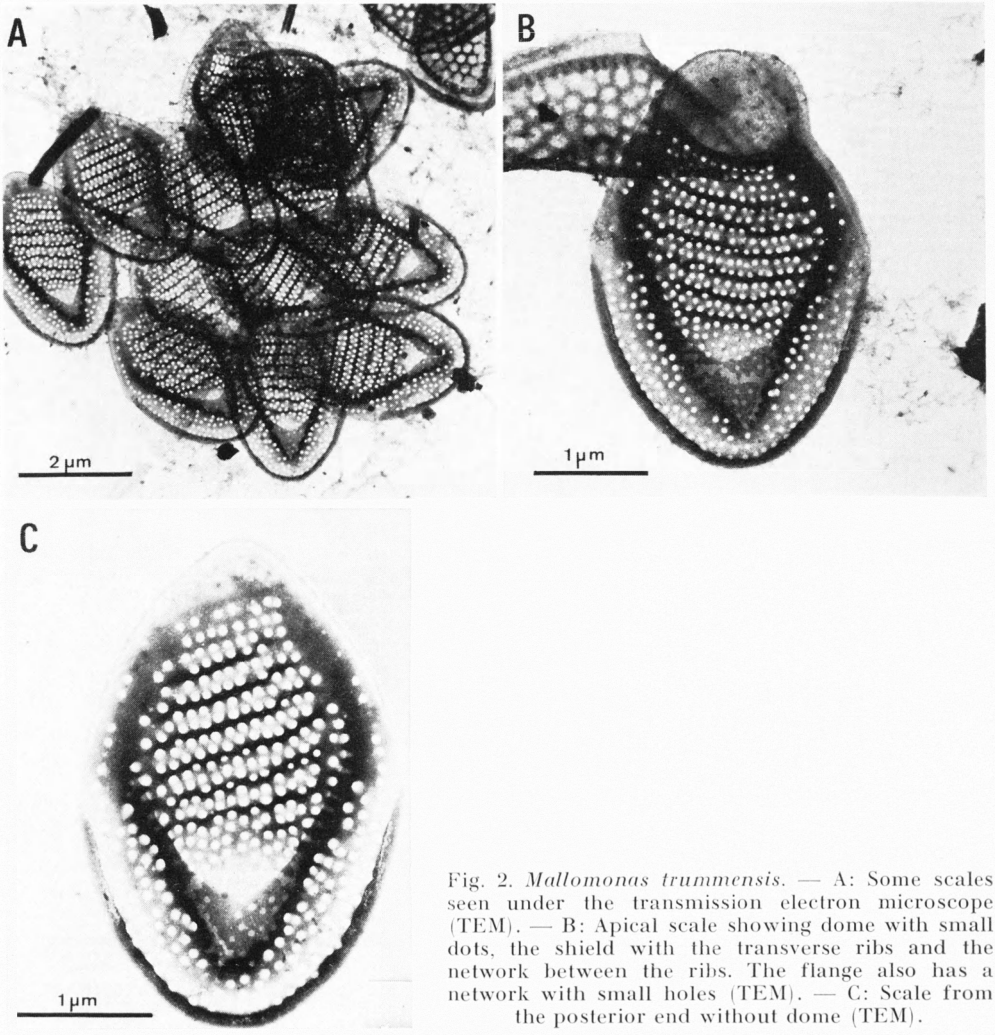

Fig. 2. *Mallomonas trummensis*. — A: Some scales seen under the transmission electron microscope (TEM). — B: Apical scale showing dome with small dots, the shield with the transverse ribs and the network between the ribs. The flange also has a network with small holes (TEM). — C: Scale from the posterior end without dome (TEM).

the dome small protuberant points also occur. On the flange there is a fine network.

The apical scales with bristles are 3×4 µm, the others 2×4 µm.

The upmost apical scales have the dome directed anteriorally and they have forwardly directed bristles 9—10 µm long, thick and serrate (Fig. 1 A). The other apical scales have bristles that are directed outwards and slightly backwards, 21—25 µm long, evenly narrowing to a point. Posterior scales have no bristles (Fig. 1 C). Cysts were not found. The alga has been named after Lake Trummen.

M. trummensis most closely resembles *M. portae-ferreae* PÉTERFI & ASMUND (1972), but this species is much larger (30—60 µm long and 8—12 µm broad) than *M. trummensis*. The ultrastructure of the scales also differs. *M. portae-ferreae* has bristles over the whole cell, while *M. trummensis* has apical bristles only (Fig. 1 A).

Samples containing *Mallomonas* species from some other lakes were investigated under the electron microscope. *M. trummensis* was found in two other lakes, viz. Södra Bergundasjön down stream from Trummen, and Ryssbysjön in another part of central southern Sweden, also in winter plankton. All these lakes with *M. trummensis* are polluted to a greater or less degree and highly eutrophic. *M. trummensis* seems to prefer eutrophic and cold water.

ACKNOWLEDGEMENTS

This investigation was supported by the Royal Physiographic Society of Lund and the Hierta-Retzius foundation. The transmission electron microscope was generously placed at my disposal by Professor CLAES WEIBULL. Thanks are also due to Mr FOLKE LARSSON and Miss BIRGITTA SANDSTRÖM at the Electron-microscopic Laboratory at the Zoological Institute. The sample from Ryssbysjön was kindly sent to me by Dr GÖRAN ROSÉN, Drottningholm. Dr TYGE CHRISTENSEN, Copenhagen, has written the latin diagnosis.

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On pollen of Campanulaceae and Related Families with Special Reference to the Surface Ultrastructure

I. Campanulaceae Subfam. Campanuloidae

Anita Dunbar

DUNBAR, A. 1975 07 08. On pollen of Campanulaceae and related families with special reference to the surface ultrastructure. I. Campanulaceae subfam. Campanuloidae. — Bot. Notiser 128: 73—101. Lund. ISSN 0006-8195.

Pollen grains of 61 species of Campanuloidae representing 18 genera have been studied by means of light microscopy and scanning electron microscopy. Similarities between some genera and species of Campanuloidae based on the sexine pattern have been found as well as compound patterns, constituting possible transitions. A line of evolution from ridges to finger-like structures is suggested. There seems to be a relation between shape of pollen grains and the nature of the apertures.

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Campanulaceae and related families such as Sphenocleaceae and Goodeniaceae, are represented all over the world. In his monograph on Campanulaceae DE CANDOLLE (1830) described 334 species belonging to 21 genera. Since then many new genera have been recognized and the family now consist of some 60—70 genera and 2,000 species (WILLIS 1966).

Most authors divide the family into three subfamilies: Campanuloidae, Lobelioidae and Cyphioidae. This division will be used in the present study.

A correlation of the pollen morphology with the taxonomy of Campanulaceae has been made by means of light microscopy by CHAPMAN (1967) who studied 31 species representing 21 genera, and by AVETISJAN (1967, 1973). AVETISJAN (1967) gave a schematic presentation of evolution based on the development of apertures from pollen with many colpi to pantoporate pollen grains. A review of the pollen literature with respect to light microscopy can furthermore be found in ERDTMAN (1952) and with respect to light microscopy and electron microscopy in DUNBAR (1973 a). Since then a cytological study on the *Campanula* species belonging to the *rotundifolia* group has been made by means of scanning electron microscopy (GESLOT & MÉDUS 1974).

The considerable variation in the pollen morphology hitherto found indicates that a more complete investigation, including that of the fine structure of the pollen surface, may resolve some of the phylogenetic and taxonomic problems.

This paper is the first of three parts, the second (DUNBAR 1975) dealing with the subfamilies Cyphioidae and Lobelioidae and the related families Goodeniaceae and Sphenocleaceae. The results are discussed together in the second part. The third part is planned to deal with the ultrastructure of sectioned pollen grains of some of the present material.

MATERIAL AND METHODS

The pollen grains have been studied by means of light microscopy and scanning electron microscopy. The material was either

Table 1. The species are arranged morphologically according to the pattern of the sexine fine structure. The numbers 1—11 and a—d indicate the different types of fine structure

Taxon	Size (μ) Polar axis×equatorial axis (E)		Shape	Aperture condition	Pore diam.	
	LM	SEMG			LM	SEMG
Campanulaceae, Campanuloidae						
Campanula garganica var. *hirsutum*	32×38	—	suboblate	4-porate	4	—
C. rapunculus	28×32	—	suboblate	3-(4-)porate	3	4
C. phyctidocalyx	36×34	—	prolate-spheroidal	4—3-porate	4	6
C. trachelium	28	—	spheroidal	3-porate	3	5
C. glomerata	27×29	—	oblate-spheroidal	3-porate	2	5
C. lactiflora	32	—	spheroidal	3-porate	4	5
C. rapunculoides	42.5×45	—	oblate-spheroidal	4-porate	—	5
C. rotundifolia	29×33	—	suboblate	4-porate	—	4
C. persicifolia	42	—	spheroidal	4-porate	—	5
C. erinus	—	30	spheroidal	3-porate	—	4
C. uniflora	36	—	spheroidal	3-porate	2	3
C. pyramidalis	34×36	—	oblate-spheroidal	3-porate	4	5
C. alliarifolia	34×36	—	oblate-spheroidal	3-porate	5	6
C. strigosa	30	—	spheroidal	3-porate	4	5
C. carpatica	36×40	—	suboblate	4-porate	3	5
C. speciosa	40	—	spheroidal	3-porate	4	5
C. medium	40	—	spheroidal	3-porate	4	5
C. trachelium f. *alba*	42×44	—	oblate-spheroidal	4-porate	5	6
C. americana	36.5×38	—	oblate-spheroidal	pantoporate, 12 pores	3.5	—
Asyneuma canescens	40	—	spheroidal	4-(5-)porate	3.5	4
Phyteuma scheuchzerii	—	30×32	suboblate	4-porate	—	3.5
Symphyandra armena	26×29	—	oblate-spheroidal	3-porate	3.5	4
S. hofmannii	28	—	spheroidal	3-porate	3	—
Edraianthus serpyllifolia	31×33	—	oblate-spheroidal	3-porate	2	5
Wahlenbergia abyssinica	—	27×30	oblate-spheroidal	3-porate	—	4.5
W. denticulata	—	32×40	oblate-spheroidal	3-porate	—	3.3
W. madagascariensis	—	32	spheroidal	3-(5-)porate	—	3
W. napiformis	E 33	—	oblate-spheroidal	3-porate	—	4
W. perrieri	—	30	spheroidal	3-porate	—	3
W. upembensis	E 33—44	—	oblate-spheroidal	(3-)4(5-) or 3-porate	—	3
W. androsaceae	—	42	spheroidal	3-porate	—	6
W. masafuerae	—	24×30	suboblate	3-porate	—	—
W. communis	—	38×45	oblate-spheroidal	3-porate	—	3.8
W. krebsii ssp. *arguta*	E 25—42	—	oblate-spheroidal	3-porate	—	4
W. subaphylla ssp. *thesioides*	—	40×45	oblate-spheroidal	3-porate	—	5
W. perrottettii	—	30	spheroidal	3-porate	—	—
W. undulata	—	E 42	oblate-spheroidal	3-porate	—	3
Adenophora aurita	—	34×36	oblate-spheroidal	4-porate	—	3.3
A. lilifolia	E 48	36×45	suboblate	4-porate	—	2
A. palustris	—	30×36	oblate-spheroidal	4-porate	—	3
A. thunbergiana	—	33×36	oblate-spheroidal	4-porate	—	3

Table 1 continued.
and the types of spinules/verrucae, respectively, see pp. 76, 77. Two numbers = compound pattern. *: could not be determined.

Sculpturing					
Sexine between spinules or entire sexine	Type (spinules/ verrucae excepted)	Spinules/ verrucae	Height of spinules SEMG	Shape of spinules	Type of spinules/ verrucae
ridges	1	spinules	0.5	basally divided	a
ridges	1	spinules	0.8	basally divided	a
ridges	1	spinules	1	basally divided	a
short ridges	1	spinules	1.5	basally divided	a
short ridges	1	spinules	0.7	basally divided	a
short ridges	1	spinules	1	basally divided	a
short ridges	1	spinules	1.6	basally divided	a
short ridges	1	spinules	0.6	basally divided	a
short ridges	1	spinules	1	basally divided	a
short ridges	1	spinules	1.2	basally divided	a
short ridges, top end bent upwards	2	spinules	1	basally divided	a
ridges, top end bent upwards	2	spinules	1.8	basally divided	a
ridges, protrusions	1, 4	spinules	1	basally divided	a
ridges, protrusions	1, 4	spinules	0.6	basally divided	a
finger-like elements	3	spinules	2	basally divided	a
protrusions	4	spinules	3.3	basally divided	a
protrusions	4	spinules	3	basally divided	a
irregular ridges, atypical	6	spinules	0.9	basally divided	a
reticulate, low relief	5	spinules	0.4	basally divided	a—b
short ridges	1	spinules	0.8	basally divided	a
short ridges	1	spinules	1	basally divided	a
ridges	1	spinules	0.6	basally divided	a
short ridges, protrusions	1, 4	spinules	1.2	basally divided	a
ridges, protrusions	1, 4	spinules	0.8	basally divided	a
short ridges, low relief	1	spinules	0.8	basally divided	a
short ridges	1	spinules	1.6	basally divided	a
short ridges, low relief	1	spinules	0.9	basally divided	a
short ridges	1	spinules	0.8	without roots	b
short ridges	1	spinules	0.8	without roots	b
short ridges	1	spinules	0.8	basally divided	a
short ridges	1	spinules	0.7	without roots	b
short ridges, low relief	1	spinules	0.7	without roots	b
short ridges/muri	1, 5	spinules	1.2	basally divided	a
short ridges-reticulate	1, 5	spinules	0.7	basally divided	a
short ridges/muri	1, 5	spinules	1.2	basally divided	b
reticulate, low relief/ridges	5, 1	spinules	0.8	basally divided	a
reticulate, low relief	5	spinules	2	without roots	b
short ridges, protrusions	1, 4	spinules	1	basally divided	a
short ridges, protrusions	1, 4	spinules	1.5	basally divided	a
short ridges, protrusions	1, 4	spinules	1	basally divided	a
protrusions, ridges	4, 1	spinules	0.9	basally divided	a

Table 1 continued.

Taxon	Size (μ) Polar axis×equatorial axis (E)		Shape	Aperture condition	Pore diam.	
	LM	SEMG			LM	SEMG
Jasione montana	22×25	—	oblate-spheroidal	3-porate	—	5
Roella amplexicaulis	—	E 38	oblate-spheroidal	3-porate	—	5
R. leptosepala	—	E 55	oblate-spheroidal	3-porate	—	4
R. muscosa	—	50	spheroidal	3-porate	—	5
Githopsis specularioides	36×40	—	suboblate	6-porate	3	—
Prismatocarpus pedunculatus	—	42×55	prolate-spheroidal	3-porate	—	4.5
Triodanis falcata	40	E 31	spheroidal	3-4-porate	1.7	3
Platycodon grandiflorum	53×55	—	oblate-spheroidal	5-6-colporate	—	—
Campanumoea lancifolia	—	25×31	suboblate	3-colporate	—	—
C. maximowiczii	—	30×35	suboblate	5-6-colporate	—	—
Canarina eminii	E 30	30×33	oblate-spheroidal	3-colporate	—	—
C. abyssinica	—	22	spheroidal	3-colporate	—	—
Ostrovskia magnifica	—	50×57	oblate-spheroidal	6-7-colpate	—	—
Cyananthus incanus	—	42×45	oblate-spheroidal	9-colpate	—	—
C. inflatus	E 36	E 33	oblate-spheroidal	9-colpate	—	—
C. microphyllus	—	E 42	oblate-spheroidal	8-colpate	—	—
C. lobatus	E 40	E 38	spheroidal	8-10-colpate	—	—
Codonopsis clematidea	40×44	E 45	oblate-spheroidal	8-colpate	—	—
C. handeliana	48×46	38×40	oblate-spheroidal	7-colpate	—	—
C. viridiflora	36×40	—	oblate-spheroidal	8-colpate	—	—

fresh or was obtained from dried specimens from the following Herbaria: BR, CONC, K, P, S, S-MB (Bot. Inst. Univ. Stockholm) and UPS. For purpose of light microscopy the pollen grains were acetolyzed, embedded in unstained glycerine jelly on slides and sealed with paraffin. For electron microscopy the fresh material was air-dried. Both the air-dried material and the herbarium material was coated with gold during evaporation. A Stereoscan MK IIa (Cambridge Scientific Instrument Co.) at the Swedish Geological Survey, Stockholm, and a Jeol, JSM U3 instrument at the Wallenberg Laboratory, Uppsala were used for examination and for taking the micrographs.

Some of the material has been treated by means of the critical point method (ANDERSSON 1950).

The terminology used to describe the surface of the pollen wall is mainly as in ERDTMAN (1952). The features revealed by scanning electron microscopy need however sometimes to be expressed more adequately, for instance finger-like structures.

OBSERVATIONS

The surface pattern except spinules/verrucae has been divided into 11 arbitrary types:

1. ridges
2. ridges, top end bent upwards
3. finger-like structures
4. protrusions
5. reticulate, low relief
6. irregular ridges, atypical
7. perforated tectum
8. pits
9. granulate
10. reticulate, high relief
11. striate

Table 1 continued.

Sculpturing					
Sexine between spinules or entire sexine	Type (spinules/ verrucae excepted)	Spinules/ verrucae	Height of spinules SEMG	Shape of spinules	Type of spinules/ verrucae
protrusions	4	spinules	—	basally divided	a
protrusions	4	spinules	1.6	without roots	b
protrusions	4	spinules	2.8	without roots	b
protrusions	4	spinules	2.5	without roots	b
protrusions	4	spinules	1.2	without roots	a
reticulate, low relief	5	spinules/ verrucae	1	without roots	a, b, c
*		verrucae	1.5		c
short ridges	1	spinules	1.5	basally divided	a
short ridges	1	spinules	2	basally divided	a
short curved ridge-like elements	6	spinules	0.8	basally divided	a
protrusions, round	4	spinules/ verrucae	1		b, c
reticulate-ridge-like	5	verrucae	—		c
protrusions, round	4	verrucae	3.5		c
perforated tectum, puncta	7	verrucae	—		c
perforated tectum, puncta	7	verrucae	—		c
perforated tectum, puncta	7	verrucae	—		c
reticulate, high relief, incomplete muri	10	—	—		d
reticulate, small lumina	5	spinules/ verrucae	—	without roots	b, c
reticulate, small lumina	5	spinules/ verrucae	—	without roots	b, c
reticulate, small lumina	5	spinules	—	without roots	b

Furthermore, the sexine (spinules/ verrucae) has been divided into 4 arbitrary types:

a. spinules, basally divided
b. spinules without "roots"
c. verrucae
d. absence of spinules/verrucae

The two types (1—11, a—d) are then combined in the description. A description of a genus is presented only when a large number of the species it comprises (WILLIS 1966) have been studied, when there is a conspicuous difference between the species of the genus and when the genus is of special significance, for instance, when providing a link between the subfamilies. Since the shape of the pollen grains changes somewhat during acetolysis, they have been measured in scanning electron micrographs (SEMG's). Both sets of data are presented where available.

Campanulaceae, Campanuloidae

CAMPANULA

Pollen grains generally spheroidal to suboblate, occasionally subprolate, ranging in size from 27 to 45 μ, porate. The pores are generally arranged equatorially (E), exceptionally in panto-position (*C. americana*). The number of pores ranges from 3 to 4 (*C. americana* 12). The pore diameter ranges from 2—5 μ (2—6 μ SEMG). The surface is covered with spinules of

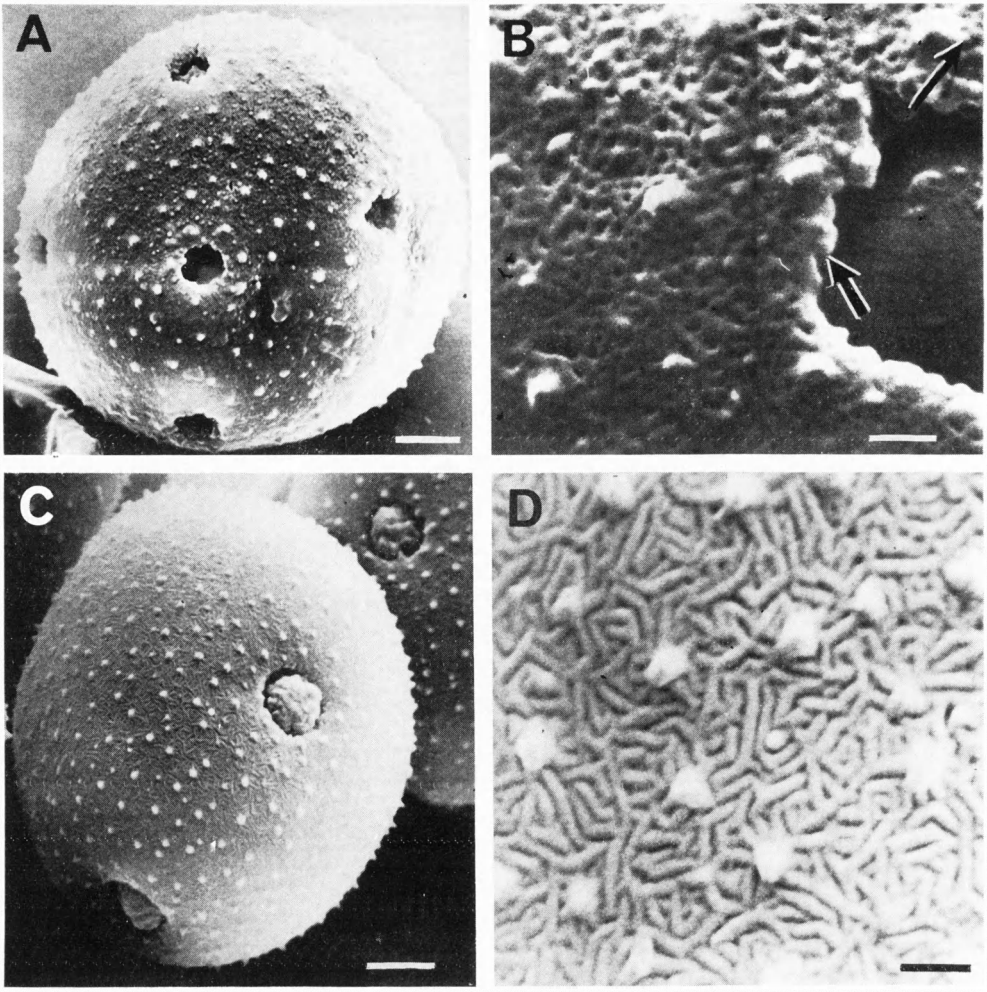
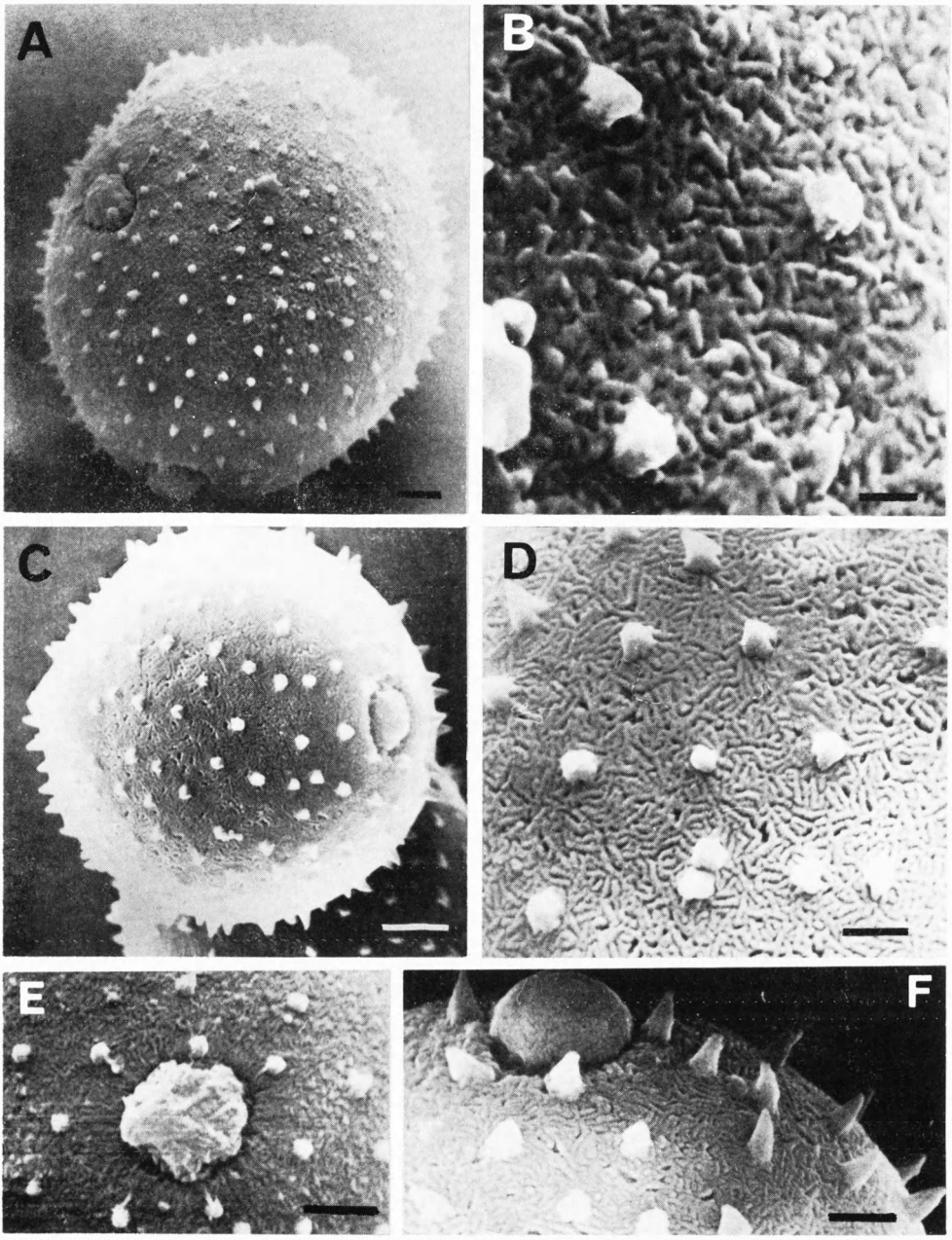


Fig. 1. *Campanula.* — A, B: *C. americana.* — A: Pantoporate pollen grain. Spinules of varying size are distributed over the surface. C. ×1,700. — B: Part of the pollen wall with a pore to the right; the margin is irregular (thick arrow). The surface of the sexine consist of a low relief reticulum with small lumina. The spinules are basally divided into short "roots" (thin arrow). C. ×9,000. Line c. 1 μ. — C, D: *C. garganica* var. *hirsutum.* — C: 4-porate pollen grain with pores equatorially arranged. Spinules of varying size are distributed over the surface. C. ×1,800. — D: The sexine surface consist of spinules and ridges occasionally branched. C ×9,000. Line c. 1 μ. — For shape, size and apertures etc. see Table 1. The line equals 5 μ in all figures unless otherwise indicated.

Fig. 2. *Campanula.* — A, B, E: *C. trachelium* f. *alba.* — A: 4-porate pollen grain with pores arranged equatorially. Spinules of varying size are distributed over the surface. C. ×1,300. — B: Part of the pollen wall with basally divided spinules and irregular structures (see p. 86), except around the pore margin where they are radially arranged (see Fig. 2 E). C. ×8,000. Line c. 1 μ. — E: Detail of a pollen grain with operculum. Note the structures extending radially from the pore margin. C. ×2,000. — C, D: *C. trachelium*



(ASPLUND 1489). — C: 3-porate pollen grain showing one pore. Spinules distributed over surface. C. ×1,800. — D: The sexine consists of short ridges and basally divided spinules. C. ×4,500. Line c. 2 μ. — F: *C. trachelium* (MAKINS 1299). Part of pollen grain with pore. The sexine consists of short ridges and basally divided spinules also occurring close to the pore. C. 4,000. Line c. 2 μ.

varying size, shape and number, the size ranging from 0.4 to 3.3 μ. The base of the spinules is divided into a varying number of "roots" which anchor the spinules to the sexine or nexine. According to the sexine pattern between the spinules the genus is divided into types (1—6). The ridges of Type 1 are about uniform in width, although the length varies. The protrusions of Type 4 are relatively close together, while the reticulum of Type 5 is in low relief with short muri and small lumina. These types occur frequently; Types 2, 3 and 6 occur occasionally.

Campanula garganica TEN. var. *hirsutum* — Fig. 1 C, D

Shape: suboblate.

Size: 32×38 μ.

Apertures: pollen grains 4-porate, pore diam. 4 μ.

Exine: 2 μ thick, sexine slightly thicker than nexine, spinules mostly 0.5 μ high, occasionally lower, irregularly spaced; ridges sometimes branched. Type 1 a.

Campanula rapunculus L. — Fig. 4 A, B, D

Shape: suboblate.

Size: 28×32 μ.

Apertures: pollen grains 3(—4)-porate, pore diam. 3 μ, 4 μ (SEMG), elongated structures cover surface of operculum (Fig. 4 B).

Exine: 2 μ thick, sexine slightly thicker than nexine, spinules irregularly spaced, mostly 0.8 μ high, lower ones occur; ridges occasionally branched (Fig. 4 D). Type 1 a.

Campanula phyctidocalyx BOISS. & NOÉ. — Fig. 4 C

Shape: prolate-spheroidal.

Size: 36×34 μ.

Apertures: pollen grains 3—4-porate, pore diam. 4 μ, 6 μ (SEMG), surface of operculum covered with granular and elongated structures.

Exine: 2 μ thick, sexine thicker than nexine, spinules mostly 1 μ high, irregularly spaced; ridges occasionally branched. Type 1 a.

Campanula trachelium L. — Fig. 2 C, D, F

Shape: spheroidal.

Size: 28 μ.

Apertures: pollen grains 3-porate, pore diam. 3 μ, 5 μ (SEMG).

Exine: 2 μ thick, sexine with spinules 1.5 μ high, somewhat irregularly spaced; short ridges. Type 1 a.

Campanula glomerata L. — Fig. 3 D, E, F

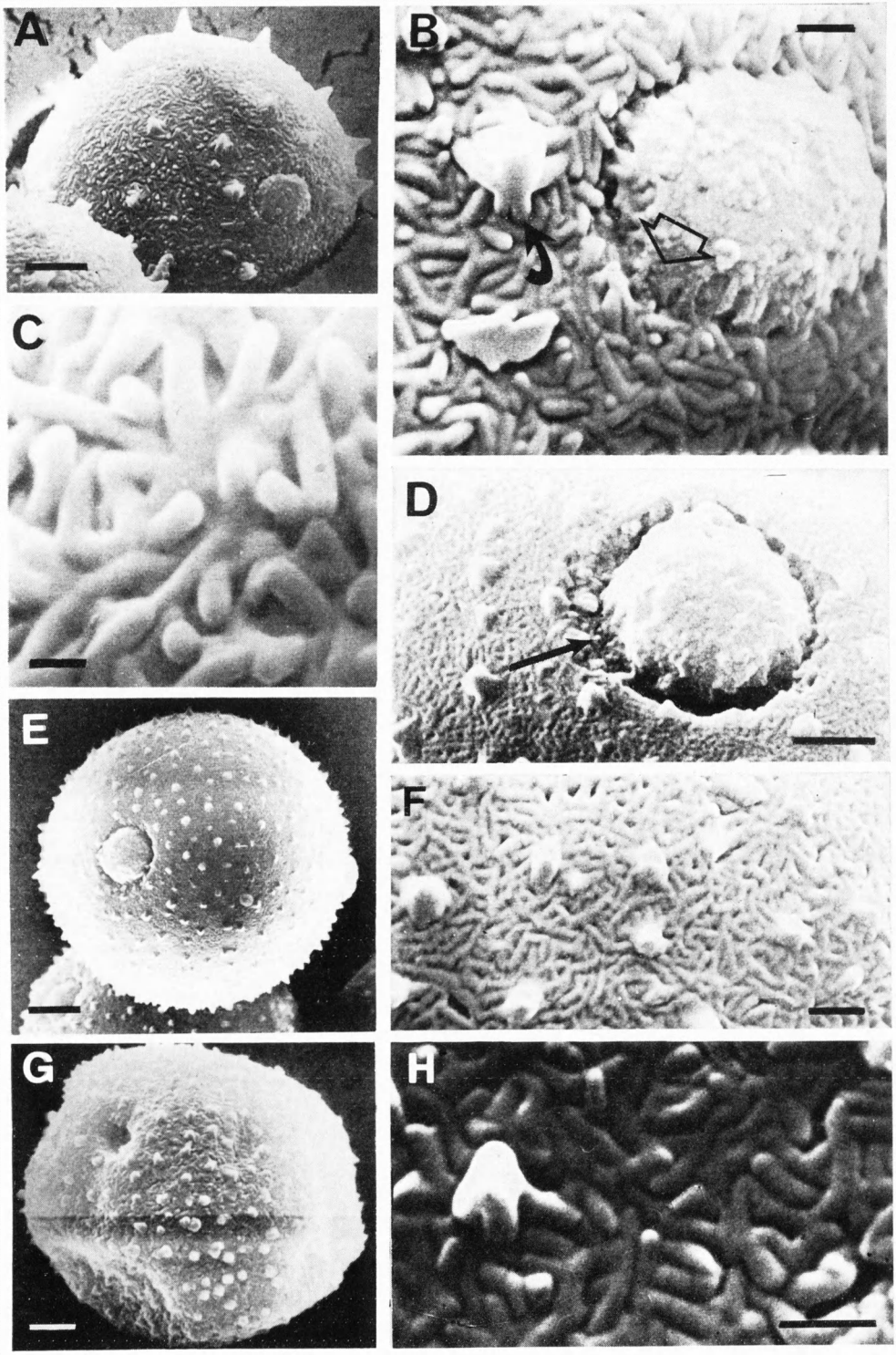
Shape: oblate-spheroidal.

Size: 27×29 μ (CHAPMAN 1967).

Apertures: pollen grains 3-porate, pore diam. 2 μ, 5 μ (SEMG), surface of operculum granular, small granules also occurring on pore margin (Fig. 3 D).

Exine: sexine with spinules mostly 0.7 μ high, irregularly spaced; short ridges. Type 1 a.

Fig. 3. *Campanula*. — A—C: *C. pyramidalis*. — A: 3-porate pollen grain showing one pore. Relatively few spinules distributed over surface. C. ×1,700. — B: Part of pollen wall showing one pore with operculum. Surface of operculum appears granulated (arrow head); spinule with rather long "roots" (arrow); short branched ridges cf. DUNBAR (1975 Fig. 6 D). C. ×8,300. Line c. 1 μ. — C: Detail of sexine surface with ridges mostly bent upwards, finger-like. C. ×15,000. Line c. 0.5 μ. — D—F: *C. glomerata*. — E: 3-porate pollen grain showing two pores. Spinules of varying size distributed over surface. C. ×1,400. — D: Part of pollen wall with pore and operculum. Small granula occur at the pore margin (arrow). Spinules basally divided. C. ×6,000. Line c. 2 μ. — F: Part of non-apertural pollen wall. Between spinules the sexine consists of short ridges. C. ×8,000. Line c. 1 μ. — G, H: *C. uniflora*. G: (BJÖRLING s.n.) 3-porate pollen grain showing one pore. Spinules are closely spaced. C. ×1,200. — H: *C. uniflora* (BERGGREN s. n.). Detail of pollen wall showing a basally divided spinule; short ridges, some with ends bent upwards. C. ×15,000. Line c. 1 μ.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Campanula lactiflora L. — Fig. 4 E, F, G
Shape: spheroidal.
Size: 32 μ.
Apertures: pollen grains 3-porate, pore diam. 4 μ, 5 μ (SEMG).
Exine: 2 μ thick, sexine with spinules mostly 1 μ high, irregularly spaced; short ridges (Fig. 4 F), the mass of ridges in places broken up showing bacula beneath the ridges (Fig. 4 G). Type 1 a.

Campanula rapunculoides L.
(DUNBAR 1973 a, b) Type 1 a.

Campanula rotundifolia L.
(DUNBAR 1973 a, b) Type 1 a.

Campanula persicifolia L.
(DUNBAR 1973 a, b) Type 1 a.

Campanula erinus L.
Shape: spheroidal.
Size: 30 μ (SEMG).
Apertures: pollen grains 3-porate, pore diam. 4 μ (SEMG).
Exine: sexine with spinules mostly 1.2 μ high, irregularly and closely spaced; short ridges. Type 1 a.

Campanula uniflora L. — Fig. 3 G, H
Shape: spheroidal.
Size: 36 μ.
Apertures: pollen grains 3-porate, pore diam. 2 μ, 3 μ (SEMG).
Exine: 1.8 μ thick, sexine thicker than nexine, spinules about 1 μ high, closely and irregularly spaced; short ridges, occasionally with ends bent upwards (Fig. 3 H). Type 2 a.

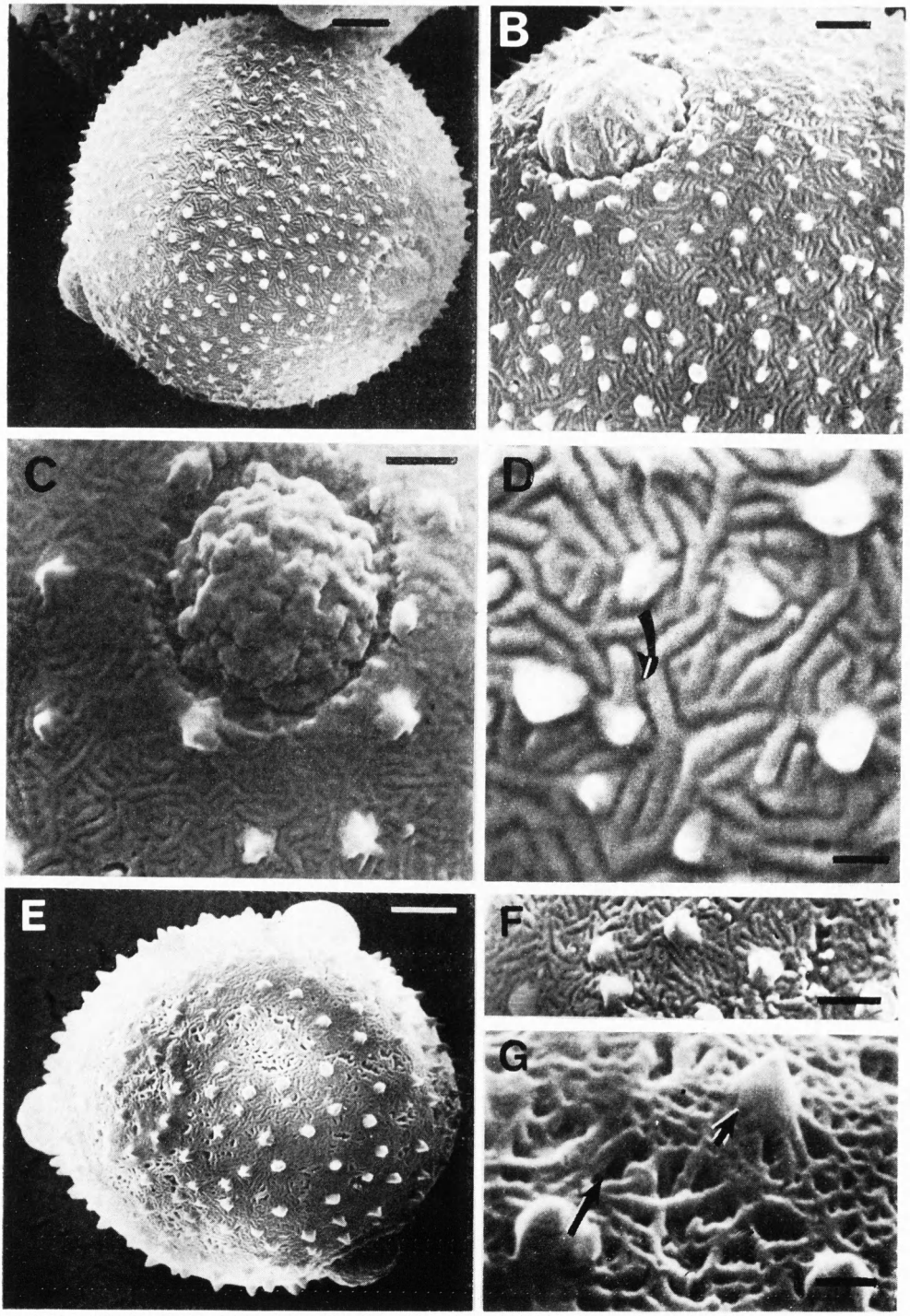
Campanula pyramidalis L. — Fig. 3 A, B, C; DUNBAR (1975 Fig. 6 D)
Shape: oblate-spheroidal.
Size: 34×36 μ.
Apertures: pollen grains 3-porate, pore diam. 4 μ, 5 μ (SEMG), surface of operculum granular (Fig. 3 B).
Exine: 2 μ thick, sexine slightly thicker than nexine, relatively few spinules, mostly 1.8 μ high, almost evenly spaced (Fig. 3 A); ridges frequently bent upwards, finger-like (Fig. 3 C). Type 2 a.

Campanula alliarifolia WILLD. — Fig. 5 A, B
Shape: oblate-spheroidal.
Size: 34×36 μ.
Apertures: pollen grains 3-porate, pore diam. 5 μ, 6 μ (SEMG), surface of operculum consisting of elongated and granular structures (Fig. 5 B).
Exine: 2.2 μ thick, sexine thicker than nexine, spinules mostly 1 μ high; short ridges, protrusions. Type 1, 4 a.

Campanula strigosa SOL.
Shape: spheroidal.
Size: 30 μ.
Apertures: pollen grains 3-porate, pore diam. 4 μ, 5 μ (SEMG).
Exine: 2 μ thick, sexine thicker than nexine, spinules mostly 0.6 μ high, irregularly spaced; ridges, sometimes branched, protrusions. Type 1, 4 a.

Campanula carpatica JACQ. — Fig. 5 C, D
Shape: suboblate.
Size: 36×40 μ.

Fig. 4. *Campanula.* — A, B, D: *C. rapunculus.* — A: 3-porate pollen grain showing two pores; surface covered with spinules of varying size. C. ×1,600. — B: Part of pollen wall showing pore with operculum; elongated structures cover operculum. Ridges of varying length between spinules. C. ×3,500. Line c. 2 μ. — D: Detail of non-apertural pollen wall. Thin structures at a lower level between main ridges (arrow); main ridges branching. C. ×15,000. Line c. 0.5 μ. — C: *C. phyctidocalyx.* Part of pollen wall showing one pore with operculum and basally divided spinules. Surface of operculum granular. Sexine between the spinules consists of branching ridges. C. ×5,000. Line c. 2 μ. — E—G: *C. lactiflora.* — E: 3-porate pollen grain. Spinules distributed over surface. Ridges situated less closely in places. C. ×1,800. — F: Detail of pollen wall with ridges between spinules. C. ×4,500. Line c. 2 μ. — G: Detail of the expanded pollen wall showing bacula (arrow) beneath ridges situated apart. Spinules basally divided (arrow-head). C. ×8,500. Line c. 1 μ.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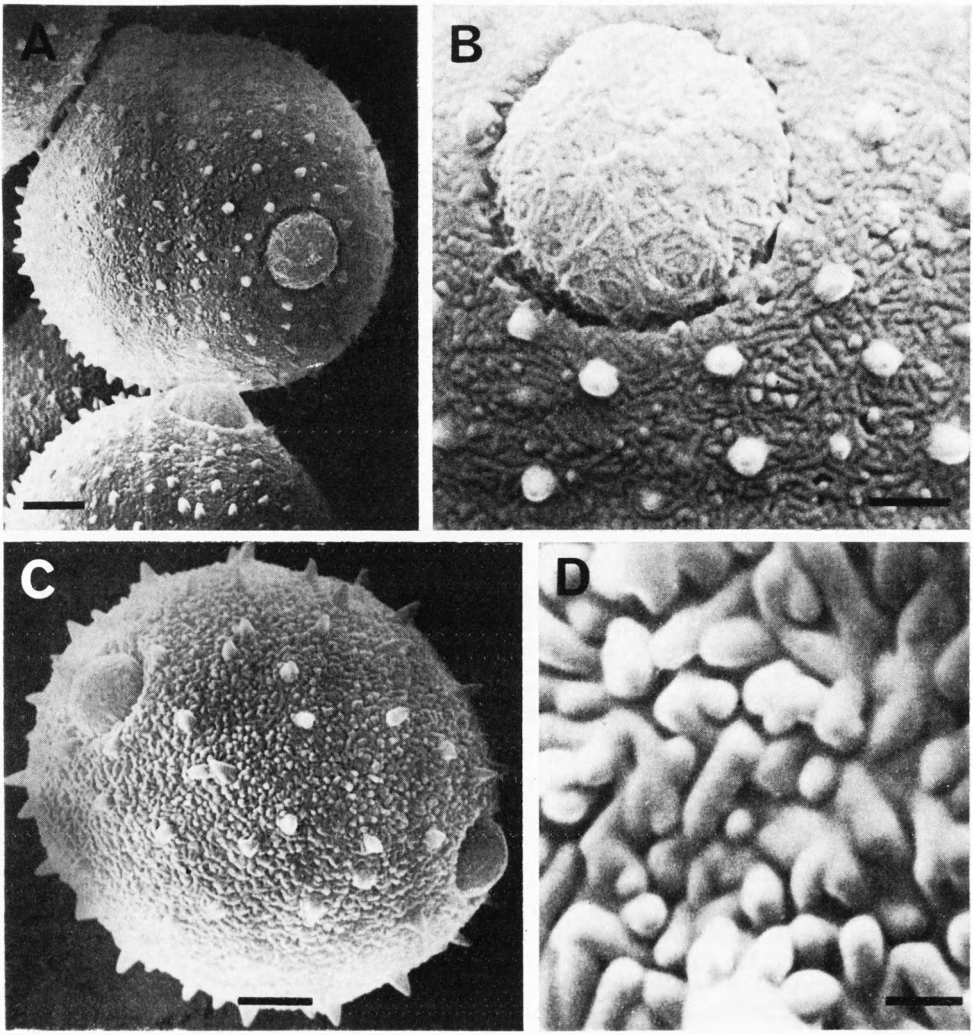


Fig. 5. *Campanula*. — A, B: *C. alliariaefolia*. — A: 3-porate pollen grain showing two pores. Spinules distributed over surface. C. ×1,700. — B: Part of pollen wall with pore and operculum. Surface of operculum shows elongated structures. Sexine between spinules consists of short ridges and protrusions. C. ×5,500. Line c. 2 μ. — C, D: *C. carpatica*. — C: 4-porate pollen grain showing two pores. Relatively few and large spinules distributed over surface. C. ×2,000. — D: Detail of pollen wall with finger-like, more or less upwardly bent structures. C. ×20,000. Line c. 0.5 μ.

Apertures: pollen grains 4-porate, pore diam. 3 μ, 5 μ (SEMG).

Exine: 2 μ thick, sexine with relatively few spinules, 2 μ high, irregularly spaced (Fig. 5 C); finger-like structures close together (Fig. 5 D). Type 3 a.

Campanula speciosa POURR. — Fig. 6 A, B

Shape: spheroidal.

Size: 40 μ.

Apertures: pollen grains 3-porate, pore diam. 4 μ, 5 μ (SEMG), operculum covered with granula and protrusions.

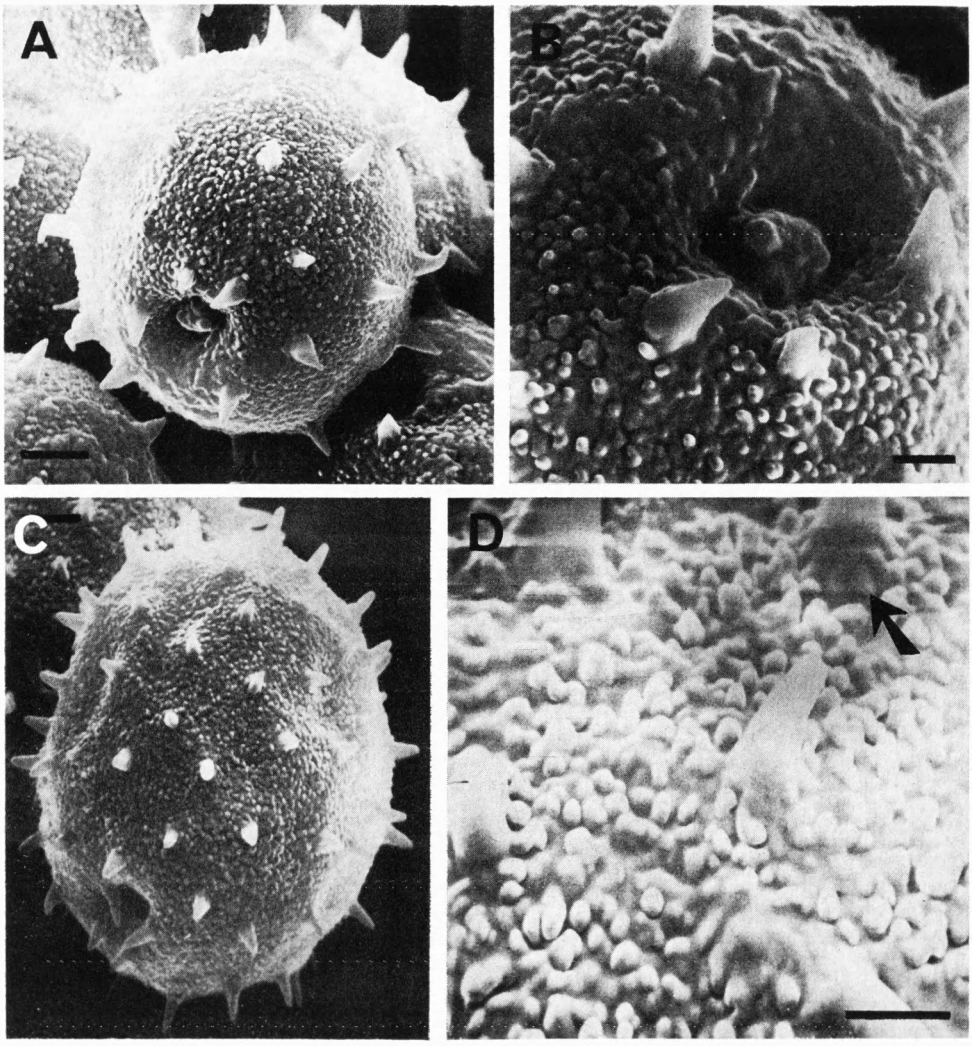


Fig. 6. *Campanula*. — A, B: *C. speciosa*. — A: 3-porate pollen grain showing one pore. Few and large spinules distributed over surface. C. ×1,800. — B: Detail of the pollen wall with a pore; operculum appears to be covered with protrusions. Verrucose-like protrusions on sexine surface. C. ×4,300. Line c. 2 μ. — C, D: *C. medium*. — C: 3-porate pollen grain with one pore visible. Large spinules distributed over surface; also occurring close to pore margin. C. ×1,500. — D: Part of pollen wall. Spinules with many "roots" (arrow). Between spinules verrucose-like protrusions. C. ×7,000. Line c. 2 μ.

Exine: 2 μ thick, sexine thicker than nexine, few spinules, 3.3 μ high, almost evenly spaced; verrucose-like protrusions close together. Type 4 a.

Campanula medium L. — Fig. 6 C, D

Shape: spheroidal.

Size: 40 μ.

Apertures: 3-porate, pore diam. 4 μ, 5 μ (SEMG).

Exine: 2 μ thick, sexine with few, evenly spaced spinules, 3 μ high, sometimes provided with many "roots" (Fig. 6 D); verrucose-like protrusions, close together. Type 4 a.

Campanula trachelium L. f. *alba* — Fig. 2 A, B, E

Shape: oblate-spheroidal.

Size: 42×44 μ.

Apertures: pollen grains 4-porate, pore diam. 5 μ, 6 μ (SEMG).

Exine: 2 μ thick, spinules mostly 0.9 μ high; irregular, very short "ridges" form an asymmetrical pattern (Fig. 2 B) except around the pore margin where they are radially arranged (Fig. 2 E). Type 6 a.

Campanula americana L. — Fig. 1 A, B

Shape: oblate-spheroidal.

Size: 36.5×38 μ (CHAPMAN 1967).

Apertures: pollen grains pantoporate, about 12 pores, 3.5 μ in diam., occasionally smaller.

Exine: spinules mostly 0.4 μ high, frequently lower (Fig. 1 A); low relief reticulum with narrow muri and small lumina (Fig. 1 B). Type 5 a—b.

ASYNEUMA

Asyneuma canescens GRISEB. & SCHENK — Fig. 7 C, D

Shape: spheroidal.

Size: 40 μ.

Apertures: pollen grains 4-porate, exceptionally 5-porate, pores equatorially arranged, pore diam. 3.5 μ, 4 μ (SEMG).

Exine: 1.5 μ thick, spinules basally divided, irregularly spaced, about 0.8 μ high, lower ones also occurring; short ridges of uniform width and varying length, sometimes branched (Fig. 7 D). Type 1 a.

PHYTEUMA

Phyteuma scheuchzerii ALL. — Fig. 7 E, F

Shape: suboblate.

Size: 30×32 μ (SEMG).

Apertures: pollen grains 4-porate, pores equatorially arranged, pore diam. 3.5 μ (SEMG).

Exine: relatively many, basally divided spinules, 1 μ high; short ridges of uniform width and varying length, sometimes branched. (Fig. 7 F). Type 1 a.

SYMPHYANDRA

Symphyandra armena (STEV.) A. DC.

Shape: oblate-spheroidal.

Size: 26×29 μ.

Apertures: pollen grains 3-porate, pores equatorially arranged, pore diam. 3.5 μ, 4 μ (SEMG), surface of operculum granular.

Exine: 2 μ thick, sexine thicker than nexine, spinules basally divided, mostly 0.6 μ high, irregularly spaced; ridges uniform in width, of varying length, occasionally branched. Type 1 a.

Symphyandra hofmannii PANT. — Fig. 9 A, B

Shape: spheroidal.

Size: 28 μ.

Apertures: pollen grains 3-porate, pores equatorially arranged, pore diam. 3 μ, surface of operculum granular.

Fig. 7. A, B: *Githopsis specularioides*. — A: 6-porate, spinulose pollen grain with equatorially arranged pores, cf. DUNBAR (1975 Fig. 6 B). Spinules close together. C. ×1,500. — B: Part of pollen wall showing pore. Spinules basally divided (arrow). Between spinules protrusions of different shapes. C. ×4,700. Line c. 2 μ. — C, D: *Asyneuma canescens*. — C: 4-porate pollen grains. Surface covered with spinules of varying size. C. ×1,000. Line c. 1 μ. — D: Part of pollen wall showing basally divided spinules and branched and irregularly curved short ridges. C. ×10,000. Line c. 0.1 μ. — E, F: *Phyteuma scheuchzerii*. — E: 4-porate pollen grains. Relatively few spinules distributed over surface. C. ×1,400. — F: Detail of pollen wall with basally divided spinule and short ridges. C. ×18,000. Line c. 0.5 μ.

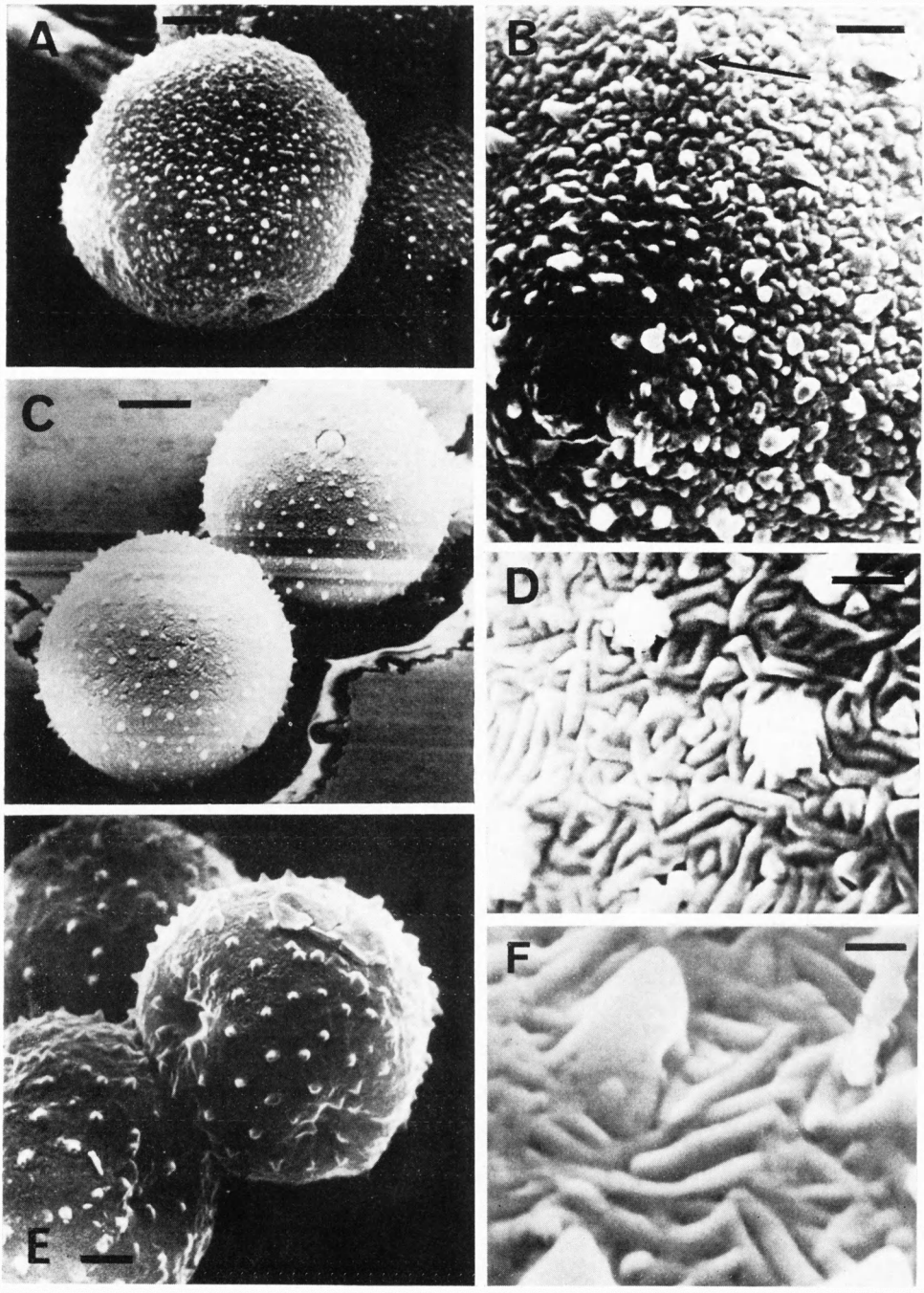


Fig. 7.

Exine: 2 μ thick, sexine thicker than nexine, spinules basally divided, about 1.2 μ high, irregularly spaced; short ridges (see *S. armena*) and protrusions. Type 1, 4 a.

EDRAIANTHUS

Edraianthus serpyllifolia (VIS.) A. DC. — Fig. 11 C, D

Shape: oblate-spheroidal.

Size: 31×33 μ.

Apertures: pollen grains 3-porate, pores equatorially arranged, pore diam. 2 μ, 5 μ (SEMG), surface of operculum smooth, occasionally provided with spinules (Fig. 11 D).

Exine: sexine with spinules fairly closely spaced, basally divided, mostly 0.8 μ high, lower ones occurring; ridges uniform in width, of varying length, occasionally branched, protrusions. Type 1, 4 a.

WAHLENBERGIA

Pollen grains slightly spheroidal-oblate, 31.5 to 45 μ, 3—5-porate, pore diameter 3—6 μ (SEMG). Surface covered with spinules of varying size, number and shape. Base of spinules sometimes appears to be divided, the "roots" always being shorter than those in the *Campanula* species. Sexine between spinules mostly consisting of short ridges (Type 1) in some species in low relief, and sometimes of low relief reticulum (Type 5) with short muri and small lumina as in the surface pattern of *Campanula americana* (see above). A transition between these patterns also occurs (Type 1, 5). Light microscopic observations on size, exine thickness and number of aperture as in THULIN (1975) if not otherwise stated.

Wahlenbergia abyssinica (RICH.) THULIN

Shape: oblate-spheroidal.

Size: 27×30 μ (SEMG).

Apertures: pollen grains 3-porate, pore diam. 4.5 μ (SEMG).

Exine: sexine with basally divided spinules mostly 0.8 μ high, lower ones also occurring, closely and irregularly spaced; short ridges, slightly curved, low relief pattern. Type 1 a.

Wahlenbergia denticulata (BURCH.) A. DC. — Fig. 12 A, B

Shape: oblate-spheroidal.

Size: 32×40 μ (SEMG).

Apertures: pollen grains 3-porate, pore diam. 3.3 μ (SEMG).

Exine: sexine with spinules mostly 1.6 μ high, basally divided, closely and irregularly spaced; short ridges occasionally branched. Type 1 a.

Wahlenbergia madagascariensis A. DC.

Shape: spheroidal.

Size: 32 μ (SEMG).

Apertures: pollen grains 3(—5)-porate, pore diam. 3 μ (SEMG).

Exine: sexine with spinules basally divided, irregularly spaced, mostly 0.9 μ high, lower ones also occurring; short ridges in low relief. Type 1 a.

Wahlenbergia napiformis (A. DC.) THULIN — Fig. 12 E, F

Shape: oblate-spheroidal.

Size: E 33 μ.

Apertures: pollen grains 3-porate, pore diam. 4 μ (SEMG), operculum spinulose.

Exine: 2 μ thick, spinules irregularly spaced, mostly 0.8 μ high, lower ones

Fig. 8. *Adenophora*. A, B: *A. aurita*. A: 4-porate pollen grain with one pore in face view. Pore margin slightly thickened. Spinules distributed over surface. C. ×1,500. — B: Part of pollen wall. Sexine consists of basally divided spinules, rounded protrusions and in between short ridges (arrow). C. ×7,600. Line c. 1 μ. — C, D: *A. palustris*. — C: 4-porate pollen grain with one pore in face view. Spinules distributed over surface. C. ×1,600. — D: Spinules, short ridges (left bottom corner) and rounded protrusions are shown. C. ×6,300. Line c. 2 μ. — E, F: *A. lilifolia*. — E: 4-porate pollen grain. Spinules distributed over surface. C. ×1,300. — F: Detail of pollen wall showing part of pore with operculum (arrow), spinules basally divided, short ridges with thickened ends and protrusions. C. ×8,600. Line c. 1 μ.

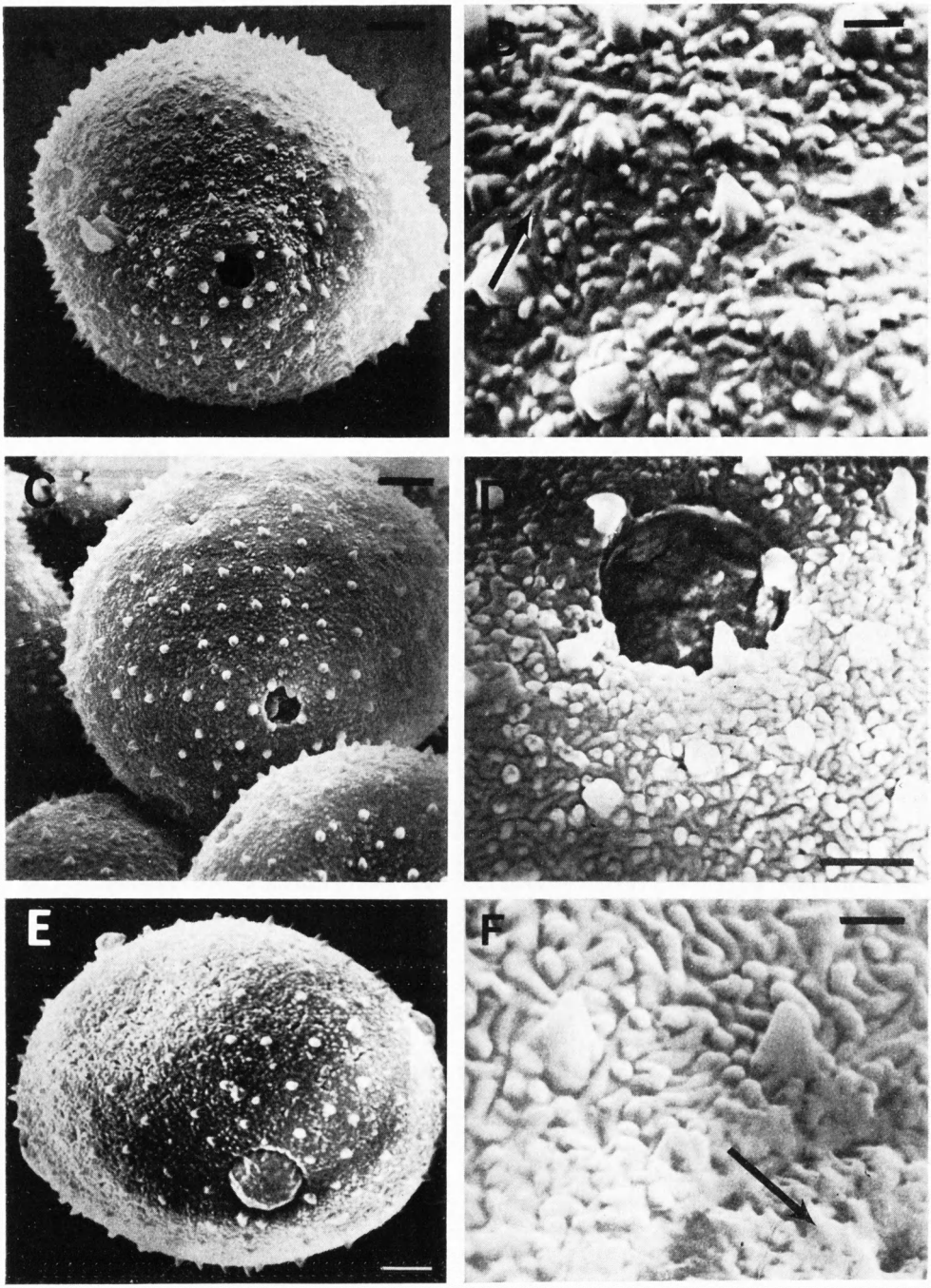


Fig. 8.

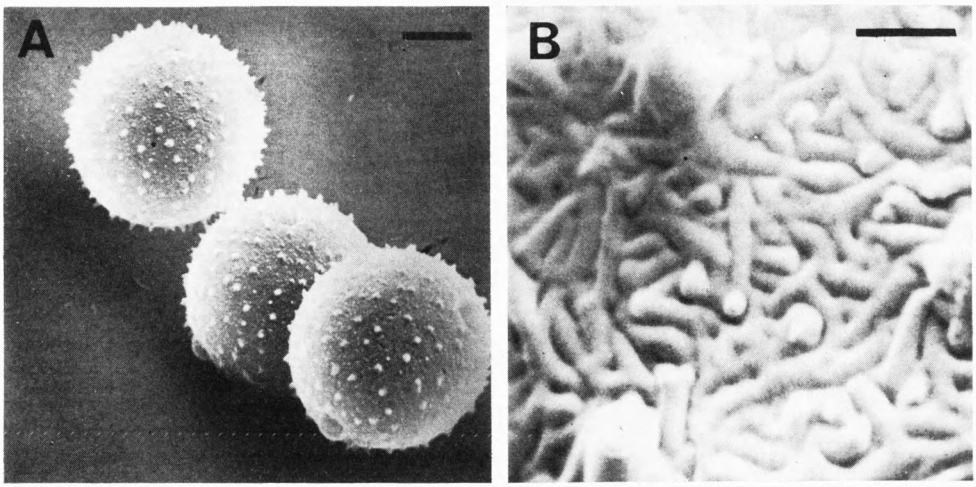


Fig. 9. *Symphyandra hofmannii.* — A: 3-porate, spinulose pollen grains with pores. C. ×940. Line c. 10 μ. — B: Part of pollen wall showing basally divided spinules, short ridges and rounded protrusions. C. ×13,000. Line c. 1 μ.

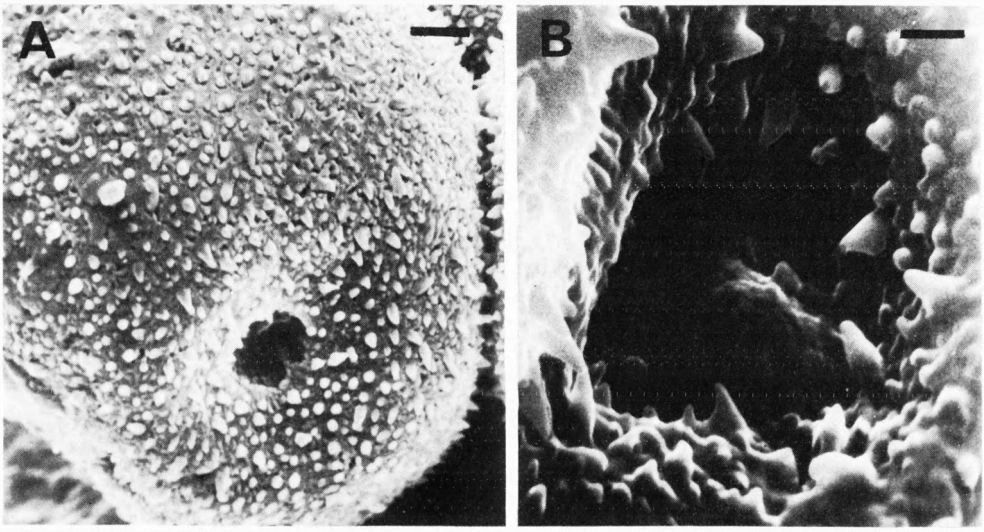
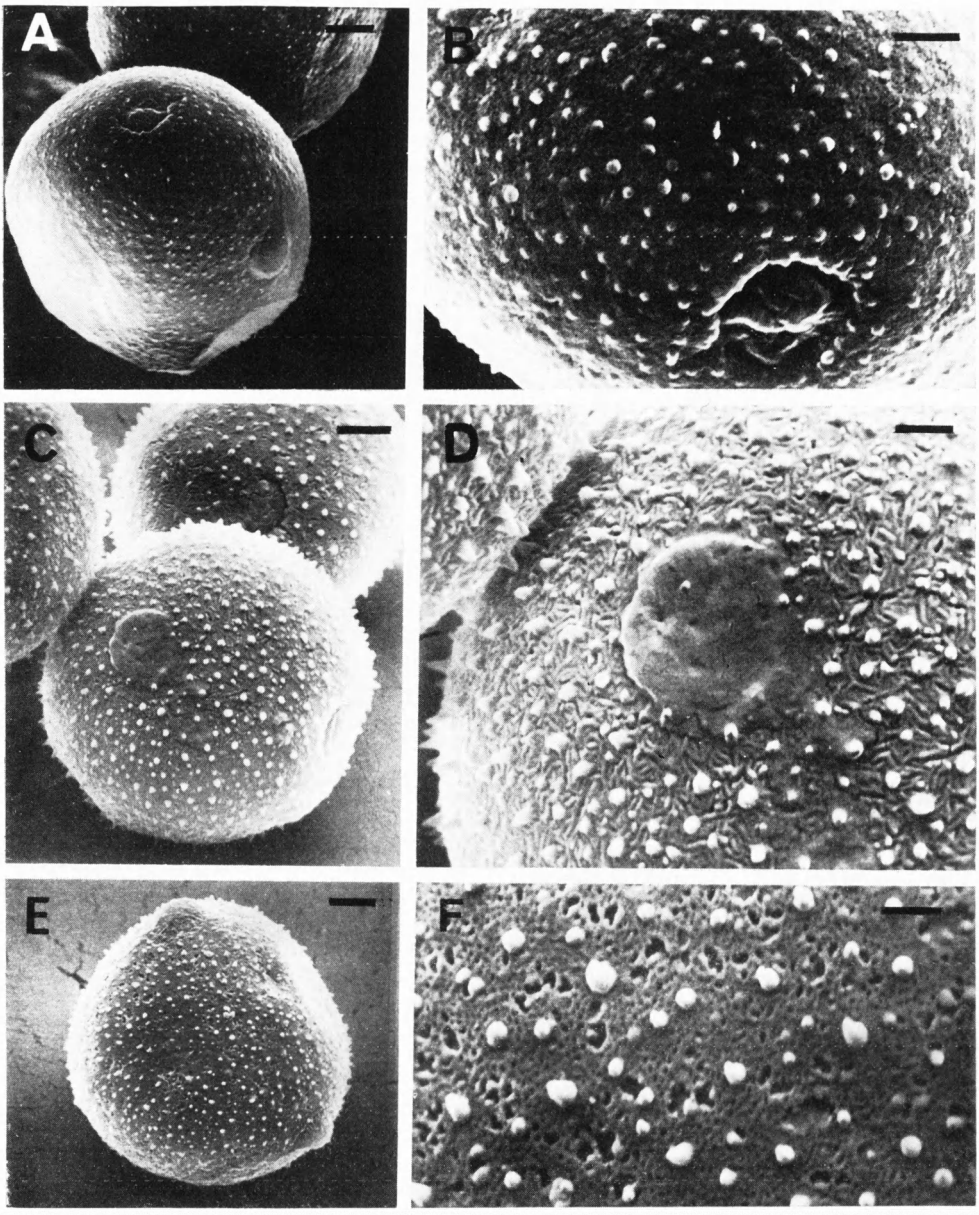


Fig. 10. *Roella muscosa.* — A: 3-porate pollen grain with pore in face view. Spinules distributed over surface. C. ×1,600. — B: Detail of pollen wall showing one pore and pore margin. Rounded protrusions between spinules. C. ×8,000. Line c. 1 μ.

Fig. 11. A, B: *Triodanis falcata.* — A: 3—4-porate pollen grain with two pores visible. The sexine surface is covered by verrucae. C. ×1,200. — B: Part of the verrucose sexine surface with pore. The verrucae are of varying size. C. ×4,200. Line c. 2 μ. — C, D:



Edraianthus serpyllifolia. — C: 3-porate pollen grains. Spinules of variable size are closely distributed over the surface. C. ×1,300. — D: Part of pollen wall with pore. Surface of operculum almost smooth although occasionally provided with small spinules. Sexine surface consists of short ridges, protrusions and basally divided spinules. C. ×3,600. Line c. 2 μ. — E, F: *Prismatocarpus pedunculatus.* 3-porate pollen grain. Spinules of different size closely distributed over surface. C. ×1,200. — F: Part of pollen wall. Sexine with spinules of varying shape and size, some of them being verrucose-like and a low relief reticulum. C. ×3,800. Line c. 2 μ.

also occurring; short ridges, somewhat curved, occasionally branched. Type 1 b.

Wahlenbergia perrieri THULIN
Shape: spheroidal.
Size: 30 μ (SEMG).
Apertures: pollen grains 3-porate, pore diam. 3 μ (SEMG).
Exine: sexine with spinules irregularly spaced, mostly 0.8 μ high, lower ones also occurring; short ridges in low relief. Type 1 b.

Wahlenbergia upembensis THULIN — Fig. 12 C, D
Shape: oblate-spheroidal.
Size: E 33—44 μ.
Apertures: pollen grains (3—)4(—5)- or 3-porate, pore diam. 3 μ (SEMG).
Exine: 2 μ thick, sexine with spinules basally divided, closely and irregularly spaced, mostly 0.8 μ high, lower ones also occurring; short ridges, occasionally branched. Type 1 a.

Wahlenbergia androsaceae A. DC.
Shape: spheroidal.
Size: 42 μ (SEMG).
Apertures: pollen grains 3-porate, pore diam. 6 μ (SEMG).
Exine: sexine with spinules mostly 0.7 μ high, less closely spaced than is usual in *Wahlenbergia*; short ridges. Type 1 b.

Wahlenbergia masafuerae (PHIL.) SKOTTSB. (author's observations)
Shape: suboblate.
Size: 24×30 μ (SEMG).
Apertures: pollen grains 3-porate.
Exine: sexine with spinules irregularly spaced, mostly 0.7 μ high, lower ones also occurring; short ridges in low relief. Type 1 b.

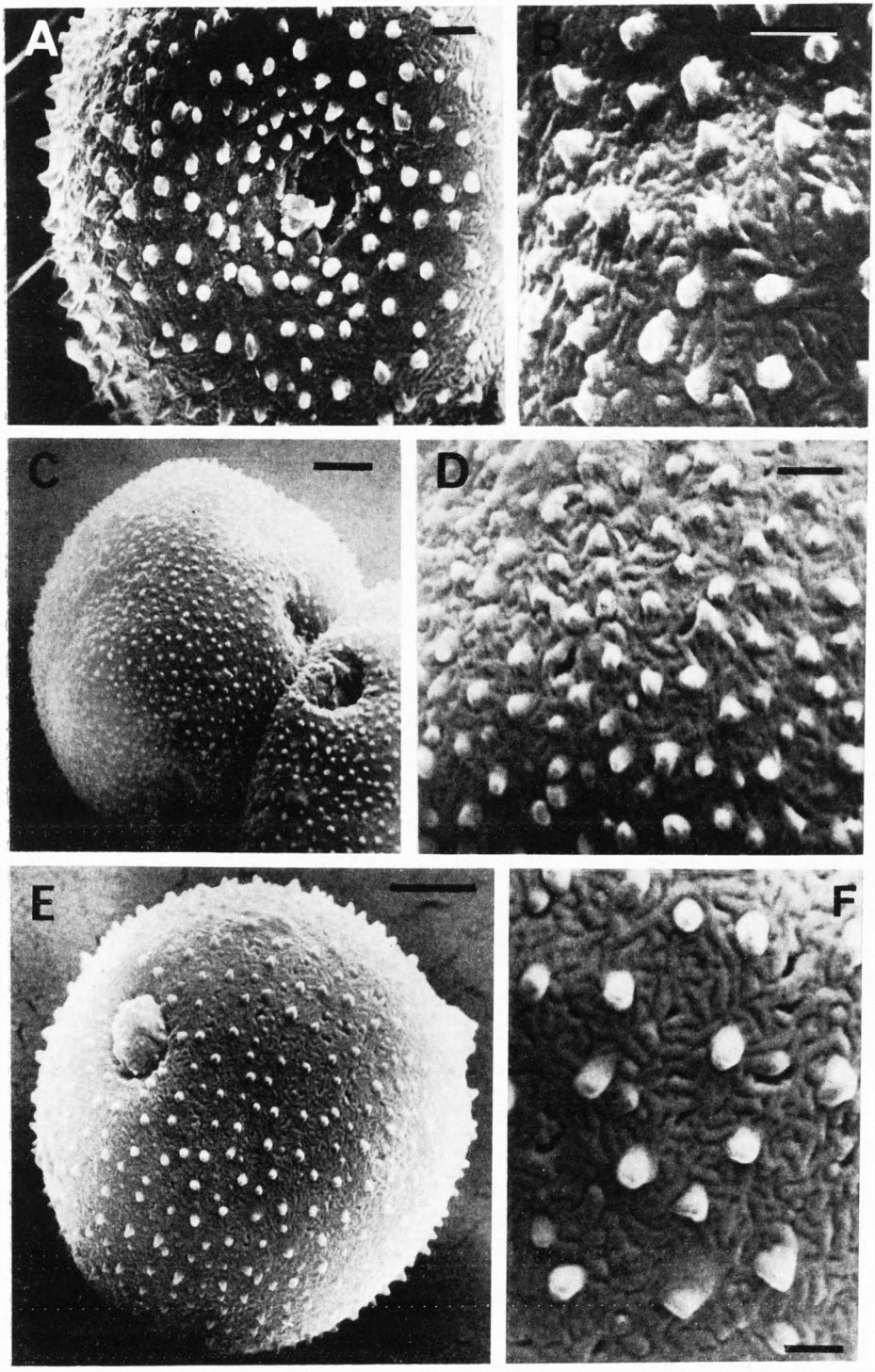
Wahlenbergia communis CAROLIN (author's observations)
Shape: oblate-spheroidal.
Size: 38×45 μ (SEMG).
Apertures: pollen grains 3-porate, pore diam. 3.8 μ (SEMG).
Exine: sexine with spinules basally divided, rather closely and irregularly spaced, mostly 1.2 μ high, lower ones also occurring; short ridges or muri of irregular shape. Type 1, 5 a.

Wahlenbergia krebsii CHAM. ssp. *arguta* (HOOK. FIL.) THULIN
Shape: oblate-spheroidal.
Size: E 25—42 μ.
Apertures: pollen grains 3-porate, pore diam. 4 μ (SEMG).
Exine: 1.5—2 μ thick, spinules mostly 0.7 μ high, irregularly spaced; short ridges, interrupted by reticulate areas. Type 1, 5 a.

Wahlenbergia subaphylla (BAK.) THULIN ssp. *thesioides* THULIN
Shape: oblate-spheroidal.
Size: 40×45 μ (SEMG).
Apertures: pollen grains 3-porate, pore diam. 5 μ (SEMG).
Exine: sexine with spinules irregularly spaced, mostly 1.2 μ high, lower ones also occurring; very short ridges/muri. Type 1, 5 b.

Wahlenbergia perrottetti (A. DC.) THULIN
Shape: spheroidal.
Size: 30 μ (SEMG).
Apertures: pollen grains 3-porate.
Exine: sexine with spinules mostly 0.8 μ high, occasionally lower, irregularly spaced; reticulate, small lumina, interrupted by areas with ridges. Type 5, 1 a.

Fig. 12. *Wahlenbergia*. — A, B: *W. denticulata*. — A: 3-porate pollen grain with one pore in face view. Spinules closely distributed over surface. Critical point treated. C. ×3,000. Line c. 2 μ. — B: Part of pollen wall with spinules and short ridges. Critical point treated. C. ×6,000. Line c. 2 μ. — C, D: *W. upembensis*. — C: 3-porate pollen grains. Spinules distributed over surface. C. ×1,600. — D: Part of pollen wall with closely spaced spinules of varying size and short ridges. C. ×4,500. Line c. 2 μ. — E, F: *W. napiformis*. — E: 3-porate pollen grain with one pore visible. Spinules of different size distributed over surface. C. ×2,400. — F: Part of pollen wall. The sexine surface consists of spinules and short, somewhat curved and branched ridges C. ×8,000. Line c. 1 μ.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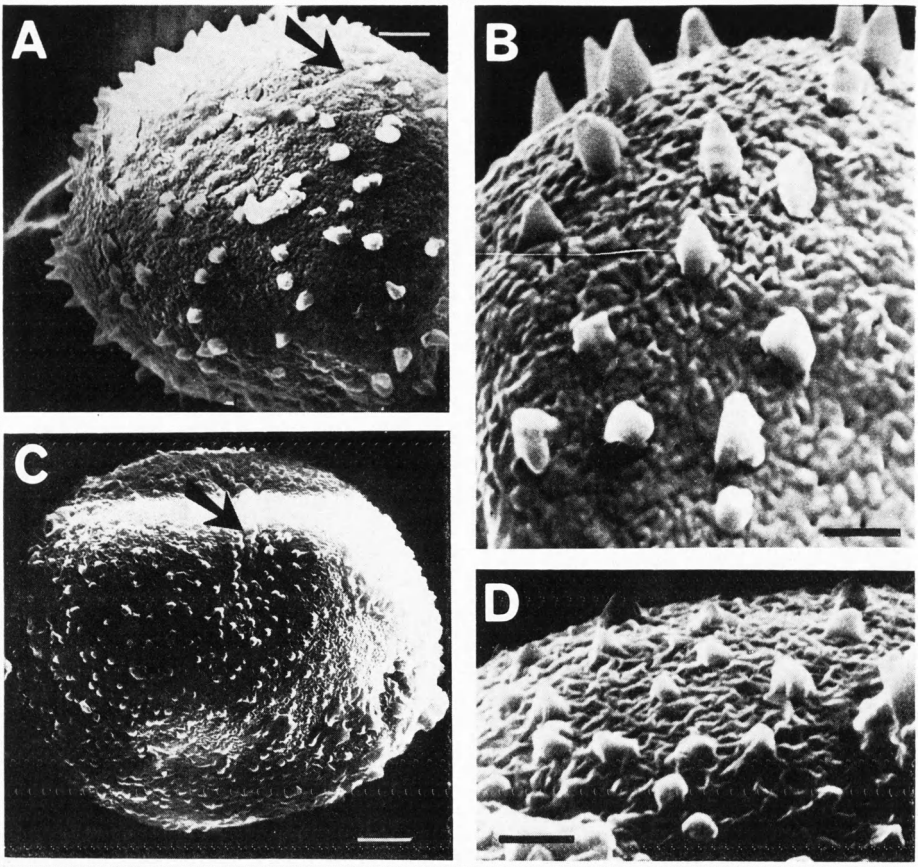


Fig. 13. *Campanumoea*. — A, B: *C. lancifolia*. — A: 3-colporate pollen grain with relatively few and large spinules. One of the compound apertures traceable (arrow). C. ×1,400. — B: Part of pollen wall with basally divided spinules and short irregular ridges. C. ×5,000. Line c. 2 μ. — C, D: *C. maximowiczii*. — C: 5—6-colporate pollen grain with spinules. One of the compound apertures traceable (arrow). C. ×1,400. — D: Part of pollen wall with basally divided spinules and short curved ridges. C. ×4,700. Line c. 2 μ.

Wahlenbergia undulata A. DC.

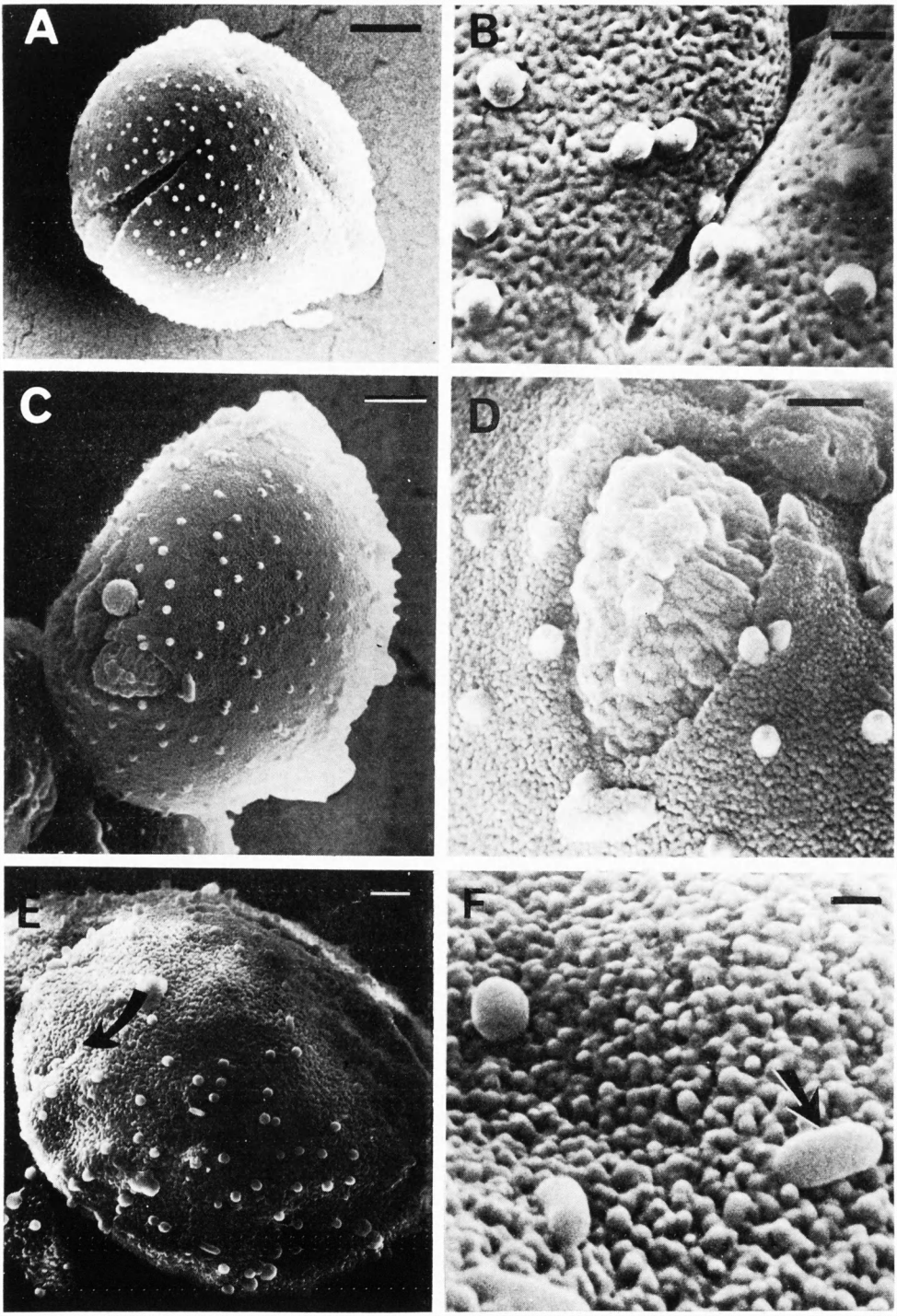
Shape: oblate-spheroidal.

Size: E 42 μ (SEMG).

Apertures: pollen grains 3-porate, pore diam. 3 μ (SEM).

Exine: sexine with spinules closely and

Fig. 14. A—D: *Canarina*. — A, B: *C. abyssinica*. — A: 3-colporate, verrucose pollen grain. C. ×1,000. Line c. 10 μ. — B: Detail of pollen wall showing part of colpus. Fine structure with partly atypical reticulum. C. ×7,600. Line c. 1 μ. — C, D: *C. eminii*. — C: 3-colporate pollen grain with very short colpi. Sexine with relatively blunt spinules. C. ×1,800. — D: Part of pollen wall with short, oval aperture. Sexine with spinules and rounded protrusions closely-placed. C. ×5,500. Line c. 2 μ. — E, F: *Ostrovskia magnifica*. — E: 6—7-colpate pollen grain in oblique polar view. Part of colpus (arrow). Verrucae very irregularly distributed over surface. C. ×1,100. EMG taken with Jeol JSM-U3 electron microscope. — F: The sexine surface consists of verrucae and closely-placed rounded protrusions of varying size. Verrucae sometimes elongated (arrow). C. ×7,000. Line c. 1 μ.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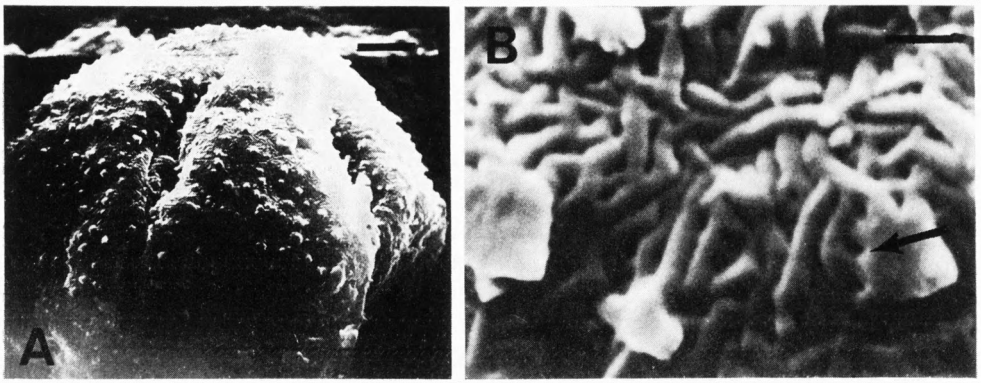


Fig. 15. *Platycodon grandiflorum*. — A: 5—6-colporate pollen grain. Two of the apertures visible. Spinules distributed over surface. C. ×1,600. — B: Detail of pollen wall showing basally divided spinules and short branched ridges forming an irregular pattern. Note connection between one ridge and more than one "root" (arrow). C. ×18,000. Line c. 0.5 μ.

irregularly distributed, mostly 2 μ high, lower ones also occurring; reticulate, low relief, small lumina. Type 5 b.

ADENOPHORA

Pollen grains oblate-spheroidal to suboblate, 30—36×36—45 μ, 4-porate. Surface covered with spinules basally divided. Sexine between spinules consisting mostly of protrusions (Type 4), short ridges occasionally occur.

Adenophora aurita FRANCH. — Fig 8 A, B

Shape: oblate-spheroidal.

Size: 34×36 μ (SEMG).

Apertures: pollen grains 4-porate, pore diam. 3.3 μ (SEMG), pore margin thickened.

Exine: sexine with spinules irregularly spaced, mostly 1 μ high, occasionally lower; short ridges, protrusions (Fig. 8 B). Type 1, 4 a.

Adenophora lilifolia L. — Fig. 8 E, F

Shape: suboblate.

Size: E 48 μ (36×45 μ SEMG).

Apertures: pollen grains 4-porate, pore diam. 2 μ (SEMG).

Exine: 3 μ, spinules almost regularly spaced, 1.5 μ high; short ridges occasionally branched, protrusions. Type 1, 4 a.

Adenophora palustris NOMAR — Fig. 8 C, D

Shape: oblate-spheroidal.

Size: 30×36 μ (SEMG).

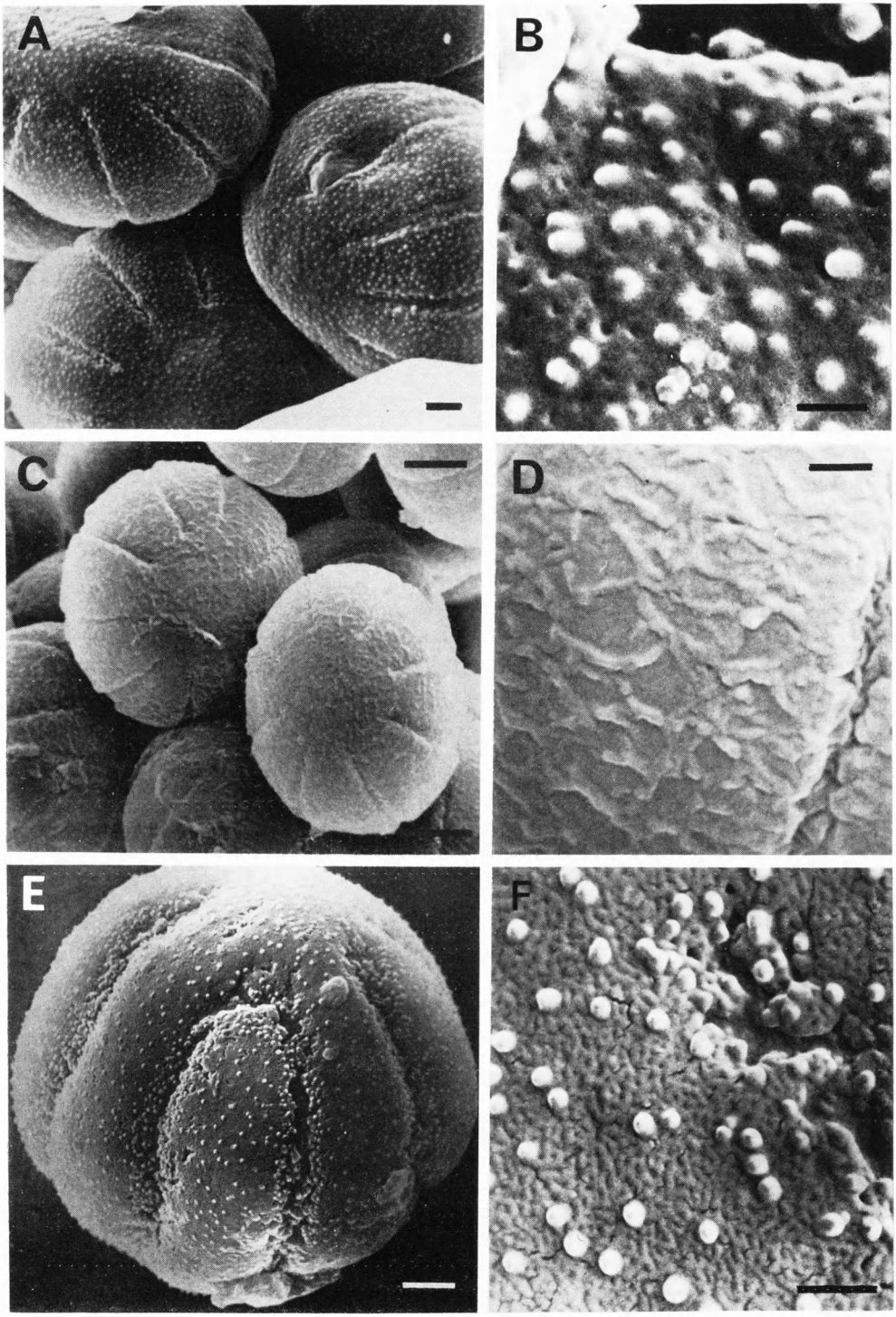
Apertures: pollen grains 4-porate, pore diam. 3 μ (SEMG).

Exine: spinules almost regularly spaced, 1 μ high; short ridges, protrusions. Type 1, 4 a.

Adenophora thunbergiana KUDO

Shape: oblate-spheroidal.

Fig. 16. A—D: *Cyananthus*. — A, B: *C. incanus*. — A: 9-colpate pollen grains. Verrucae closely distributed over sexine surface, also occurring on colpus membrane. C. ×1,100. — B: Part of pollen wall showing colpus at the top. Small puncta are seen in tectum. C. ×10,000. Line c. 1 μ. — C, D: *C. lobatus*. C: 8—10-colpate pollen grains in polar view. C. ×900. Line c. 10 μ. — D: Detail of pollen wall with part of colpus to the right. Reticulate sexine surface with incomplete muri. C. ×4,600. Line c. 2 μ. — E, F: *Codonopsis clematidea*. — E: 8—10-colpate pollen grain. Spinule and/or verrucae irregularly distributed over surface. C. ×1,500. — F: Part of pollen grain towards polar region. The sexine consists of irregularly spaced verrucae and between them of a reticulum with short, thick muri and very small lumina. C. ×6,500. Line c. 2 μ.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Size: 33×36 µ (SEMG).

Apertures: pollen grains 4-porate, pore diam. 3 µ (SEMG).

Exine: spinules almost regularly spaced, 0.9 µ high; relatively few ridges between protrusions. Type 4, 1 a.

JASIONE

Jasione montana L.
(DUNBAR 1973 a, b) Type 4 a.

ROELLA

Pollen grains suboblate-oblate spheroidal (ERDTMAN 1952), E 38—55 µ, 3-porate. Spinules of varying size, without "roots", cover the surface. Between them the sexine consists of small, rounded protrusions (Type 4).

Roella amplexicaulis DOD.

Shape: oblate-spheroidal.

Size: E 38 µ (SEMG).

Apertures: pollen grains 3-porate, pore diam. 5 µ (SEMG).

Exine: spinules closely and irregularly spaced, of varying size, mostly 1.6 µ high; small rounded protrusions. Type 4 b.

Roella leptosepala SOND.

Shape: oblate-spheroidal.

Size: E 55 µ (SEMG).

Apertures: pollen grains 3-porate, pore diam. 4 µ (SEMG).

Exine: spinules of varying size up to 2.8 µ high, closely spaced; rounded protrusions. Type 4 b.

Roella muscosa THUNB. — Fig. 10 A, B

Shape: spheroidal.

Size: 50 µ (SEMG).

Apertures: pollen grains 3-porate, pore diam. 5 µ (SEMG).

Exine: spinules of varying size up to 2.5 µ high, closely spaced; rounded protrusions. Type 4 b.

GITHOPSIS

Githopsis specularioides NUTT. — Fig. 7 A, B; DUNBAR (1975 Fig. 6 B)

Shape: suboblate.

Size: 36×40 µ.

Apertures: pollen grains 6-porate, pores arranged equatorially, pore diam. 3 µ.

Exine: 2 µ thick, basally divided spinules (Fig. 7 B), 1.2 µ high; club-like to verrucose-like protrusions close together (Fig. 7 B). Type 4 a.

PRISMATOCARPUS

Prismatocarpus pedunculatus (BERG.) A. DC. — Fig. 11 E, F

Shape: prolate-spheroidal.

Size: 42×55 µ (SEMG).

Apertures: pollen grains 3-porate, pore diam. 4.5 µ (SEMG).

Exine: spinules mostly 1 µ high and verrucae somewhat lower, closely spaced; low relief reticulum. Type 5 a, b, c.

TRIODANIS

Triodanis falcata (TEN.) MC VAUGH — Fig. 11 A, B

Shape: spheroidal.

Size: 40 µ (E 31 µ SEMG).

Apertures: pollen grains 3—4-porate, pore diam. 1.7 µ, 3 µ (SEMG).

Exine: 1.8 µ thick, verrucae mostly 1.5 µ high, lower ones also occurring; pattern of tectum could not be determined. Type - c.

PLATYCODON

Pollen grains oblate-spheroidal, 53×55 µ, 5—6-colporate. The sexine resembles that of *Campanula persicifolia,* for example, with a distinct feature of basally divided spinules and short branching ridges (Type 1 a).

Platycodon grandiflorum JACQ. — Fig. 15 A, B

Shape: oblate-spheroidal.

Size: 53×55 µ.

Apertures: pollen grains 5—6-colporate.

Exine 1.5 µ thick, sexine with basally divided spinules, irregularly spaced, mostly 1.5 µ high, lower ones also occurring; short ridges occasionally branched. Type 1 a.

CAMPANUMOEA

Pollen grains suboblate, 25—30×31—35 µ, 3—6-colporate. The sexine differs in the two species investigated in *Campanumoea*. Spinules of *C. lancifolia* are comparatively large in relation to size of pollen grains, those of *C. maximowiczii* being smaller; spinules of both species basally divided, the "roots" being shorter than those in the *Campanula* species. According to the sexine pattern between the spinules the genus is divided into Types 1 and 6.

Campanumoea lancifolia (REXB.) MERR. — Fig. 13 A, B

Shape: suboblate.

Size: 25×31 µ (SEMG).

Apertures: pollen grains 3-colporate.

Exine: relatively few and large, basally divided spinules, mostly 2 µ high irregularly spaced, with short "roots"; short ridges. Type 1 a.

Campanumoea maximowiczii HONDA — Fig. 13 C, D

Shape: suboblate.

Size: 30×35 µ (SEMG).

Apertures: pollen grains 5—6-colporate.

Exine: basally divided spinules, closely and irregularly spaced, mostly 0.8 µ high, lower ones also occurring; short, curved ridge-like structures. Type 6 a.

CANARINA

Pollen grains spheroidal to oblate-spheroidal, 22 µ to 30×33 µ, 3-colporate, length of colpus differs considerably in the two species investigated, (Fig. 14 A, C). Surface covered with blunt spinules in *C. eminii*, in *C. abyssinica* with verrucae. Sexine between verrucae in *C. abyssinica* with reticulum-like pattern (Type 5), that between spinules in *C. eminii* consisting of protrusions.

Canarina eminii ASCHERS. — Fig. 14 C, D

Shape: oblate-spheroidal.

Size: E 30 µ (30×33 µ SEMG).

Apertures: pollen grains 3-colporate, very short colpus (Fig. 14 C).

Exine: 2 µ thick, sexine with blunt spinules mostly 1 µ high, irregularly spaced; rounded protrusions close together. Type 4 b—c.

Canarina abyssinica ENGL. — Fig. 14 A, B

Shape: spheroidal.

Size: 22 µ (SEMG).

Apertures: pollen grains 3-colporate, colpus membrane granular.

Exine: sexine with verrucae mostly 1 µ high, irregularly spaced; reticulum-like pattern with short "muri". Type 5 c.

OSTROVSKIA

Pollen grains oblate-spheroidal, 50×57 µ, 6—7-colpate. Sexine surface covered with verrucae of varying shape. Sexine between verrucae consisting of closely spaced protrusions (Fig. 14 F), similar to those of *Canarina eminii* (Fig. 14 D).

Ostrovskia magnifica RGL. — Fig. 14 E, F

Shape: oblate-spheroidal.

Size: 50×57 µ (SEMG).

Apertures: pollen grains 6—7-colpate.

Exine: sexine with very irregularly spaced verrucae, round or elongated, up to 3.5 µ high; protrusions, sometimes appearing to consist of subunits. Type 4 c.

CYANANTHUS

Pollen grains spheroidal, 36—42 µ and oblate-spheroidal, 42×45 µ, 8—10-colpate. Except in *C. lobatus*, sexine surface covered with verrucae, also present on the colpus membrane. Sexine between verrucae consisting of perforated tectum, except in *C. lobatus* provided with reticulum in high relief, sometimes with incomplete muri.

Cyananthus incanus HOOK. FIL. & THOMS. — Fig. 16 A, B

Shape: oblate-spheroidal.

Size: 42×45 µ (SEMG).

Apertures: pollen grains 9-colpate, colpus membrane verrucose.

Exine: verrucae closely and irregularly spaced; tectum perforated by small puncta of about equal size. Type 7 c.

Cyananthus inflatus HOOK. FIL. & THOMS.
Shape: oblate-spheroidal.
Size: E 36 µ (E 33 µ SEMG).
Apertures: pollen grains 9-colpate, colpus membrane verrucose.
Exine: 2 µ thick, verrucae closely and irregularly spaced; tectum perforated by small puncta of equal size. Type 7 c.

Cyananthus microphyllus EDGEW.
Shape: oblate-spheroidal.
Size: E 42 µ (SEMG).
Apertures: pollen grains 8-colpate, colpus membrane verrucose and granular.
Exine: verrucae closely and irregularly spaced; tectum perforated by small puncta of equal size. Type 7 c.

Cyananthus lobatus WALL. — Fig. 16 C, D
Shape: spheroidal.
Size: E 40 µ (ERDTMAN 1952); (E 38 µ SEMG).
Apertures: pollen grains 8—10-colpate.
Exine: sexine about as thick as nexine, sexine reticulate in high relief, long, irregularly shaped muri, occasionally incomplete. Type 10 d.

CODONOPSIS

Pollen grains spheroidal, 48 µ and oblate-spheroidal, 36—40×40—44 µ, 7—8-colpate, colpi longer than in *Cyananthus,* occasionally anastomosed at the poles (Fig. 16 E). Small spinules and/or verrucae cover sexine surface, increasing in number on margin of aperture. Sexine between spinules consists of a low relief reticulum with thick, short muri and very small lumina.

Codonopsis clematidea SCHRENK — Fig. 16 E, F
Shape: oblate-spheroidal.
Size: 40×44 µ (E 45 SEMG).
Apertures: pollen grains 8-colpate.
Exine: 2 µ thick, sexine with spinules and/or verrucae closely and irregularly spaced; reticulate, low relief, small lumina. Type 5 b—c.

Codonopsis handeliana NANNF. — DUNBAR (1975 Fig. 6 C)
Shape: oblate-spheroidal.
Size: 48×46 (38×40 µ SEMG).
Apertures: pollen grains 7-colpate.
Exine: 2 µ thick, sexine with spinules and/or verrucae irregularly spaced, accumulating at aperture margin; low relief reticulum, small lumina. Type 5 b—c.

Codonopsis viridiflora MAXIM.
Shape: oblate-spheroidal.
Size: 36×40 µ.
Apertures: pollen grains 8-colpate.
Exine: 2 µ thick, sexine surface with closely spaced spinules; low relief reticulum with small lumina. Type 5 b.

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APPENDIX. SPECIMENS INVESTIGATED

Adenophora aurita FRANCH., China 1934, FRANCH. s.n. det. Y. NANNFELDT (S). — *A. lilifolia* (L.,) BESS., cult. Hort. UPS. ex THOMPSON & MORGAN (UPS). — *A. palustris* NOMAR, cult. 1974 Hort. Berg. ex (GB). — *A. thunbergiana* KUDO, cult. 1974 Hort. Berg. ex (GB).

Asyneuma canescens (W. & K.) GRISEB. & SCHENK, cult. 1974 (UPS).

Campanula alliariaefolia WILLD., Caucasus, cult. 1974 Hort. Berg. ex (WA). *C. americana* L., cult. Hort. Ups. ex Sudbury, Mass., U. S. A. C. G. ALM s. n. 1951 (UPS). — *C. carpatica* JACQ., Carpathian, cult. 1974 Hort. Berg. — *C. erinus* L., Spain 1968, STRANDHEDE et al. 501 (S-MB). — *C. garganica* TEN. var. *hirsutum,* cult. 1974 Hort. Kew ex WATERER & Sons, Twyford, England (K). — *C. glomerata* L., Sweden 1945, C. G. ALM & H. SMITH 362 (UPS). — *C. lactiflora* M. B., Caucasus, Vacratot 70 cult. 1970 Hort. Berg. (SBT). — *C. medium* L., France 1952, SONSTER 1286 (K). — *C. persicifolia* L., Sweden 1970, A. DUNBAR s. n., det. Å. NILSSON. — *C. phyctidocalyx* BOISS. & NOÉ, cult. 1974 (K) ex (E). — *C. pyramidalis* L., cult. 1974 Hort. Berg. det. L. KERS. — *C. rapunculoides* L., Sweden 1970, A. DUNBAR s. n., det. Å. NILSSON. — *C. rapunculus* L., cult. 1974 Hort. Berg. det. L. KERS. — *C. rotundifolia* L., Sweden 1970, A.DUNBAR s.n., det. Å. NILSSON. — *C. speciosa* POURR., Spain 1974, H. & H. E. WANNTORP, K. BREMER, B. SVENSSON 90 (S-MB). — *C. strigosa* SOL., cult. Hort. UPS. ex Copenhagen 1965 (UPS). — *C. trachelium* L., England 1937, F. K. MAKINS 1299 (K); Sweden, E. ASPLUND 1489 (K). — *C. trachelium* L., f. *alba* cult. Hort. Kew ex J. FORBES Ltd., Hawick, Scotland (K). — *C. uniflora* L., Greenland 1891, J. A. BJÖRLING s. n. (S-MB); Norway 1892, J. BERGGREN s. n. (S-MB), Sweden 1904, W. NETZEL s. n. (S-MB).

Campanumoea lancifolia (REXB.) MERR., Sumatra 1928, R. TOROES 763 (S); China 1931, N.STEWARD, C. CHIAO & H. CHEO 291 (S). — *C. maximowiczii* HONDA, China 1964, M. MIZUSHIMA 17497 (S).

Canarina abyssinica ENGL., Kenya 1962, IRWIN s. n. (UPS). — *C. eminii* ASCHERS. ex SCHWEINF., Kenya 1948, O. HEDBERG 158 (UPS).

Codonopsis clematidea SCHRENK, China 1933, C. B. CLARKE det. E. WALKER s. n. (S); C. B. CLARKE cult. Hort. UPS. ex Hort. Vilar (UPS). — *C. handeliana* NANNF., China 1934, J. NANNFELDT 11086 (S). — *C. viridiflora* MAXIM., China 1925, J. ROCK 12738(S).

Cyananthus incanus HOOK. FIL. & THOMS., Tibet 1938, LUDLOW, SHERIFF & TAYLOR 6020 (UPS). — *C. inflatus* HOOK. FIL. & THOMS., Tibet 1947, LUDLOW, SHERIFF & ELLIOTT 14497 (S). — *C. lobatus* WALL. ex BENTH., Bhutan 1949, LUDLOW, SHERIFF & HICKS 17221 (S). — *C. microphyllus* EDGEW., cult. Hort. UPS. ex Trädgårdsamat. Spånga 62, Sweden (UPS).

Edraianthus serpyllifolia (VIS.) A. DC., Albania 1916, I. DÖRFLER 239 (UPS).

Githopsis specularioides NUTT., California 1958, R. ALAVA 2086 (UPS).

Jasione montana L., Sweden 1970, A. DUNBAR s. n., det. Å. NILSSON.

Ostrovskia magnifica RGL., Afghanistan 1969, REGEL 462 (K).

Phyteuma scheuchzerii ALL., Switzerland 1942, W. KOCH 42/293 (UPS).

Platycodon grandiflorum (JACQ). A. DC., cult. 1974 Hort. Ups. ex THOMPSON & MORGAN, Ipswich, England (UPS); — China 1955, BRYNYIN-TJA s. n. (S).

Prismatocarpus pedunculatus (BERG.) A. DC., S. Africa 1972, K. BREMER 328 (S).

Roella amplexicaulis W. DOD., S. Africa 1968, J. SIDEY 4144 (S). — *R. leptosepala* SOND., Cape Province 1937, E. WALL s. n. (S). — *R. muscosa* THUNB., Cape Province 1937, HAFSTRÖM s. n. (S).

Symphyandra armena (STEV.) A. DC., cult. 1974 Hort. Berg. ex (O). — *S. hofmannii* PANT. cult. 1974 Hort. Berg. (SBT).

Triodanis falcata (TEN.) MC VAUGH, Greece 1933, F. GUIOL 2315 (UPS).

Wahlenbergia abyssinica (RICH.) THULIN, Tanzania 1970, M. THULIN 314 (UPS). — *W. androsaceae* A. DC., Cape Province 1963, H. SCHLIEBEN 9821 (S); Cape Province 972, K. BREMER 413 (S). — *W. communis* CAROLIN, S. Australia 1967, B. COPLEY 1680 (UPS). — *W. denticulata* (BURCH.) A. DC., S. W. Africa 1934, K. DINTER (S). — *W. krebsii* CHAM. ssp. *arguta* (HOOK. FIL.) THULIN, Ethiopia 1971, THULIN 1392 (UPS). — *W. madagascariensis* A. DC., Madagascar 1950, M. R. BENOIST 469 (P). — *W. masafuerae* (PHIL.) SKOTTSB., Juan Fernandez, C. & I. SKOTTSBERG 428 (UPS). — *W. napiformis* (A. DC.) THULIN, Kenya 1970, THULIN 298 (UPS). — *W. perrieri* THULIN, Madagascar 1960, COURS 5731 (P); Madagascar 1956, BOSSER 9978 (O). — *W. perrottetii* (A. DC.) THULIN, Nigeria 1957, HEPPER 1020 (BR). — *W. subaphylla* (BAK.) THULIN, subsp. *thesioides* THULIN, Tanzania 1970, THULIN & MHORO 1166 (UPS). — *W. undulata* A. DC., S. Africa 1920, TH. FRIES & ROB. 3010 (UPS). — *W. upembensis* THULIN, Katanga 1953, ROBYNS 3959 (BR).

On pollen of Campanulaceae and Related Families with Special Reference to the Surface Ultrastructure

II. Campanulaceae Subfam. Cyphioidae and Subfam. Lobelioidae; Goodeniaceae; Sphenocleaceae

Anita Dunbar

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22 species representing 14 genera have been studied by means of light microscopy and scanning electron microscopy. Pollen morphology suggests that Cyphioidae is a link between the two other subfamilies Campanuloidae and Lobelioidae. As yet there is no evidence that supports a connection between Campanuloidae and Lobelioidae. A similarity in ultrastructure between Goodeniaceae and Campanulaceae has been found.

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This paper is the second of two parts, the first being (DUNBAR 1975). This part deals with two subfamilies of Campanulaceae, Cyphioidae and Lobelioidae. The families Goodeniaceae and Sphenocleaceae are briefly dealt with. For further details see DUNBAR (1975).

OBSERVATIONS

For material and methods, terminology and the division of the surface pattern into arbitrary types see DUNBAR (1975).

Campanulaceae, Cyphioidae

CYPHIA

Cyphia assimilis SCHEEPERS

Shape: prolate.

Size: 48×35 μ.

Apertures: pollen grains 3-colporate, colpi constricted at equator.

Exine: 1.5 μ thick, sexine surface almost smooth but for a finely granular pattern. Type 9 d.

Cyphia bulbosa L. — Fig. 5 F

Shape: prolate.

Size: 54×39 μ (ERDTMAN 1952).

Apertures: pollen grains 3-colporate.

Exine: sexine almost smooth but for a finely granular pattern. Type 9 d.

PARISHELLA

Parishella californica GRAY — Fig. 1 A, B

Shape: oblate-spheroidal.

Size: 32×36 μ.

Apertures: pollen grains 6-colpate.

Exine: 2 μ thick, sexine with spinules mostly 1 μ high, closely and irregularly spaced; small pits in tectum, closely-placed, of equal size. Type 8 b.

NEMACLADUS

Nemacladus rubescens GREENE — Fig. 1 C, D

Shape: spheroidal.

Size: 27 μ (E).

Apertures: pollen grains 3-colporate, colpi obliquely arranged at varying angles or parallel to pollen axis.

Exine: 1.8 μ thick, sexine surface with spinules almost regularly spaced, about 1 μ high; small pits in tectum, closely-placed, of equal size. Type 8 b.

CYPHOCARPUS

Pollen grains prolate-spheroidal, 44—52×40—46 μ, 3-colporate, reticulate with muri in high relief and lumina of varying shape. Protrusions occur in lumina, they are more conspicuous in *C. psammophilus* than in *C. innocuus* or *C. rigescens.*

Cyphocarpus psammophilus RICARD — Fig. 1 E, F

Shape: prolate-spheroidal.

Size: 44×40 μ.

Apertures: pollen grains 3-colporate.

Exine: 2.4 μ thick, sexine slightly thicker than nexine, high relief reticulate, lumina 4—6-angular, smaller in size towards apocolpia; protrusions sometimes consisting of compound structures with up to three, occasionally more, subunits protruding either unattached from centre of lumina or attached to a murus. Type 10, 4 d.

Cyphocarpus innocuus SAND.

Shape: prolate-spheroidal.

Size: 52×46 μ.

Apertures: pollen grains 3-colporate.

Exine: 2 μ thick, sexine slightly thicker than nexine, high relief reticulate, lumina of varying shape and size, generally decreasing in size towards apocolpia; 1—4 small protrusions, sometimes attached to muri, mostly unattached, occur in many lumina. Type 10, 4 d.

Cyphocarpus rigescens MIERS

Shape: prolate-spheroidal.

Size: 44×40 μ.

Apertures: pollen grains 3-colporate, colpus membrane granular.

Exine: 2 μ thick, sexine slightly thicker than nexine, high relief reticulate, lumina of varying shape and size, generally smaller on apocolpia; protrusions occur in some lumina. Type 10, 4 d.

Campanulaceae, Lobelioidae

LAURENTIA

Pollen grains prolate-spheroidal, 26×24 μ and prolate, 33—46×24—32 μ, 3-colporate except *L. petraea* 3-colpate. Sexine reticulate to striate. Protrusions occur in the lumina of some species. They are less conspicuous however (Fig. 2 b) than those in *Cyphocarpus* species of the subfamily Cyphioidae. (Fig. 1 F).

Laurentia petraea (F. v. M.) WIMM. — Fig. 2 A, B

Shape: prolate.

Size: 46×32 μ.

Apertures: pollen grains 3-colpate.

Exine: 2 μ thick, sexine reticulate with broad muri, lower than in *Cyphocarpus;* low protrusions of varying size and number occur in lumina. Type 10, 4 d.

Laurentia carnosula (HOOK. & ARN.) — Fig. 2 C, D

Shape: prolate.

Size: 33×24 μ (SEMG).

Apertures: pollen grains 3-colporate.

Exine: sexine striate, lirae branched, with transverse connections situated lower in the sexine. As the lirae are situated somewhat apart in the equatorial region small "lumina" occur between them: low protrusions occasionally occur in these lumina. Type 11, 4 d.

Laurentia michelii A. DC.

Shape: prolate-spheroidal.

Size: 26×24 μ.

Apertures: pollen grains 3-colporate.

Exine: 2 μ thick, sexine thicker than nexine, striate with branched lirae, connected at a lower level and situated somewhat apart, especially in the equatorial region where small "lumina" occur; no

Table 1. The species are arranged morphologically according to the pattern of the sexine fine structure. The numbers 1—11 and a—d indicate the different types of fine structure and the types of spinules/verrucae, see DUNBAR (1975 pp. 76, 77).

Taxon	Size (μ) Polar axis× equatorial axis (E)		Shape	Aperture condition
	LM	SEMG		
Campanulaceae, Cyphioidae				
Cyphia assimilis	48×35		prolate	3-colporate
C. bulbosa	54×39		prolate	3-colporate
Parishella californica	32×36		oblate-spheroidal	6-colpate
Nemacladus rubescens	E 27		spheroidal	3-colporate
Cyphocarpus psammophilus	44×40		prolate-spheroidal	3-colporate
C. innocuus	52×46		prolate-spheroidal	3-colporate
C. rigescens	44×40		prolate-spheroidal	3-colporate
Campanulaceae, Lobelioidae				
Laurentia petraea	46×32		prolate	3-colpate
L. carnosula		33×24	prolate	3-colporate
L. michelii	26×24		prolate-spheroidal	3-colporate
Lobelia anceps		25×17	prolate	3-colpate
L. dortmanna	29×22		subprolate	3-colpate
L. zeylanica	26×22		subprolate	3-colpate
Isotoma anemonifolius	42×30	36	subprolate	3-colporate
Palmerella debilis	22×17		prolate-spheroidal	3-colporate
Downingia elegans	44×32	E 36	prolate	3-colporate
Siphocampylus biserratus	30×24		subprolate	3-colporate
Pratia angulata	30×21.5		prolate	3-colporate
Grammatotheca bergiana		30×25	subprolate	3-colporate
Goodeniaceae				
Scaevola cerastifolia		38×31	subprolate	3-colporate
S. koenigii	48×44		prolate-spheroidal	3-colporate
Sphenocleaceae				
Sphenoclea zeylanica	17.5×15		subprolate	3-colporate

protrusions have been found in these lumina. Type 11 d.

LOBELIA

Lobelia anceps L. FIL. — Fig. 3 C, D

Shape: prolate.

Size: 25×17 μ (SEMG).

Apertures: pollen grains 3-colpate, colpus membrane granular.

Exine: sexine reticulate to reticulate-striate, muri and/or lirae increase in width at poles, lumina irregular in size. Type 10, 11 d.

Lobelia dortmanna L. — Fig. 3 A, B

Shape: subprolate.

Size: 29×22 μ.

Apertures: pollen grains 3-colpate.

Exine: 2 μ thick, sexine reticulate-striate, muri and/or lirae variable in width, narrow bridges connect the lirae at a somewhat lower level; small rounded lumina. Type 10, 11 d.

Lobelia zeylanica L. — Fig. 3 E, F

Shape: subprolate.

Size: 26×22 μ.

Apertures: pollen grains 3-colpate, colpi occasionally anastomosed at the pole (Fig. 3 E).

Exine: 2 μ thick, sexine striate, lirae closely-placed, branched and connected at a lower level by thin bridges. Type 11 d.

Table 1 continued.

Sculpturing					
Sexine between spinules or entire sexine	Type (spinules/ verrucae excepted)	Spinules/ verrucae	Height of spinules SEMG	Shape of spinules	Type of spinules/ verrucae
almost smooth, nano-granulate	9				d
almost smooth, nano-granulate	9				d
pits in tectum	8	spinules	1	without roots	b
pits in tectum	8	spinules	1	without roots	b
reticulate, protrusions	10,4				d
reticulate, protrusions	10,4				d
reticulate, protrusions	10,4				d
reticulate, protrusions	10,4				d
striate, protrusions	11,4				d
striate	11				d
reticulate-striate	10,11				d
reticulate-striate	10,11				d
striate	11				d
reticulate, protrusions	10,4				d
striate-reticulate	11,10				d
striate	11				d
striate	11				d
striate	11				d
striate	11				d
perforated tectum, puncta	7	spinules	0.7	without roots	b
perforated tectum, puncta	7	spinules	0.3	without roots	b
granular	9				d

ISOTOMA

Isotoma anemonifolius KNIGHT — Fig. 2 E, F

Shape: spheroidal.

Size: 42×30 μ (36 μ SEMG).

Apertures: pollen grains 3-colporate, colpus membrane granular.

Exine: 2 μ thick, sexine thicker than nexine, sexine high relief reticulate, muri about equal in width, 3—5 angular lumina increasing in size in non-apertural parts of the pollen grains, rather small at aperture margin and also at poles; protrusions of varying size and number occur in most lumina. Type 10, 4 d.

PALMERELLA

Palmerella debilis GRAY var. *serrata* GRAY

Shape: prolate-spheroidal.

Size: 22×17 μ (CHAPMAN 1967).

Apertures: pollen grains 3-colporate.

Exine: sexine striate-reticulate, lirae and/or muri curved, the space between them small and irregular. Type 11, 10 d.

DOWNINGIA

Downingia elegans DOUGL. — Fig. 4 A, B

Shape: prolate.

Size: 44×32 μ.

Apertures: pollen grains 3-colporate.

Exine: 2 μ thick, sexine thicker than nexine, striate, lirae branched, uniform in width and connected at a lower level by bridges thinner than main lirae; flattened protrusions occur on lirae (Fig. 4 B). Type 11 d.

SIPHOCAMPYLUS

Siphocampylus biserratus (CAV.) A. DC. — Fig. 4 C, D

Shape: subprolate.

Size: 30×24 μ.

Apertures: pollen grains 3-colporate, colpi constricted equatorially, colpus membrane granular.

Exine: 1.5 μ thick, striate, lirae uniform in width, branched and connected at a lower level by thin bridges. Type 11 d.

PRATIA

Pratia angulata HOOK. FIL. — Fig. 4 E, F

Shape: prolate.

Size: 30×21.5 μ (ERDTMAN 1952).

Apertures: pollen grains 3-colporate.

Exine: sexine striate, branched lirae closely-placed. Type 11 d.

GRAMMATOTHECA

Grammatotheca bergiana (CHAM.) PRESL

Shape: subprolate.

Size: 30×25 μ (SEMG).

Apertures: pollen grains 3-colporate, colpus membrane granular.

Exine: sexine striate, branched lirae closely-placed. Type 11 d.

Goodeniaceae

SCAEVOLA

Scaevola cerastifolia SKOTTSB. — Fig. 5 C, D

Shape: subprolate.

Size: 38×31 μ (SEMG).

Apertures: pollen grains 3-colporate, colpus membrane granular, surface of operculum covered with elongated structures.

Exine: sexine with spinules irregularly spaced, mostly 0.7 μ high; tectum perforated by puncta of similar size and uniform shape. Type 7 b.

Scaevola koenigii VAHL — Fig. 5 A, B, Fig. 6 A

Shape: prolate-spheroidal.

Size: 48×44 μ.

Apertures: pollen grains 3-colporate, lalongated ora (Fig. 6 A), colpus membrane granular.

Exine: 4 μ thick at the thinnest places, sexine thicker than nexine, varies considerably in different parts of pollen grain, being thickest below the poles, c. 5 μ; spinules about 0.3 μ high, irregularly spaced; tectum perforated by puncta of uniform size and shape. Type 7 b.

Sphenocleaceae

SPHENOCLEA

Sphenoclea zeylanica GAERTN. — Fig. 5 E

Shape: subprolate.

Size: 17.5×15 μ (CHAPMAN 1967).

Fig. 1. A, B: *Parishella californica*. — A: 6-colpate pollen grains. Spinules closely distributed over surface. C. ×950. Line c. 10 μ. — B: Part of pollen wall. Sexine provided with spinules. Small pits of uniform size occur in the tectum. C. ×4,000. Line c. 2 μ. — C, D: *Nemacladus rubescens*. — C: 3-colporate pollen grain. Spinules are almost uniformly distributed over sexine surface. C. ×2,000. — D: Detail of wall with part of aperture visible. Rounded protrusions on colpus membrane (arrow). Pits are seen in the tectum. C. ×4,700. Line c. 2 μ. — E, F: *Cyphocarpus psammophilus*. — E: 3-colporate, reticulate pollen grain showing two of its apertures. C. ×2,000. — F: Detail of pollen wall with part of colpus to the left. The reticulum consists of muri in high relief, and 4—6-angular lumina. Protrusions in lumina, sometimes consisting of compound units. C. ×7,000. Line c. 1 μ. — For shape, size and apertures etc. see Table 1. The line equals 5 μ in all figures unless otherwise indicated.

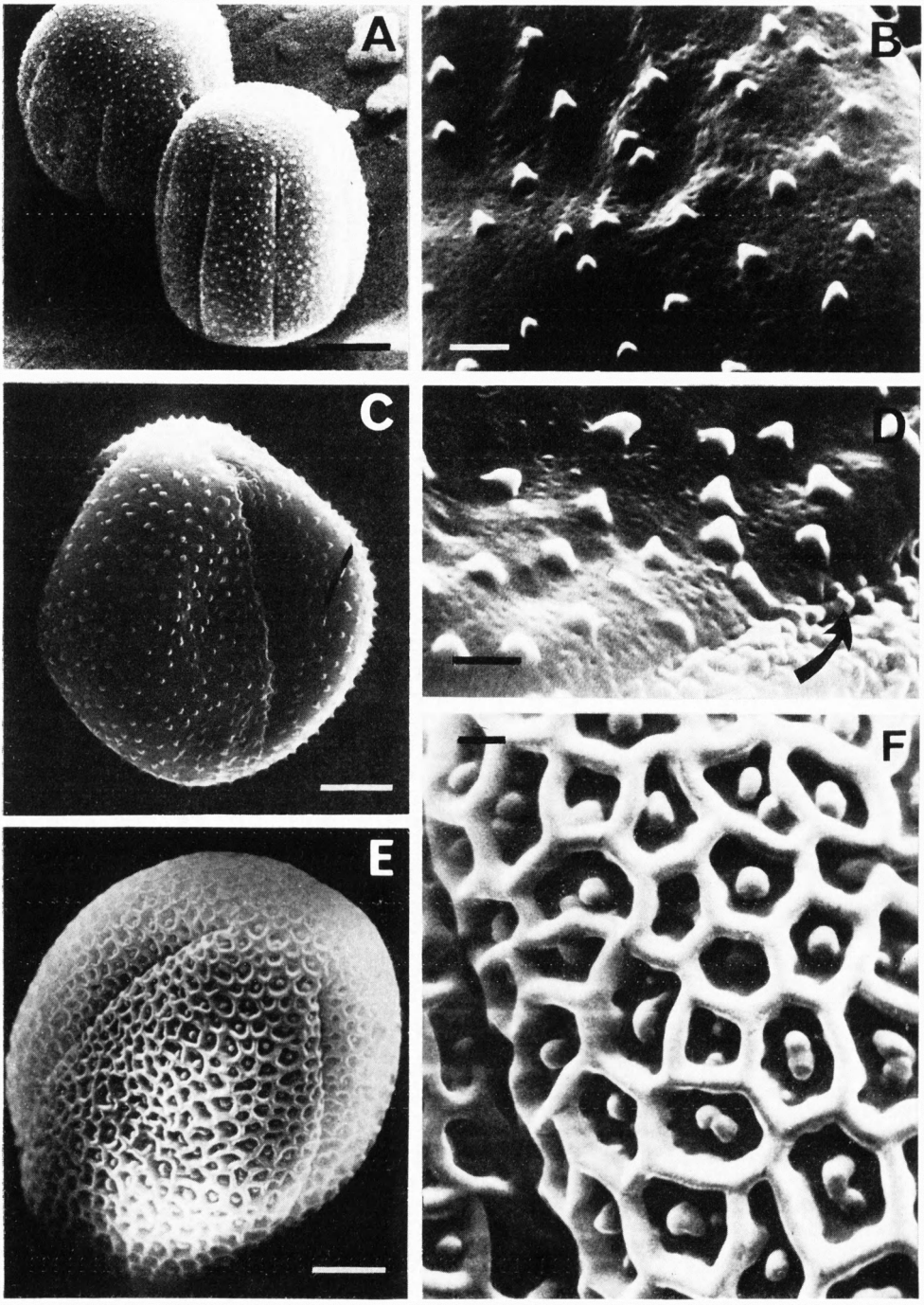


Fig. 1.

Apertures: pollen grains 3-colporate.
Exine: sexine granular with rounded protrusions of varying size. Type 9 d.

DISCUSSION

The relationship between the three subfamilies of Campanulaceae is not easily discerned. No direct similarity between the sexine pattern of pollen grains in the Campanuloidae and Lobelioidae has so far been detected but there is evidence however, that the Cyphioidae can be regarded as a connecting link (see below) between the other two subfamilies (Fig. 8).

The pollen grains in the Lobelioidae are either 3-colpate or 3-colporate. This fact may indicate that phylogenetically the subfamily would have a position near to the genera of Cyphioidae, or to those Campanuloidae that have 3-colpate/colporate apertures. AVETISJAN (1967) pointed out that the 3-colporate pollen grains in Sphenocleaceae, Lobeliaceae and Cyphiaceae show a general similarity to the tropical species of the bell-shaped ones with colporate pollen, for example *Canarina, Campanumoea, Platycodon* and *Pentaphragma* (Campanuloidae). The author regarded these as having common ancestors possibly with 3-colporate or related types of apertures. Other characters however, such as fine structure of the sexine, support that the Campanuloidae and Lobelioidae are remote, since the reticulate/striate pattern in high relief (Type 10, 11) of Lobelioidae are absent in the genera of Campanuloidae (Fig. 8). Moreover Lobelioidae, as far as has been investigated, lacks spinules while most Campanuloidae pollen are spinulose or verrucose.

The fine structure in Cyphioidae points to a connection between the two other subfamilies. Genera with spinulose pollen grains and genera with pollen grains lacking spinules belong to this subfamily. A distinct sexine pattern (Type 10, 4 d) can be discerned in both Cyphioidae *(Cyphocarpus)* and Lobelioidae *(Laurentia, Isotoma)*. The similarity between Cyphioidae and Campanuloidae is less distinct. There is however a resemblance between the 8—10-colpate pollen grains of *Cyananthus* (Campanuloidae) and the 6-colpate pollen grains of *Parishella* (Cyphioidae). In some of the *Cyananthus* species the tectum is perforated with puncta of about equal size, while there are only pits in the tectum of *Parishella*. Further ontogenetical studies may reveal a closer relationship.

That lines of evolution have proceeded in Campanuloidae is indicated by the shape, number and position of the apertures (AVETISJAN 1967, 1973, DUNBAR in press). AVETISJAN (1973) stated that colpate, colporate and colpate-porate pollen grains are typical of all families and genera of Campanulaceae found in tropical zones, and that porate apertures constitute one of the most important characters in the new type of pollen grains of the family distributed in temperate zones. This author moreover suggested that the evolution in *Campanula* pollen can be seen in the decrease in length of spinules in association with an increase in numbers of pores. As far as concerning the genus *Campanula* my observations agree with this interpretation (DUNBAR 1975 Table 1). In addition to decrease in height of spinules, a change in fine structure is also evident

Fig. 2. A—D: *Laurentia*. — A, B: *L. petraea*. — A: 3-colpate, reticulate, pollen grains. C. ×2,700. Line c. 10 μ. — B: Detail of pollen wall with thick muri and lumina of varying size. Low protrusions of varying size occur in the lumina. C. ×7,000. Line c. 1 μ. — C, D: *L. carnosula*. — C: 3-colporate, striate pollen grain with one colpus in face view. C. ×1,800. — D: Detail of pollen wall with colpus to the right. Branched lirae connected at lower level. C. ×3,500. Line c. 2 μ. — E, F: *Isotoma anemonifolius*. — E: 3-colporate pollen grain. Reticulate sexine. Colpus membrane with small, closely-placed protrusions. C. ×1,500. — F: Detail of reticulate pollen wall. Note the bacula (arrow). Structures on muri are artefacts. Small protrusions occur in lumina. C. ×6,000. Line c. 2 μ.

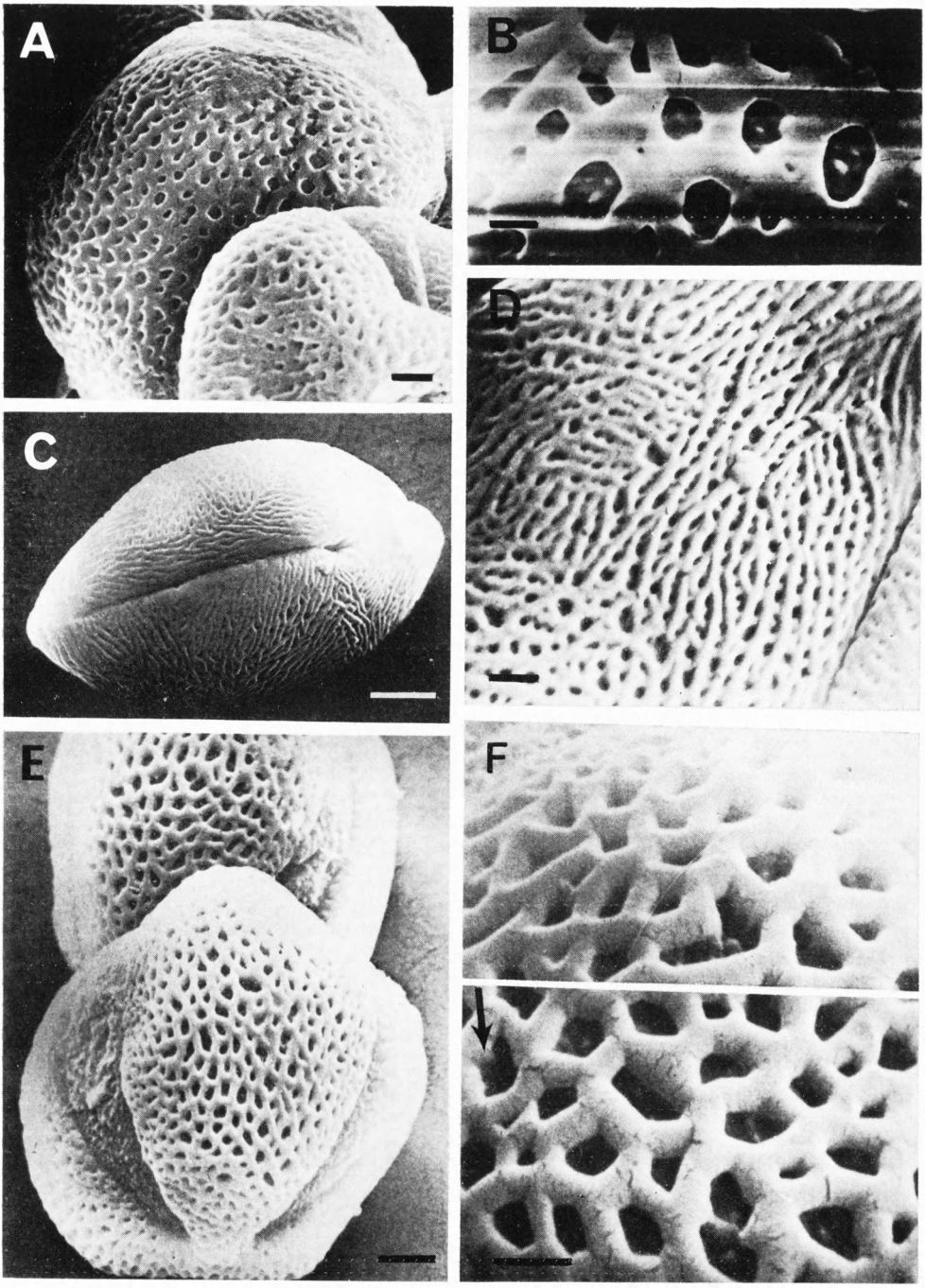


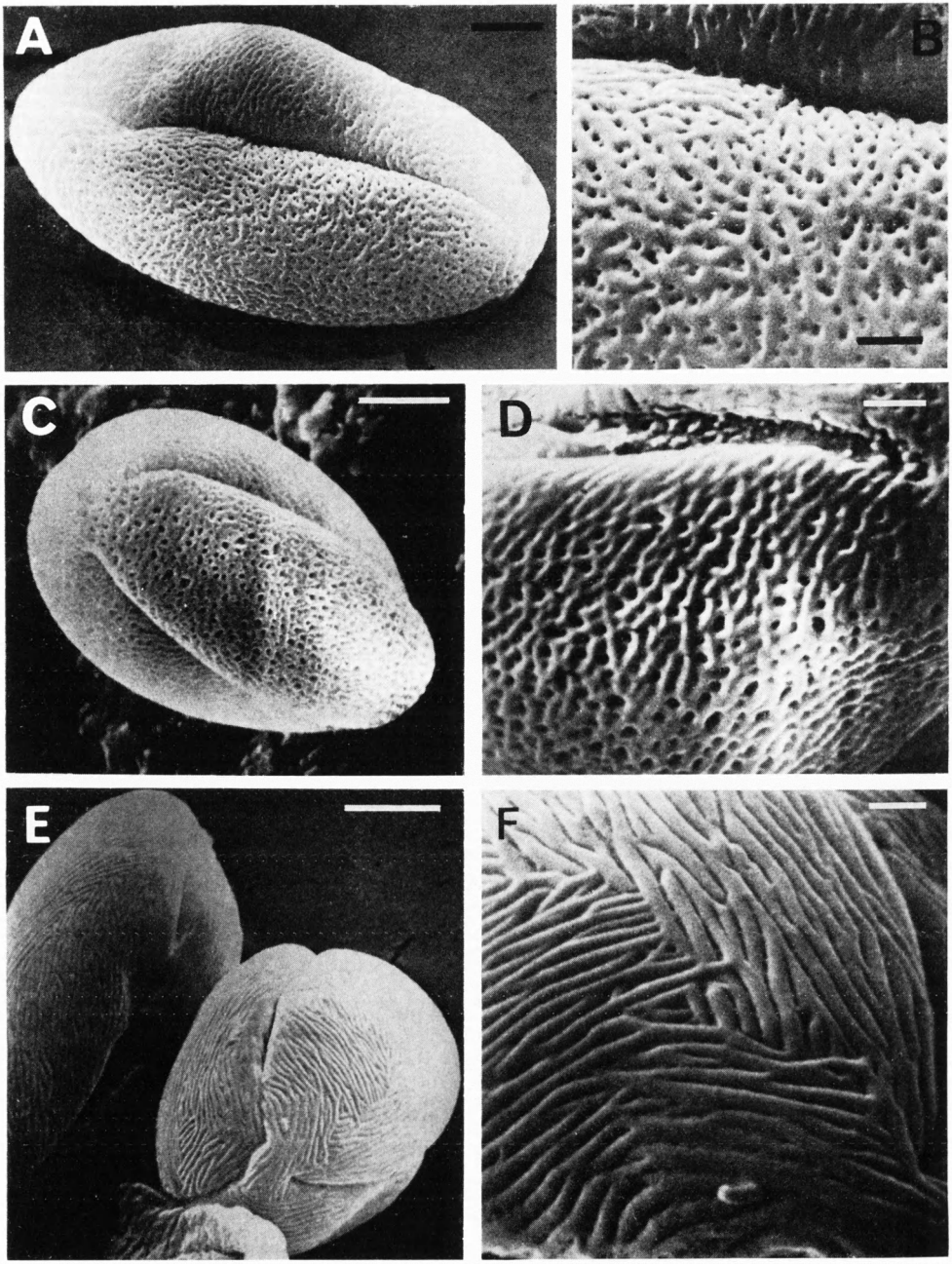
Fig. 2.

(Fig. 7). If, however, the height of spinules in the porate Campanuloidae pollen in general is compared, there is no definite association between this character and numbers of pores. Hence, the height of spinules can hardly be regarded as a character to be relied upon in the genus *Campanula* either. A reliable character is, however, known to be provided by the sexine ultrastructure, the specific patterning of the pollen grain. In *Campanula* a line of evolution can now be traced from the pattern of ridges to finger-like structures (Fig. 9). This line stands in direct relationship to a reduction of the inflorescence, illustrated by the following: (1) *C. rapunculoides:* sexine pattern: ridges; cymous flowers; and *C. persicifolia:* sexine pattern: ridges; 4—6 flowers; (2) *C. uniflora:* sexine pattern: ridges, top end bent upwards; flowers solitary; (3) *C. carpatica:* sexine pattern: finger-like structures; flowers solitary.

Ontogenetically all three sexine patterns probably develop from the slender structures of uniform thickness of the young pollen wall formed by branching of probacula (DUNBAR 1973 a). This mode of exine formation (i. e. branching of probacula) also known for the sexine formation in *Gerbera jamesonii* in Compositae (SOUTHWORTH 1970) may be regarded as an advanced development compared to the development leading to a more common type of sexine provided with protrusions, *Jasione montana,* for example (DUNBAR 1973 c). If and how the type of pattern of low relief reticulum is related to the other surface patterns in the porate Campanuloidae cannot be decided at present. It is of significance, however, that this pattern although slightly modified, also occurs on the surface of colpate pollen grains in the genus *Codonopsis* provided with 7—8 apertures (Fig. 9). Moreover it occurs together with the pattern of ridges in some species of *Wahlenbergia* (Fig. 9). It cannot be entirely excluded that this compound sexine pattern provides a transition between the two sexine patterns. A similar phenomenon may be due for the pollen grains of the genus *Adenophora* (Fig. 9) and *Edraianthus serpyllifolia* (DUNBAR 1975 Table 1), where the compound sexine pattern consists of protrusions and ridges. The 4-porate pollen grains of *Adenophora* may provide a transition between, on one hand the 3- and 4-porate *Campanula* pollen with ridges, and on the other hand the 6-porate pollen grains of *Githopsis specularioides,* the surface pattern of which consists of only protrusions (Fig. 9).

The delimition of the genera in Campanuloidae is still open for discussion. In the genus *Campanula* doubt is still justified with regard to its homogeneity (GADELLA 1966) despite the fact that many genera have been split off. The results of my investigation support this statement. While short ridges and basally divided spinules with distinct "roots" (Type 1a) is by far the commonest pattern in the genus, *C. americana* has a low relief reticulum resembling the pattern in some *Wahlenbergia* species. Moreover the spinules are very short and the base not too distinctly divided. As regards apertures *C. americana* differs markedly from all other species of the porate Campanuloidae, being the only one with pantoporate pollen grains. Although there is an increase in pore numbers in Campanuloidae the pores are equatorially arranged. *C. americana* is by virtue of its sexine pattern closer to some of the *Wahlenbergia* species and to *Prismato-*

Fig. 3. *Lobelia.* — A, B: *L. dortmanna.* — A: 3-colpate pollen grain with one colpus in view. Reticulate-striate sexine. C. ×2,000. — B: Detail of pollen wall with part of colpus. Muri or lirae connected by thin bridges at slightly lower level. C. ×4,200. Line c. 2 μ. — C, D: *L. anceps.* — C: 3-colpate pollen grain with two colpi visible. C. ×2,400. — D: Detail of pollen wall with part of colpus. Small granula on colpus membrane. Sexine reticulate



to reticulate-striate. C. ×8,500. Line c. 1 μ. — E, F: *L. zeylanica*. — E: Pollen grain in polar view. Two colpi anastomosing at pole. Sexine surface striate. C. ×2,500. — F: Part of pollen wall towards one pole. Long, branched lirae connected at lower level. C. ×7,600. Line c. 1 μ.

carpus than to the other *Campanula* species. GADELLA (1964) suggested that *C. americana* should be removed from the *Campanula* genus on both cytological and morphological evidence, and placed in the monotypic genus *Campanulastrum*.

The Asiatic plant *Platycodon grandiflorum* has 5—6-colporate pollen grains along with a sexine pattern closely resembling some species of *Campanula*, e. g. the European plant *C. persicifolia* (Type 1a). This similarity of fine structure points to a close affinity between the two genera in spite of distance of geographical distribution. Differences in type of aperture may indicate that the evolution from colporate to porate apertures has proceeded more slowly, being a more rigid character than the sexine pattern. In addition the porate nature of the pollen grains of *Campanula persicifolia* could be influenced by the European distribution of the plant in a temperate zone (see above). It could be expected that ontogenetically the pollen wall of *Platycodon* would develop in a similar way to *Campanula rapunculoides* or *C. persicifolia* with branching probacula.

In many *Campanula* species, in some *Wahlenbergia* species and in *Asyneuma, Phyteuma, Adenophora, Symphyandra* and *Platycodon*, for example, the basally divided spinules (DUNBAR 1973 a, b, c, GESLOT & MÉDUS 1974) are a conspicuous character. GESLOT and MÉDUS (1974) suggested that one of the basal ramifications of the spinules is in contact with more than one ridge in the hybrids of *Campanula rotundifolia* subsection *Heterophylla*. I have, however, not observed this feature in the present material. In contrary, several "roots" are observed to be connected to one ridge. It is of ontogenetical significance that where no ridges occur, the "roots" are in direct contact with the non-sculptured surface between protrusions for instance, and that there seems to be no direct contact between protrusions and "roots". In this case probably the ramified spinule-base develops from the lower part of the sexine, in both cases their future shape determined during the critical period of early wall formation while the protectum and probacula are still influenced by the primexine template. (DUNBAR 1973 a, c).

The different shapes of the pollen grains in Campanulaceae appear to be related to the type of the apertures. Mostly the porate pollen grains are spheroidal to oblate-spheroidal; the 3-colporate ones are frequently prolate, while those having 5 or more colpi increase equatorially in width along with the increase in aperture number. The shape of the pollen grains however, is changed after acetolysis, being more natural when air-dried.

As regards related families the tectum in *Scaevola* (Goodeniaceae) is perforated by puncta of uniform shape. This pattern is also recognized in Campanulaceae in most of the *Cyananthus* species. *Sphenoclea zeylanica* (Sphenocleaceae) on the other hand, has a smooth surface from which round protrusions of varying size arise, a pattern which has no relationship whatever with any genera in Campanulaceae. Goodeniaceae hence appears in some respects to be palynologically closer to Campanulaceae than is Sphenocleaceae. On the other hand the nature of the apertures (lalongated ora) in *Scaevola* pollen is not

Fig. 4. A, B: *Downingia elegans*. — A: 3-colporate pollen grain with one colpus visible. Striate sexine. C. ×1,600. — B: Part of pollen wall. Adjacent lirae connected at lower level. Flattened protrusions on lirae (arrow). C. ×15,000. Line c. 0.5 μ. — C, D: *Siphocampylus biserratus*. — C: Pollen grain in oblique polar view with two colpi visible. Colpi equatorially constricted. Striate sexine surface. C. ×2,000. — D: Detail of pollen wall with part of colpus. Protrusions on colpus membrane. Lirae connected at lower level. C. ×5,000. Line c. 2 μ. — E, F: *Pratia angulata*. — E: 3 colporate pollen grain with two colpi visible. Striate sexine. ×2,200. — F: Detail of pollen wall. Lirae closely-placed, branching to become again fused. C. ×7,200. Line c. 1 μ.

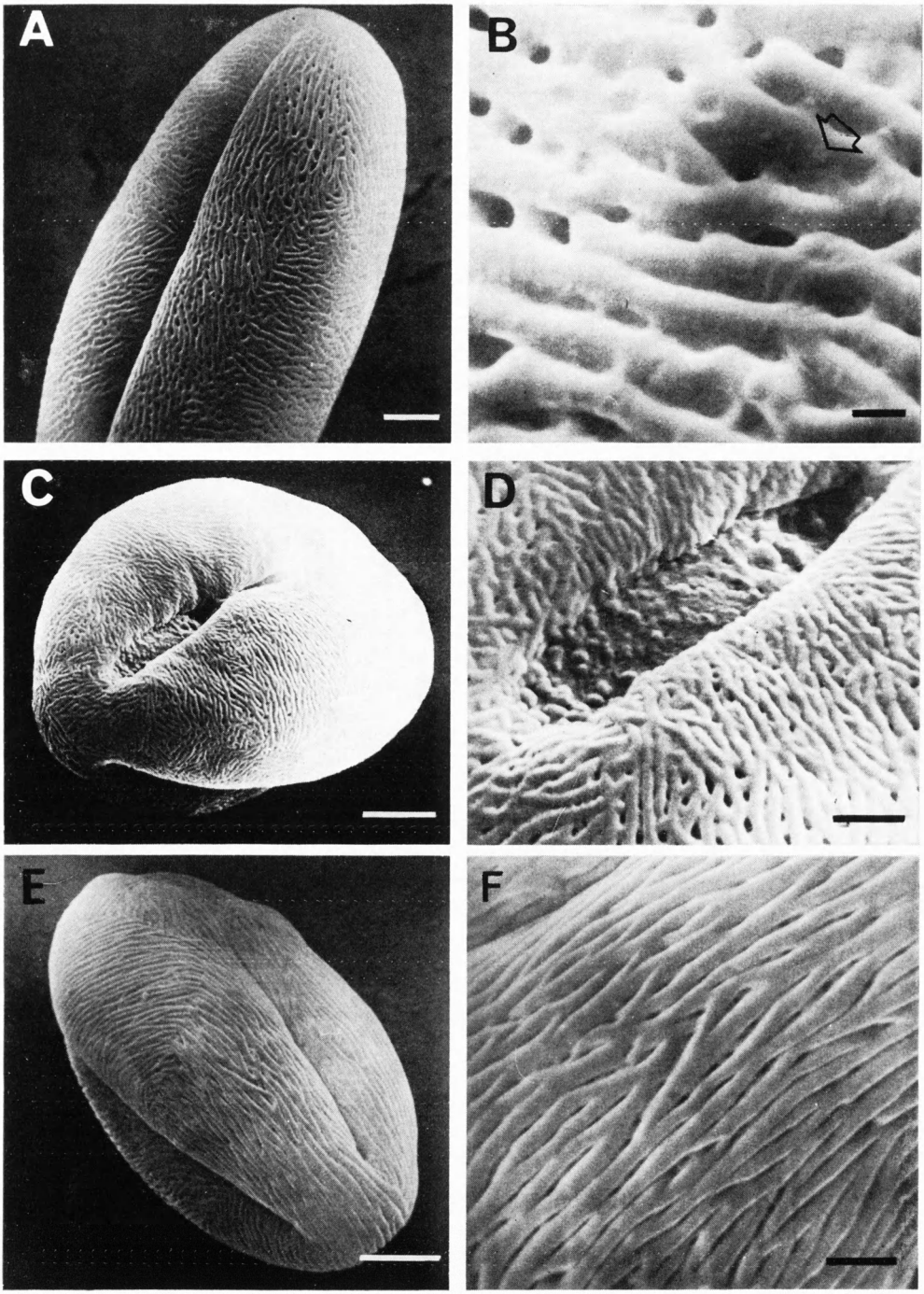


Fig. 4.

seen in any pollen grains of Campanulaceae, nor is the considerable variation in the thickness of the sexine also described by DUIGAN (1961) in *Scaevola ramosissima* (Pl. XVI, Fig. 3) and *Goodenia pinnatifida* (Pl. XV, Fig. 20). Finally it should be noted that JENSEN et al. (1975) found an essential difference between the plants of the two families Goodeniaceae and Campanulaceae.

ACKNOWLEDGEMENTS

I am indebted to Professor O. HEDBERG and Dr M. THULIN for valuable discussions and to Dr S. NILSSON for valuable discussions and for reading the manuscript. I wish to thank Mrs M. GREENWOOD PETERSSON for correcting the English and the staff of the Palynological Laboratory for skilful technical assistance, and I wish to express my sincere thanks to the Directors and the Curators of the various Herbaria for allowing me to sample polleniferous material and for sending specimens.

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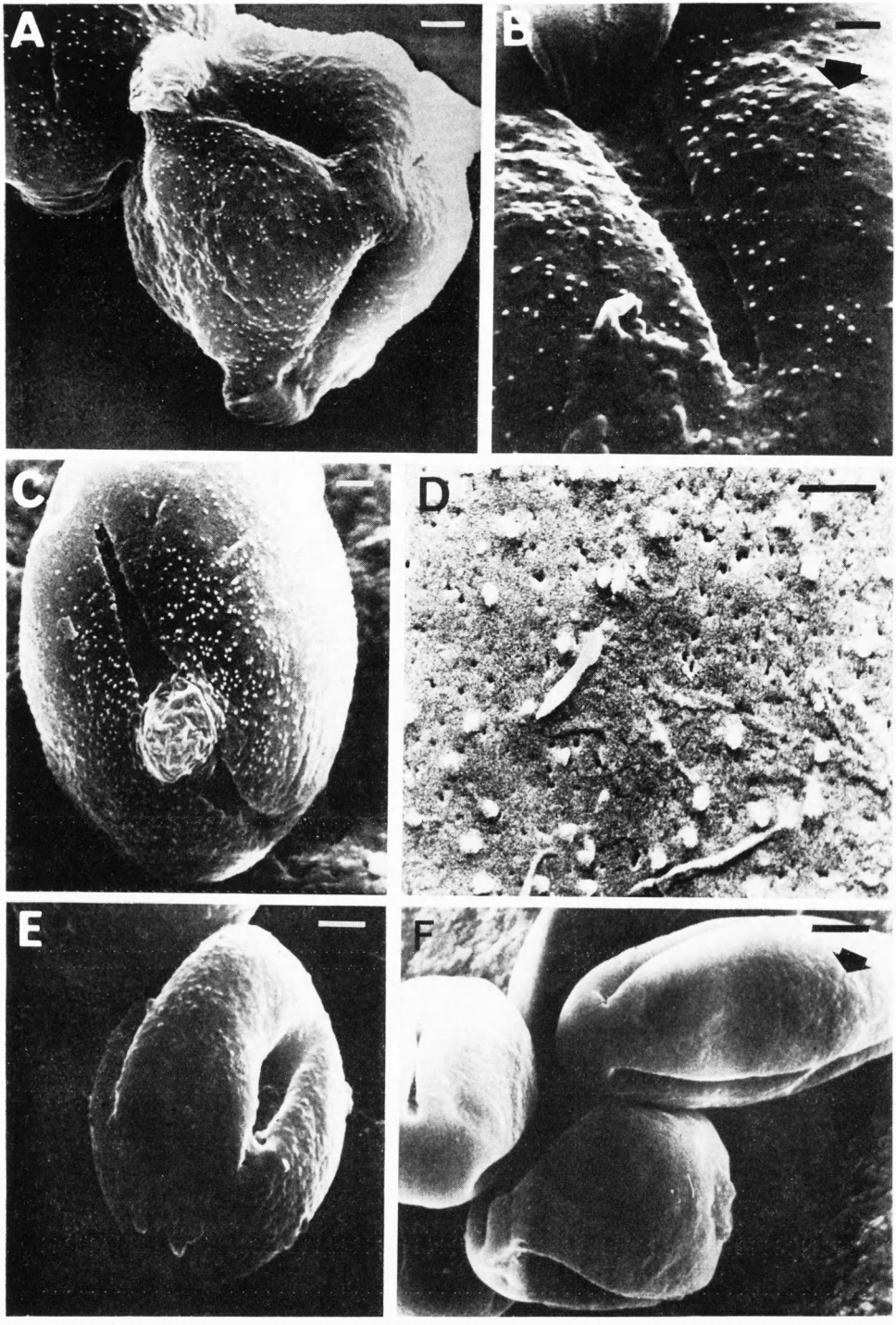
APPENDIX. SPECIMENS INVESTIGATED

Campanulaceae, Cyphioidae

Cyphia assimilis SCHEEPERS, S. Africa 1967, J. SCHEEPERS s. n. (S). — *C. bulbosa* L., Cape Province 1938, E. WALL s. n. (S); Berg., Cape Province 1911, R. E. FRIES s. n. (UPS).

Fig. 5. A—D: *Scaevola*. — A, B: *S. koenigii*. — A: 3-colporate pollen grain. Sexine with very small spinules. C. ×1,300. — B: Detail of pollen wall with part of colpus, see also Fig. 6 A. Between spinules puncta of uniform shape visible (arrow). C. ×3,200. Line c. 2 μ. — C, D: *S. cerastifolia*. — C: 3-colporate pollen grain showing one compound aperture. Curved, irregular structures on operculum. Pollen wall covered with small, irregularly distributed spinules. C. ×1,200. — D: Part of pollen wall with puncta in tectum. C. ×5,500. Line c. 2 μ. — E: *Sphenoclea zeylanica*. 3-colporate pollen grain. Sexine with rounded protrusions of different size. C. ×3,000. Line c. 2 μ. — F: *Cyphia bulbosa*. 3-colporate pollen grains. Sexine almost smoth; finely granular pattern however traceable (arrow). C. ×800. Line c. 10 μ.


A
B
C
D
E
F

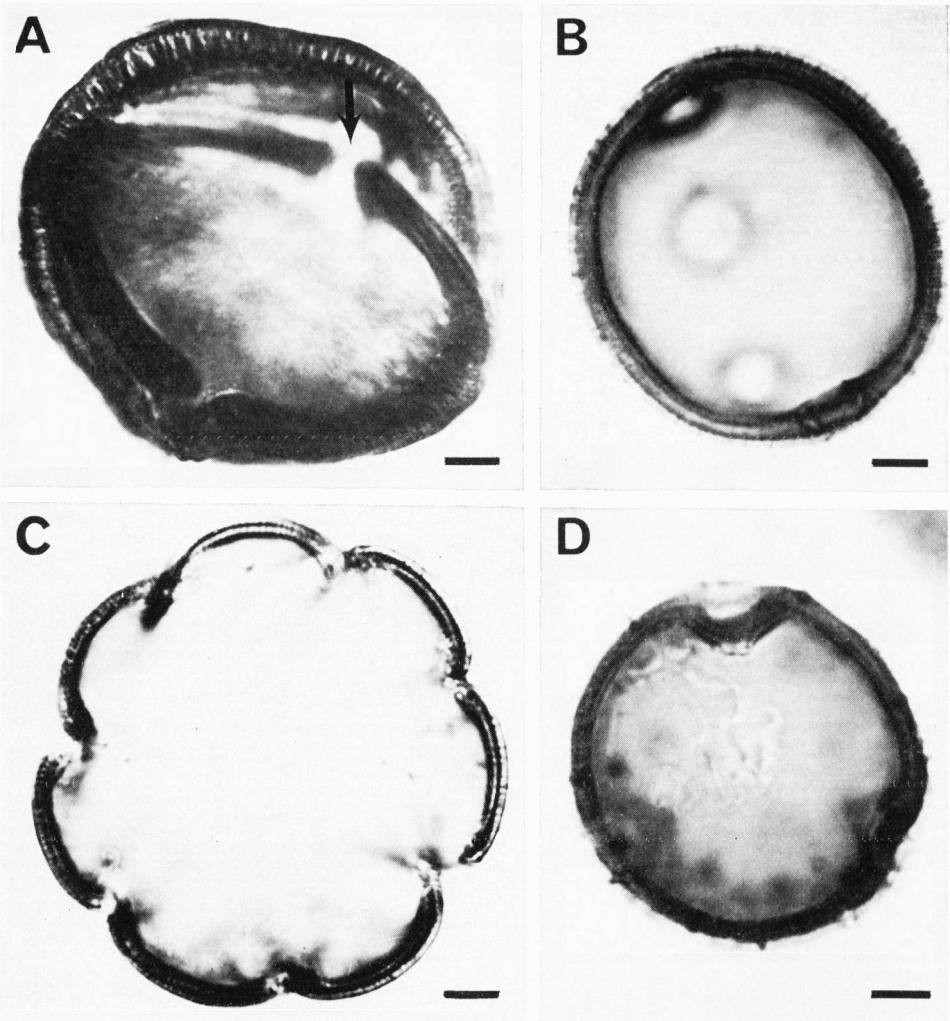


Fig. 6. A: *Scaevola koenigii*. Two of the three compound apertures are shown. Note lalongate ora (arrow), and thick layer of exine with bacula, exine varying in thickness with thickest areas below pole. C. ×1,500. — B: *Githopsis specularioides*. Four of the 6 equatorially arranged pores are shown. Surface closely beset with spinules. C. ×1,500. — C: *Codonopsis handeliana*. Equatorial view of 7-colpate pollen grain with relatively thin exine layer. C. ×1,500. — D: *Campanula pyramidalis*. 3-porate pollen grain. Two of the pores visible. C. ×1,500. All pollen grains are acetolysed.

Cyphocarpus innocuus SAND., Chile 1956, C. JILES 3092 (CONC). — *C. psammophilus* RICARD, Chile 1971, Marticorena, RODRIGUEZ & WELDT 1766 (CONC). — *C. rigescens* MIERS, Chile 1973, Marticorena, MATTHEI & QUEZADA 472 (CONC).

Nemacladus rubescens GREENE, California 1949, KECK, BAKER, DANSEREAU & NORDENSKIOLD 6241 (UPS).

Parishella californica GRAY, California 1957, C. SMITH 5452 (S).

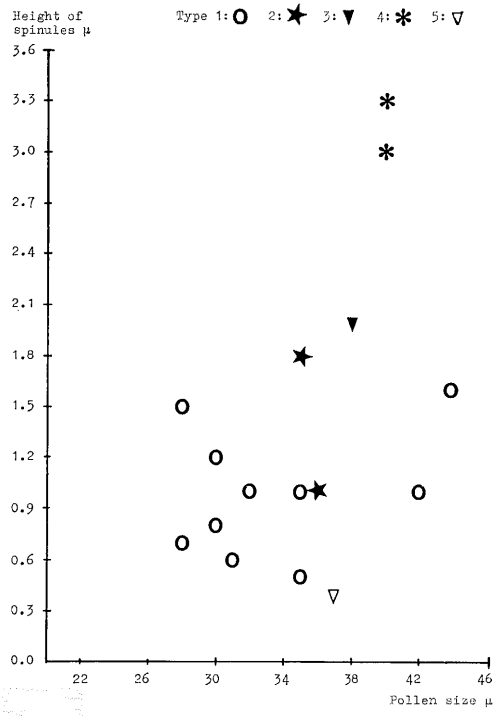


Fig. 7. Height of spinules in relation to the size of pollen grains and the pattern of sexine in *Campanula*. A change in the surface pattern along with a decrease in the height of spinules is obvious. The types of surface pattern (see DUNBAR 1975 p. 76) are indicated by the symbols 1—5.

Lobelioidae

Downingia elegans (DOUGL.) TORR., cult. Hort. UPS. ex Hort. Berg. & (GOET) (UPS).

Grammatotheca bergiana (CHAM.) PRESL, South Africa 1972, K. BREMER 571 (UPS).

Isotoma anemonifolius KNIGHT, Australia 1944, M. CLEMENS s. n. (S).

Laurentia carnosula (HOOK. & ARN.) GRAY, U. S. A. 1952, H. MASON s. n. (S); U. S. A., Wyoming 1963, C. L. & M. W. PORTER 9412 (UPS). — *L. michelii* A. DC., Spain 1960, D. HUMMEL det. C. A. TORÉN (S). — *L. petraea* (F. v. M.) WIMM., cult. Hort. UPS. ex Adelaide, Australia (UPS).

Lobelia anceps L. FIL., Kenya 1970, M. THULIN 302 (UPS). — *L. dortmanna* L., Sweden 1885, C. REUTERMAN s. n. (S-MB). — *L. zeylanica* L., Ceylon 1974, H. & H. E. WANNTORP 2857 (S-MB).

Palmerella debilis GRAY var. *serrata* GRAY, U.S.A., Senor Canyon, 1949, H. POLLARD s. n. (S).

Pratia angulata HOOK. FIL., New Zealand 1949, C. SKOTTSBERG s. n. (S).

Siphocampylus biserratus (CAV.) A. DC., Peru 1940, E. ASPLUND 11286 (UPS).

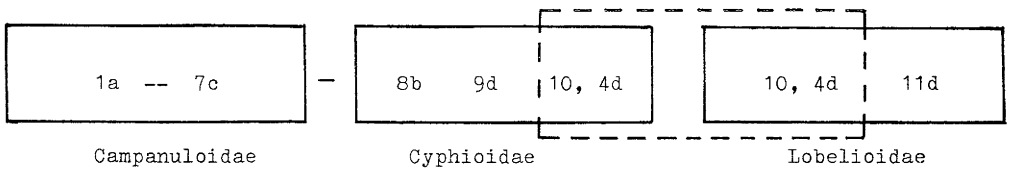


Fig. 8. Schematical, hypothetical representation of relationships between the subfamilies of Campanulaceae. For types of sexine pattern, indicated by numbers and letters, see DUNBAR (1975 pp. 76, 77).

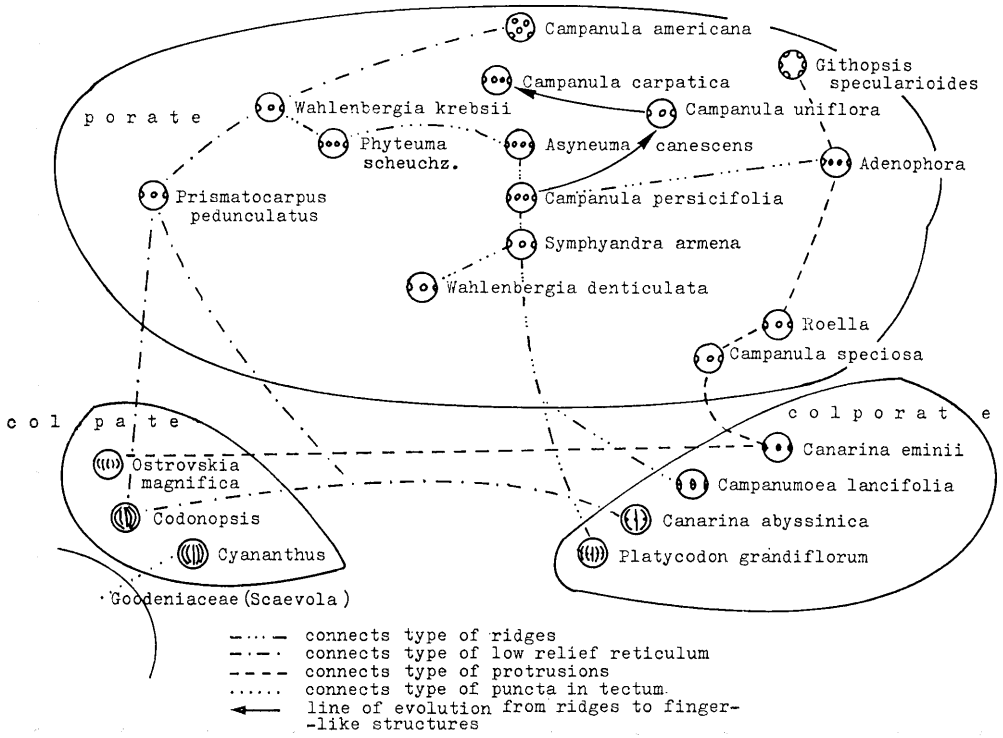


Fig. 9. Similarities between some of the genera and species of Campanuloidae (DUNBAR 1975 Table 1), and a possible line of evolution of the sexine pattern. The pollen grains are represented schematically, the porate above the colpate-colporate and the 6—12-porate above the 3—4-porate ones. One pattern of sexine ultrastructure between spinules/verrucae is demonstrated at some of the main levels of apertural evolution, two patterns at each level. The fourth shows a relationship between Campanulaceae (Campanuloidae) and Goodeniaceae.

Goodeniaceae

Scaevola cerastifolia SKOTTSB., Hawaiian Islands 1948, F. FAGERLIND s. n. (S). — *S. koenigii* VAHL, Ceylon 1974, H. & H. E. WANNTORP 2850 (S-MB).

Sphenocleaceae

Sphenoclea zeylanica GAERTN., Madagascar 1954, P. MORAT 799 (P).

A System of Classification of the Angiosperms to be Used to Demonstrate the Distribution of Characters

Rolf Dahlgren

DAHLGREN, R. 1975 07 08. A system of classification of the angiosperms to be used to demonstrate the distribution of characters. — Bot. Notiser 128:119—147. Lund. ISSN 0006-8195.

A system of classification of the angiosperms is presented down to family level. The angiosperms are divided into 34 superorders, 27 in the dicotyledons and 7 in the monocotyledons. They are: Magnolianae, Rafflesianae, Ranunculanae, Nymphaeanae, Rutanae, Aralianae, Asteranae, Dillenianae, Thymelaeanae, Violanae, Celastranae, Solananae, Campanulanae, Hamamelidanae, Rosanae, Proteanae, Myrtanae, Saxifraganae, Balanophoranae, Plumbaginanae, Primulanae, Theanae, Cornanae, Gentiananae, Loasanae, Lamianae and Caryophyllanae — and Alismatanae, Lilianae, Typhanae, Zingiberanae, Commelinanae, Arecanae and Aranae.

Short diagnoses of the superorders and orders are given, and the families in each order are enumerated. The system deviates considerably from other current systems.

The system is presented graphically as a phylogenetic tree in transection, each order being represented by a branch; the thickness of this is roughly proportional to the number of species in the order. In determining the relative position of the orders in the system as many characters as possible have been used, the similarities having been weighed against dissimilarities.

In forthcoming articles the distribution of a number of presumably important characters will be placed in their respective positions in this system.

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The system presented here is based on the distribution within the families and higher taxa of the angiosperms of a considerable number of characters: chemical as well as embryological, anatomical, cytological, palynological and in particular gross morphological characters.

It has been devised progressively without undue consideration being paid in the first stages to any particular of the previous systems, and constructed so as to account for trends in variation between main groups. In a number of cases the position of a family may coincide with its position in another system; in other cases there is no agreement with the position in any other system. Admittedly, where evidence has been weak or about equal for two or more alternatives, particular consideration has been paid to the position of the group in current systems, for instance in those proposed by THORNE 1968, TAKHTAJAN 1969, CRONQUIST 1968, MELCHIOR 1964 and HUTCHINSON 1973. Recent convincing arguments presented in the literature have been accepted as far as possible. Needless to say, the classification proposed here is preliminary in particular as regards small, little-known families, but it may nevertheless serve its purpose.

The aim in presenting this system is

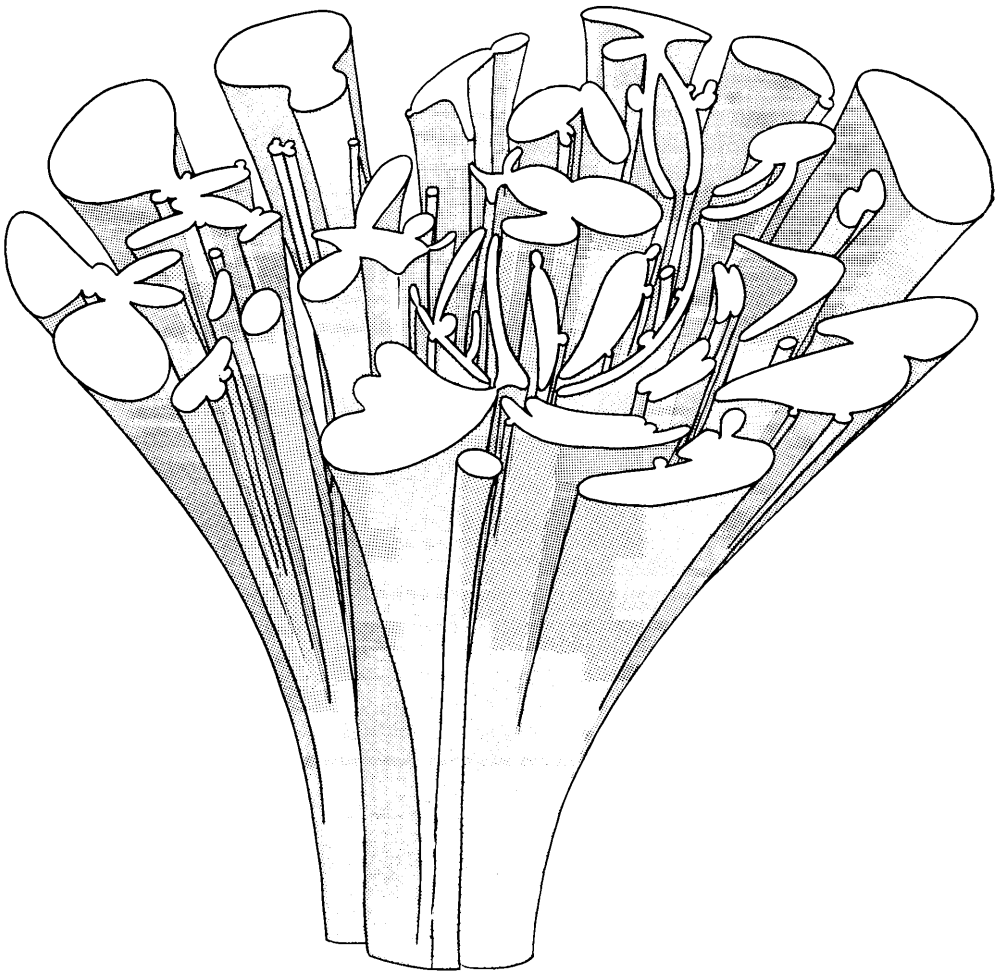

Fig. 1. The present angiosperm system pictured as the transection of an imaginary phylogenetic tree. Details of connections between branches should not be considered as having great significance.

twofold. The prime consideration has been the graphic representation of the angiosperms in the form of a two-dimensional model or "map" (Fig. 2), on which the distribution of selected characters can be demonstrated by shading. This diagram represents an imaginary phylogenetic tree (Fig. 1) in transection. — Secondly, having demonstrated the occurrence of a considerable number of characters the aim is to use the accumulated evidence to improve and reconstruct the system. Certain deficiencies in this system will inevitably present themselves as the repeated occurrence of spots in the same place on the "maps".

Among the numerous problems encountered, some are connected with the circumscription of families. Where heterogeneity in formerly broadly circumscribed

families is great, such as in Saxifragaceae s. lat. and Liliaceae s. lat., I have preferred to split. To recognize smaller entities sometimes placed within these families as families themselves is a useful means of taking into account their mutual differences and the fact that some should possibly be placed at a distance from the others. In dividing up the two collective families mentioned and the related families I have been influenced by two papers by HUBER (1963 and 1969), although I have not adhered in detail to the classification proposed in them. — I have not found it possible to place in my system all the small and little-known families recognized by AIRY SHAW (1973). Many of the observations by AIRY SHAW have been taken into consideration, but knowledge is often very incomplete. The status and position in the system of the small families, it is hoped, will eventually be made clearer in future monographic studies.

The short descriptions given below are not meant to be exhaustive in any way, nor are they meant to be consistent by giving the same characters for each group. The intention is merely to present some of the most characteristic features of each superorder and order. The data are compiled with the help of a number of textbooks and separate articles. Among the most important of the former are METCALFE & CHALK 1950, ERDTMAN 1952, HEGNAUER 1963—1973, DAVIS 1966 and AIRY-SHAW 1973.

THE ANGIOSPERM SYSTEM DEPICTED AS THE TRANSECTION OF AN EVOLUTIONARY TREE

To present orders or families of angiosperms as a two-dimensional model is no innovation. Where this has been done the relative position of the groups has been determined by the degree of mutual similarity. One disadvantage is that the reader, and sometimes even the constructor of the system, has been inclined to look upon the system of groups of now living plants as an evolutionary tree, where some groups are regarded as descendants of others in the diagram. This applies in particular to HUTCHINSON 1969. Evidence for this type of evolutionary tree is usually sparse or lacking. The present Magnoliales in particular is often regarded as an ancestral group, other groups being frequently indicated as shooting out of it like lateral buds.

The introduction here of a third dimension, time, in Fig. 1 is intended to prevent any such misinterpretation. It must be said that practically nothing is known about the course of evolution in the angiosperms, so that the tree must be presented in such a generalized form that no evolutionary details are shown. Even the two-dimensional representation of the angiosperms involves a tremendous number of problems.

Two principles are adhered to:

(1) *The orders are represented as imaginary transections of branches roughly proportional in size to the number of species in the order,* although the size of the smallest groups has been sufficiently exaggerated to allow details to be clearly visible.

(2) *The orders exhibiting the greatest degree of similarity are placed closest together.* In the hypothetical ideal state the many similarities and differences when judged in conjunction would give some measure of the distance between the groups. For practical reasons, however, a numerical estimation is not possible. Firstly, only a fraction of the possibly important characters are known in a sufficient number of plant groups (and very seldom in a sufficient number of species in each group), and only a certain number of the characters can be presented in a diagram and used or evaluated in phylogenetic calculations. Secondly, not all characters are of equal phylogenetic value, a fact that should receive more consideration

in numerical taxonomy. And to what extent is it possible to give an adequate relative measure or factor for each character? One and the same difference may be of great taxonomic importance in one part of the system but of little significance in another. It is also a well-known fact, for example, that conspicuous morphological effects are sometimes caused by comparatively small genetic changes. Further, many similarities are due to convergence (see DAHLGREN 1970 and 1971).

In the course of evolution the different characters have probably developed along entirely independent lines of evolution from a common primitive ancestor. Thus certain conservative ("ancient", "primitive") characters may have persisted in some descendants, others in other descendants.

Is it then at all possible to construct a reasonably functionable two-dimensional diagram for the orders and families of angiosperms?

The answer is presumably in the negative. To place groups in exactly those positions that reflect their affinities becomes increasingly difficult when consideration has to be taken to the number of species in each group. For example, large "bubbles" may prevent other, related groups from meeting in the model, and small groups cannot be extended so as to approach sufficiently close to other groups showing great similarity. In any system, it seems, some families or orders apparently appropriately placed at the same time show several perhaps phylogenetically important similarities to one or more remotely placed group which in turn appears to occupy an appropriate position.

It is imperative that botanists should persevere with the construction of systems of the type outlined above or of other types to survey the many groups of angiosperms. The need is pedagogic rather than scientific.

After all, a two-dimensional model offers greater scope for the expression of affinities than do linear sequences of families and orders. Moreover, as the orders are illustrated as transections it is possible to extend these in any direction so as to meet demands of affinities between groups. The transections may be circular, linear or even slightly branched. The shape in these cases does not necessarily have any connections with the relationships of the families *within* the order, but aims at bringing the orders into a position that reflects their affinities.

Abbreviations used in text:

alt.: alternatively	incl.: including
esp.: especially	occas.: occasionally
excl.: excluding	usu.: usually

DICOTYLEDONEAE

Magnolianae

Mainly woody; vascular elements variable, primitive to advanced; leaves mostly alternate, usu. exstipulate; cells containing ethereal oils present in most families; flowers hypo- to epigynous; stamens often flat; microsporangia often below stamen apex; pollen grains binucleate, usually with 1, 2 or no apertures, seldom 3-colpate; apocarpy dominant; ovules mostly anatropous, usu. crassinucellate, bi- (seldom uni-)tegmic; integuments thick; endosperm usu. cellular ab initio; benzylisoquinoline alkaloids usu. present; ellagic acid lacking.

Magnoliales: woody; leaves usu. exstipulate; stomata often paracytic; vessels occas. absent; sieve tube plastids usu. with protein; nodes usu. 3- to multilacunar; flowers well-developed, acyclic or usu. spirocyclic, generally not with urceolate receptacle, often 3-merous; microsporangia usu. below stamen apex; pollen grains usu. tectate and with one or no aperture; apocarpy dominant; carpels several to numerous; stigma often decurrent; endosperm formation usu. cellular; plants sometimes rich in tannins. — *Winteraceae, Degeneriaceae, Himantandraceae, Magnoliaceae, Annonaceae, Cannellaceae, Myristicaceae, Eupomatiaceae.*

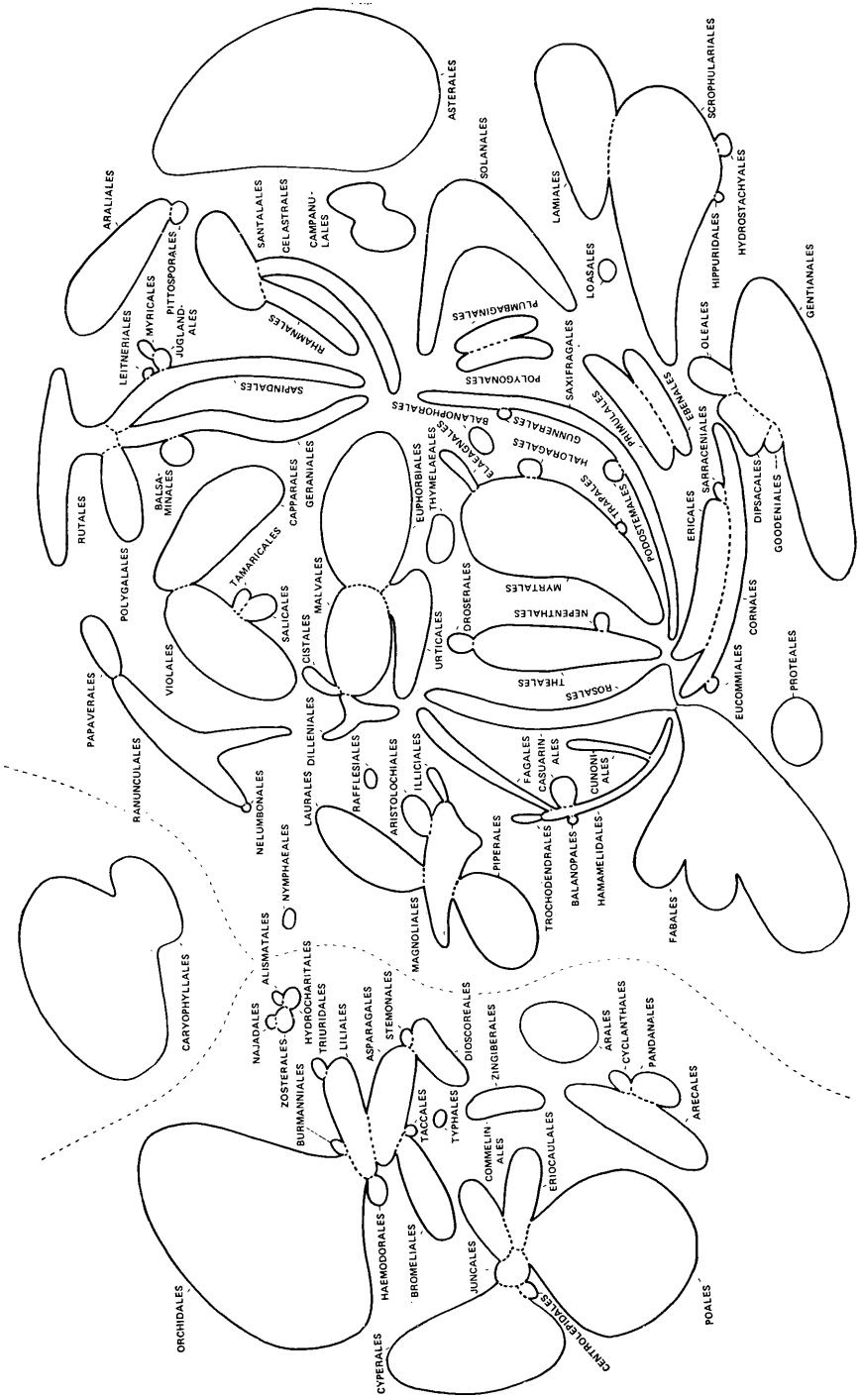

Fig. 2. The present angiosperm system (cf. Fig. 1). The size of each order roughly corresponds to its number of species. Orders with great similarity are placed next to each other as far as possible. Further explanations in the text.

Laurales: usu. woody; mainly exstipulate; stomata para- or anomocytic; nodes usu. unilacunar; perforations of vessels variable; sieve tube plastids usu. with starch (except in Calycanthaceae); flowers well developed; receptacle often urceolate; perianth often 3-merous; microsporangia usu. on stamen apex, often opening by 2—4 valves; pollen grains usu. tectate and inaperturate or occas. with 1 or 2 apertures; carpels one or several; ovules one or few per carpel, bitegmic; endosperm cellular or nuclear ab initio, seeds often without endosperm. — *Monimiaceae* (incl. *Siparunaceae* and *Atherospermataceae*), *Trimeniaceae, Lauraceae, Idiospermaceae, Austrobaileyaceae, Gomortegaceae, Amborellaceae, Calycanthaceae, Hernandiaceae, Lactoridaceae, Chloranthaceae, Gyrocarpaceae* (position of the last three families not quite certain).

Aristolochiales: largely herbs, but also woody, often climbers; medullary rays broad; stomata anomocytic; vessels with simple perforations; sieve tube plastids with protein; flowers cyclic, usu. epigynous; perianth double or usu. simple, in latter case syntepalous, usu. zygomorphous; stamens free or usu. united to a gynostemium; pollen grains tectate or occas. semitectate, inaperturate or occas. with 1—many apertures; (apocarpy or) usu. syncarpy; ovules numerous, bitegmic; endosperm formation cellular; fruit usu. capsular; seeds rich in fatty oils; cells with ethereal oils and benzylisoquinoline alkaloids (magnoflorin type) characteristic. — *Aristolochiaceae.*

Piperales: shrubs, climbers or mostly herbs; leaves alternate, simple, entire, often carnose; stipules lacking or small and united with petiole; atactostele; vascular strands scattered or in 1—2 whorls; vessels usu. with simple perforations; flowers in spike or spadix, uni- or bisexual, naked; stamens 1 or more; anthers opening by splits; pollen grains tectate, without or with one aperture; carpels 1—5; pistil often pseudomonomerous, syn- or paracarpous, usu. with one basal or subbasal, uni- or bitegmic ovule; embryo sac usu. tetrasporic; endosperm cellular or nuclear ab initio; seeds with richly developed perisperm containing starch; ethereal oils in all parts; tannins lacking. — *Saururaceae, Piperaceae* (incl. *Peperomiaceae*).

Illiciales: woody, often lianes; leaves alternate (to whorled), exstipulate; stomata anomocytic; hairs lacking; vessels with scalariform perforations; sieve tube plastids with starch; idioblasts with ethereal oils in all parts; flowers acyclic or spirocyclic, uni- or bisexual; perianth not clearly differentiated into sepals and petals; stamens 4 to numerous, often broad, occas. fused to a ± globose synandrium; pollen grains semitectate and 3- or 6-colpate, often syncolpate; carpels 5 to numerous, free, each with 1—5 ovules; endosperm cellular ab initio; carpels either forming separate fruits or a collective fruit; seeds rich in endosperm, with oil; plants poor in tannins. — *Illiciaceae, Schisandraceae.*

Rafflesianae

Carnose, chlorophylless parasites invading hosts with cell rows or cork-clad cell masses; scale-like leaves usu. present; vascular system often lacking; atactostele in Hydnoraceae, vessels here with simple perforations; stomata abnormal; flowers bi- or unisexual; floriferous shoots differentiated endogenously; perianth simple; synandrium or ring-like androecium on inner side of tepals; pollen grains inaperturate or with 2—3 apertures, binucleate; female flowers epigynous; carpels 3—8; usu. paracarpy; placentation parietal; ovules numerous, tenuinucellate, bi- or unitegmic; endosperm formation cellular or nuclear; embryo little differentiated; plants tanniniferous.

Rafflesiales: *Rafflesiaceae, Hydnoraceae.*

Ranunculanae

Herbaceous or woody; atactostele common in herbs; vessels with simple perforations; leaves usu. exstipulate; stomata usu. anomocytic; flowers hypogynous; perianth usu. 5-, 3- or 2-merous, honeyleaves common; stamens usu. numerous, in a spiral, developing centripetally; pollen grains usu. 3-colpate, binucleate; apocarpy to paracarpy; carpels numerous to one; ovules uni- or bitegmic; usu. crassinucellate or pseudocrassinucellate; endosperm formation usu. nuclear; no perisperm but endosperm usu. present; cells with ethereal oils lacking; benzylisoquinoline alkaloids usu. present; tannins and many polyphenolics, such as ellagic acid lacking.

Nelumbonales: aquatic herbs; rhizome with laticiferous ducts; leaves long-petiolate, peltate; atactostele; vessels with scalariform perforations present in rhizome; flowers large; tepals in spiral; stamens numerous, linear; microsporangia below stamen apex; pollen grains 3-colpate; receptacle obconical, on upper side with monocarpellate cavities; each carpel with 1 subapical, bitegmic, crassinucellate ovule; endosperm cellular ab initio; nutlets one-seeded; endo- and perisperm lacking in seed; benzylisoquinoline bases recorded in the group. — *Nelumbonaceae.*

Ranunculales: woody or often herbaceous; leaf base often dilated; atactostele with scattered vascular strands common in herbs; stomata usu. anomocytic; flowers actinomorphous to median-zygomorphous, hemicyclic to cyclic; perianth in one to several whorls, often 3- or 5-merous; petaloid staminodes with basal nectary often present; stamens often many, sometimes in whorls of 3; anthers opening by splits or valves; apocarpy dominant, sometimes syncarpy occas. combined with pseudomonomery; carpels 1 to numerous; ovules usu. crassi- or pseudocrassinucellate, uni- or bitegmic; endosperm usu. nuclear (seldom cellular) ab initio; seeds rich in endosperm; benzylisoquinoline alkaloids of rather advanced types common; cyanogenic compounds occasional. — *Lardizabalaceae, Menispermaceae, Sargentodoxaceae, Kingdoniaceae, Ranunculaceae, Circaeasteraceae, Hydrastidaceae, Glaucidiaceae, Podophyllaceae, Nandinaceae, Berberidaceae* (incl. *Leonticaceae*).

Papaverales: usu. herbaceous; atactostele with one whorl of vascular strands common; laticiferous sacs or ducts present; flowers 3- or usu. 2-merous, tri-, bi- or transversally monosymmetric, in determinate or indeterminate inflorescences; sepals 3 or 2, often caducous; petals 2+2 or 3+3; stamens numerous or 2+2, or derived in number from 2+2; anthers opening by splits; gynoecium paracarpous, of 2 to numerous carpels; placentas parietal; stigmas carinal or (and) commissural; ovules crassinucellate, bitegmic; endosperm nuclear ab initio; seeds with endosperm rich in oil; with advanced types of benzylisoquinoline alkaloids. — *Papaveraceae, Hypecoaceae, Fumariaceae.*

Nymphaeanae

Aquatic herbs; atactostele; vessels lacking; leaves entire to dissected; intravaginal or lateral stipules occas. present; flowers spirocyclic, hypo- or epigynous; perianth often 5- or 3-merous; stamens 6 to numerous, developing centripetally, usu. flat; thecae often lateral, below stamen apex; pollen grains tectate, with one aperture, binucleate; apocarpy to (pseudo-) syncarpy; gynoecium often enclosed by receptacle; stigmas often decurrent; placentation laminal; ovules bitegmic (except in Ceratophyllaceae), crassinucellate; endosperm formation cellular, helobial or occas. nuclear; seeds with endo- and perisperm and with small embryo; tannins (and gallic acid, sometimes also ellagic acid) present; benzylisoquinoline alkaloids lacking.

Nymphaeales: *Cabombaceae, Nymphaeaceae* (incl. *Euryalaceae*), *Barclayaceae, Ceratophyllaceae.*

Rutanae

Woody or herbaceous; leaves compound or simple, generally exstipulate; vessels usu. with simple perforations; wood, bark and leaves often with resins or ethereal oils in cavities, ducts or glands; flowers hypogynous and often 5-merous; choripetaly or apetaly; obdiplostemony common, also diplo- or haplostemony; pollen grains mostly binucleate (except, e. g. in many Geraniales and some Rutales); intra- or extrastaminal disc often present; carpels usu. 2—5; apocarpy to syncarpy; ovules usu. anatropous, bitegmic (except in Juglandales and Myricales in particular), and crassinucellate (except in Balsaminales and many Geraniales); endosperm formation usu. nuclear (in some groups intermediate); tannins usu. rich; benzylisoquinoline alkaloids only in some Rutaceae; saponins common in many families.

Rutales: woody, leaves usu. alternate, exstipulate; bark and leaves often with secretory cells, ducts, or cavities with resin and ethereal oils; flowers hypogynous, actinomorphous, usu. with 5 sepals and 5 petals; androecium haplo- or usu. obdiplostemonous; filaments free or united to a tube; annular intrastaminal disc typical; carpels usu. 2—5;

apo- or eusyncarpy; each carpel usu. with 1—2 epitropous (occas. atropous or campylotropous), usu. bitegmic ovules; seeds with or without endosperm; triterpenoids and saponins with pentacyclic terpene acids common; condensed tannins and other phenolics often very rich; ellagic acid rare; tendency to accumulate silicic acid; alkaloids common; benzylisoquinoline alkaloids in some genera of Rutaceae. — *Rutaceae* (incl. *Flindersiaceae*), *Cneoraceae, Surianaceae, Simaroubaceae, Kirkiaceae, Burseraceae, Meliaceae.*

Polygalales: mainly woody; leaves usu. simple, opposite or alternate, often stipulate (always in Malpighiaceae); secretory cells and lysigenous secretion cavities or ducts common; inflorescence usu. a raceme; flowers usu. zygomorphous; sepals basally nectariferous; petals usu. 5 or 3, free or occas. fused with filaments; stamens 1—5 or 6—12, in Malpighiaceae usu. 5+5 (obdiplostemony); filaments often connate; anthers sometimes with pores; pollen grains usu. binucleate, occas. trinucleate; eusyncarpy; carpels (1—)2—3, usu. with one ovule; embryo sac mono- or tetrasporic; seeds usu. with endosperm; saponins with triterpene sapogenins characteristic; condensed tannins and quebrachitol and polygalitol frequent; galli- and ellagi-tannins lacking. — *Malpighiaceae, Trigoniaceae, Vochysiaceae, Xanthopyllaceae, Polygalaceae, Krameriaceae, Emblingiaceae* (position uncertain).

Sapindales: usu. woody; stipules present or absent; mucilage cells and ducts or cells with balsam (mono- and triterpenes), saponins or tannins common; flowers usu. ± zygomorphous; sepals usu. 5, petals 5, often clawed; haplo- or often diplostemony; stamens free, some often reduced; carpels usu. 2—3, free or usu. ± fused (eusyncarpy); ovules apotropous (cf. Rutales), usu. bitegmic; seeds occas. arillate; endosperm usu. lacking and embryo large, rich in oils, protein or starch; condensed tannins usu. rich; occas. ordinary (e. g. ellagi-) tannins; triterpene saponins common, also quebrachitol and polygalitol. — *Coriariaceae, Anacardiaceae* (incl. *Pistaciaceae*), *Podoaceae, Julianaceae, Akaniaceae, Uapacaceae* (position uncertain), *Sapindaceae, Aitoniaceae, Aceraceae, Hippocastanaceae, Sabiaceae* (position uncertain), *Meliosmaceae, Koeberliniaceae.*

Juglandales: woody; usu. trees; leaves compound, digitate or imparipinnate, usu. exstipulate, with glands containing ethereal oils and resin; stomata anomocytic; vessels with scalariform or usu. simple perforations; bark rich in tannins; flowers usu. unisexual, in panicles, compound spikes, or catkins; bracts and bracteoles occas. enlarging; perianth simple; male flowers with 1—5 tepals and a variable number of stamens; pollen grains usu. porate; female flowers epigynous, with 4 or less, small or obsolete perianth lobes; pistil bicarpellate, unilocular; ovules 1(—2), basal, atropous, unitegmic, crassinucellate, chalazogamous; drupe or nut; seed without endosperm; embryo large, oil-rich; plants rich in polyphenolics (incl. various tannins, myricetin and ellagic acid); naphthoquinones typical; citrullin found in Juglandaceae. — *Rhoipteleaceae, Juglandaceae.*

Myricales: woody; shrubs or trees; leaves simple, entire to lobate, exstipulate, usu. with peltate glands and enlarged epidermis cells with ethereal oils; vessels usu. with scalariform (to simple) perforations; flowers unisexual, naked, in spikes, with bract and bracteoles, male with 4—8 stamens; pollen grains 3-porate; pistil bicarpellate, unilocular, with one basal, atropous, unitegmic ovule; fruit usu. a drupe; seed without endosperm, with oil-rich embryo; chemistry mainly as in Juglandales, in which Myricales could well be included. — *Myricaceae.*

Leitneriales: woody; leaves alternate, simple, exstipulate; hairs simple or glandular; secretory ducts with resinous contents at margin of pith and in leaf midveins; vessels small, with simple perforations; flowers unisexual, dioecious, in erect spikes, solitary in axil of bract; male naked, with 3—12 stamens; pollen grains 3—6-colporate; female hypogynous, with one whorl of small, unequal perianth scales; pistil monomerous; stigma decurrent; ovule solitary, lateral, bitegmic; drupe; seed with thin endosperm and large, straight embryo; bark rich in tannins. — *Leitneriaceae.*

Geraniales: mostly herbs; leaves opposite or alternate, simple or compound; ethereal oils occas. in glands, occas. in wood of trees and shrubs; flowers usu. actinomorphous, bisexual; disc usu. absent; obdiplostemony with one whorl often staminodial, or haplostemony; heterostyly common; pollen grains usu. colpate (to colporate), occas. porate, binucleate or often trinucleate; pistil eusyncarpous, often with 3—5 stylodia; ovules bitegmic, crassi- to tenuinucellate; endosperm formation nuclear or occas. intermediate; fruit variable, often a schizocarp; seeds with oil or protein (in Oxalidaceae also starch); polyphenolics common (occas. ellagic acid); plants rich in oxalates, sometimes also in saponins and alkaloids, tropane deri-

vatives in Erythroxylaceae. — *Zygophyllaceae* (should probably be further divided), *Nitrariaceae, Peganaceae, Balanitaceae, Ancistrocladaceae, Erythroxylaceae, Dirachmaceae* (position uncertain), *Geraniaceae, Ledocarpaceae, Vivianiaceae, Biebersteiniaceae* (alt.: in Rosales), *Ixonanthaceae, Humiriaceae, Hugoniaceae, Linaceae, Lepidobotryaceae, Averrhoaceae, Oxalidaceae, Hypseocharitaceae.*

Balsaminales: mainly herbs, often with semitransparent stem without sclerenchyma; leaves simple, alternate, opposite or in whorls; exstipulate; flowers in racemes, zygomorphous, bisexual; of sepals at least the two foremost often reduced, the back, median sepal helmet-like and often spurred; petals unequal, the lateral on each side often fused; stamens 5, filaments free, but anthers connate to a corona-like structure around the stigma; pollen shed apically; pollen grains 3—4-colpate; disc lacking; pistil eusyncarpous, 5-carpellary; ovules bi- (to almost uni-) tegmic, tenuinucellate; embryo sac mono- or bisporic; endosperm helobial (intermediate) ab initio; fruit a carnose explosion capsule; seeds with oil and protein, seed oil with glycerides of acetic acid and parinaric acid; calcium oxalate raphides common; naphthoquinone derivatives typical; leucoanthocyanins and other polyphenolics common. — *Balsaminaceae.*

Aralianae

Woody or herbaceous; leaves usu. alternate; vegetative parts and usu. also fruit with schizogenous ducts with mucilage, resin and ethereal oils; flowers usu. actinomorphous, (4—)5-merous; stamens usu. 5, alternating with petals; pollen grains usu. 3-colporate, free, trinucleate; pistil 2—5-carpellate; ovules unitegmic, crassinucellate, pseudo-crassinucellate or usu. tenuinucellate; endosperm nuclear ab initio; seeds with much endosperm containing oil (rich in petroselinic acid) and protein; embryo small; ethereal oils, resins, gums, triterpene saponins, furo- and pyrano-coumarins, caffeic acid derivatives and polyacetylenes present; tannins, leucoanthocyanins and ellagic acid as well as iridoids lacking.

Araliales: woody or herbaceous, leaves simple, entire, deeply and often repeatedly dissected or compound; leaf base usu. wide-ned into a sheath; vessels with scalariform or usu. simple perforations; herbaceous stems often hollow; inflorescences usu. compound umbels (of apparently dichasial origin); flowers epigynous; calyx teeth usu. small; petals free, usu. white, yellow or rose; stamens free on an epigynous disc (stylopodium); stylodia usu. separate; pistil 5—2-carpellate, eusyncarpous; each locule with one pendulous, crassi-, pseudocrassi- or tenuinucellate ovule; drupe, berry or usu. schizocarp with 2 nut-like mericarps. — *Araliaceae, Torricelliaceae* (alt.: in Cornales), *Apiaceae.*

Pittosporales: woody; shrubs or lianes; leaves opposite or whorled, simple, entire, evergreen, exstipulate; vessels with simple perforations; stomata paracytic; flowers hypogynous, usu. bisexual and sympetalous; anthers dehiscing by spits or pores; pistil 2(—5)-carpellate, usu. paracarpous, unilocular, with 2(—5) parietal placentas; ovules numerous, anatropous, tenuinucellate; capsule, berry or dry fruit; chemistry very similar to that in Araliales; saponins and coumarins present. — *Pittosporaceae.*

Asteranae

Woody or herbaceous; leaves alternate or opposite, exstipulate; laticiferous and resiniferous canals, secretory canals and cavities, glandular hairs, etc. often present; stomata usu. anomocytic; vessels usu. with simple (occas. scalariform) perforations; flowers in heads with green to scarious involucral bracts and usu. flat to conical receptacle; flowers epigynous, actinomorphous or zygomorphous; the latter often peripheral ("ray-florets"); calyx teeth usu. replaced by pappus; sympetaly; petals tubular or 3 or 5 forming tongue or 1 or 2 lips; anthers introrse, connate to a tube; pollen grains usu. porate or (3-)colporate, trinucleate; carpels (and stylar lobes) 2; locule one; ovule solitary, basal, erect, anatropous, unitegmic, tenuinucellate; endosperm nuclear or cellular ab initio, without haustoria; fruit an achene; seed without endosperm; embryo straight, rich in fatty oils; subterranean parts of perennials usu. with inulin; polyacetylenes, triterpenes and flavones usu. present; pyrrolizidine alkaloids and other alkaloids in some

genera; tannins, ellagic acid and iridoids lacking.

Asterales: *Asteraceae.*

Dillenianae

Woody or herbaceous; leaves usu. simple, stipulate or exstipulate; stellate and peltate hairs as well as mucilage cells common; flowers actinomorphous (or strongly reduced), bi- or unisexual, hemicyclic or cyclic, hypogynous, when well developed usu. 5-merous in calyx and corolla; choripetaly; stamens often (?primarily) in 2 whorls, outer often reduced but inner often attaining to high number; stamens when numerous with centrifugal development; filaments often fused into fascicles or to a tube or column; pollen grains binucleate or (in part of Euphorbiales and in *Ulmus*) trinucleate; carpels 1 to numerous, free or united, sometimes secondarily numerous; placentation usu. central in syncarpous gynoecia; ovules bitegmic and crassinucellate; obturator common; endosperm nuclear ab initio, in seed often rich in oil and protein (occas. starch); among polyphenolics tannins and myricetin richly present, leucodelphinidin often present, ellagic acid usu. lacking; glucosinolates largely lacking.

Dilleniales: mostly woody, leaves usu. evergreen, simple to lobate or compound, exstipulate; vessels with scalariform perforations; sclereid idioblasts common; flowers hemicyclic; bracteoles often several; sepals 3—5; petals 2—5, brightly coloured; stamens usu. numerous, sometimes developing centrifugally, often dilated apically (spathulate); pollen grains 3-colpate or 3-colporate; apocarpy predominant; carpels 1—numerous, each with 1 to numerous ovules; follicles, usu. with arillate seeds; these rich in amyloid or oils; polyphenolics such as leucodelphinidin, leucoanthocyanin and myricetin known in Dilleniaceae; quercetin and kaempferol in Paeoniaceae. — *Paeoniaceae, Dilleniaceae* (possibly not so closely related).

Cistales: shrubs and herbs; leaves usu. opposite, entire, often stipulate; vessels small, with simple perforations; trichomes often stellate or peltate; in *Cistus* glandular hairs with balsam and aethereal oils; flowers well developed; sepals 5—3; petals usu. 5, thin, brightly coloured; stamens on hypogynous disc, numerous, developing centrifugally, pollen grains 3-colporate; pistil paracarpous; carpels usu. 3—5; style simple, sometimes obsolete; placentation parietal; fruit capsular; endosperm rich in starch; caffeic acid absent; polyphenolics such as myricetin and leucodelphinidin common. — *Cistaceae, Bixaceae* (approaches Cochlospermaceae in Malvales).

Malvales: woody or herbaceous; leaves simple or digitate, usu. stipulate; cells, sacs or ducts with mucilage common; vessels with simple perforations; flowers usu. large, showy, usu. 5-merous and bisexual; petals free, often contorted in bud; stamens principally in 2 whorls, outer often reduced, inner multiplied, often forming a column; pollen grains 3-colpate to polyporate; carpels 2 to numerous; free stylodial branches or a single style; syncarpy or (probably secondarily) apocarpy; placentation in syncarpous pistils usu. central; fruit variable, often a capsule or schizocarp; seeds with variable amount of (sometimes no) endosperm; endosperm with oil, protein and sometimes starch; glycerides with cyclopropene fatty acids frequent; ellagic acid and myricetin only occas. present; balsam with tri-, mono- and sesquiterpenes esp. in Dipterocarpaceae. — *Sphaerosepalaceae* (alt.: in Thymelaeales) *Cochlospermaceae, Elaeocarpaceae, Sterculiaceae, Huaceae* (position uncertain), *Tiliaceae, Dipterocarpaceae, Bombacaceae, Malvaceae, Neuradaceae* (alt. in Geraniales or Rosales).

Urticales: woody or herbaceous; leaves entire to digitate, usu. stipulate; leaf lamina often with oblique base; hairs of stellate, glandular, stiff and other types; cystoliths common; cells with tanniniferous or mucilage contents typical; laticiferous cavities or ducts in Moraceae; vessels with simple perforations; inflorescence often carnose and head-, plate- or urn-shaped; flowers simple, reduced, usu. unisexual; tepals 5, 4 or 2+2, inconspicuous; stamens few, usu. opposite tepals; pollen grains porate; pistil usu. bicarpellate, sometimes pseudomonomerous; with 2 or 1 stigmas; only one locule fertile; ovule solitary; chalazogamy predominant; nut or drupe, occas. capsule; alkaloids common; tannins and polyphenolics rare or absent; latex with resin, wax, rubber etc. in Moraceae. — *Ulmaceae, Hymenocardiaceae, Moraceae, Cannabaceae, Urticaceae.*

Euphorbiales: woody or herbaceous, some stem-succulents; leaves alternate or opposite, usu. simple and stipulate; lamina often with oblique base; trichomes stellate, peltate, glandular, stinging, etc.; mucilage cells often present; tannin and latex vessels usu. present;

flowers often in pseudanthia (e. g. cyathia), unisexual, with double or simple perianth or none; stamens numerous to 1; pollen grains variable, bi- or trinucleate; pistil eusyncarpus, 3-carpellate, each carpel with few or usu. one ovule; obturator usu. present; fruit usu. a schizocarp with 3 cocci; seeds with endosperm rich in oil or occas. starch; latex with various tannins, rubber, ethereal oils, etc. usu. present; cyanogenic glycosides common; also alkaloids of various kinds, benzylisoquinoline alkaloids in *Croton*; glucosinolates in *Drypetes*, which is perhaps wrongly placed in Euphorbiaceae (ETTLINGER, priv. comm.). — *Euphorbiaceae* (should probably be divided into several families), *Pandaceae*, *Aextoxicaceae* (position of last two families uncertain), *Picrodendraceae* (alt.: in Sapindales).

Thymelaeanae

Mostly woody; leaves entire, alternate or opposite, exstipulate; stem with tough pericycle fibres; internal phloem usu. present; vessels with simple perforations; mucilage cells common; stomata anomocytic; flowers usu. actinomorphous, 4 (—5)-merous, hypogynous, bi- or unisexual, usu. with hypanthium; petals occas. present or petal- or scale-like structures or tufts of hairs often in throat of hypanthium; stamens in 2 or 1 whorls; pollen grains 3-colporate to polyporate, tri- or in Dichapetalaceae binucleate; pistil simple, usu. monomerous or pseudomonomerous but sometimes 2—12-carpellate; ovary usu. unilocular, with one pendulous, epitropous, bitegmic, crassinucellate or (in Dichapetalaceae) tenuinucellate ovule; obturator usu. present; endosperm nuclear ab initio; fruit usu. a nut or drupe; seed with little or no endosperm; embryo straight; toxic substances and coumarin derivatives (daphnin etc.) common in Thymelaeaceae; organic fluorid compounds in Dichapetalaceae; flavonoids common; tannins not accumulated; leucoanthocyanins found but ellagic acid lacking.

Thymelaeales: *Dichapetalaceae, Thymelaeaceae* (the two families doubtfully related; Dichapetalaceae perhaps closer to Euphorbiaceae).

Violanae

Woody or herbaceous; vessels usu. with simple perforations; trichomes often stellate; flowers actinomorphous, bisymmetric or zygomorphous, hypo- or epigynous; perianth double, 5-, 4- or 2-merous or absent; androgynophore or gynophore common; androecium haplo- or diplostemonous, or with numerous stamens usu. developing centrifugally; pollen grains binucleate or (in Brassicaceae and Frankeniaceae) trinucleate; gynoecium usu. paracarpous; carpels usu. 3 or 2; placentas usu. parietal; ovules usu. numerous, anatropous or campylotropous, usu. bitegmic (except, e. g., in most of Salicales) and crassinucellate (except in several families in Capparales); endosperm nuclear ab initio; tannins and various polyphenolics rare (except in Salicales and Tamaricales); cyanogenic compounds often present; glucosinolates typical of Capparales.

Violales: woody or herbaceous, often climbers; leaves simple or often digitate, usu. stipulate; laticiferous ducts and internal phloem sometimes present; flowers actinomorphous or sometimes zygomorphous, usu. 5-merous, hypo- or epigynous; corona structures and androgynophore often present; pollen grains usu. 3-colporate; paracarpy dominant; carpels usu. 3; ovules anatropous; seeds usu. with straight embryo; endosperm usu. well-developed; cyanogenic compounds accumulated in several families; tannins and many polyphenolic compounds sparse to absent (but ellagic acid etc. known in Begoniaceae); glucosinolates in Caricaceae only. — *Flacourtiaceae* (incl. *Lacistemataceae*), *Passifloraceae, Dipentodontaceae, Scyphostegiaceae, Violaceae, Turneraceae, Malesherbiaceae, Achariaceae, Cucurbitaceae, Begoniaceae, Datiscaceae* (position uncertain), *Caricaceae* (alt.: in Capparales).

Tamaricales: usu. woody; leaves small, often ericoid or scale-like, exstipulate; epidermis often with salt glands; flowers small, actinomorphous, usu. 4- or 5-merous, haplo- or diplostemonous; disc usu. present; pollen grains free, usu. 3-colpate, bi- or trinucleate; pistil paracarpous, unilocular, 2—5-carpellate; each carpel with 2 or more crassi- or tenuinucellate ovules; embryo sac mono- or tetrasporic; loculicidal capsule; seeds with

copious endosperm; leucoanthocyanins, tannins and pinitol present, ellagic acid in Tamaricaceae. — *Tamaricaceae, Frankeniaceae.*

Salicales: woody; leaves simple, stipulate; leaf traces with closed vascular strands; stomata paracytic; hairs usu. unicellular; flowers in spikes or catkins; unisexual, dioecious, naked; cup-shaped receptacle or lobate nectar gland present; stamens 2 or more; pollen grains 3-colporate or nonaperturate; pistil paracarpous; carpels 2; ovules with inner integument usu. reduced; capsules small; seeds basally hairy; tannins and phenolic glucosides like salicin and populin present; no ellagic acid. — *Salicaceae.*

Capparales: mostly herbaceous; leaves usu. alternate, usu. exstipulate; protein-storing ("myrosin") cells usu. present; stomata usu. anomocytic or anisocytic; hairs mainly unicellular, simple or branched; inflorescence indeterminate; flowers usu. bisymmetric or zygomorphous, with sepals and petals; pollen grains 3-colpate or 3-colporate, binucleate or in Brassicaceae trinucleate; carpels usu. 2, occas. 3, 5 or more; pistil usu. paracarpous with parietal placentas; ovules campylotropous or anatropous, usu. bitegmic, crassi- or tenuinucellate; seeds with large, oil-rich, often folded embryo, usu. without endosperm; glucosinolates present; seed oils in some families with erucic acid; tannins and many polyphenolic compounds largely lacking; certain protoalkaloids often present. — *Limnanthaceae, Tropaeolaceae* (alt.: these in Geraniales), *Bretschneideraceae* (alt.: in Sapindales), *Salvadoraceae* (alt.: in Celastrales or Oleales), *Moringaceae, Resedaceae, Tovariaceae, Capparaceae, Pentadiplandraceae, Brassicaceae, Gyrostemonaceae, Bataceae* (alt.: the last two families in a separate order).

Celastranae

Mainly woody plants; in some families parasites; leaves alternate or opposite, usu. simple but occas. compound; stipulate or exstipulate; idioblasts with mucilage and tanniniferous contents and crystals of calcium oxalate common; flowers in determinate inflorescences, actinomorphous, usu. small, (3—)4—5-merous, with double or in Santalales in particular with simple perianth, hypo- to epigynous; stamens usu. in one whorl (occas. in two) alternating with or opposite petals; pollen grains usu. colporate, bi- or (in part of Celastrales) trinucleate; intrastaminal disc common; pistil eusyncarpous, usu. 2—5-carpellate with separate loculi; each locule usu. with 1—2 ascending ovules; these bi-, uni- or ategmic (in Santalales usu. strongly reduced), crassi- or tenuinucellate; endosperm cellular or nuclear ab initio; endosperm usu. copious in seed (fruit), rich in oil; condensed tannins present in all orders, often in rich quantities; iridoids lacking; chemical relationships otherwise somewhat obscure. The superorder is likely to be heterogeneous, as may also be some of its orders, in particular Celastrales.

Celastrales: leaves simple or occas. compound, often glabrous, stipulate or exstipulate; hairs of simple construction; vessels with scalariform or simple perforations; intraxylary phloem or ducts with guttapercha occas. present; idioblasts with tannins and druses or simple crystals of calcium oxalate common; sepals and petals usu. present, but inconspicuous, hypo- to perigynous; petals usu. free; stamens usu. 4—5, alternating with petals; pollen grains usu. 3-colporate, bi- or trinucleate; pistil 1—5-carpellate; ovules well-developed, erect or ascending, crassi- or tenuinucellate, bi- or more seldom unitegmic; endosperm formation usu. nuclear (but cellular in Aquifoliaceae and some Buxaceae, for example); seeds with or without endosperm, often arillate, rich in oil or occas. wax; guttapercha and dulcitol often present; tannins usu. present, but ellagic acid lacking. — Probably not a natural order. The first five families show affinities to Euphorbiales, Flacourtiaceae in Violales and perhaps to Hamamelidales; Geissolomataceae shares some features with Hamamelidales others with Oleales; Staphyleaceae is often placed in Sapindales; the last three families, finally, have a very preliminary position in Celastrales. — *Buxaceae, Simmondsiaceae, Stylocerataceae, Didymelaceae, Barbeyaceae, Geissolomataceae, Avicenniaceae, Staphyleaceae, Sphenostemonaceae, Aquifoliaceae, Celastraceae* (incl. *Hippocrateaceae*), *Stackhousiaceae, Siphonodontaceae, Goupiaceae, Lophopyxidaceae, Montiniaceae.*

Santalales: woody or herbaceous, mostly parasites on trees; leaves opposite or alternate; vessels with simple perforations; schizogenous resiniferous ducts occas. present; cells with mucilage and tannins usual; flowers usu. haplo- or homochlamydeous, occas.

with calyx or calyculus; tepals variable; stamens in one (or 2) whorl(s), opposite tepals; disc usu. lacking; pistil 1—3(—5)-loculate; each locule usu. with one tenuinucellate ovule, or this not differentiated, ovule when discernible usu. without (occas. with 1—2) integument(s); endosperm cellular ab initio; berry, drupe or nut; endosperm usu. well-developed, rich in oils; tannins common in some families, sometimes leucoanthocyanin, myricetin and ellagic acid; triglycerides of acetylenic fatty acids in some families; acculumation of silicic acid common in leaves, triterpenes common. — *Olacaceae* (incl. *Octoknemaceae* and *Erythropalaceae*), *Opiliaceae, Loranthaceae, Misodendraceae, Santalaceae, Eremolepidaceae, Viscaceae.*

Rhamnales: leaves simple or compound, opposite or alternate; stipules usu. small; hairs simple; crystals common; vessels with simple perforations; flowers usu. greenish or yellowish-white, hypogynous or occas. epigynous; petals inconspicuous, often small, hood-like, sometimes fused and shed at anthesis in one part; stamens 4—5, opposite petals; pollen grains usu. 3-colporate, bi- or trinucleate (apertures operculate in Leeaceae); pistil eusyncarpus, 2—8-locular; ovules bitegmic, crassinucellate; endosperm nuclear ab initio; drupe, capsule or berry; seeds rich or (espec. in Rhamnaceae) poor in endosperm, containing fatty oils and protein, but not starch; leucoanthocyanins usu. and ellagic acid often present; organic acids such as oxalic and malonic acids common; anthraquinone glycosides and cyclopeptide alkaloids in Rhamnaceae; pentacyclic triterpene acids in Vitaceae. Relationships not fully verified. — *Rhamnaceae, Vitaceae, Leeaceae* (position uncertain).

Solananae

Mostly herbs but also woody plants; leaves usu. alternate, exstipulate; intraxylary phloem in some families; vessels with simple perforations; inflorescences usu. determinate; flowers usu. actinomorphous, hypogynous, usu. 5-merous, 4-cyclic, sympetalous; sepals, petals and stamens in alternating whorls; pollen grains variable, bi- or trinucleate; pistil bicarpellate, eusyncarpous; ovules 2 to numerous per locule, unitegmic, usu. tenuinucellate; endosperm nuclear or cellular ab initio; fruit variable; seeds rich in oil; tropane alkaloids, nicotine and steroidal saponins esp. in Solanaceae; pyrrolizidine alkaloids in Boraginaceae; derivatives of caffeic acid and flavonols common; tannins usu. lacking; iridoids absent.

Solanales: *Solanaceae, Goetzeaceae, Nolanaceae, Convolvulaceae* (incl. *Humbertiaceae*), *Cuscutaceae, Cardiopterygiaceae, Cobaeaceae, Polemoniaceae, Hydrophyllaceae, Ehretiaceae, Boraginaceae, Wellstediaceae, Lennoaceae, Hoplestigmataceae.*

Campanulanae

Herbs or shrubs; leaves usu. alternate, entire, and exstipulate; glandular hairs lacking; laticiferous ducts present in phloem; vessels with simple perforations; flowers actinomorphous or zygomorphous, usu. epigynous, tetracyclic, 5-merous; calyx usu. with green lobes; corolla sympetalous, in zygomorphous flowers deeply parted medially and with unequal lobes; anthers 5, introrse, free or connate to a tube; pollen grains variable, bi- or occas. trinucleate; gynoecium 2—5-carpellate, eusyncarpous; ovules several to numerous, unitegmic, tenuinucellate; endosperm cellular ab initio, with terminal haustoria; fruit usu. capsular; seeds usu. with endosperm; accumulation in perennials of inulin; latex with alkaloids and chelidonic acid only in Lobeliaceae, but caffeic acid in particular in Campanulaceae; tannins and iridoids lacking.

Campanulales: *Campanulaceae, Pentaphragmataceae, Lobeliaceae, Sphenocleaceae* (position uncertain).

Hamamelidanae

Woody plants; leaves usu. alternate, simple, stipulate or exstipulate; stomata anomocytic or paracytic; stellate, peltate and glandular hairs common; vessels occas. lacking, usu. present and with scalariform or simple perforations; usu. compact spikes, heads or catkins, their components often triads of flowers; chiefly anemogamy; flowers usu. unisexual, hypo- or epigynous; perianth often 4-merous, usu.

more or less reduced, simple or lacking; filaments usu. long, slender; anthers dehiscing longitudinally; pollen grains often porate and smooth, always binucleate; carpels free (apocarpy) or ± fused (eusyncarpy) but with free stylodia, often only one locule developed; ovules usu. bitegmic (unitegmic in Balanopales and part of Fagales and Cunoniales) and crassinucellate; chalazogamy common; endosperm usu. nuclear ab initio, but cellular in esp. Trochodendrales; seeds rich in oil, protein and occas. starch; tannins and other polyphenolics rich, in some groups ellagic acid; cells with ethereal oils and benzylisoquinoline alkaloids lacking; iridoids usu. lacking (present in *Liquidambar* and *Daphniphyllum*).

Trochodendrales: leaves stipulate or exstipulate; vessels either lacking (then solely tracheids) or with oblique end walls and scalariform perforations (many bars); sclereid and secretory idioblasts often present; flowers actinomorphous, naked or with simple perianth of small, bract-like tepals, occas. in synanthia, mono- or bisexual; stamens 4—numerous; pollen grains 3-colpate with colpi occas. tending to be pore-like; carpels free, 1—numerous, when several in one whorl, usu. with decurrent stigma; ovules few to numerous; endosperm cellular ab initio; follicle, multifollicle or cluster of nutlets; seeds usu. with oil-rich endosperm; polyphenolics like leucodelphinidin and quercetin (in Cercidiphyllaceae also ellagic acid) usu. present. — *Trochodendraceae, Tetracentraceae, Eupteleaceae, Cercidiphyllaceae.*

Hamamelidales: leaves stipulate; trichomes simple or stellate; vessels present, usu. with scalariform perforations; secretory ducts in Altingiaceae; flowers hypo- to epigynous, often in compact, determinate or indeterminate inflorescences, cyclic or hemicyclic; perianth double, simple or lacking, when present often 4-merous; stamens in one or occas. 2 whorls; pollen grains usu. 3-colpate, rarely polyporate; carpels usu. 2 (occas. more and free), more or less syncarpous; stigma usu. decurrent; each locule with 1—numerous, usu. pendulous ovules; endosperm nuclear (or occas. cellular) ab initio; capsule or nut; seeds usu. with copious endosperm, with oil and protein; tannins, leucoanthocyanins and myricetin typical; sometimes ellagic acid; shikimic and quinic acids known in Hamamelidaceae; iridoids rare (see above). — *Myrothamnaceae, Hamamelidaceae, Platanaceae, Altingiaceae, Daphniphyllaceae, Rhodoleiaceae* (position uncertain).

Casuarinales: branches sulcate; leaves whorled, fused with the stem for one internode and appearing with tips at following node; stomata paracytic; trichomes simple or branched; vessels with scalariform or usu. simple perforations; flowers axillary along branch ends, extremely reduced, unisexual, monoecious; male with 2 small prophylls, 2 small tepals and one stamen with long, thin filament; pollen grains 3-por(or)ate; female flowers in cone-like inflorescence, with 2 prophylls and a unilocular bicarpellary pistil; only one locule fertile, with 2—4 ovules; chalazogamy; few to many monosporic embryo sacs developed; winged nut; seed without endosperm, with oil-rich embryo; tannins rich, esp. in the bark; polyphenolics including ellagic acid, catechin and leucoanthocyanins present. — *Casuarinaceae.*

Fagales: leaves stipulate; stomata anomocytic; vessels with scalariform or simple perforations; flowers usu. unisexual and monoecious, in small, dichasial units often in catkins; male naked or with simple perianth and 2 or more stamens; pollen grains with 3—7 pori or colpi; female flowers naked or epigynous, pistil syncarpous, 3- or 2-carpellate; each locule with 1—2 uni- or bitegmic ovules; chalazogamy; fruit usu. a 1-seeded nut; embryo large, rich in oil and occas. starch; tannins and triterpenes very rich; tannins made up of ellagic and gallic acids and catechin; often shikimic and quinic acids; nitrogen transported in the form of citrullin in Betulaceae. — *Fagaceae, Corylaceae, Betulaceae.*

Balanopales: leaves exstipulate; stomata anomocytic; vessels large, with scalariform perforations; flowers unisexual, dioecious; male in catkins, with perianth of a single scale and usu. 5—6 stamens; pollen grains 3—4-colpoidate, minutely spinulose; female flowers solitary, in an involucre of bracts, naked (?), 2(—3)-carpellate, 2- or 3-locular; each locule with 2 sub-basal unitegmic ovules; drupe; bark very rich in tannins and triterpenes. — *Balanopaceae* (position uncertain).

Cunoniales: trees or shrubs; leaves alternate or often opposite, simple or compound, with or without stipules; unicellular (rarely also multicellular glandular) hairs present; vessels with scalariform (or sometimes with simple) perforations; flowers actinomorphous, hypogynous to half or entirely epigynous; perianth double or simple, usu. 5-merous; stamens 4 to numerous, often of same or

double the number of petals; anthers dehiscing longitudinally; pollen grains usu. colporate, occas. porate, usu. with 2—8 apertures, binucleate (as far as known); carpels usu. 2, rarely up to 5 or more, free or usu. united (eusyncarpous) in ovary region, then usu. with free stylodia; ovules few to numerous, bitegmic or (in Bruniaceae) unitegmic, crassinucellate; endosperm nuclear ab initio; follicles or capsule, seeds with copious endosperm; embryo small; tannins probably always rich, chemistry otherwise little known. The families show affinities with Hamamelidales, Rosales and Saxifragales; possibly a heterogeneous group. — *Cunoniaceae, Iteaceae, Brunelliaceae, Eucryphiaceae, Baueraceae, Bruniaceae.*

Rosanae

Woody or herbaceous; leaves usu. alternate, simple or compound and usu. with well-developed stipules; stomata anomocytic or in Fabales often paracytic; intraxylary phloem lacking; vessels usu. with simple perforations; flowers actinomorphous or zygomorphous, hypo- or perigynous (epigynous in Malaceae); perianth usu. double and 5- (or 4-)merous; synsepaly common, more seldom sympetaly (viz. in some Mimosaceae); stamens usu. in 2 or more whorls, usu. 5 or more in each, free or united to a tube or sheath; pollen grains variable, usu. 3-colporate, binucleate; carpels 1—numerous, usu. free; ovules ana- or campylotropous, usu. bitegmic (but unitegmic in a great part of Rosaceae), crassinucellate; endosperm nuclear ab initio; seeds usu. without endosperm; condensed tannins and gallo- and ellagi-tannins and other polyphenolics common; saponins common; iridoids lacking.

Rosales: woody or herbaceous; mucilage cells common; flowers actinomorphous or zygomorphous; floral receptacle exceptionally variable, often urceolate, flat, columnar or conical; perianth usu. 5-merous; petals free or sometimes lacking; haplo- or diplostemony or usu. numerous (then centripetally developing) stamens in successive whorls tending to 5-mery; stamens free; intrastaminal disc common; carpels 1 to numerous, usu. free (fused with receptacle in Malaceae); ovules usu. 1—2 per carpel, anatropous, bi- or unitegmic; embryo rich in fatty oils; in some groups ellagic acid; triterpenes and saponins common, often also sorbitol, cyanogenic compounds and fruit acids. — *Crossosomataceae, Rosaceae, Malaceae, Amygdalaceae, Connaraceae, Melianthaceae* (position uncertain), *Chrysobalanaceae* (alt.: in Fabales).

Fabales: woody or herbaceous; leaves usu. compound (or secondarily simple); flowers actinomorphous, or zygomorphous, in indeterminate inflorescences; perianth usu. double, 4—5-merous; petals free, lower coherent in Fabaceae; sympetaly common in Mimosaceae; aestivation of petals valvate, descending or ascending; stamens usu. 5+5 (diplostemony), also 4, 5, 4+4, numerous or otherwise; pistil usu. solitary, often stipitate, with long style; ovules 1—numerous, ana- or campylotropous; endosperm often with chalazal haustorium; fruit normally a legume; seeds often arillate; embryo with fat, protein and often starch; ellagic acid, quinolizidine alkaloids, triterpene saponins and isoflavones common. — *Mimosaceae, Caesalpiniaceae, Fabaceae.*

Proteanae

Mainly woody plants; leaves alternate, entire to deeply and finely dissected, exstipulate; hairs when present mostly unicellular; stomata usu. paracytic; vessels narrow, with simple perforations; flowers uni- or bisexual, ± actinomorphous, often in compact spikes or heads; female spikes sometimes cone-like; flowers often ornithogamous; perianth simple; tepals 4, usu. fused to a tube with valvate lobes; stamens 4, opposite tepals and usu. fused with these; pollen grains usu. triangular, 2—3-porate, binucleate; pistil monocarpellate; style often thickened into a pollen presenter; ovules numerous to one, bitegmic, crassinucellate; endosperm nuclear ab initio; follicle, capsule, nut or drupe; seeds without endosperm, sometimes with 3—8 cotyledons, lacking starch but rich in protein and fat; flavonol derivatives, leucoanthocyanins, arbutin, condensed tannins, aluminium and cyanogenic compounds characteristic; alkaloids and ellagi-tannins lacking or rare. Chemical contents somewhat reminiscent of those in Fabanae, otherwise great similiarities to Thymelaeaneae.

Proteales: *Proteaceae.*

Myrtanae

Woody or herbaceous; leaves usu. opposite, simple, entire; intraxylary phloem common; vessels usu. with simple perforations; stomata usu. anomocytic; flowers usu. actinomorphous, generally 4-merous; usu. epi- or perigynous, often with hypanthium; on edge of this: calyx lobes, petals and 1—2 whorls of stamens; latter occasionally numerous and then developing centripetally; petals free; pollen grains usu. colpate or colporate, generally binucleate or in Melastomataceae and Haloragaceae trinucleate; pistil eusyncarpous, usu. 2- or 4-carpellate, in Elaeagnales monocarpellate, usu. with one style; ovules usu. bitegmic and crassinucellate; endosperm usu. nuclear ab initio; seeds usu. without endosperm or with little endosperm; polyphenolics incl. galli- and ellagi-tannins and condensed tannins usu. in rich quantities; caffeic acid usu. lacking.

Myrtales: woody or herbaceous; stipules usu. rudimentary but present, occas. large and interpetiolar; schizolysigenous secretory cavities esp. in Myrtaceae; sclereid-idioblasts common; flowers often with hypanthium; perianth usu. double, but petals occas. lacking; haplo- or diplostemony or stamens numerous; connective often thick or carnose; capsule or berry; seeds usu. without or with little endosperm with fatty oils (starch in Myrtaceae only); accumulations of aluminium and calcium oxalate common. — *Lythraceae* (incl. *Sonneratiaceae*), *Punicaceae, Rhizophoraceae* (incl. *Anisophyllaceae*), *Dialypetalanthaceae* (position uncertain), *Crypteroniaceae, Combretaceae, Oliniaceae, Melastomataceae* (incl. *Memecylaceae*), *Penaeaceae, Myrtaceae* (incl. *Heteropyxidaceae*), *Onagraceae*.

Elaeagnales: woody; leaves simple, entire, usu. alternate, exstipulate; stem and leaves with stellate or peltate hairs; crystal needles or crystal sand common; intraxylary phloem lacking; flowers actinomorphous, epigynous, with hypanthium; perianth simple (corolla lacking); stamens 4 or 8, on edge of hypanthium; pollen grains usu. 3-colporate; pistil monocarpellate, with one basal, anatropous ovule; nut; seed with little endosperm and straight embryo containing oil and aleuron (no starch), occas. enclosed by carnose being perianth; L-quebrachitol typical; ellagic acid, quercetin and other polyphenolics present; myricetin and caffeic acid lacking; accumulation of simple indole bases, sinapic acid and saponins. Perhaps close to Thymelaeales, Rhamnales or Proteales. — *Elaeagnaceae*.

Trapales: aquatic annual herbs with floating rosettes of leaves with dissected caducous stipules; crystal raphides lacking; epidermis sometimes with mucilage and oil cells; petiole with aerenchyma; intraxylary phloem present; flowers solitary in leaf axils, perigynous, with 4-merous calyx, corolla and androecium; pollen grains tricolpate; folded intrastaminal disc present; pistil bicarpellate, bilocular, with single style; each locule with one pendulous, anatropous ovule; endosperm not formed at all; fruit a nut enclosed by the perianth; seed with large embryo, rich in starch; cotyledons unequal. — *Trapaceae*.

Haloragales: herbs, partly aquatic; leaves opposite or in whorls, from simple and entire or serrate to finely dissected, exstipulate; flowers small, often spicate, bi- or unisexual, usu. 4-merous, with simple or double perianth and 2 or 1 whorls of stamens; pollen grains colpate to porate, with 1—7(—16) apertures; pistil 2—4-loculed, each with one pendulous ovule; endosperm cellular (possibly occas. nuclear) ab initio; suspensor haustorium formed; nut, drupe or schizocarp; endosperm rich in oil; embryo straight; plant rich in polyphenolics such as ellagic acid and quercetin; also cyanogenic compounds and saponins. Alternative position: near Saxifragales. — *Haloragaceae*.

Saxifraganae

Woody or usu. herbaceous; vessels with scalariform or simple perforations; flowers usu. actinomorphous, with double or occas. strongly reduced perianth, usu. 5-merous, sometimes 4—2-merous; petals when present usu. free; obdiplostemony or haplostemony; pollen grains free or occas. in dyads, binucleate; carpels often 2, free or often more or less fused, with 2 (or 1) locules, generally with free stylodia; ovules usu. numerous, always bitegmic and usu. crassinucellate (tenuinucellate e.g. in Podostemales); endosperm usu. cellular ab initio (not formed at all in Podoste-

males); seeds with variable amount of endosperm, this never with starch; plants usu. rich in tannins and other polyphenolics, such as leucoanthocyanins and ellagic acid (except in Podostemales); iridoids lacking; saponins occas. present.

Saxifragales: woody or herbaceous; leaves simple or compound, with or without stipules; vessels usu. with simple perforations; flowers actinomorphous, usu. 5-merous, hypo- or epigynous, usu. with free petals; obdiplostemony or haplostemony; stamens usu. free; pollen grains free; variation from apocarpy to syncarpy; carpels usu. 2—5 (or more); stylodia often free; ovules usu. numerous, apotropous; endosperm formation cellular or intermediate; fruit (apocarpous gynoecia) multifollicle, or (syncarpous gynoecia) capsule, berry etc.; seeds with little (Crassulaceae) or usu. much endosperm; sedoheptulose often present. — *Crassulaceae, Penthoraceae, Saxifragaceae, Fouquieriaceae* (position uncertain), *Francoaceae, Brexiaceae* (position uncertain), *Cephalotaceae, Tremandraceae, Vahliaceae, Ribesiaceae, Greyiaceae* (position uncertain).

Podostemales: usu. small, herbaceous, annual or perennial fresh-water aquatics found in running water; roots usu. dorsiventral, flat, often green and assimilatory, liverwort-like, adhering to stones; silicate bodies often present in periphery of lobes; secretory ducts usu. present; stem reduced, often dorsiventrally flattened; stomata lacking; flowers bi- or unisexual, solitary or in small often dichasial inflorescences, often basally with a "spathella"; tepals usu. lacking or 2—5, hypogynous; stamens 1, 2, 4 or more, occas. in 2 whorls, when 2 often fused by their filaments; pollen grains free or in dyads; pistil usu. bicarpellate; ovules several, anatropous, tenuinucellate; embryo sac bisporic; endosperm not formed at all; capsule; seeds small, with straight, thick embryo; silicate bodies and laticiferous or resin ducts typical as is also accumulation of salts. — *Tristichaceae, Podostemaceae.*

Gunnerales: small to giant herbs; leaves basal, long petiolate, stipulate; cortex of stems rich in slime containing colonies of algae (*Nostoc*); upper parts of stem polystelic; vessels with simple perforations; inflorescence branched, usu. shorter than leaves, carnose, with numerous small, bi- or unisexual, epigynous flowers; perianth simple, 2- or 4-merous; stamens 2; pollen grains free, 3-colpate; pistil bicarpellate, unilocular, with one subapical, pendulous, crassinucellate ovule; embryo sac tetrasporic (of Peperomia-type); endosperm cellular ab initio; small drupe; seed rich in endosperm, with small embryo; plants rich in tannins; ellagic and caffeic acids and saponins present. — *Gunneraceae.*

Balanophoranae

Parasitic, chlorophylless, red, yellow, brown or whitish plants forming large, often branched underground tubercles possibly partly of root nature and partly containing host tissue; floriferous branches usu. differentiated endogenously in these; stems usu. with bract-like, alternate, opposite or whorled leaves; inflorescence carnose, branched or unbranched, spike-like; flowers unisexual; male with 2—8 (usu. 3—4) tepals and 1—8 (or more) free or fused stamens with one- or several-chambered anthers; pollen grains bi- or trinucleate, inaperturate or aperturate; female flowers naked or epigynous with few tepals, in extreme cases archegonium-like; carpels (5—)3—1; placenta central; ovules 1 or more, usu. ategmic and tenuinucellate, often completely undifferentiated and fused with pericarp; embryo sac monosporic; endosperm cellular ab initio; nut or achene; endosperm with oil; embryo acotyledonous; Cynomoriaceae with tannins. The homogeneity of the group is questionable.

Balanophorales: *Balanophoraceae, Cynomoriaceae.*

Plumbaginanae

Woody or herbaceous; leaves usu. alternate, simple, exstipulate or with ochrea; trichomes and stomata variable; vessels with simple perforations; flowers hypo- to perigynous, with simple or double, usu. 3- or 5-merous perianth; perianth members free or connate; stamens in one or two 3- or 5-merous whorls; pollen grains variable, trinucleate; pistil syncarpous, unilocular, usu. 3- or 5-carpellate, with only one ovule; this orthotropous or anatropous, bitegmic and crassinucellate; en-

dosperm nuclear ab initio; seeds with endosperm rich in simple starch grains and protein, without perisperm; plants rich in polyphenolics, incl. condensed tannins and quinones, lacking betalains.

Plumbaginales: leaves exstipulate, without ochrea, usu. with glandular hairs or salt glands; flowers 5-merous, synsepalous and sympetalous; stamens 5, epipetalous; pollen grains usu. 3- or 5-colpate to polyporate; pistil 5-carpellate; ovule anatropous, with long funiculus; embryo sac usu. tetrasporic (of various types); obturator usu. present; capsule; seed with straight embryo; naphthoquinones, flavonols such as myricetin, leucoanthocyanins and often ellagic acid present. — *Plumbaginaceae, Limoniaceae.*

Polygonales: ochrea usu. present; nodes often prominent; flowers usu. inconspicuous; perianth often white, pink, brown or hyaline, either double and 3-merous or simple and 5-merous, when double the inner whorl sometimes enclosing fruit; stamens in one or usu. two 3-merous, sometimes collaterally doubled whorls; pollen grains variable, 3-colpate to polyporate; gynoecium (2- or) 3-carpellate, with free stylodia; ovule orthotropous or occas. anatropous; embryo sac monosporic; nutlet; embryo straight or curved; plants rich in oxalic acid, polyphenolic compounds (incl. tannins) and anthraquinones; saponins largely lacking. — *Polygonaceae.*

Primulanae

Woody or herbaceous; leaves usu. simple; vessels usu. with simple perforations; flowers usu. actinomorphous and hypogynous, generally sympetalous; stamens in 1, 2 or 3 whorls; pollen grains colpate or colporate, usu. binucleate, pistil syncarpous, 1-, 2- or pluri-locular; ovules usu. bitegmic and tenuinucellate; endosperm nuclear ab initio or cellular in some Ebenales; seeds rich or poor in endosperm; saponins, quinones and polyphenolics present, esp. leucoanthocyanins and tannins derived from them characteristic of most families.

Primulales: woody or herbaceous; leaves usu. exstipulate; stomata usu. anomocytic; capitate glandular hairs common; flowers usu. 5-merous; stamens 5, opposite petals, occas. also staminodes alternating with these; pollen grains binucleate; pistil unilocular, with simple style and free, central placentation; ovules usu. numerous, occas. solitary, bitegmic or rarely unitegmic; berry, capsule or drupe; seeds usu. rich in endosperm (with oil and cellulose) and with straight embryo; triterpene saponins (neutral sapogenins), leucoanthocyanins and benzoquinones common. — *Myrsinaceae, Aegiceratataceae, Theophrastaceae, Primulaceae, Coridaceae.*

Ebenales: woody, usu. with alternate, entire leaves, with or without caducous stipules; ducts with guttapercha in certain groups; wood often hard, heavy and dark; flowers actinomorphous, 3—7-merous; sepals occas. in 2 whorls; petals in one or more whorls, occas. with dorsal petaloid appendices; stamen whorls usu. 2—3, isomerous with and alternating with petals; anthers introrse or extrorse, opening by splits or pores; pollen grains bi- or sometimes trinucleate; disc absent; pistil eusyncarpous, usu. 2—12-carpellate, with 2 or more locules; ovules uni- or bitegmic; endosperm formation nuclear or cellular; berry or drupe; seeds with variable amount of endosperm; polyphenolics (but not ellagic acid), triterpenes and saponins common; in Ebenaceae naphthoquinone derivatives. Probably heterogeneous. Perhaps more closely related to Sapindales or Celastrales than to Primulales. — *Ebenaceae, Sapotaceae, Lissocarpaceae, Styracaceae.* (Symplocaceae is placed in Theales.)

Theanae

Woody or herbaceous; leaves usu. alternate, with or without stipules; vessels usu. with simple perforations; stomata variable; flowers actinomorphous, spirocyclic or cyclic, usu. hypogynous and with 5-merous calyx and corolla; petals when present free; stamens (4—)5 to numerous, when numerous often in fascicles and usu. with centrifugal development; pollen grains usu. binucleate; gynoecium usu. 2—5-carpellate, para- or eusyncarpous, in ovary region sometimes apocarpous; ovules usu. bitegmic, generally tenuinucellate except in Nepenthales and part of Droserales; endosperm nuclear ab initio (except in Marcgraviaceae); various polyphenolics (often tannins) common, sometimes alkaloids.

Theales: mainly woody; leaves simple, usu. entire; schizogenous secretion ducts sometimes present; vessels with scalariform or more often simple perforations; stamens usu. numerous, often in fascicles; anthers opening by splits or pores; pollen grains usu. free, 3-colporate, usu. binucleate; carpels 2—c. 20, usu. 3—5; stylodia often separate; seeds usu. without or with little endosperm and with well developed embryo, rich in oil but usu. without starch; tannins and various other polyphenolics common, also ellagic acid; often triterpene saponins, alkaloids, anthraquinones and coumarins; aluminium accumulation common. — *Stachyuraceae, Ochnaceae, Quiinaceae, Medusagynaceae, Scytopetalaceae* (position uncertain), *Sarcolaenaceae, Strasburgeriaceae, Oncothecaceae, Theaceae* (incl. *Sladeniaceae* and *Tetrameristaceae*), *Pentaphylacaceae, Marcgraviaceae, Caryocaraceae, Pelliceriaceae, Napoleonaceae, Bonnetiaceae, Foetidiaceae, Lecythidaceae, Symplocaceae, Clusiaceae* (incl. *Hypericaceae*), *Ancistrocladaceae, Elatinaceae* (position of last two families uncertain).

Nepenthales: herbs or lianes; leaves alternate, often heteromorphic, sometimes forming specialized pitcher (ascidium) with operculum, in other cases with a pair of apical elastic hooks, often glanduliferous; petioles with peripheral ring of fibres; stem cortex with 2 zones, outer with thick-walled fibrous cells, inner with thin-walled cells; lianes with anomalous secondary growth; flowers actinomorphous, bi- or unisexual; perianth 5-merous and double (with various reductions of calyx) or 4(—3)-merous and simple; petals (tepals) free; disc absent; stamens often numerous, ± free or united to a column; pollen grains free or in tetrads, binucleate, apertures 3 or obscure; carpels 2, 4, or 5; pistil para- or eusyncarpous; ovules numerous, crassinucellate; fruit capsular, occas. with equatorial wing; seeds with wing-like projection; endosperm rich (occas. with starch); embryo small. (*Dioncophyllum* contains the naphthoquinone plumbagin, also found in *Drosera* and various other plants.) — *Nepenthaceae, Dioncophyllaceae* (relationship uncertain).

Droserales: mostly herbs, seldom woody at base; leaves exstipulate; either glandular hairs with proteolytic secretion or fimbriate appendages secreting mucilage usu. present; vessels with simple perforations; flowers bisexual, hypogynous (to half epigynous); stamens free, (4—)5 or 10 to 20, one whorl sometimes transformed into variable, often digitate, gland-tipped staminodia; pollen grains free or in tetrads, 3-colpate, 3-colporate or 7—polyporate, bi- or trinucleate; pistil 3—5-carpellate, unilocular, with parietal or basal placentas; free stylodial branches or commissural stigmas; ovules crassi- to tenuinucellate; fruit capsular; testa often with wing-like projections; naphthoquinones in Droseraceae; polyphenolics common, occas. ellagic acid and cyanogenic compounds. — *Droseraceae, Lepuropetalaceae, Parnassiaceae.*

Cornanae

Woody or partly herbaceous; leaves usu. simple, occas. compound; vessels usu. with scalariform perforations, esp. in woody members; flowers usu. 4—5-merous, actinomorphous, hypo- to epigynous, generally with double perianth; sympetaly or choripetaly; androecium usu. obdiplostemonous or haplostemonous, occas. with more than 10 stamens; pollen grains simple or in tetrads, usu. 3-colporate, binucleate or in Cornales often trinucleate; pistil usu. eusyncarpous and 2—5-carpellate; ovules unitegmic, usu. tenuinucellate, endosperm usu. cellular ab initio, often with terminal haustoria; seeds usu. rich in endosperm and with small embryo; polyphenolics usu. rich, often galli- and ellagitannins; iridoids present in all orders and most families (but not constantly).

Ericales: usu. woody; vessels usu. with scalariform perforations; leaves usu. simple, entire, often ericoid or coriaceous, exstipulate; flowers 5- or 4-cyclic, hypo- or epigynous; corolla often campanulate; obdiplostemony or haplostemony; filaments usu. free; anthers introrse, dehiscing by splits or often by apical pores; pollen grains often in tetrads; intrastaminal disc common; pistil usu. 5—3-carpellate, style usu. simple; ovules tenuinucellate; endosperm usu. with terminal haustoria; capsule or berry; seeds small; ellagic acid, leucoanthocyanins and tannins common, also phenolic heterosides such as arbutin; triterpenes in cuticula; mono- and sesquiterpenes common; iridoids known in about half of the families. — *Actinidiaceae* (incl. *Saurauiaceae*), *Clethraceae, Cyrillaceae, Roridulaceae, Ericaceae, Monotropaceae, Pyrolaceae, Epacridaceae, Diapensiaceae, Byblidaceae* (position uncertain), *Empetraceae, Grubbiaceae* (position uncertain).

Sarraceniales: herbs; leaves alternate, basal, pitcher-like, tubuliform or funnel-shaped, of complicated construction, with a lid projection over the mouth; pitcher with several zones of glands and hairs; vascular strands

scattered; vessels with scalariform perforations; flowers hypogynous, with double or simple perianth; sepals 3—6; petals when present usu. 5, free; stamens 12 to numerous, often in groups; pollen grains simple, often polycolporate; pistil 3—5-carpellate; style apically 5-lobate or umbellular; ovules tenuinucellate; seeds numerous, rather small. — *Sarraceniaceae.*

Eucommiales: tree; leaves alternate, simple, exstipulate; latex cells with guttapercha esp. in phloem of stems and leaves; vessels with simple perforations; hairs unicellular, simple; flowers unisexual, dioecious, naked; stamens 6—10; pollen grains 3-colpate (colpi unequal); carpels 2; pistil eusyncarpous, one locule abortive; stylodia separate; ovules 2, apical, pendulous, tenuinucellate; samara; bark with condensed tannins; iridoids present; types of iridoids (incl. ajugol, harpagide etc.) indicating relationship with Lamiales. — *Eucommiaceae.*

Cornales: woody or occas. herbaceous; leaves simple to compound, often opposite, usu. exstipulate; vessels often with scalariform perforations in woody members, usu. simple in herbaceous; flowers without epicalyx; sepals and petals usu. 4 or 5; synsepaly and sympetaly common; haplo- or obdiplostemony or numerous stamens (with centrifugal development); anthers usu. dehiscing longitudinally; pollen grains free, binucleate or trinucleate; intrastaminal disc esp. in haplostemonous taxa; pistil 2—5-carpellate, often with free stylodia; ovules crassi- to tenuinucellate; endosperm usu. cellular ab initio (except in Garryaceae and some Alangiaceae); often gallic and ellagic acids and leucoanthocyanins; saponins, resins and caffeic acid usu. absent. — *Garryaceae, Alangiaceae, Cornaceae* (incl. *Aucubaceae, Helwingiaceae, Griseliniaceae, Mastixiaceae, Melanophyllaceae* and *Curtisiaceae*), *Davidiaceae, Nyssaceae, Icacinaceae, Escalloniaceae, Columelliaceae, Stylidiaceae* (incl. *Donatiaceae*), *Hydrangeaceae, Alseuosmiaceae, Sambucaceae, Adoxaceae.* (Possibly also the monogeneric *Dulongiaceae, Tribelaceae, Eremosynaceae, Pterostemonaceae* and *Tetracarpaeaceae* belong here.)

Gentiananae

Woody or herbaceous; leaves usu. opposite, entire or compound, with or without stipules; vessels usu. with simple perforations (except, e.g. in Menyanthaceae); intraxylary phloem in some groups; flowers 5- or 4-merous, actinomorphous to zygomorphous or asymmetric, usu. bisexual, hypo- to epigynous; calyx often reduced and sometimes pappus-like; corolla sympetalous; stamens in one whorl alternating with petals, often only 1—4; pollen grains usu. 3-colporate, bi- or trinucleate (varible in several families); pistil 5—2-(usu. 2-)carpellate, usu. eusyncarpous, some locule(s) often aborted; ovules few to solitary in each locule, unitegmic, tenuinucellate; endosperm cellular ab initio or in Gentianales usu. nuclear; seeds with or without endosperm containing fatty oils and proteins but not starch; iridoids (chiefly seco-iridoids) usu. present; caffeic acid usu. present; tannins usu. lacking; triterpenes common.

Dipsacales: woody or herbaceous, usu. with opposite, simple or compound, exstipulate leaves; intraxylary phloem lacking; flowers usu. in determinate inflorescences, from actinomorphous to zygomorphous or asymmetric, epigynous, usu. 5-merous; epicalyx often present; calyx often reduced and/or pappus-like; petals never contorted in bud; stamens 5—1; pollen grains usu. 3-colpate or 3-colporate, usu. trinucleate; pistil 5—2-carpellate; one carpel often sterile; ovules few or 1 per locule; endosperm cellular ab initio; seeds with or without endosperm, rich in fatty oils; iridoids, caffeic acid and often saponins present. The order is possibly heterogeneous; Caprifoliaceae shows many similarites to Cornales. — *Caprifoliaceae, Valerianaceae, Triplostegiaceae, Dipsacaceae, Morinaceae, Calyceraceae* (position of last two families somewhat uncertain).

Oleales: woody; leaves usu. opposite, exstipulate, simple or compound; intraxylary phloem lacking; peltate and glandular hairs common; sclereids common in mesenchyma; stomata usu. anomocytic; flowers in determinate types of inflorescences, bisymmetric; perianth whorls 4-merous; stamens 2, transverse; pollen grains usu. binucleate; carpels 2; flowers occas. naked and unisexual; pollen grains free, usu. 3-colporate, binucleate; pistil 2-locular, with 1—2 ovules in each locule; endosperm cellular ab initio; seeds with or without endosperm; tannins, leucoanthocyanins, etc. lacking; ethereal oils in some genera; free terpenic acids common. — *Oleaceae.*

Goodeniales: herbs or shrubs; leaves usu. alternate, exstipulate; glandular and non-

glandular hairs and sclerenchymatous idioblasts present; stomata anomocytic or paracytic; laticiferous vessels absent (cf. Campanulanae); flowers hypo- or epigynous, 5-merous, zygomorphous; calyx 5-lobed; corolla 1- or 2-lipped; stamens 5; anthers free or connivent around style; pollen grains binucleate; pistil bicarpellate, 1—2-locular, style simple, widened in upper part into pollen-cup; each locule with 1 (or more) erect or ascending ovule; endosperm cellular ab initio; drupe, nut or capsule; seed with or without endosperm; calcium oxalate druses common; caffeic and chlorogenic acids and usu. ursolic acid present; saponins and inulin often accumulated. — *Goodeniaceae* (incl. *Brunoniaceae*).

Gentianales: woody or herbaceous; leaves usu. simple and entire, opposite or not, exstipulate or often with interpetiolar stipules; intraxylary phloem in some families; laticiferous ducts in Apocynaceae and Asclepiadaceae; inflorescences usu. determinate; flowers actinomorphous; petals often contorted in bud; pollen grains often in tetrads (often in pollinia), bi- or trinucleate; pistil bicarpellate, eusyncarpous or paracarpous or in ovary region secondarily apocarpous; ovules few to numerous; endosperm cellular or generally nuclear ab initio; seeds often rich in endosperm; embryo small; tannins lacking; seco-iridoids common (lacking in Asclepiadaceae); accumulation of aluminium and of alkaloids, especially indole alkaloids derived from iridoids common; cardenolides in Apocynaceae and Asclepiadaceae; caffeic acid common (except in Gentianaceae). — *Loganiaceae* (incl. *Antoniaceae, Spigeliaceae, Strychnaceae* and *Potaliaceae*), *Buddlejaceae* (alt.: in Scrophulariales), *Retziaceae, Rubiaceae* (incl. *Theligonaceae*), *Menyanthaceae, Gentianaceae, Apocynaceae, Asclepiadaceae* (incl. *Periplocaceae*).

Loasanae

Herbs or occas. shrubs, often climbers; leaves alternate or opposite, exstipulate; trichomes variable, incl. simple, hook-like or stinging types; cystoliths common; intraxylary phloem lacking; vessels with simple perforations; inflorescence usu. determinate; flowers actinomorphous, bisexual, usu. epigynous, usu. 5-merous; petals usu. free, occas. basally connate; stamens 5, 5+5 or secondarily numerous; staminodia present in some genera; pollen grains variable, colpate, colporate or porate, binucleate; pistil usu. 3—5-carpellate, usu. unilocular, with parietal placentas; ovules hemianatropous to anatropous, unitegmic, tenuinucellate; endosperm cellular ab initio, with terminal haustoria; capsule or nut; seeds with endosperm containing oil and fat; tannins lacking; caffeic acid, iridoids and druses of calcium oxalate found in leaves.

Loasales: *Loasaceae*.

Lamianae

Woody or herbaceous; leaves alternate or opposite (or in whorls), exstipulate; intraxylary phloem usu. lacking; vessels usu. with simple perforations; flowers usu. hypogynous, generally zygomorphous (or strongly reduced); sepals and petals 5-merous (but often bilabiate); synsepaly and sympetaly (naked and monochlamydous forms occur esp. in the small orders); staminal whorl alternating with petals, usu. reduced to 4 or 2 (occas. 1) stamens; pollen grains variable, binucleate or trinucleate; gynoecium usu. bicarpellate, 1-, 2- or (secondarily) 4-locular; style usu. simple; ovules 1, 2 or numerous per carpel, unitegmic, tenuinucellate; endosperm usu. cellular ab initio, often with terminal haustoria, occas. helobial; fruit often a capsule or 4-partite schizocarp; seeds with or without endosperm; with fatty oils; tannins and polyphenolics incl. ellagic acid, myricetin and leucoanthocyanins lacking; caffeic acid, ferulic acid and triterpenes common; iridoids (but not seco-iridoids) present in most families (Hydrostachyales not known in this respect).

Scrophulariales: woody or herbaceous; some parasites or semiparasites; leaves opposite or alternate; intraxylary phloem rare; inflorescences usu. thyrses, racemes or spikes; flowers usu. zygomorphous, usu. 5-merous (Plantaginaceae 4-merous); stamens usu. 4 or 2; pollen grains usu. binucleate; colporate or porate; pistil bicarpellate, bilocular or sometimes unilocular; ovules 1 to numerous per carpel; endosperm usu. with micropylar and chalazal haustoria; fruit variable, usu.

a capsule, never a 4-partite schizocarp; seeds with fatty oils; saponins and stachyose common. — *Scrophulariaceae, Selaginaceae, Globulariaceae, Lentibulariaceae, Plantaginaceae, Pedaliaceae, Trapellaceae, Martyniaceae, Orobanchaceae, Gesneriaceae, Bignoniaceae, Henriqueziaceae, Myoporaceae, Acanthaceae* (incl. *Thunbergiaceae* and *Mendonciaceae*).

Hippuridales: erect, aquatic herb; leaves in whorls of 6—12, linear, entire; peltate hairs with multicellular head present; flowers small, in leaf axils, often bisexual (but also unisexual, male or female), epigynous; ovary monocarpellate, subapically with one slightly lateral style, one stamen and a small, simple 2—4-lobate perianth borne near the top of the ovary; pollen grains 4—6-colpate, trinucleate; one locule with one apical, pendulous ovule; with suspensor haustorium but not endosperm haustoria; small drupe with endospermless seed; embryo large; caffeic and ferulic acids present; iridoids of same type as in Scrophulariales (aucubin). — *Hippuridaceae.*

Hydrostachyales: partly submerged freshwater aquatics with short, tuber-like stem; leaves in rosette, simple or divided 1—3 times, partly covered with scale-like excrescences; inflorescence spicate, on unbranched leafless peduncle with a ring of vascular bundles; flowers naked, unisexual, each in the axil of a bract, usu. with a tuft of hairs on each side; male with one stamen, its extrorse anther longitudinally divided into two monothetic halves; pollen grains in tetrads, probably inaperturate, binucleate; pistil bicarpellate, paracarpous, with 2 parietal placentae and 2 free stylodia; ovules several to numerous; endosperm with micropylar haustorium; small capsule with numerous, small, endospermless seeds; druses of calcium oxalate in vegetative parts. — *Hydrostachyaceae.*

Lamiales: woody or herbaceous; leaves opposite; plants usu. covered with glandular hairs containing ethereal oils; stems often quadrangular; inflorescence usu. a thyrse or raceme; flowers hypogynous, actinomorphous or usu. zygomorphous, often bilabiate; stamens 5 or usu. 4 or 2; pollen grains usu. 3- or 6-colpate, bi- or trinucleate; pistil usu. bicarpellate; style usu. simple, often gynobasic; ovules 2 per carpel, with micropyle directed downwards; usu. drupe or 4-partite schizocarp with one-seeded mericarps; seeds rich in fatty oils (in Lamiaceae often with linolic and linolenic acids); tendency to produce essential oils in glandular hairs and to produce and accumulate diterpenes; otherwise chemically similar to Scrophulariales. — *Verbenaceae* (incl. *Stilbaceae*), *Callitrichaceae, Lamiaceae* (incl. *Tetrachondraceae*).

Caryophyllanae

Mostly herbs; succulents common; abnormal secondary growth common; vessels with simple perforations; sieve tube plastids with characteristic protein bodies; inflorescences mainly determinate; flowers usu. actinomorphous, hypogynous to epigynous, usu. 4—5-merous; perianth variable; involucre occas. present; sepals nearly always present, usu. green, occas. (in Portulacaceae) deeply bilabiate; petals (or petaloid staminodia) of various types, cyclic or spirally set; haplo- or diplostemony or numerous centrifugally developing stamens; pollen grains variable, often polyporate, trinucleate; pistil usu. syncarpous, 2—5-carpellate, unilocular with central placentation or sometimes otherwise; ovules campylotropous or amphitropous, usu. bitegmic, crassinucellate; endosperm nuclear ab initio; seeds usu. with curved embryo encircling a richly developed perisperm with compound starch grains; plants with betalains instead of anthocyanins (except in Caryophyllaceae and perhaps Molluginaceae); tendency of accumulating acids, esp. oxalic acid; saponins common; pinitol present in some families (absent in Amaranthaceae, Chenopodiaceae and Portulacaceae); alkaloids occasional.

Caryophyllales: *Phytolaccaceae, Agdestidaceae, Stegnospermataceae, Achatocarpaceae, Nyctaginaceae, Aizoaceae, Molluginaceae* (? distinct from preceding), *Didiereaceae, Cactaceae, Portulacaceae, Hectorellaceae, Basellaceae, Chenopodiaceae, Dysphaniaceae, Halophytaceae, Amaranthaceae, Caryophyllaceae.*

MONOCOTYLEDONEAE

Alismatanae

Chiefly aquatic herbs, often with rhizomes; leaves linear, band-like or differentiated into petiole and lamina; intravaginal stipules frequent; stomata usu. lacking

or when present the neighbouring cells with or without oblique divisions; schizogenous ducts in some families; flowers from actinomorphic, with 3+3 (or more) stamens and 3 (or more) carpels, to reduced, naked, unisexual, sometimes with one stamen or one carpel only; perianth in some families regarded as functionally replaced by laminar connective outgrowths; filaments narrow, with apical microsporangia; pollen grains with one or no apertures, free or in tetrads, usu. trinucleate; apocarpy; placentation laminal or submarginal; ovules usu. bitegmic, crassi- or pseudocrassinucellate; endosperm formation helobial or sometimes nuclear; nutlets or follicles; seeds without endosperm; leucoanthocyanins rare or absent.

Alismatales: secretory ducts present; flowers hypogynous, in panicles or similar inflorescences, usu. with 3 greenish to white outer tepals ("sepals") and 3 whitish to pink, petaloid inner ones; pollen grains 2—30-porate; carpels 3 to numerous, with laminar to laminar-basal placentation; ovules 1 or more, pseudocrassinucellate; embryo sac bisporic; follicles or nuts; seeds with horseshoe-like, curved embryo; rhizomes with starch and sugars; no anthocyanin pseudobases. — *Alismataceae, Limnocharitaceae.*

Hydrocharitales: secretory ducts lacking; flowers solitary or in cymose inflorescences, often enclosed by a spathe, hypo- or usu. epigynous, often unisexual and dioecious; tepals usu. 3+3, outer 3 often sepaloid, occas. (Aponogetonaceae) 1—3 (by reduction); stamens in one or more, usu. 3-merous whorls; pollen grains usu. with one distal aperture; apocarpy in hypogynous flowers; placentation laminal to lateral or basal; ovules usu. several to numerous, usu. anatropous and bitegmic (unitegmic in some Aponogetonaceae), crassinucellate; embryo sac monosporic; fruit variable; seeds with straight embryo; anthocyanin pseudobases often present. — *Butomaceae, Hydrocharitaceae, Aponogetonaceae.*

Zosterales: leaves variable, usu. stipulate; secretory ducts common in leaves; hairs and stomata usu. lacking; flowers bi- or unisexual; naked (except, perhaps, in Scheuchzeriaceae), perianth then sometimes functionally replaced by what is considered to be petal-like outgrowths from connectives; stamens 3+3 or fewer, sometimes only 1; pollen grains simple or in dyads or tetrads, globose to thread-like, inaperturate; carpels 6—1, free or slightly fused in centre; ovules usu. 1—2, atropous or anatropous, crassi- or pseudocrassinucellate; embryo sac monosporic; follicles, nutlets or schizocarp; calcium oxalate usu. lacking; rhodoxanthin sometimes present; anthocyanin pseudobases probably lacking; cyanogenic compounds found in the first two families. — *Scheuchzeriaceae, Juncaginaceae, Potamogetonaceae* (incl. *Ruppiaceae*), *Zosteraceae, Posidoniaceae, Zannichelliaceae, Cymodoceaceae.*

Najadales: fresh- and brackish-water plants; branching at least partly sympodial; leaves subopposite (!), linear, often toothed, dilated at base, with intravaginal scales; stomata lacking; flowers terminal (?), unisexual, usu. monoecious; male basally with 2 scales (bracteoles), consisting otherwise of an almost sessile anther enclosed in a thin, apically 2-lobate, flask-shaped sheath (perianth?); pollen grains ellipsoidal, inaperturate; female flowers usu. naked, consisting perhaps of one carpel, but apically with 2—4 stylar branches; ovule solitary, basal, anatropous, crassinucellate; nutlet; seed with reticulate testa. — *Najadaceae.*

Lilianae

Herbs or somewhat woody plants without or occas. with abnormal secondary thickening growth; leaves usu. linear or lanceolate, occas. petiolate, alternate (rarely opposite); neighbouring cells of stomata with or without divisions, these oblique or non-oblique; vessels usu. present in root only (or lacking altogether); flowers 3-merous; tepals usu. 3+3, usu. of similar colour and texture in the two whorls; stamens 3+3, 3 or less, free or connate; pollen grains usu. with one (occas. 2—3) aperture(s), usu. binucleate (except in some parasitic groups and one genus of Bromeliales); pistil usu. 3-carpellate, usu. para- or eusyncarpous, occas. apocarpous or almost so (mainly Triuridales); ovules usu. bitegmic, crassinucellate, pseudocrassinucellate or (Orchidales, Burmanniales, Triuridales, etc.) tenuinucellate; endosperm not formed in Orchidales, otherwise nuclear or often helobial ab initio; endosperm when present usu.

without starch; steroidal saponins and leucoanthocyanins very common.

Dioscoreales: climbers and creepers; usu. with thick tubular rhizome rich in starch and with abnormal secondary thickening; vascular strands often in one or more rings; leaves often opposite, simple, to digitately compound, petiolate, rarely stipulate; trichomes and glands variable; stomata: neighbouring cells with irregular divisions; idioblasts with resin or tannins common; flowers small, usu. unisexual; stamens 3 or 3+3, in former case 3 staminodes; connective tip often extended; pollen grains with 1, 2, 3 or 4 variable apertures; ovary 3-locular; ovules 2 or more per carpel, usu. crassinucellate; embryo sac monosporic; endosperm nuclear ab initio; capsule or berry; seeds often winged; endosperm with cellulose; embryo occas. with terminal plumula; steroidal saponins and tropane alkaloids as well as leucoanthocyanins and other polyphenolics (incl. tannins) common; raphides common. — *Dioscoreaceae* (incl. *Stenomeridaceae* and *Trichopodaceae*).

Stemonales: erect or climbing perennial herbs with rhizome; leaves alternate, opposite or whorled; flowers hypogynous; tepals 2+2, 3+3 or 4+4, green or coloured; stamens of same number as tepals, often flat; connective projecting beyond the latrorse or introrse thecae; pistil of 2—5 carpels, either unilocular with parietal placentas or 3—5-locular with central placentas; septal nectaries lacking; ovules 2—many, with multilayered outer integuments; endosperm formation nuclear or helobial; berry or capsule; seeds often with elaiosome formed from raphe or hilum; seeds rich in endosperm containing fat and aleurone and also often starch, but not cellulose; certain alkaloids and poisonous saponins (with diosgenin as sapogenin) known in the order. — *Stemonaceae* (incl. *Croomiaceae*), *Trilliaceae*.

Asparagales: herbs or shrub-like plants, occas. with abnormal secondary thickening growth; bulbs, rhizomes or roots serving as storage organs; vessels restricted to roots, with scalariform to simple perforations; leaves often succulent; raphides of calcium oxalate and mucilage cells common; stomata: neighbouring cells usu. with divisions, oblique or non-oblique; flowers usu. pentacyclic; tepals 3-merous, *not* with variegated pattern of drop-like dots, outer and inner similar, basally without nectaries (except in Philesiaceae); anthers usu. basi- or dorsifixed, usu. introrse; pollen grains usu. with one aperture; gynoecium syncarpous; carpels 3, usu. with septal nectaries; ovules crassi-, pseudocrassi- or tenuinucellate; outer layer of testa black, incrusted with melanin layer; inner integument collapsed in testa; embryo sac bi- or monosporic; endosperm nuclear or helobial ab initio; fruit usu. berry or capsule; endosperm seldom with starch; saponins, calcium oxalate (esp. raphides) and chelidonic acid common; alkaloids in some families. — *Smilacaceae, Philesiaceae* (incl. *Luzuriagaceae* and *Petermanniaceae*), *Ruscaceae, Convallariaceae, Asparagaceae, Dracaenaceae* (incl. *Nolinaceae, Asteliaceae* and *Dianellaceae*), *Hypoxidaceae, Tecophileaceae* (incl. *Walleriaceae, Cyanastraceae* and *Eriospermaceae*), *Phormiaceae, Xanthorrhoeaceae* (incl. *Dasypogonaceae*), *Aphyllanthaceae, Asphodelaceae, Anthericaceae, Ixioliriaceae, Agavaceae, Phormiaceae, Hemerocallidaceae, Hyacinthaceae, Alliaceae, Amaryllidaceae*.

Taccales: perennial herbs with tubercular rhizome rich in starch; vessels with scalariform perforations present in roots; leaves usu. in basal rosette, petiolate, entire or deeply dissected, with parallel nerves and anastomosing side-veins; flowers in sympodial umbel-like inflorescences; involucre usu. of 4 broad leaves; bracts long and filiform; flowers epigynous; tepals 3+3, similar; stamens 3+3; anthers short, broad, introrse, with conspicuous connective; filaments short, epitepalous; anther walls formed almost as in dicotyledons; pollen grains with one aperture; ovary unilocular; placentas parietal; inner integument multilayered; fruit berry-like but dehiscing irregularly; seeds with horny endosperm containing fat and aleurone. — *Taccaceae*.

Haemodorales: terrestrial or (Pontederiaceae) aquatic herbs; leaves distichous, linear or with petiole and lamina; stomata usu. with neighbouring cells with or without oblique divisions; glandular hairs and raphides often present; vessels often with scalariform perforation; flowers usu. zygomorphous; tepals 3+3, hypo- or epigynous, petaloid, often fused into tubular or bilobate structures; stamens 3+3, 3 or 1 plus staminodes; pollen grains usu. with 2—3 apertures, occas. in tetrads; gynoecium eusyncarpous, 3-carpellate; septal nectaries usu. present; ovules usu. crassinucellate; embryo sac monosporic; endosperm formation helobial; nut or capsule; endosperm with starch; embryo small; chemistry little known, the order possibly heterogeneous. — *Haemodoraceae* (incl. *Conostylidaceae*), *Pontederiaceae, Philydraceae*.

Liliales: mostly herbs, without secondary thickening; rhizomes and bulbs in most taxa;

roots usu. *not* thick storage organs (except in Alstroemeriaceae); leaves usu. *not* succulent and not differentiated into petiole and lamina; stomata: neighbouring cells apparently usu. without divisions; vegative organs usu. *not* with raphides or mucilage in cells or ducts; inflorescence usu. terminal on shoot; flowers 5- or 4-cyclic; tepals in two whorls, outer and inner similar or dissimilar, often variegated with drop-shaped dots; nectaries usu. present at base of tepals (septal-nectaries usu. lacking); stamens 3+3 or 3; anthers basi- or medifixed, introrse or extrorse; pollen grains with one aperture; carpels 3; apo- or usu. syncarpy; ovules usu. numerous, crassi- or tenuinucellate; endosperm formation nuclear or helobial; fruit never a berry; seeds never with dark melaniferous testa, its inner integument intact; endosperm without starch; alkaloids largely absent; steroidal saponins usu. present (except in some Alstroemeriaceae). — *Colchicaceae, Iridaceae* (incl. *Geosiridaceae*), *Alstroemeriaceae, Liliaceae* (incl. *Calochortaceae*), *Melanthiaceae* (incl. *Petrosaviaceae* and *Tricyrtidaceae*).

Triuridales: small, chlorophylless, whitish, yellow, red or violet saprophytes with mycorrhiza; leaves small, bract-like; flowers in cymose inflorescence, small, actinomorphous, usu. unisexual, with 3 or 6(—10) tepals sometimes extended into tails; stamens 3 or 6, with short filaments; pollen grains smooth, inaperturate, trinucleate; apocarpy; carpels free, small, numerous, developing into small nutlets or follicles; ovules tenuinucellate; embryo sac monosporic; endosperm nuclear ab initio; seed endosperm with protein and fat. — *Triuridaceae.*

Burmanniales: autotrophic or saprophytic, with or without chlorophyll; probably with mycorrhiza; leaves linear (when green) or bract-like (when chlorophylless); flowers solitary and often terminal or in various inflorescences, actinomorphous or occas. (Corsiaceae) zygomorphous, always epigynous; tepals 3+3, similar or usu. dissimilar in the two whorls, often with bizarre projections; stamens 3+3 or 3, free or united with tepal tube; pollen grains free, without or with 1(—3) aperture(s), bi- or trinucleate; ovary 3- or 1-locular, with central or parietal placentation; ovules numerous, tenuinucellate; embryo sac bisporic; endosperm formation helobial (or sometimes cellular ?); capsule; seeds diminutive, with little endosperm. — *Burmanniaceae, Corsiaceae, Thismiaceae.*

Orchidales: perennial herbs; roots or stem often swollen storage organs; leaves linear to circular; stomata: neighbouring cells variable, with or without divisions, these usu. oblique; raphides of calcium oxalate common; mucilage cells particularly in succulent taxa; flowers usu. zygomorphous, solitary or in spike; usu. bisexual; tepals 3+3, inner median one usu. forming a labellum (directed downwards by resupination); this or other tepals often with a spur; stamens 3, 2 or usu. 1 (= the lateral of inner whorl or the median of outer whorl or both); stamens united with style to a gynostegium; pollen grains free, in tetrads, in massulae, or in pollinia; stigmatic lobes 3, one often sterile, extended into a rostellum; ovary 3- or 1-locular; ovules numerous, tenuinucellate; embryo sac mono- or bisporic; endosperm usu. not formed at all; glucosides and alkaloids rich. — *Apostasiaceae, Cypripediaceae, Orchidaceae.*

Bromeliales: herbs, often with large, coarse leaf rosette; leaves linear or lanceolate, sessile, often serrate and xeromorphous, sometimes stiff or tough; stomata: neighbouring cells as far as known with oblique divisions; vessels with simple or occas. scalariform perforations; flowers actinomorphous, hypo- or epigynous; tepals 3+3, similar or dissimilar; stamens 3+3 to numerous; pollen grains occas. in tetrads, with 1 or occas. 2 apertures, bi- (or occas. tri-)nucleate, gynoecium syncarpous, 3-locular; septal nectaries usu. present; ovules numerous, crassi- or pseudocrassinucellate; embryo sac monosporic; endosperm formation (where known) helobial; berry or capsule; endosperm rich in starch, lacking fat; embryo small; alkaloids lacking; steroidal saponins sometimes present. The order approaches Commelinales (Commelinanae) in e.g. the starchy endosperm. — *Bromeliaceae, Velloziaceae.*

Typhanae

Glabrous, perennial herbs with creeping, starch-rich rhizome; leaves distichous, linear; stomata: neighbouring cells with oblique divisions; mucilage cells in vegetative parts; calcium oxalate as raphides and in other forms; inflorescence unbranched or branched, with spikes or heads, upper with male, lower with female flowers, these hypogynous, with 3+3 tepals or naked (though then with numerous scattered trichomes); stamens usu. 2, 3 or 6; anthers extrorse; connective distally broad; pollen grains occas. in tetrads, with one aperture, binucleate; gy-

noecium monocarpellate, with one pendulous, anatropous, bitegmic, crassinucellate ovule; endosperm formation helobial; drupe or nutlet; endosperm with starch, aleurone and fatty oil; embryo small, straight; plants rich in polyphenolics such as leucoanthocyanins and tannins.

Typhales: *Sparganiaceae, Typhaceae.*

Zingiberanae

Often large, occas. tree-like, usu. glabrous herbs with starch-rich rhizomes; leaves petiolate, with broad, usu. lanceolate or linear-oblong, pinnately veined lamina; sheaths occas. forming a "false stem" (in Musaceae); stomata: neighbouring cells with divisions, non-oblique or usu. oblique; silicate cells (stegmata) and raphides sometimes present; inflorescence usu. with monochasial units; flowers zygomorphous or asymmetric, usu. epigynous; tepals 3+3, often inconspicuous, outer usu. smaller than inner; syntepaly common; stamens 6—5 or reduced to 1, in latter case (1—)3—5 often transformed into large, showy petaloid staminodia; pollen grains with one or no aperture, binucleate; pistil eusyncarpous or paracarpous; carpels 3; ovules usu. numerous, crassinucellate; embryo sac usu. monosporic; endosperm helobial or nuclear ab initio; seeds arillate, with peri- and endosperm rich in starch; calcium oxalate present in diverse forms; silicic acid common; ethereal oil present in vegetative parts and testa in Zingiberaceae; polyphenolics such as leucoanthocyanins and flavonols common.

Zingiberales: *Lowiaceae, Heliconiaceae, Musaceae, Strelitziaceae, Zingiberaceae, Costaceae, Marantaceae.*

Commelinanae

Herbs and graminids, often tufted; stem often hollow, with compact nodes; leaves usu. linear, generally with basal sheath, almost never with distinct petiole and lamina; hyaline ligula common at edge of sheath; stem usu. with vessels; stomata: neighbouring cells nearly always with non-oblique divisions; epidermis cells often with silicate bodies; inflorescences spikes, heads or cymose assemblages; flowers entomogamous or usu. anemogamous, hypogynous; perianth members 3+3, 3 or less than 3, often lacking (differentiated into sepals and petals in Commelinales); stamens 3+3, 3, or less; pollen grains single or in tetrads, usu. with one aperture, generally trinucleate (except at least, in Commelinales and some genera of Cyperales); pistil 3-, 2- or possibly 1-carpellate; ovules usu. bitegmic, crassi-, pseudocrassi- or tenuinucellate; endosperm usu. nuclear ab initio (except at least in Juncales); seeds with endosperm rich in starch; saponins and alkaloids sporadic or lacking.

Commelinales: perennial herbs; leaves entire, usu. linear to lanceolate, sheath closed; mucilage ducts and raphides of calcium oxalate at least in Commelinaceae; only druses or single crystals known in the other families; vessels present in stem; flowers usu. bisexual, actinomorphous to zygomorphous; tepals usu. 3+3, outer usu. green and sepaloid or hyaline, inner petaloid; stamens usu. 3+3; anthers basifixed; pollen grains with 1 (occas. 0 or 3) apertures; pistil 3-carpellate, 3-locular; style single; stigmas 1—3; placentation usu. central; ovules crassi- or tenuinucellate; embryo sac mono- or bisporic; fruit usu. a loculicidal capsule; endosperm rich in starch, protein and often oil; embryo small, undifferentiated, apical, often separated from endosperm. — *Commelinaceae, Cartonemataceae, Mayacaceae, Xyridaceae, Abolbodaceae, Rapateaceae.*

Eriocaulales: annual or perennial herbs with rosettes of usu. spirally set, linear or filiform leaves; crystal raphides lacking; flowers numerous, small, unisexual, monoecious or dioecious, in pedunculate heads enclosed by an involucrum; flowers usu. actinomorphous; tepals 3+3 or 2+2; outer dry, chaffy, inner scarious to hyaline; stamens half the number of or in same number as tepals; pollen grains spiraperturate; style with 2—3 or more branches; pistil 2—3-locular; each locule with one tenuinucellate ovule; small loculicidal capsules; seeds with well-developed, mealy endosperm rich in starch. — *Eriocaulaceae.*

Juncales: graminids, usu. tufted, usu. either annuals or rhizomatous perennials; leaves usu. tristichous, narrow, flat or terete, with open or closed sheath, often with ligule; flowers usu. anemophilous, bisexual, in cymose inflorescence; bracteoles often several per flower; tepals 3+3, bract-like, of similar texture, green to brown or black, often marginally hyaline; stamens 3+3, free; pollen grains in tetrads, trinucleate, with one aperture; pistil 3-carpellate, 3- or 1-locular; stylodial branches 3; ovules crassinucellate; endosperm formation helobial; capsule loculicidal; seeds often with elaiosome; endosperm enclosing the small, straight embryo; tannins common; calcium oxalate lacking; silicic acid rich; anthocyanins lacking, replaced by glucosides of luteolinidin. — *Juncaceae, Thurniaceae.*

Cyperales: graminids, usu. herbaceous, often rhizomatous, normally with 3-angular to terete, marrow-filled stem; leaves usu. tristichous, narrow, with closed sheath; epidermis cells often with silicate bodies of conical shape; stomata of poaceous type; spikelets, often in compound systems; flowers (or flower-like synanthia) uni- or bisexual, naked or with 3, 3+3 or numerous scales, bristles or hairs; stamens usu. 3 or less, with thin filaments; 3 microspores in each tetrad degenerating and incorporated in wall of fourth which becomes a functional pollen grain; this bi- or trinucleate, with one aperture; pistil 2—3-carpellate, unilocular, with 2—3 long stigmatic branches; locule with one basal, anatropous, crassinucellate ovule; endosperm nuclear ab initio; nutlet; endosperm starchy; embryo basal; tanniferous cells common; calcium oxalate absent or rare. — *Cyperaceae.*

Centrolepidales: graminids, usu. annual and growing in tufts; leaves not distichous, concentrated basally; stomata of poaceous type; silicate bodies and calcium oxalate probably lacking; inflorescence usu. a short spike or head with distichous bracts; these in their axils with male or female flowers or bisexual (? flowers or) synanthia, the flowers usu. interpreted as being unisexual, naked and assembled in small synanthia with 1—3 hyaline bracts; male interpreted as consisting of a single tetra- or bisporangiate (or 2—1 bisporangiate) anther(s); pollen grains monoporate, 2-(? or 3-)nucleate; female flowers usu. interpreted as monocarpellate; carpels 2 or more together on same or different levels; ovule one per carpel, pendulous, orthotropous, pseudocrassinucellate (or crassinucellate); endosperm probably nuclear ab initio; fruit usu. dehiscent; endosperm starchy; embryo peripheral. — *Centrolepidaceae.*

Poales: graminids, usu. with hollow stems; leaves distichous, band-like; sheath usu. open, with membranous ligule; stomata: neighbouring cells usu. with non-oblique divisions; one small subsidiary cell on each side of the stoma; "short cells" present, with rounded, saddle-shaped or quadratic (but not conical) bodies of silicate; bracts of spikelets usu. distichous, lowest two usu. empty (= "glumes"), others floriferous (= "lemmae"), opposite these usu. 2-keeled "paleae" (bracteoles or product of 2 outer tepals); flowers usu. bisexual; tepals 3+3 or usu. 3—2 and small ("lodiculae"); stamens 3+3 or usu. 3 (—2 or 1); pollen grains with one usu. circular aperture, usu. trinucleate; ovary 3- or usu. unilocular, with 3 or usu. 2 stigmatic branches; ovule solitary, basal to apical, usu. pseudocrassinucellate; embryo sac monosporic; endosperm nuclear ab initio; berry, nutlet or usu. caryopsis; embryo small, lateral; endosperm large, rich in simple or compound starch grains; calcium oxalate absent or scanty; cyanogenic compounds common; leucoanthocyanins lacking; coumarin and silicic acid generally present. — *Restionaceae* (incl. *Anarthriaceae*), *Ecdeiocoleaceae, Flagellariaceae, Joinvilleaceae, Poaceae.*

Arecanae

Tree-like or usu. at least large plants; usu. with woody stem, but secondary growth usu. lacking or weak; leaves usu. large, simple or secondarily divided; frequently fan- or feather-like or 2-cleft; vessels present in stem, with scalariform or simple perforations; raphides and simple crystals of calcium oxalate usu. present; stomata: neighbouring cells usu. with non-intersecting oblique divisions; stegmata of silicic acid in Arecaceae only; inflorescence usu. a compound panicle or spike; flowers usu. small, hypogynous, usu. with 3+3, 4, 3 or no tepals; stamens numerous, 9, 6, 3 or less, free or united in various ways; pollen grains with one circular or tripartite, occas. 2 aperture(s), binucleate; carpels variable, often 3 or 4, free or fused in various ways; ovules bitegmic, usu. crassinucellate; endosperm

probably mostly nuclear ab initio; endosperm copious, horny, rich in fat, protein and often hemicellulose; condensed tannins and other polyphenolics such as leucoanthocyanins common in Arecales and Cyclanthales, saponins in Arecales.

Arecales: trees, shrubs or lianes with monopodial growth; aerial stem often unbranched; leaves usu. in rosette; lamina entire in juvenile stage, divided and feather- or fan-like in adult stage; "lobes" V- or A-shaped in transection; leaf base often with ligule ("hastula"); isodiametric "stegmata" with silicic acid often present (resemblance to Poales!); flowers in simple or compound panicles or spadices, relatively small, usu. actinomorphous and unisexual; tepals 3+3, 9 or more; pollen grains with one pore or 3-lobate aperture; carpels 3, free or united; locules usu. separate; berry or drupe; seeds large; endosperm well developed, rich in fat, aleurone and cellulose; embryo small, lateral, with cotyledonary haustorium; calcium oxalate and silicic acid common. Many similarities to Poales and possibly closely related with this. — *Arecaceae.*

Pandanales: dioecious trees, shrubs or lianes, often with supporting aerial roots; strong primary and partially secondary growth, but not formed from a continuous cambium ring; leaves usu. narrow, often marginally dentate, in rosettes; raphides and mucilage cells or ducts common; inflorescences spadix, head or panicle, supported by spathe rich in ethereal oils; flowers naked or occas. with rudimentary tepals; stamens on a peltate or otherwise-shaped floral axis; pollen grains monoporate; female flowers with few to numerous carpels, para- or eusyncarpous; embryo sac mono- or bisporic; berries or drupes; seeds with endosperm containing oil and protein; embryo small; tannins and polyphenolics absent. — *Pandanaceae.*

Cyclanthales: large perennial herbs or somewhat woody plants or lianes; leaves usu. alternate, petiolate, with broad, usu. 3-nerved, usu. 2-cleft lamina, mucilage ducts occas. present; spadix unbranched, monoecious, with male and female flowers alternating in groups or rings on the surface; male flowers with 6 or more basally united stamens; tepals irregular or rudimentary; pollen grains free, with 1—2 apertures; female flowers usu. with 4 carnose tepals alternating with the 4 stylar lobes of a paracarpous pistil; ovules numerous, pseudocrassinucellate; endosperm formation helobial; fruits berry-like, seeds small, rich in horny endosperm containing fat and aleurone; embryo small; saponins and polyphenolics common. In chemical characters intermediate between Arales and Arecales. — *Cyclanthaceae.*

Aranae

Mostly herbs with rhizomes rich in starch, occas. root climbers, epiphytes and aquatics; some strongly reduced and rootless; leaves usu. alternate and petiolate, with entire (seldom lobate or compound) lamina; stomata: neighbouring cells usu. with divisions; stomata "paracytic", "tricytic", etc.; trichosclereids common; laticiferous (usu. rows of intact) cells in some genera; calcium oxalate occurring as raphides, druses, etc.; cells containing ethereal oils occas. present; inflorescence a carnose spadix basally supported by a spathe; flowers minute, bi- or unisexual, usu. with 3+3 or 2+2 or no tepals, these when present usu. prismatic or scale-like; stamens from 3+3 to 1; pollen grains with variable number (1—4) and character of apertures; bi- or trinucleate; pistil monomerous or 2—3-merous and eusyncarpous; ovules bitegmic, varying in number, appearance and position; nucellus variable; endosperm cellular ab initio (!), with chalazal haustorial cell; seeds with or without endosperm; plants occas. with ethereal oil in cells or schizogenous ducts or cavities; calcium oxalate, polyphenolics and cyanogenic compounds common.

Arales: *Araceae, Lemnaceae.*

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Iridoid Compounds, Their Occurrence and Systematic Importance in the Angiosperms

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Naturally occurring iridoid compounds are divided into ten groups on biosynthetic grounds, demonstrated or postulated. Iridoid-bearing genera of plants are tabulated according to the iridoids found in them.

Iridoid compounds are found in thirteen orders within the superorders Hamamelidanae, Cornanae, Gentiananae, Loasanae and Lamianae (sensu DAHLGREN). The mutual relationships of the orders are discussed with regard to the groups of iridoids found, together with other characters. Arguments for a monophyletic origin of these orders are presented, and the traditional "Sympetalae" is rejected as a natural group.

The results of an investigation for iridoids in 44 species from 36 families are recorded in an appendix. Iridoid glucosides have been detected or identified for the first time in the families Retziaceae, Dipsacaceae, Calyceraceae, Roridulaceae, Stylidiaceae, Sarraceniaceae and Goodeniaceae. Comments on the systematic position of the last four families are presented.

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The iridoids (for general structure see Fig. 1) form a homogeneous group of monoterpenoid compounds that are found as constituents of a number of orders in the dicotyledons.

The presence of compounds such as these in a given group of plants is considered by many taxonomists (e.g. HEGNAUER 1966 b, 1969, 1971, KUBITZKI 1969, MEEUSE 1970, BATE-SMITH 1972, BATE-SMITH and SWAIN 1966) to be a valuable (chemical) character. It is used together with other characters to relate all iridoid-containing taxa and thus suggesting a common origin for them.

On account of the abundant occurrence of iridoids in certain orders of the "Sympetalae" (e.g. Gentianales, Lamiales, Scrophulariales) and their complete absence in others (e.g. Asterales, Campanulales), HEGNAUER (1964 p. 544), using additional chemical evidence, argued for a revision of this subclass (Asteridae) of TAKHTAJAN's system (1959).

KUBITZKI (1969) has made use of the presence of iridoids as an important character connecting the Rosalian and the Guttiferalian complexes. In CRONQUIST's system (1968) these are both derived from Magnoliidae which, however, completely lacks iridoids. The presence of iridoids in some parts of the traditional Rosiflorae and their absence in other parts, has been used by MEEUSE (1970) in support of a polyphyletic origin for the dicotyledons.

The distribution of ellagic acid in dicotyledons has been extensively studied by BATE-SMITH (1972) who also recognized the presence of iridoids as a taxonomically valuable character, partly over-

lapping with and partly complementary to ellagic acid in distribution.

The aims of the present study are: (1) to give a survey of the different types of iridoids occurring in nature and as far as possible to classify them on biosynthetic grounds; (2) to give an account of and to evaluate the distribution of iridoids in general, as well as of the various groups within them, as found in the angiosperm system (of DAHLGREN 1975), and finally (3) to make use of the iridoids in conjunction with other categories of characters (morphological, embryological, anatomical, palynological and additional chemical characters) to re-evaluate the position of certain plant groups.

This paper will bring up to date information on the iridoids found in higher plants. For the occurrence of iridoid glucosides reported before 1971 we have quoted from the reviews of PLOUVIER and FAVRE-BONVIN (1971) and CORDELL (1974). In addition, the current literature has been covered up to the end of 1974. Data on iridoid alkaloids are taken from SNIECKUS (1968) and BROSSI et al. (1971) supplemented by WILLAMAN and LI (1970), HEGNAUER (1973 pp. 137 & 731, Rubiaceae) with additional more recent data.

Finally, a limited number of species have been investigated experimentally by the authors. Most of them were selected because of their similarities to iridoid-containing groups, using the DAHLGREN (1975) system.

IRIDOIDS: BIOSYNTHETIC CLASSIFICATION AND OCCURRENCE

Biosynthesis and Definition

The iridoids are terpenoid in origin. Numerous experiments making use of the in vivo incorporation of radioactive compounds have established that mevalonic acid (**1**, Fig. 1) is a precursor of the iridoid compounds (INOUYE 1971, CORDELL 1974, GROSS 1970). Geranyl pyrophosphate (**2**) is an intermediate in the formation of the "basic" iridoid skeleton depicted as **3** (where the carbon atoms are numbered). Most of the glucosides (glucose seems to be the obligatory sugar) contain this skeleton, although often with some modification. Thus C-11 is sometimes missing and C-10 also in a few cases. One example is known where none of these carbon atoms are found. Nepetalactone (**4**) and loganin (**5**) have been chosen as examples of single iridoids containing the basic carbocyclic skeleton.

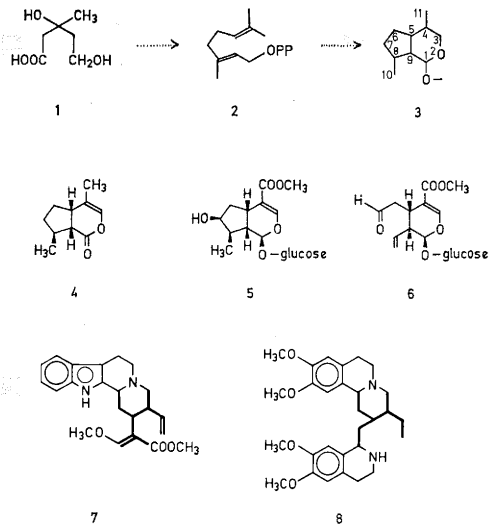

Fig. 1. Examples of iridoid structures (**3**—**8**).

The seco-iridoids form the largest class of iridoid compounds found both as glucosides and, more commonly, in modified forms as "complex" alkaloids. We have chosen secologanin (**6**) as an example of a glucoside, and corynantheine (**7**) and emetine (**8**) as examples of complex alkaloids. Secologanin is formed biosynthetically from loganin (**5**) by cleavage of the 7,8-bond of the latter compound, thus leaving an aldehyde function at C-7. Condensation of this aldehyde group with tryptophane or 3,4-dihydroxyphenylalanine (DOPA) gives rise to the alkaloids.

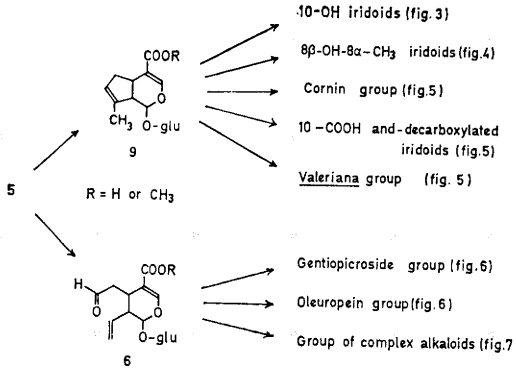

Fig. 2. Classification of carbocyclic and seco-iridoids.

The stereochemistry shown at C-5 and C-9 (**4**, **5** and **6**, hydrogen atoms pointing upwards) is common to all iridoids containing the basic or the seco-skeleton in non-rearranged form.

In an attempt to classify the iridoid compounds, one can use either arbitrarily chosen functional features or paths of biosynthesis. The latter possibility is obviously to be recommended in dealing with products of living organisms. However, as too little biosynthetic research has been carried out on the glucosides it will be necessary to use the chemical features, thereby choosing such functionalities as are thought to reflect biosynthetic relationships.

From the biosynthetic experiments so far carried out, it appears that loganin (**5**) may be a key intermediate in the formation of most other compounds.

A primary sub-division into seco-iridoids and iridoids containing the carbocyclic skeleton is self-evident on biosynthetic grounds, as secologanin is an intermediate compound in the synthesis of all other seco-iridoids so far investigated (CORDELL 1974, INOUYE et al. 1974 c). The results of biosynthetic research justify a sub-division of the seco-compounds into three groups (see Fig. 2 and comments to Figs. 6 and 7). Among the iridoids with the carbocyclic skeleton only a single class, the 10-hydroxylated compounds, has been relatively thoroughly investigated (INOUYE 1971). Using well-established biosynthetic mechanisms combined with structural features of the compounds, we have divided the non-seco iridoids into five subgroups as shown in Fig. 2. We have postulated 10-desoxy-geniposide (**9**) as an intermediate in the synthesis of all these subgroups and will give our reasons for this in the comments. In connection with each group we have tabulated the occurrence of all compounds in families and genera among the dicotyledons.

The above classification may be used for purposes of botanic taxonomy on the conditions that the same compound is always formed biosynthetically in the same way, and that the ability to produce iridoids at all has arisen once only in the dicotyledons. These assumptions have been made here, and seem to be supported by the distribution of iridoids in the angiosperm system.

Carbocyclic Iridoids

Group I. 10-hydroxylated Compounds (Fig. 3)

The glucosides of this group are placed together on the basis of common structural features, i.e. the presence of a 10-hydroxy group and a double bond or an epoxide function in the five-membered ring. Evidence for the biosynthetic connection between the compounds exists (INOUYE 1971, INOUYE et al. 1972), except for **14** and **20**. The scheme is essentially that presented by INOUYE, again with the exception of **14** and the group of compounds represented by **20** (plumieride group). Corroboration of the structural and biosynthetic evidence is found in the fact that the compounds are occasionally found to occur together in the plants. Thus **10** and **18** are found in *Cornus suecica* (JENSEN et al. 1973 a), **10**

and **19** in *Gardenia jasminoides* (INOUYE et al. 1969 c), **11** and **12** in Garrya sp. (JENSEN and NIELSEN unpubl.), **11**, **16** and **17** in *Paederia scandens* (INOUYE et al. 1969 a), and finally **12** and **13** occur together in a number of genera (see Table 1).

The inclusion of **14** and **20** in this group calls for comments. As can be seen from Table 1, melittoside (**14**) has so far been found solely in Lamiaceae, in which aucubin (**12**) is not found at all. On the other hand catalpol (**13**), a compound derived from aucubin, is frequently found in this family. As the ability to introduce a hydroxy group at C-5 is an established faculty of Lamiaceae (see Group II), we find the inclusion of **14** warranted. Plumieride (**20**) is the only glucoside of a group of compounds where the gardenoside (**19**) aglucone is combined with an acetoacetic acid residue. The biosynthesis of **20** has been investigated (YEOWELL and SCHMID 1964).

In Table 1 we have tabulated the reported occurrence of the 10-hydroxylated iridoids in plants. Some trends are apparent from the table. Compounds late in the biosynthetic scheme (the decarboxylated compounds **12**, **13** and **14** in Fig. 3) are found to occur only sporadically in some families often considered to be more primitive. On the other hand, they occur in a large number of genera in the more "advanced" families.

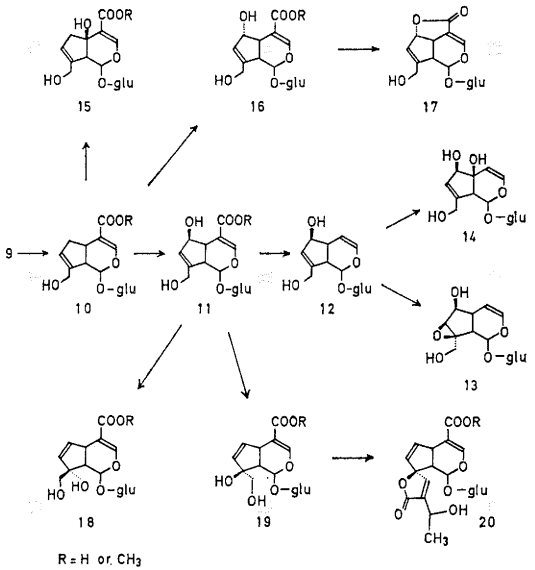

Fig. 3. Iridoids of Group I (10-hydroxylated compounds).

Group II. 8β-oxy-8α-methyl Compounds (Fig. 4)

These glucosides are grouped together because of a presumed common biogenetic origin, i.e. the formation of the 8-hydroxy-compounds by the opening of an epoxide ring. This structural feature is found in **21**, **27** and **31**. Structurally, these compounds are closely related to **13**, except that they lack the 10-hydroxy function. This points to a biosynthetic formation of the group under study closely parallel to that of Group I except that the initial step, the oxidation of **9** to **10**, has not taken place. Thus, hypothetically, **9** may be oxidised in position 5 and/or 6, followed by epoxidation at 7,8 to give the possible immediate precursors of **22**, **24** (hydrolytic opening) and **23** and **25** (reductive opening). An alternative pathway could be involved in the formation of the compounds lacking functionality at position 7. Instead of reductive opening of an epoxide ring these compounds could be formed by the addition of water to a 7,8-double bond. Decarboxylation followed by reactions analogous to those above may give rise to the remaining compounds, except **30**. Assuming a common basic biosynthesis of the iridoid glucosides, we suppose the methyl group of **30** to be formed by the reduction of a carboxylic acid derivative. That this may in fact be the case is indicated by the occurrence of a C-11-methyl group in other iridoids (see Fig. 5, and comments).

The group as a whole must be regarded as generally more advanced than the 10-

Table 1. Distribution of iridoids of Group I (10-hydroxylated compounds, Fig. 3).

Geniposide (**10**) incl. genipin and its 1-gentiobioside
Cornaceae: *Cornus* [1]
Rubiaceae: *Gardenia*,[3, 23] *Genipa* [2, 15]

Scandoside (**11**)
Garryaceae: *Garrya* [4]
Rubiaceae: *Gardenia*,[23] *Paederia* [2]

Aucubin (**12**) incl. 10-glucosyl-aucubin, agnuside, odontoside, melampyrosid,[25] and other esters
Eucommiaceae: *Eucommia* [2, 26]
Cornaceae: *Aucuba* [2]
Garryaceae: *Garrya* [2]
Ericaceae: several species [5]
(Apocynaceae: *Thevetia* [6])
Buddlejaceae: *Buddleja* [2]
Globulariaceae: *Globularia* [2, 8]
Hippuridaceae: *Hippuris* [2]
Lentibulariaceae: *Utricularia* [2]
Orobanchaceae: *Lathraea* [2, 7]
Plantaginaceae: *Plantago* [2]
Scrophulariaceae: *Angelonia*,[7] *Antirrhinum*,[2, 7] *Aureolaria*,[7] *Bartsia*,[2] *Bellardia*,[7] *Bungea*,[7] *Campylanthus*,[7] *Castilleja*,[7] *Celsia*,[7] *Chelone*,[7] *Collinsia*,[2, 7] *Cordylanthus*,[7] *Dermatobotrys*,[7] *Diascia*,[7] *Erinus*,[7] *Euphrasia*,[2, 7] *Freylinia*,[2] *Hebe*,[7] *Hemiphragma*,[7] *Lagotis*,[7] *Leptandra*,[7] *Leptorrhabdus*,[7] *Limosella*,[7] *Linaria*,[2, 7] *Lindenbergia*,[7] *Mazus*,[7] *Melampyrum*,[2, 7, 25] *Odontites*,[2, 7] *Orthanta*,[7] *Orthocarpus*,[7] *Ourisia*,[7] *Parahebe*,[7, 8] *Parentucellia*,[7] *Pedicularis*,[2, 7] *Pentstemon*,[2, 7] *Phygelius*,[7] *Rehmannia*,[7] *Rhinanthus*,[2, 7] *Russelia*,[7] *Scrophularia*,[2, 7] *Sutera*,[7] *Synthyris*,[7] *Teedia*,[7] *Tetranema*,[7] *Verbascum*,[2, 7] *Veronica*,[2, 7] *Veronicastrum*,[2] *Wulfenia* [7]
Verbenaceae: *Vitex* [2, 9]
Callitrichaceae: *Callitriche* [2]

Catalpol (**13**) incl. catalposide, methylcatapol, globularin, picroside, amphicoside,[10] and other esters
Buddlejaceae: *Buddleja* [2]
Bignoniaceae: *Amphicome*,[10] *Catalpa* [2]
Globulariaceae: *Globularia* [2]
Lentibulariaceae: *Pinguicula* [2]
Martyniaceae: not named [11]
Myoporaceae: not named [11]
Plantaginaceae: *Plantago* [2]
Hippuridaceae: *Hippuris* [2]
Scrophulariaceae: *Bungea*,[7] *Castilleja*,[7] *Celsia*,[7] *Chelone*,[7] *Collinsia*,[7] *Dermatobotrys*,[7] *Euphrasia*,[7] *Hebe*,[8] *Hemiphragma*,[7] *Lagotis*,[7] *Leptandra*,[7] *Leptorrhabdus*,[7] *Limosella*,[7] *Lindenbergia*,[7] *Mazus*,[7] *Melampyrum*,[7] *Odontites*,[7] *Orthanta*,[7] *Ourisia*,[7] *Parahebe*,[7] *Paulownia*,[2] *Pedicularis*,[7] *Pentstemon*,[7] *Phygelius*,[7] *Picrorhiza*,[2] *Rehmannia*,[7] *Rhinanthus*,[7] *Russelia*,[7] *Scrophularia*,[7] *Sutera*,[7] *Synthyris*,[7] *Teedia*,[7] *Tetranema*,[7] *Verbascum*,[2, 7] *Veronica*,[2, 7, 8] *Wulfenia*,[7] *Zaluzianskya* [7]
Callitrichaceae: *Callitriche* [2]
Lamiaceae: *Hemiandra*,[11] *Salazaria*,[11] *Scutellaria* [11]

Macfadienoside [24] (=5-hydroxy-catalpol)
Bignoniaceae: *Macfadyena* [24]

Melittoside (**14**) incl. monomelittoside
Lamiaceae: *Melittis*,[2, 11] *Prasium*,[11] *Sideritis*,[11] *Stachys* [11]

Theviridoside (**15**) incl. theveside
Apocynaceae: *Cerbera*,[12] *Thevetia* [2]

Daphylloside (**16**, R=Me) incl. "galium glucoside" [13] (**16**, R=H), asperuloside, desacetyl-asperuloside (**17**) and paederoside
Altingiaceae: *Liquidambar* [2]
Daphniphyllaceae: *Daphniphyllum* [2]
Eucommiaceae: *Eucommia* [2]
Ericaceae: *Vaccinium* [2]
Escalloniaceae: *Escallonia*,[2] *Polyosma* [14]
Hydrangeaceae: *Fendlera* [14]
Icacinaceae: *Apodytes* [14]
Davidiaceae: *Davidia* [14]
Apocynaceae: *Alstonia* [2]
Rubiaceae: *Allacophania*,[15] *Anthospermum*,[15] *Argostemma*,[15] *Asperula*,[2, 15] *Borrea*,[15] *Bouvardia*,[15] *Callipeltis*,[15] *Coccocypselum*,[15] *Coprosma*,[2, 15] *Coussarea*,[15] *Crucianella*,[2] *Damnacanthus*,[15] *Diodia*,[15] *Galium*,[2, 15] *Gardenia*,[2] *Hydnophytum*,[15] *Lasianthus*,[15] *Morinda*,[2, 15] *Oldenlandia*,[2, 15] *Paederia*,[2, 15] *Pentanisia*,[15] *Pentas*,[15] *Perama*,[15] *Phuopsis*,[15] *Phyllis*,[15] *Plocama*,[15] *Pomax*,[15] *Psychotria*,[15] *Relbunium*,[15] *Richardsonia*,[15] *Rubia*,[2, 14] *Saprosma*,[15] *Spermacoce*,[15] *Trianolepis*,[15] *Theligonum*,[14] *Vaillantia* [15]
Globulariaceae: *Globularia* [2]
Orobanchaceae: *Orobanche* [2]

Monotropein [20] (**18**, R=H) incl. vaccinoside [18]
Altingiaceae: *Liquidambar* [2]
Ericaceae: *Arctostaphylos*,[2, 16] *Oxycoccus*,[2, 16] *Tripetaleia*,[17] *Vaccinium*[2, 16, 18]
Monotropaceae: *Monotropa*,[2] *Monotropastrum* [2]
Pyrolaceae: *Chimaphila*,[2] *Pyrola* [2]
Cornaceae: *Cornus* [1]

Stylidiaceae: *Stylidium* [19]
Rubiaceae: *Asperula*,[2, 21] *Galium* [2, 16]
Globulariaceae: *Globularia* [2]

Gardenoside (**19**)
Rubiaceae: *Gardenia*,[2] *Macrosphyra*[15]

Plumieride (**20**) incl. other plumeria compounds and allamandicines [22]
Apocynaceae: *Allamanda*,[22] *Plumeria* [2]

[1] JENSEN et al. 1973 a. — [2] PLOUVIER & FAVRE-BONVIN 1971. — [3] ENDO & TAGUCHI 1970. — [4] JENSEN & NIELSEN unpubl. — [5] INOUYE 1971 p. 308. — [6] PARIS & ETCHEPARE 1966; this occurrence was not confirmed later (STICHER & SCHMID 1969, STICHER 1970). — [7] KOOIMAN 1970. — [8] GRAYER-BARKMEIJER 1973. — [9] RIMPLER 1972 a and b. — [10] KAPOOR et al. 1971. — [11] KOOIMAN 1972. — [12] INOUYE & NISHIMURA 1972. — [13] KOOIMAN (1969) isolated "galium glucoside" from seeds of *Galium aparine* and offered the structure **16** (R=H) for the compound. The data given for "galium glucoside" (m.p. and $[\alpha]_D$) are almost identical to those of desacetyl-asperulosidic acid (**16**, R=H) prepared by INOUYE et al. (1969 b). — [14] KOOIMAN 1971. — [15] KOOIMAN 1969. — [16] SWIATEK & KOMOROWSKI 1972. — [17] YASUE et al. 1971. — [18] SAKAKIBARA et al. 1971. — [19] See Appendix. — [20] According to KOOIMAN (1971), **16** (R=H) and **18** are not distinguishable by paper chromatography. Thus, monotropein-occurrences may here have been recorded under daphylloside and vice versa. — [21] STICHER 1971 a. — [22] KUPCHAN et al. 1974. — [23] INOUYE et al. 1974 b. — [24] BIANCO et al. 1974 a; this report was included after the text had been finished. — [25] AHN & PACHALY 1974. — [26] BIANCO et al. 1974 b.

hydroxylated compounds, as it includes reactions additional to those found in the latter group, in particular the opening of the epoxide ring.

No biosynthetic work has been reported on this group of iridoids.

The reported occurrence of these compounds is shown in Table 2. It can be seen that biosynthetically advanced compounds are restricted almost entirely to Lamianae. Verbenaceous plants, on which only few phytochemical investigations have as yet been carried out, show a remarkable similarity to Lamiaceae with regard to the iridoid glucosides so far reported.

Information on the further occurrence and the biosynthetic pathways of this interesting group of glucosides will probably prove of great use for taxonomic purposes.

Group III. Cornin Group (Fig. 5)

The biosynthesis of cornin (**33**) has been investigated to some extent (HORODYSKY et al. 1969, INOUYE et al. 1969 d, 1972). Thus it has been shown that desoxy-loganic acid (**57**, R=R′=H) gives a very high in vivo incorporation into cornin in *Verbena officinalis*. This, combined with the identical configuration at C-8, could point to a direct route to cornin by oxidation at the 6-position in desoxy-loganic acid as proposed by

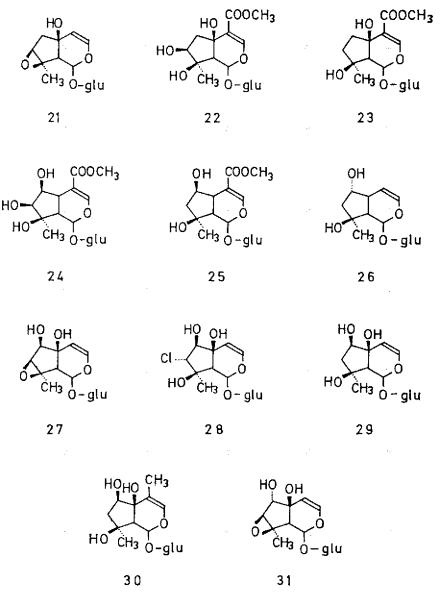

Fig. 4. Iridoids of Group II (8β-oxy-8α-methyl substituted compounds).

Table 2. Distribution of iridoids of Group II (8β-oxy-8α-methyl substituted compounds, Fig. 4).

Galiridoside (**21**)
Lamiaceae: *Galeopsis*,[1] *Lamium*,[2] *Leonurus*[8]

Lamiide (**22**)
Lamiaceae: *Lamium*[1]
Verbenaceae: *Caryopteris*,[4] *Chascanum*[3]

Caryoptoside (=5-desoxy-lamiide)
Verbenaceae: *Caryopteris*[4]

Ipolamiide (**23**) incl. reptoside[15]
Eucommiaceae: *Eucommia*[16]
Lamiaceae: *Lamium*,[1] *Ajuga*[15]

Lamalbide (**24**)
Lamiaceae: *Lamium*[5, 6]
Verbenaceae: *Caryopteris*[4]

Shantziside (**25**)
Rubiaceae: *Gardenia*[7]

Ajugol (**26**) and ajugoside
Eucommiaceae: *Eucommia*[16]
Lamiaceae: *Ajuga*,[8] *Leonurus*,[8, 9] *Melittis*[8]

Antirrhinoside (**27**)
Scrophulariaceae: *Antirrhinum*,[1, 10] *Anarrhinum*,[10] *Asarina*,[10] *Chaenorrhinum*,[10] *Galvezia*,[10] *Kickxia*,[10] *Linaria*,[1, 14] *Maurandia*,[10] *Cymbalaria*[12]

Linarioside (**28**)
Scrophulariaceae: *Cymbalaria*,[12] *Linaria*[11]

Harpagide (**29**) incl. esters
Eucommiaceae: *Eucommia*[16]
Pedaliaceae: *Harpagophytum*[1]
Scrophulariaceae: *Scrophularia*[1, 10]
Lamiaceae: *Ajuga*,[1, 10] *Betonica*,[1] *Galeopsis*,[1, 10] *Eremostachys*,[10] *Lagochilus*,[9] *Lamium*,[2] *Leucas*,[10] *Melittis*,[1, 10] *Molucella*,[10] *Stachys*,[1, 10] *Teucrium*,[1, 10] *Trichostema*[10]
Verbenaceae: *Caryopteris*[4]

Lamiol (**30**) and lamioside
Lamiaceae: *Lamium*[1]

Procumbide (**31**)[13]
Pedaliaceae: *Harpagophytum*[1, 13]

[1] PLOUVIER & FAVRE-BONVIN 1971. — [2] WIEFFERING & FIKENSCHER 1974. — [3] RIMPLER 1972 b. — [4] RIMPLER, H.; pers. comm. — [5] BRIESKORN & AHLBORN 1973. — [6] EIGTVED et al. 1974. — [7] INOUYE et al. 1974 b. — [8] GUISO et al. 1974 b. — [9] WEINGES et al. 1973. — [10] KOOIMAN 1970. — [11] KITAGAWA et al. 1972. — [12] KAPOOR et al. 1974. — [13] Revised structure by BIANCO et al. 1971. — [14] STICHER 1971 b. — [15] GUISO et al. 1974 a, this report was included after the text had been finished. — [16] BIANCO et al. 1974 b.

INOUYE et al. (1972). The finding of griselinoside (**36**) in *Griselinia littoralis* (Table 3), also with a 6-keto group suggests, however, that a mechanism of more general occurrence may be in operation. Thus desoxy-geniposide (**9**), having C-6 and C-10 in allylic positions liable to oxidation, provides a conceivable precursor for both **33** and **36**. The latter compound is highly oxidized at both C-6 and C-10, and **11** suggests itself as one of the steps between **9** and **36**. Reduction of the double bond in **11** combined with the oxidation of the hydroxy groups at C-6 and C-10 provides **36**. If a mechanism such as this is involved in the formation of **36**, the 6-keto group in cornin could presumably be formed analogously from **9** without the initial oxidation at C-10. In fact, HÄNSEL (1966) has proposed this biosynthetic pathway to cornin. The co-occurrence of **33** and **36** in Cornaceae points to a common mechanism in the formation of these compounds.

The three compounds **32**—**34** are here grouped together because of an obvious structural relationship in addition to the co-occurrence of **32** and **33** in *Cornus florida* (JENSEN et al. 1973 b) and of **33** and **34** in *Verbena hastata* (RIMPLER and SCHÄFER 1973). The few records of the group are presented in Table 3.

Group IV. 10-carboxyl and 10-decarboxylated Iridoids (Fig. 5)

The compounds of this small group have all been discovered very recently except for unedoside (**37**, R=H). Unedoside has been reported to have the opposite

Table 3. Distribution of iridoids of Groups III, IV and V (Fig. 5).

Group III. Cornin Group

Dihydrocornin (**32**)
Cornaceae: *Cornus* [1]

Cornin (**33**)
Cornaceae: *Cornus* [1]
Verbenaceae: *Verbena* [2, 3]

Hastatoside (**34**)
Verbenaceae: *Verbena* [3]

Group IV. 10-carboxyl and 10-decarboxylated Compounds

Forsythide (**35**, R=H)
Oleaceae: *Forsythia* [4]

Griselinoside (**36**)
Cornaceae: *Griselinia* [5]

Unedoside (**37**, R=H)
Ericaceae: *Arbutus* [2]
Verbenaceae: *Stilbe* [6, 13]

Stilbericoside (**37**, R=OH)
Verbenaceae: *Stilbe* [13]

Decaloside (**38**)
Loasaceae: *Mentzelia* [7]

Deutzioside (**39**, R=H)
Hydrangeaceae: *Deutzia* [8]
Loasaceae: *Mentzelia* [9]

Scabroside (**39**, R=OH)
Hydrangeaceae: *Deutzia* [10]

Group V. Valeriana Group

Valtrate (**40**, R=isovaleroyl) incl. dihydrovaltrate (**41**, R=isovaleroyl, R′=isocaproyl), other nonglucosidic compounds and valerosidate
Valerianaceae: *Centranthus*,[2] *Fedia*,[2] *Valeriana*,[2, 14] *Valerianella* [2]

Villoside (**42**)
Valerianaceae: *Patrinia* [11]

Patrinoside (**43**, R=isovaleroyl)
Valerianaceae: *Patrinia* [12]

[1] JENSEN et al. 1973 b. — [2] PLOUVIER & FAVRE-BONVIN 1971. — [3] RIMPLER & SCHÄFER 1973. — [4] INOUYE & NISHIOKA 1973. — [5] JENSEN & NIELSEN unpubl. — [6] RIMPLER 1972 c. — [7] DANIELSON et al. 1973. — [8] BONADIES et al. 1974. — [9] DANIELSON & HAWES 1973. — [10] ESPOSITO & GUISO 1973. — [11] TAGUCHI et al. 1973. — [12] TAGUCHI & ENDO 1974. — [13] RIMPLER & PISTOR 1974. — [14] POPOV et al. 1974.

stereochemistry of that shown in Fig. 5, at C-6, C-7 and C-8 (GEISSMAN et al. 1966). The structure shown has recently been proposed by RIMPLER and PISTOR (1974).

Compounds **37**—**39** have lost C-10, presumably by decarboxylation, and thus seem to have a biogenetic origin in common with **35** and **36**. No biosynthetic experiments on the compounds have yet been reported. Derivation from 10-hydroxylated compounds is conceivable using the reactions shown in Fig. 3 beside the oxidation to a 10-carboxylic acid function followed by decarboxylation, and finally the formation of the reduced functions at C-11. An indication that the methyl group in **39** is actually formed by reduction of a carboxylic acid function is found in the co-occurrence of decaloside (**38**) and deutzioside (**39**, R=H) in *Mentzelia decapetala* (DANIELSON et al. 1973, DANIELSON and HAWES 1973), where **38** is a probable precursor of **39**. It has been shown for cornin (**33**), plumieride (**20**) and actinidine (see GROSS 1970, CORDELL 1974) that scrambling takes place between C-3 and C-11 in the early biosynthetic steps. This indicates a common high state of oxidation for C-3 and C-11.

The very scattered distribution is shown in Table 3.

Group V. Valeriana Compounds (Fig. 5)

This group of iridoids is restricted in occurrence to the Valerianaceae and shows structural features seldom or never encountered in other iridoids. The CH_2-OR function at C-11 is common to all these compounds, R representing either an acyl

Table 4. Distribution of iridoids of Group VI (simple seco-iridoids, Fig. 6).

Secologanin (**6**) incl. secologanic acid (**49**), foliamenthin, cantleyoside and other derivatives

Adoxaceae: *Adoxa* [1]
Cornaceae: *Cornus*,[2] *Corokia* [1]
Davidiaceae: *Davidia* [1]
Hydrangeaceae: *Hydrangea* [4]
Icacinaceae: *Cantleya* [3]
Caprifoliaceae: *Diervilla*,[1] *Dipelta*,[1] *Kolkwitzia*,[1] *Lonicera*,[3] *Symphoricarpus*,[1] *Weigela* [1]
Menyanthaceae: *Menyanthes*,[3] *Villarsia* [4]
Dipsacaceae[15]: *Dipsacus*,[4] *Scabiosa* [4]
Calyceraceae: *Acicarpha* [4]
Goodeniaceae[15]: *Scaevola*,[4] *Selliera* [4]
Apocynaceae: *Catharanthus*,[6] *Rhazya*,[6] *Vinca* [7]
Loganiaceae: *Strychnos* [5]

Morroniside (**47**) incl. oliveridine [6]

Adoxaceae: *Adoxa* [1]
Cornaceae: *Cornus* [8]
Sambucaceae: *Sambucus* [9]
Sarraceniaceae: *Darlingtonia*,[4] *Sarracenia* [4]
Gentianaceae: *Gentiana* [6, 10]
Caprifoliaceae: *Lonicera* [3]
Valerianaceae: *Patrinia* [11]

Kingiside (**48**) incl. jasminine [12, 13, 14]

Caprifoliaceae: *Lonicera* [3]
Oleaceae: *Jasminum*,[13, 14] *Ligustrum*,[13, 14] *Olea* [3, 12]

[1] JENSEN & NIELSEN unpubl. — [2] JENSEN et al. 1973 c. — [3] PLOUVIER & FAVRE-BONVIN 1971. — [4] See Appendix. — [5] BISSET & CHOUDHURY 1974. — [6] CORDELL 1974 p. 229. — [7] GUARNACCIA et al. 1974. — [8] ENDO & TAGUCHI 1973. — [9] JENSEN & NIELSEN 1974. — [10] INOUYE & NAKAMURA 1971. — [11] TAGUCHI et al. 1973. — [12] HART et al. 1971. Note that the present compound is not identical with jasminin in Table 5. — [13] HART et al. 1968. — [14] HART et al. 1969. — [15] Dipsacaceae and Goodeniaceae have for some time been suspected to contain iridoid glucosides. For an account, see HEGNAUER (1966 a pp. 24 and 213).

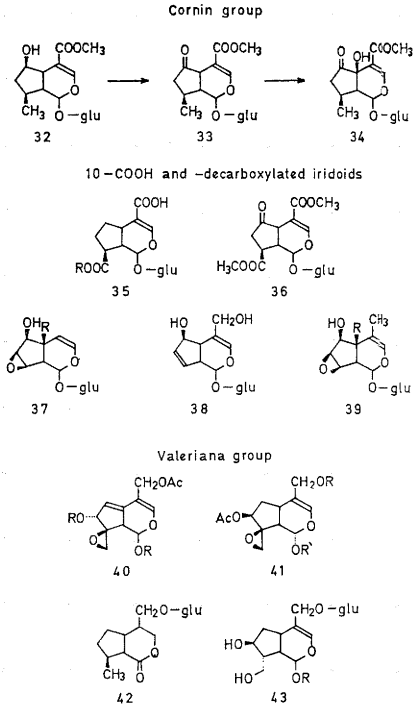

Fig. 5. Iridoids of Groups III, IV and V.

or glucosyl moiety. A 5,6-double bond is found in some compounds, and esterification at various positions (including C-1) with isovaleric or isocaproic acid is common. The non-glucosidic compounds are here represented by acetoxy-valtrate (**40**) and dihydrovaltrate (**41**), while the three known glucosides are represented by villoside (**42**) and patrinoside (**43**). No biosynthetic work has been reported, but the co-occurrence of patrinoside (**43**), loganin (**5**) and morroniside (**47**) in *Patrinia villosa* combined with the uniform structural relationships within the group suggests a biosynthetic origin in common with other iridoids with the carbocyclic skeleton. In Fig. 2 we have postulated that 10-desoxy-geniposide (**9**) is a precursor of the group.

Seco-Iridoids

Group VI. Simple Seco-Iridoids (Fig. 6)

The seco-iridoids have been shown to be derived biosynthetically from loganin (**5**) with secologanin (**6**) as an apparently

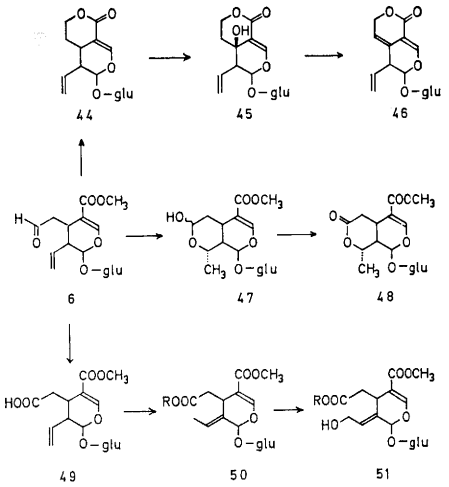

Fig. 6. Seco-iridoids of Groups VI, VII and VIII.

obligatory intermediate to the more advanced compounds (CORDELL 1974).

Among the glucosides only three advanced groups have been separated from the more primitive (or diverse) compounds: the gentiopicroside group, the oleuropein group and the complex alkaloids.

In Table 4 we have presented the occurrence of the biochemically most primitive compounds, viz. secologanin (**6**) and its derivatives morroniside (**47**) and kingiside (**48**). The latter compound is not really primitive, but we have included it here as it has so far only been found in a few species.

Group VII. Gentiopicroside Group (Fig. 6)

This group of compounds has been well investigated biosynthetically (INOUYE 1971) and the compounds forming the sequence are all found as naturally occurring compounds — and often together (Table 5). In the group are also included some terpenoid bases derived from the glucosides either biogenetically or formed as artefacts during the isolation of the compounds from the plants.

Table 5. Distribution of seco-iridoids of Groups VII and VIII (Fig. 6).

Group VII. Gentiopicroside Group

Sweroside (**44**) incl. amarogentin, amaroswerin, bakankosin, trifloroside[3] and amaropanin[4]

Cornaceae: *Cornus*[1]
Caprifoliaceae: *Lonicera*[2]
Menyanthaceae: *Menyanthes*[2]
Gentianaceae: *Centaurium*,[2] *Gentiana*,[3, 4] *Swertia*[2]
Apocynaceae: *Vinca*[6]
Loganiaceae: *Anthocleista*,[5] *Strychnos*[2]

Swertiamarin (**45**) incl. fontaphillin[7]

Gentianaceae: *Swertia*[2]
Oleaceae: *Fontanesia*[7]
Loganiaceae: *Anthocleista*[2]

Gentiopicroside (**46**) incl. erythrocentaurin, gentianin, gentioflavoside[9] and gentioflavine

Gentianaceae: *Centaurium*,[9] *Chlora*,[2] *Cicendia*,[2] *Gentiana*,[2] *Lomatogonium*,[8] *Ophelia*,[8] *Pleurogyne*[2]
Dipsacaceae: *Dipsacus*,[2] *Succisa*[13]
Oleaceae: *Fontanesia*[7]
Loganiaceae: *Anthocleista*,[2, 5] *Fagraea*[8]

Group VIII. Oleuropein Group

Oleuropein (**50**, R=3,4-dihydroxy-phenyl-ethyl) incl. ligstroside[11] (**50**, R=4-hydroxy-phenyl-ethyl), 10-hydroxy-ligstroside[11] (**51**, R=4-hydroxy-phenyl-ethyl), nüzhenid[10] and jasminin[2]

Oleaceae: *Fraxinus*,[12] *Jasminum*,[2] *Ligustrum*,[10, 11] *Olea*[2]

[1] ENDO & TAGUCHI 1973. — [2] PLOUVIER & FAVRE-BONVIN 1971. — [3] INOUYE et al. 1974 d. — [4] WAGNER & VASIRIAN 1974. — [5] CHAPELLE 1973. — [6] BHAKUNI & KAPIL 1972. — [7] BUDZIKIEWICZ et al. 1967. — [8] WILLAMAN & LI 1970. — [9] POPOV & MAREKOV 1971 a. — [10] INOUYE & NISHIOKA 1972. — [11] ASAKA et al. 1972. — [12] JENSEN & NIELSEN unpubl. — [13] TORSELL 1964.

Group VIII. Oleuropein Group (Fig. 6)

This small group is very homogeneous, and the compounds are easily recognizable by the double bond in the 8,9-position. They often contain a *p*-hydroxy-phenyl-ethyl moiety esterified with the C-7 carboxyl group. As with the gentiopicro-

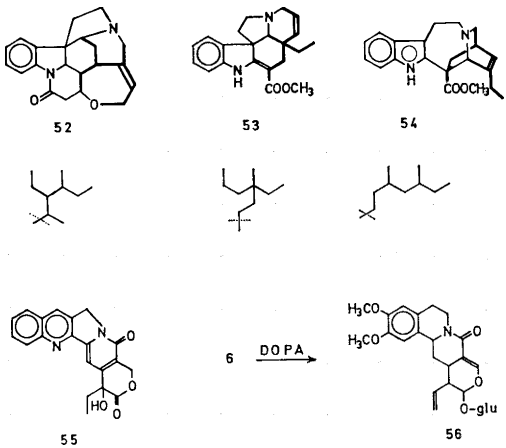

Fig. 7. Complex iridoid alkaloids. Group IX.

side group some alkaloids are included. There appears to be some doubt about details of the pathway of biosynthesis (INOUYE et al. 1974 c), but it seems that the group as a whole is formed via secologanin (**6**). The occurrence reported is confined solely to genera of Oleaceae (see Table 5).

Group IX. Complex Iridoid Alkaloids (Fig. 7)

Only a few examples of this very large group of compounds, comprising hundreds of indole alkaloids, are shown (**7**, **8**, in Fig. 1 and **52**—**56**, in Fig. 7). Biochemical evidence (CORDELL 1974) proves that the group as a whole is biosynthesized from secologanin by condensation with tryptophane (or tryptamine) to give the indole alkaloids (**7**, **52**—**54**), and, after rearrangement of these also the quinoline alkaloids (e.g. **55**) of the group. We have included here a small group of isoquinolines (**8**, **56**), the "ipecac alkaloids", which are formed analogously from secologanin and DOPA. Some compounds of the latter type contain an indole group but these are presumably formed by a secondary reaction of an isoquinoline precursor with tryptophane.

In Table 6 we have compiled the reported occurrence of Group IX according to increasing complexity of the molecules. Regarding the indole alkaloids it is presumed (CORDELL 1974) that the biosynthetic sequence in the formation of the rearranged skeletons is:

corynanthe (incl. strychnos) → aspidosperma → iboga alkaloids.

The iridoid moieties of the three alkaloid types are exemplified below by compounds **52**, **53** and **54**, respectively. The corynanthe group here includes all compounds with intact seco-iridoid skeleton (the bond marked by a dotted line may have been broken, leaving only 9 carbon atoms). The cinchona alkaloids, which formally are not indole alkaloids at all, are nevertheless formed from these (CORDELL 1974) and are therefore included in the corynanthe group. Like the cinchona alkaloids, camptothecine (**55**) is formally a quinoline alkaloid but is probably derived from the corynanthe group. Here we have arbitrarily allowed it to form a subgroup of its own as it is the only one of these alkaloids that occurs solely in the Cornales.

In the aspidosperma and iboga groups a 3-carbon unit has migrated to another position and is attached by a different carbon atom to the main carbon chain (see Fig. 7).

Table 6 shows that the reported occurrence of this very large group of compounds is restricted to a few families. The DOPA-derived ipecac alkaloids are found only in three families and can be considered primitive in this context.

As regards the main group of indole alkaloids two occurrences in Table 6 are entirely unexpected, viz. *Pouteria* (Sapotaceae) and *Enantia* (Annonaceae), which allegedly are sources of yohimbine (HEGNAUER 1973 p. 296) and quinidine (HEGNAUER 1964 p. 118), respectively. Until recently yohimbine was believed to occur in *Alchornea* (Euphorbiaceae) (HEGNAUER 1966 a p. 122). Recent investigations (RAY-

Table 6. Distribution of iridoid compounds of Group IX (complex iridoid alkaloids, Fig. 7).

Ipecac alkaloids (e.g. **8** and **56**)
(Araliaceae: *Hedera* [14])[11]
Alangiaceae: *Alangium* [1, 2]
Icacinaceae: *Cassinopsis* [1]
Rubiaceae: *Cephaelis*,[1] *Pogenopus*,[1] *Psychotria* [1]

Camptothecine (**55**)
Nyssaceae: *Camptotheca* [2]
Icacinaceae: *Mappia* [2]

Indole alkaloids of corynanthe type (e.g. **7** and **52**)
(Annonaceae: *Enantia* [3])[11]
(Sapotaceae: *Pouteria* [3])[11]
(Ericaceae: *Vaccinium* [5])[11]
Oleaceae: *Ligustrum*,[7] *Olea* [7]
Apocynaceae: *Alstonia*,[3] *Amsonia*,[3] *Aspidosperma*,[3] *Bleekeria*,[4] *Catharanthus*,[3] *Conopharyngia*,[3] *Diplorrhyncus*,[3] *Excavatia*,[3] *Gabunia*,[3] *Geissospermum*,[3] *Gonioma*,[3] *Hunteria*,[3] *Melodinus*,[3] *Ochrosia*,[3] *Picralima*,[3] *Pleiocarpa*,[3] *Rauwolfia*,[3] *Rhazya*,[3] *Stemmadenia*,[3] *Tabernaemontana*,[3] *Tonduzia*,[3] *Vallesia*,[3] *Vinca*,[3] *Voacanga* [3]
Loganiaceae: *Gardneria*,[6] *Gelsemium*,[3] *Mostuea*,[3] *Strychnos* [3]
Rubiaceae: *Adina*,[3] *Anthocephalus*,[8] *Antirrhea*,[3] *Cinchona*,[3] *Corynanthe*,[3] *Coutarea*,[3] *Isertia*,[9] *Ladenbergia*,[9] *Mitragyna*,[3] *Neonauclea*,[9] *Ourouparia*,[3] *Pauridiantha*,[9, 10] *Pausinystalia*,[3] *Pseudocinchona*,[3] *Remijia*,[3] *Sarcocephalus*,[9] *Stelecantha*,[10] *Timonius*,[9] *Uncaria* [3]

Indole alkaloids of aspidosperma (e.g. **53**) and iboga (e.g. **54**) types
Apocynaceae: *Alstonia*,[3] *Amsonia*,[3] *Aspidosperma*,[3] *Callichilia*,[3] *Catharanthus*,[3] *Conopharyngia*,[3] *Craspidospermum*,[12] *Crioceras*,[13] *Ervatamia*,[3] *Gabunia*,[3] *Gonioma*,[3] *Haplophyton*,[3] *Hunteria*,[3] *Kopsia*,[3] *Melodinus*,[3] *Pleiocarpa*,[3] *Rejoua*,[3] *Rhazya*,[3] *Schizogynia*,[3] *Stemmadenia*,[3] *Tabernaemontana*,[3] *Vallesia*,[3] *Vinca*,[3] *Voacanga* [3]

[1] BROSSI et al. 1971. — [2] See references in CORDELL 1974. — [3] SNIECKUS 1968. — [4] SAINSBURY & WEBB 1972. — [5] JANKOWSKI et al. 1974. — [6] SAKAI et al. 1971. — [7] SCHNEIDER & KLEINERT 1972. — [8] BROWN et al. 1974. — [9] HEGNAUER 1973 pp. 140 and 730. — [10] BOUQUET & FOURNET 1972. — [11] See comments in the text. — [12] KAN-FAN et al. 1971. — [13] CAVÉ et al. 1971. — [14] MAHRAN et al. 1972.

MOND-HAMET and GOUTAREL 1965, HART et al. 1970) have not confirmed this.

The two former reports must both be treated with reserve until the botanical identity of the material used in the chemical investigations has been checked by botanists. In the case of *Enantia polycarpa*, the original report of which we have seen (BUZAS et al. 1959, BUZAS and EGNELL 1965), nothing is said about this matter, but three different lots of bark were all found to contain quinidine as a minor alkaloid with palmatine as the major one. Palmatine is a benzyl-isoquinoline alkaloid and the two types of alkaloids are, except for this one case, mutually exclusive in plants.

Recently MAHRAN et al. (1972) have reported the isolation of emetine (**8**) in five varieties of *Hedera helix* (Araliaceae). In an attempt to repeat this, the authors have found that the contents of emetine, if present at all, is below 1 ppm (dry leaves).

In addition, a mention should be made on a possible iridoid indole alkaloid in *Vaccinium oxycoccus* (JANKOWSKI et al. 1971, JANKOWSKI 1973, JANKOWSKI et al. 1974). The carbon skeleton of the structures presented is not that of a true iridoid, but as the structures appear to be inconsistent with the chemical data (JOULE 1973

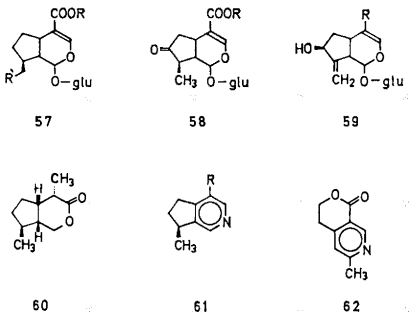

Fig. 8. Unclassified iridoids. Group X.

Table 7. Distribution of iridoids of Group X (primitive or otherwise non-classified iridoids, Fig. 8).

Desoxy-loganin (**57**, R′=H, R=Me) incl. desoxy-loganic acid
- Apocynaceae: *Vinca* [2]
- Loganiaceae: *Strychnos* [1]
- Lamiaceae: *Physostegia* [3]

Adoxoside (**57**, R′=OH, R=Me)
- Adoxaceae: *Adoxa* [4]
- Sambucaceae: *Viburnum* [4]

Loganin (**5**) incl. loganic acid and cantleyin [8]
- Alangiaceae: *Alangium* [5]
- Cornaceae: *Cornus*,[6] *Mastixia* [3]
- Hydrangeaceae: *Hydrangea* [3]
- Icacinaceae: *Cantleya* [7]
- Caprifoliaceae: *Lonicera*,[3] *Symphoricarpus* [4]
- Gentianaceae: *Swertia* [5]
- Menyanthaceae: *Menyanthes* [3]
- Apocynaceae: *Catharanthus*,[5] *Rhazya*,[5] *Vinca* [2]
- Loganiaceae: *Strychnos* [3]
- Rubiaceae: *Mitragyna* [5]
- Oleaceae: *Jasminum* [8]
- Valerianaceae: *Patrinia* [9]
- Scrophulariaceae: *Veronica* [10]

Ketologanin (**58**, R=Me) incl. syringopicroside (**58**, R=4-hydroxy-phenyl-ethyl)
- Apocynaceae: *Vinca* [2]
- Loganiaceae: *Strychnos* [1]
- Oleaceae: *Syringa* [3]

Antirrhide (**59**, R=H) and gardoside [18] (**59**, R=COOMe)
- Rubiaceae: *Gardenia* [18]
- Scrophulariaceae: *Antirrhinum* [3]

Nepetalactones (e.g. **4**) incl. matatabioles, myodesertine and others
- Actinidiaceae: *Actinidia* [3]
- Myoporaceae: *Myoporum* [3]
- Orobanchaceae: *Boschniakia* [13]
- Lamiaceae: *Nepeta* [3, 11]

Iridoid pyridine alkaloids incl. actinidine (**61**, R=Me), tecostidine (**61**, R=CH_2OH), indicain (**61**, R=CHO), plantagonine (**61**, R=COOH) and others (but not gentianine)
- Actinidiaceae: *Actinidia* [3]
- Gentianaceae: *Erythrea*,[12] *Gentiana* [3]
- Valerianaceae: *Valeriana* [3]
- Apocynaceae: *Rauwolfia*,[3] *Seytanthus* [3]
- Bignoniaceae: *Incarvillea*,[12] *Stenolobium*,[12] *Tecoma* [3, 12]
- Orobanchaceae: *Boschniakia* [13]
- Plantaginaceae: *Plantago* [12]
- Scrophulariaceae: *Pedicularis* [12]

Iridoids of unknown structure
- Cornaceae: *Curtisia* [4]
- Roridulaceae: *Roridula* [14]
- Retziaceae: *Retzia* [14]
- Gentianaceae: *Gentiana* [20]
- Rubiaceae: *Feretia* [19]
- Acanthaceae: *Cardanthera* [15]
- Scrophulariaceae: several genera [16]
- Selaginaceae: several genera [16]
- Lamiaceae: several genera [17]
- Verbenaceae: *Durantha*,[17] *Stachytarpheta* [17]

[1] BISSET & CHOUDHURY 1974. — [2] BHAKUNI & KAPIL 1972. — [3] PLOUVIER & FAVRE-BONVIN 1971. — [4] JENSEN & NIELSEN unpubl. — [5] CORDELL 1974. — [6] ENDO & TAGUCHI 1973. — [7] SEVENET et al. 1971. — [8] HART et al. 1971. — [9] TAGUCHI et al. 1973. — [10] GRAYER-BARKMEIJER 1973. — [11] SASTRY et al. 1972. — [12] WILLAMAN & LI 1970. — [13] SAKAN et al. 1967. — [14] See Appendix. — [15] WIEFFERING 1966. — [16] KOOIMAN 1970. — [17] KOOIMAN 1972. — [18] INOUYE et al. 1974 a. — [19] The structure offered by DELAVEAU et al. (1974) for "feretoside" appears not to be in accordance with the data given in the paper. — [20] POPOV & MAREKOV 1971 b.

p. 199, 1974 p. 291), the possibility of iridoid origin should still be considered.

Group X. Primitive or Otherwise Non-classified Iridoids (Fig. 8)

The iridoids so far described are all thought to be derived either from desoxy-geniposide (**9**) or from secologanin (**6**), which in turn are both derived from loganin (**5**). The glucosides in the bio-synthetic pathway before **6** and **9** must then inherently be present in all those plants which produce the more advanced compounds.

In Table 7 these "primitive" iridoids have been listed together with some compounds that are not easily classified on the basis of their structures. Desoxy-loganin (**57**, R=Me, R′=H) has been found to be the precursor of loganin (**5**) (INOUYE et al. 1972), and both these com-

Table 8. Distribution of iridoid groups among families. Orders according to the system of DAHLGREN 1975.

Order	Family (group of iridoid)
Hamamelidales	Altingiaceae (I), Daphniphyllaceae (I)
Ericales	Actinidiaceae (X), Roridulaceae (X), Ericaceae (I, IV), Pyrolaceae (I), Monotropaceae (I)
Cornales	Hydrangeaceae (I, IV, V, VI), Sambucaceae (VI, X), Adoxaceae (VI, X), Cornaceae (I, III, IV, VI, VII, X), Garryaceae (I), Alangiaceae (IX, X), Davidiaceae (I, VI), Nyssaceae (IX), Escalloniaceae (I), Icacinaceae (I, VI, IX, X), Stylidiaceae (I)
Sarraceniales	Sarraceniaceae (VI)
Eucommiales	Eucommiaceae (I, II)
Oleales	Oleaceae (IV, VI, VII, VIII, IX, X)
Gentianales	Loganiaceae (VI, VII, IX, X), Buddlejaceae (I), Retziaceae (X), Rubiaceae (I, II, IX, X), Gentianaceae (VI, VII, X), Menyanthaceae (VI, VII, X), Apocynaceae (I, VI, VII, IX, X)
Dipsacales	Caprifoliaceae (VI, VII, X), Valerianaceae (V, VI, X), Dipsacaceae (VI, VII), Calyceraceae (VI)
Goodeniales	Goodeniaceae (VI)
Loasales	Loasaceae (IV)
Scrophulariales	Scrophulariaceae (I, II, X), Selaginaceae (X), Globulariaceae (I), Plantaginaceae (I, X), Myoporaceae (I, X), Martyniaceae (I), Orobanchaceae (I, X), Lentibulariaceae (I), Bignoniaceae (I, X), Pedaliaceae (II), Acanthaceae (X)
Hippuridales	Hippuridaceae (I)
Lamiales	Verbenaceae (I, II, III, IV, X), Callitrichaceae (I), Lamiaceae (I, II, X)

pounds are thus primitive. Adoxoside (**57**, R=Me, R′=OH) with a 10-hydroxy group, should be formally classified with the other compounds having this functionality — and indeed is possibly derived from geniposide (**10**) by reduction of the double bond. However, as secologanin (**6**), which is also found in *Adoxa,* is thought (see CORDELL 1974) to be produced from loganin (**5**) via 10-hydroxyloganin (not shown), a 10-hydroxylating enzyme must be involved and adoxoside could be a by-product of the enzyme working on **57** (R′=H). We have therefore included adoxoside as a primitive compound.

Gardoside (**59**; R=COOMe) occurs together with geniposide (**10**) in *Gardenia jasminoides,* and INOUYE et al. (1974 a) consider that the former may be formed by an allylic rearrangement of the latter. Thus it may be better to place gardoside and the decarboxylated form antirrhide (**59**; R=H) in Group I. We have, however, retained these compounds in Group X. Ketologanin (**58**) has previously been thought to be a precursor of the oleuropein group (INOUYE 1971), but this apparently is not the case (INOUYE et al. 1974 c).

The non-glucosidic monoterpenes (e.g. nepetalactone (**4**) and iridomyrmecine (**60**)) and monoterpenoid alkaloids (e.g. **61** and **62**) with the basic iridoid skeleton have also been included in Table 7, together with some compounds thought or known to be iridoids but with unknown structures. In the review by PLOUVIER and FAVRE-BONVIN (1971 p. 1700) the stereoformulae in their Fig. 1 should be interchanged with those of the enantiomers in order to conform with the formulae in the original papers referred to.

SYSTEMATIC EVALUATION OF THE OCCURRENCE OF DIFFERENT IRIDOIDS EXPRESSED IN TABLES 1—7

General Trends

From the tables it can be seen that in two cases only has the same genus been reported to contain both of the main

groups of iridoids, viz. seco-compounds (Groups VI—IX) and the compounds belonging to Groups I—V. These are *Cornus* (see below under Cornales) and *Davidia*. The latter is monotypic and appears to be the only species reported to contain both types of compounds. In addition *Alstonia,* Apocynaceae, (having Group I and IX iridoids) may possibly be another example of this, but the finding of asperuloside dates from 1880 and is most dubious.

The tables and figures show that the biosynthetically more advanced compounds generally occur in the families and orders usually considered to be the most advanced. However, as mentioned above in connection with Fig. 3, this is not necessarily true when a single taxon is considered. One explanation may be that when producing the more advanced compounds the plants must first synthesize precursors of these. Mutations causing loss of a single enzyme may thus give rise to "advanced" plants producing primitive iridoids or none at all. This is presumably the case with Asclepiadaceae and a considerable number of genera in Lamiaceae.

In the tables shown here we have used biosynthetic pathways (demonstrated or postulated) as a criterion for classification. From the tables, however, it can be seen that some types of reactions (demonstrated by the compounds produced) are almost solely found in families generally considered to be advanced. Thus the ability to hydroxylate the 5-position of the iridoid skeleton, to epoxidize at various positions and to esterify the compounds with aromatic acids is extremely common in Lamianae. On the other hand the products resulting from these reactions occur only sporadically in Ericanae (*Vaccinium, Deutzia*), and not at all in Hamamelidanae.

Hamamelidales

Only two genera of this order are known to contain iridoid compounds (Group I), viz. *Liquidambar* (Altingiaceae) and *Daphniphyllum* (Daphniphyllaceae). The two families differ from all other iridoid-bearing taxa in having bitegmic ovules. The endosperm, which in most other iridoid-containing orders except Gentianales (and Garryaceae and Alangiaceae in Cornales) is cellular ab initio, is also probably nuclear ab initio in the genera mentioned. Other members of Hamamelidales and adjacent orders such as Cunoniales, have been investigated for iridoids. They are lacking at least in samples of *Trochodendron, Tetracentron, Cunonia* and *Staavia* investigated by us, and according to WINDE (1959) also in several genera in Hamamelidaceae. *Liquidambar* and *Daphniphyllum* both have reduced flowers and seem to agree well with other members of Hamamelidales. The iridoids indicate a close relationship between Hamamelidales and Cornales.

Ericales

About half the families in the order are known to produce iridoids. These belong either to Group I (Ericaceae, Pyrolaceae and Monotropaceae) or to Group X, the group of unknown or otherwise unclassified compounds, (Actinidiaceae and Roridulaceae). In addition, *Byblis* is suspected to contain iridoids (GIBBS 1974). One species from each of the remaining families except Epacridaceae has been investigated in the course of this project, but no iridoids have been detected. Ericales is thus heterogeneous as regards the occurrence of iridoids. However, the three first-mentioned families all produce Group I compounds. Further investigations are needed, especially in the smaller families. Grubbiaceae may be wrongly placed in Ericales, though FAGERLIND (1947) found close embryological and morphological agreement with other families of this order. For further observations on Roridulaceae see Appendix.

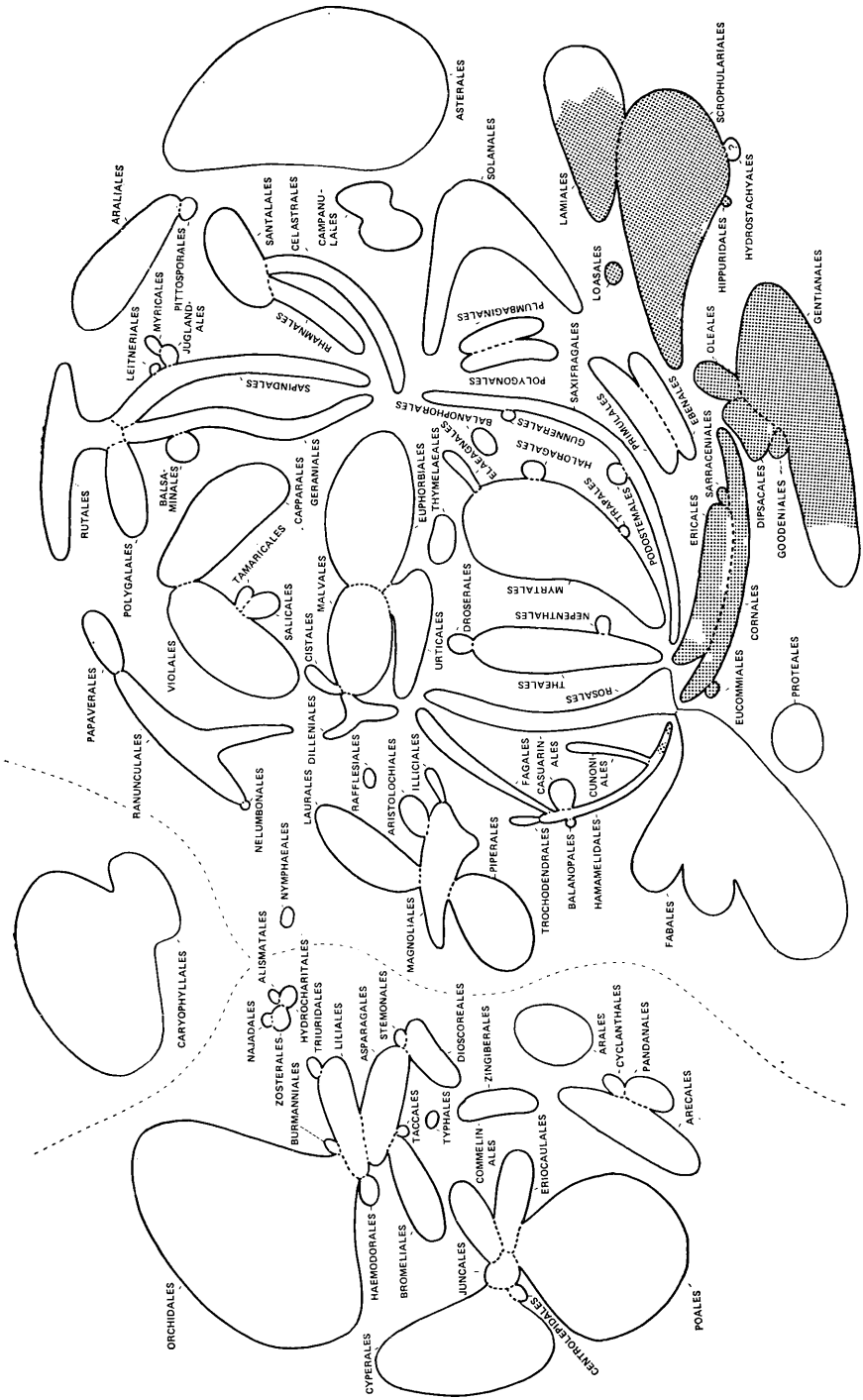

Fig. 9. Documented distribution of iridoid compounds in the angiosperm system. The area of each family from where iridoids are known has been shaded in its entirety except for Lamiaceae, where it is known that the iridoids are restricted to certain groups of genera.

Sarraceniales

The two genera investigated in this small order were both found to contain the primitive seco-iridoids belonging to Group VI. In this respect they agree well with the adjacent order Cornales although certain genera of Ericales seem to agree somewhat better in morphological features (see Appendix). Embryologically, Sarraceniales resembles both of the two orders mentioned. As far as we can see, it should not be placed near Papaverales as in certain other modern systems. We have also investigated one member of each of two other families sometimes considered to be closely related to Sarraceniaceae, viz. Droseraceae and Nepenthaceae, but these did not contain iridoid glucosides (see Appendix).

Eucommiales

This monotypic order comprising *Eucommia ulmoides* is unusual in having unisexual naked flowers and ducts containing gutta-percha. It has usually been placed in or near Urticales or Hamamelidales, but the monothetic, tenuinucellate ovules with ab initio cellular endosperm speaks against this. The presence of iridoids also supports a position removed from them. The embryological features agree well with Cornales and other iridoid-containing orders. The species also agrees with certain Lamianae, e.g. Lamiaceae and Scrophulariaceae, in the presence of iridoids belonging to both Group I and Group II (BIANCO et al. 1974 b). In spite of this, in the present system it has been placed in a separate order near Cornales awaiting further evidence. (The *Ulmus*-like fruits and naked, unisexual flowers probably represent derived features.)

Cornales

This appears to be a relatively homogeneous order in the sense that all the families, though not all the members, investigated contain iridoid compounds of some kind. However, as regards the groups of iridoids the order displays more diversity than any other, as iridoids belonging to Groups I, III, IV, VI, IX and X are present.

This diversity is also displayed within some of the families of the order. Thus in Icacinaceae, Davidiaceae, Hydrangeaceae and Cornaceae there are some members with seco-iridoids and some with more or less advanced iridoids belonging to Groups I, III and IV. Even within a single genus, *Cornus,* iridoids belonging to Groups I, III and IV are found, although in different species, and most species prove to have no iridoids at all (JENSEN et al. 1975). As far as is known no other genus displays such diversity as regards iridoids, but *Cornus* is known to be very variable in other characters as well and is often divided into several minor groups of species sometimes treated as genera.

Of special interest is the co-occurrence of camptothecine (Group IX, **55**) in Nyssaceae and Icacinaceae and ipecac alkaloids (e.g. **8**, **56**) in Alangiaceae and Icacinaceae. Although camptothecine itself has so far not been found in Gentianales it is a representative of a class of indole alkaloids very often found in this order, thus forming a chemical link between Cornales and Gentianales. The same can be said of the ipecac alkaloids as this type of compound is also found in Rubiaceae.

As emphasized by HUBER (1963), whose circumscription of Cornales largely agrees with the one accepted here (DAHLGREN 1975), there is close agreement between Cornales and Ericales. This includes the embryological characters such as the usually ab initio cellular endosperm, unitegmic ovules, and frequent endosperm haustoria, and the anatomical characters, such as the often scalariform perforation of the vessels, as well as the floral and vegetative morphology. Thus Diapensiaceae could well be treated in either order but is here placed in Ericales.

These orders are placed well apart from

Araliales (see below) and also from Saxifragales which practically always has bitegmic ovules and also seems to be entirely lacking in iridoids. Further investigations are needed before this can be concluded with certainty. For the position of Stylidiaceae in Cornales see Appendix.

Oleales

This order consists of a single family, Oleaceae, which is mainly characterized by iridoid compounds of Groups VI, VII and VIII, the last group not being found elsewhere. As these compounds are known to be derived from secologanin and as the family also contains complex alkaloids its proximity to the order Gentianales is well-established. Only a few genera have so far been investigated and a more detailed knowledge of the chemistry of the order is desirable.

Dipsacales

The presence of seco-iridoids is a common feature of the order being found within all families except Morinaceae of which only a single species has been investigated (see Appendix). The type of seco-iridoids suggests close relationship with Gentianales, Oleales and Goodeniales, but also with certain families in Cornales and with Sarraceniales. Valerianaceae occupies a singular position in also producing iridoids of Group V with an intact five-ring. These compounds, although they are biochemically closely related to Groups I—IV, are known from Valerianaceae only and display some special features not found elsewhere. They can be interpreted as being products of a secondary evolution within the family. Thus the order could have a common ancestor that produced seco-iridoids only.

One of the weaknesses of this system (DAHLGREN 1975) is apparent in the fact that there seems to be an almost indefinable borderline between Cornales and Dipsacales as regards morphological features. This close relationship is also reflected in the iridoids. The order Dipsacales may possibly represent a heterogeneous assemblage of families. The flowers have perhaps proceeded to sympetaly and zygomorphy or asymmetry in the perianth, oligomery in the androecium, epigyny, and few pendulous apical ovules, along more than one line of evolution from different ancestors in a pre-Cornales where several of these features are found separately.

The position of Calyceraceae in Dipsacales is discussed in the Appendix.

No definite conclusions can be drawn from the absence of iridoids in *Morina* (Morinaceae). It should be kept in mind that there are differences in various details between *Morina* (*longifolia*) and the members of Dipsacaceae (see VIJAYARAGHAVAN and SARVESHWARI 1968 pp. 383—402). This evidence casts doubt upon the close relationship between Morinaceae and Dipsacaceae.

Goodeniales

Further evidence will be presented in the Appendix, in support of treating Goodeniaceae (incl. Brunoniaceae) as a separate order, Goodeniales. Goodeniaceae is usually included in Campanulales, but does not seem to belong there at all.

So far only a few members of the order have been investigated for iridoids. The compound found suggests relationship with both Dipsacales and Gentianales.

Gentianales

The families of Gentianales are mainly characterized by the occurrence of seco-iridoids, exceptions being Retziaceae, Buddlejaceae and Asclepiadaceae. Retziaceae, which is monotypic, has been investigated in the course of the present project, resulting in the detection of an iridoid, but the material was too limited to permit determination of its structure (see Appendix).

Table 9. Iridoid-bearing orders and their families (whether these contains iridoid compounds or not). The figures given refer to genera and species of each family. They are highly approximative and mostly in accord with AIRY-SHAW 1973.

HAMAMELIDANAE (other orders than Hamamelidales omitted here)

Hamamelidales: Myrothamnaceae (1: 2), Hamamelidaceae (23: 80), Platanaceae (1: 10), Altingiaceae (2: 10), Daphniphyllaceae (1: 10), Rhodoleiaceae (1: 1)

CORNANAE

Ericales: Actinidiaceae (3: 350), Clethraceae (1: 120), Cyrillaceae (3: 13), Roridulaceae (1: 2), Ericaceae (50: 1,350), Pyrolaceae (3: 30), Monotropaceae (12: 21), Epacridaceae (30: 400), Diapensiaceae (6: 20), Byblidaceae (1: 2), Empetraceae (3: 10), Grubbiaceae (2: 5)

Sarraceniales: Sarraceniaceae (3: 17)

Eucommiales: Eucommiaceae (1: 1)

Cornales: Garryaceae (1: 18), Alangiaceae (2: 20), Cornaceae (12: 100), Davidiaceae (1: 1), Nyssaceae (2: 10), Icacinaceae (58: 400), Escalloniaceae (7: 150), Columelliaceae (1: 4), Stylidiaceae (6: 150), Hydrangeaceae (10: 115), Alseuosmiaceae (3: 11), Sambucaceae (2: 240), Adoxaceae (1: 1), and, perhaps, some smaller families (see DAHLGREN 1975 p. 138)

GENTIANANAE

Dipsacales: Caprifoliaceae (11: 250), Valerianaceae (13: 400), Triplostegiaceae (1: 2), Dipsacaceae (8: 150), Morinaceae (1: 17), Calyceraceae (4: 40)

Oleales: Oleaceae (29: 600)

Goodeniales: Goodeniaceae (15: 300)

Gentianales: Loganiaceae (22: 548), Buddlejaceae (6: 150), Retziaceae (1: 1), Rubiaceae (500: 6,000), Menyanthaceae (5: 33), Gentianaceae (80: 900), Apocynaceae (180: 1,500), Asclepiadaceae (175: 2,200)

LOASANAE

Loasales: Loasaceae (15: 250)

LAMIANAE

Scrophulariales: Scrophulariaceae (215: 2,700), Selaginaceae (5: 300), Globulariaceae (2: 30), Lentibulariaceae (4: 170), Plantaginaceae (3: 270), Pedaliaceae (12: 50), Trapellaceae (1: 2), Martyniaceae (3: 13), Orobanchaceae (13: 180), Gesneriaceae (120: 2,000), Bignoniaceae (120: 650), Henriqueziaceae (2: 13), Myoporaceae (2: 85), Acanthaceae (250: 2,500)

Hippuridales: Hippuridaceae (1: 1)

Hydrostachyales: Hydrostachyaceae (1: 30) (iridoids present?)

Lamiales: Verbenaceae (75: 3,000), Callitrichaceae (1: 25), Lamiaceae (180: 3,500)

In Buddlejaceae, *Buddleja* has been reported to contain Group I iridoids typical of Scrophulariales but not of Gentianales. However, iridoids of Group I are found in a large part of Rubiaceae and a few species of Apocynaceae, though none of the iridoids in these families are identical with those in Buddlejaceae.

Seco-iridoids are relatively common in the order having been reported in Menyanthaceae, Gentianaceae, Loganiaceae and Apocynaceae. The presence of this group of iridoids links these families with Dipsacales, Goodeniales and Oleales in all of which seco-iridoids are predominant, and also with Sarraceniales and families within Cornales.

The complex alkaloids are characteristic of Gentianales, being widely distributed in Loganiaceae, Rubiaceae and Apocynaceae. The few scattered occurrences outside this order, viz. in Cornales and Oleales, indicate a common ancestry for the three orders.

The apparently complete absence of iridoid compounds in the florally most

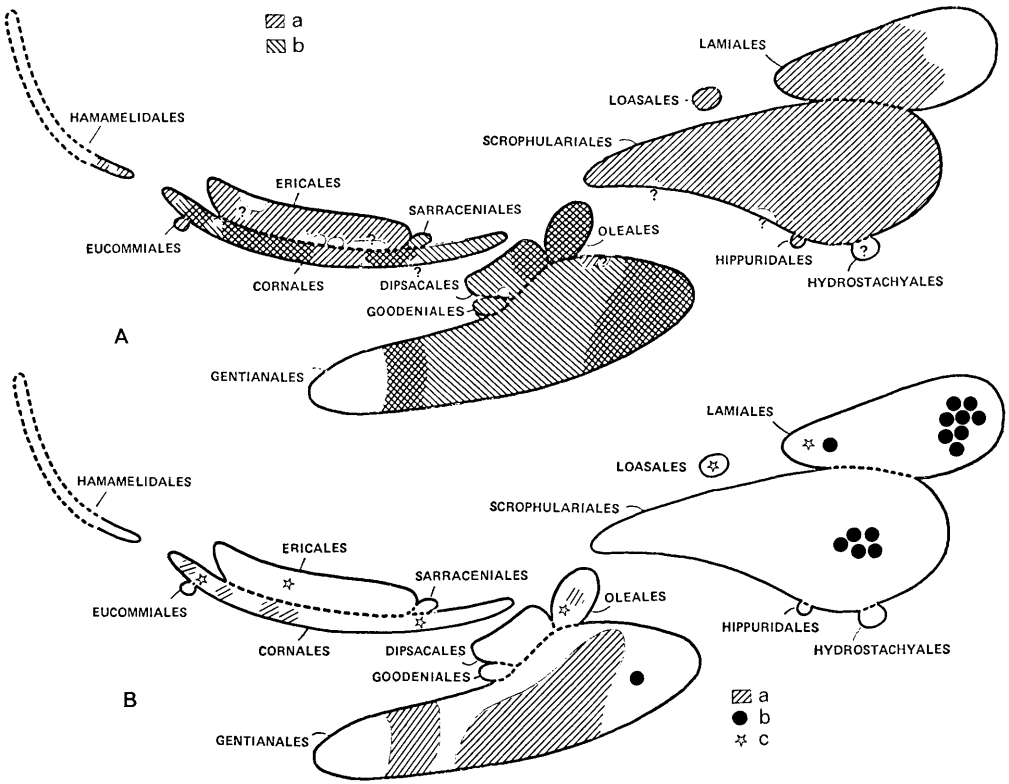

Fig. 10. — A: a: Distribution of carbocyclic iridoids (Groups I—V and X) if seco-iridoids are not present; b: Distribution of seco-iridoids (Groups VI—IX). Families where both kinds occur are checkered. — B: a: Occurrence of "complex" iridoid alkaloids (Group IX), the records are numerous in Rubiaceae and Apocynaceae; b: occurrence of iridoid glucosides of Group II; c: occurrence of iridoid glucosides of Group IV.

advanced of the families, Asclepiadaceae, is of great interest. The close connection between this and Apocynaceae is demonstrated by many morphological features and also by other chemical characters (see HEGNAUER 1964 p. 223). Lack of iridoids could here be interpreted as being a derived character.

The types of iridoids present in most families of Gentianales support the view that the order is largely a natural one. Some slight doubt still remains as to whether Retziaceae and Buddlejaceae belong here and the families are kept separate from Loganiaceae where they are otherwise likely to be included.

Loasales

In Loasaceae, the only family in the order, a single species (of *Mentzelia*) has so far been reported to contain iridoids. Compounds of the same group are known mainly from Cornales and Lamiales. On account of the unitegmic ovules, the ab initio cellular endosperm, and the terminal endosperm haustoria, etc., Loasaceae has long been recognized as diverging from the other families in Violales (Parietales). It was placed by HALLIER (1912) in Campanulales and by TAKHTAJAN (1969) in Polemoniales. None of these groups, however, contain iri-

doids. A place near Lamiales-Scrophulariales or, perhaps, Cornales is more satisfactory from this point of view. However, Loasaceae is morphologically rather isolated even here and should be treated as a separate order.

See also note on p. 180.

Scrophulariales

No seco-iridoids have been found in this large order. The iridoid compounds known are restricted to Groups I, II and X, which all have the basic iridoid skeleton. A gradient of complexity can be seen in the Group I compounds found in the order.

Some taxa contain aucubin (**12**) alone, i.e. Orobanchaceae and some genera of Scrophulariaceae (c. 20 % of the total number of species found to contain **12** and/or **13**). Some contain aucubin in admixture with catalpol (**13**), i.e. Globulariaceae, Lentibulariaceae, Plantaginaceae and approximately 70 % (as defined above) of Scrophulariaceae. Catalpol alone is found in Martyniaceae, Myoporaceae, Bignoniaceae and some genera of Scrophulariaceae (c. 10 %; see KOOIMAN 1972).

The two compounds often occur esterified with aromatic acids (for a comprehensive summary see GRAYER-BARKMEIJER 1973), and in this form have only been found in one case among the "more primitive" orders, viz. in Ericaceae, Ericales.

Compounds of Group II are less often encountered in the order, but a few occurrences are known from Scrophulariaceae and one from Pedaliaceae.

In addition to the compounds mentioned some apparently simple iridoid-derived pyridine alkaloids (Group X) have been discovered in Scrophulariales. They occur in Bignoniaceae, Orobanchaceae, Plantaginaceae and Scrophulariaceae.

Of the families not mentioned above Selaginaceae (KOOIMAN 1970) and Acanthaceae (WIEFFERING 1966) are suspected to contain iridoids, while none have yet been reported from Trapellaceae and Gesneriaceae.

Taxonomically, Scrophulariales does not seem to be controversial. The families usually resemble one another closely and generally speaking the order is easily distinguished on morphological features. It is evident that Solanaceae should not be included in the order. Like the other families placed in Solanales (according to the system accepted here, DAHLGREN 1975), such as Polemoniaceae, Convolvulaceae and Boraginaceae (WINDT 1959), Solanaceae seems to lack iridoids entirely (KOOIMAN 1971 p. 397).

Scrophulariales is distinguished from Gentianales and other orders of Gentiananae in lacking seco-iridoids.

Hippuridales

This monotypic order contains advanced iridoid glucosides belonging to Group I and identical with those found in a number of families of Scrophulariales. Like this order, it lacks tannins and gallic and ellagic acids. The unitegmic ovules and the ab initio cellular endosperm in combination with these features point to a position close to Scrophulariales, perhaps near Plantaginaceae or Scrophulariaceae. This position has been suggested by HEGNAUER (1966 b p. 267). The epigyny and reduced perianth in this connection seem to be of no great significance, but in combination with the whorled leaves, for example, may justify treating the family Hippuridaceae as a separate order.

Hydrostachyales

No chemical investigations have been reported from this order consisting of the small family Hydrostachyaceae. The present taxonomic position has been proposed by JÄGER-ZÜRN (1965).

Lamiales

Like Scrophulariales, this large order is characterized by a complete lack of seco-iridoids. Iridoid glucosides belonging to Group I have been reported from all three families. These are the only iridoids found in Callitrichaceae. The close affinity between this and the other families in the order has now been fully established. As regards composition of iridoids it agrees, however, equally well with Scrophulariales.

Group II iridoids appear to be characteristic of certain groups of genera in the other two families in Lamiales, Lamiaceae and Verbenaceae, where their diversity is greatest. Biochemically the known Group II iridoids are in general more advanced than those belonging to Group I. This would support the view often expressed that Lamiales is more advanced than Scrophulariales. However, they have doubtless evolved along more or less parallel lines.

Verbenaceae also contains Group III compounds, otherwise known only in Cornaceae, and Group IV compounds, known also in Oleaceae, Cornaceae, Hydrangeaceae, Ericaceae and Loasaceae.

Not all the genera of Verbenaceae or Lamiaceae contain iridoids. They are lacking in certain groups of genera, some of which are quite large. In Lamiaceae there seems to be a high degree of correlation between the presence of iridoids and other characters such as pollen grain morphology and number of nuclei in mature pollen grains (see KOOIMAN 1972). This opens up new possibilities, and prompts to similar investigations in other families.

SYMPETALAE, A POLYPHYLETIC GROUP

"Sympetalae" or at least most orders in this somewhat ill-defined group, has long been acknowledged as a presumably natural (i.e. monophyletic) group. This applies in particular to those orders of Sympetalae that according to TAKHTAJAN (1969) comprise the subclass Asteridae, viz. Dipsacales, Gentianales, Polemoniales, Scrophulariales (including Solanaceae), Lamiales, Campanulales, Calycerales and Asterales.

This group is characterized by 5- or 4-merous, tetracyclic flowers with sepals, petals and stamens in alternating whorls and with generally 2 carpels; further by the sympetalous corolla, unitegmic tenuinucellate ovules and generally by ab initio cellular endosperm.

Now, chemical evidence does not entirely support the view that this group is natural. The presence of iridoids in certain orders and families provides a rather distinct dividing line between Dipsacales, Gentianales, Scrophulariales (excluding Solanaceae) and Lamiales on the one hand and the remaining orders on the other. Furthermore, they are more or less closely connected with Oleales, Cornales, Ericales, Sarraceniales, Eucommiales and Hippuridales (s. str.). Certain orders thus need to be broken up; in particular Goodeniales must be excluded from Campanulales and Loasales from Violales. This is in fact supported by embryological and gross morphological characters. It should also be stressed that in general most of the characters considered typical of Asteridae are also found within orders outside this subclass, for instance within Oleales, Cornales and Ericales.

On the other hand those sympetalous orders that lack iridoids, viz. Campanulales, Solanales, Asterales and Pittosporales, show a varying degree of similarity in chemical as well as morphological characters to other orders. This applies in particular to Araliales which in its turn approaches Rutales.

Chemical characters apart from the presence of iridoids support the demarcation between the iridoid-containing groups on the one hand and at least some of the sympetalous groups not containing iri-

doids on the other. Thus in the iridoid-bearing orders necin and tropane alkaloids are almost completely absent but are found in some of the other orders. Polyacetylenes are typical of Campanulales, Asterales, Pittosporales and Araliales (and are also known in Rutales), but are, as it seems, lacking in the iridoid-containing orders.

This and additional evidence can be taken to indicate a double or possibly even multiple ancestry for the "Sympetalae" (or TAKHTAJAN's Asteridae), whereas Ericales, for example, which is sometimes placed in the subclass Dilleniidae, is closely connected with the families of Cornales (sensu DAHLGREN) most families of which are found in TAKHTAJAN's Rosidae.

PHYLOGENETIC CONSIDERATIONS. SUMMARY

An increasing degree of complexity and variety in the iridoid compounds can be seen when proceeding from Hamamelidales (in Hamamelidanae) through the orders in Cornanae thence either to Gentiananae or to Lamianae.

The few occurrences of iridoids so far registered in Hamamelidanae belong exclusively to Group I, which presumably represents the primary compounds. This type is also found in the other superorders and has its most complex forms in Lamianae.

The orders in Cornanae have probably developed iridoids at an early stage and these have successively attained to great diversity. This applies in particular to Cornales which contain a great variety of iridoids belonging to Groups I, III, IV, VI, IX and X. The seco-iridoids apparently evolved first in Cornales. This is indicated by the presence in contemporary forms of mostly primitive compounds of Groups VI and IX.

One evolutionary branch connected with the early Cornanae is probably Gentiananae where the iridoids have further evolved along more or less distinct biosynthetic lines (to compounds belonging to Groups VII and VIII). A further development of the Group IX compounds has also taken place. As regards the iridoids Gentiananae is thus clearly connected with Cornanae, and these superorders are probably of common origin. The Group V compounds are found solely in Valerianaceae and have presumably evolved within primitive members of this family.

Lamianae contains biochemically advanced iridoids belonging to Groups I, II, III and IV. This suggests a common origin for this superorder and Cornales in Cornanae, possibly also with Gentianae. At an early stage Cornales, with its great variety of iridoid types, could have given rise to primitive Lamianae where Group II iridoids have developed. This group of iridoids is not found in Cornales, whereas the other groups appear in Cornales as well as Lamianae.

Primitive Gentianales and primitive Lamianae, on the other hand, may also be of common origin as far as iridoids are concerned. Buddlejaceae, which morphologically is related to Loganiaceae and chemically is related to Scrophulariales, is thus intermediate and may represent a relict from common ancestors. The one known occurrence in Rubiaceae of a Group II glucoside, shantziside (**25**), points to a possible connection between Lamianae and Rubiales.

The iridoids so far discovered in the plant orders mentioned support the conclusion that these groups make up a relatively homogeneous and probably monophyletic group. The restriction of iridoid compounds mainly to groups with unitegmic ovules suggests that they developed along an evolutionary line where the ovules were just about to evolve from the bitegmic to the unitegmic condition. Altingiaceae and Daphniphyllaceae, both in Hamamelidales, are perhaps relicts of primitive iridoid-bearing groups with bitegmic ovules. Floral reduction has

here proceeded further than in most of the other iridoid-bearing groups. This connection between Hamamelidales and Cornanae is of particular interest while also raising some phylogenetic problems.

APPENDIX I. MATERIALS AND METHODS

Investigations for iridoid glucosides were made on single species from selected families of the dicotyledons.

Individual compounds were identified by comparison of ^{1}H-NMR-spectra with those of authentic compounds. The spectra were recorded at 90 MHz on a Bruker HX-90E instrument with a deuterium lock. The solvents were D_2O and $CDCl_3$ with DSS and TMS, respectively, used as standards.

Generally 20—50 g samples of fresh plant material or 2—10 g of herbarium material were extracted with EtOH, evaporated, dissolved in water and extracted with $CHCl_3$ and Et_2O to remove fats, etc. The aqueous solution was filtered through a column of neutral Al_2O_3 followed by washing with water. The eluate was concentrated and fixed on a column of silica gel, and iridoid and other glycosides eluted with acetone. The stages of purification were checked by ^{1}H-NMR with D_2O as a solvent, and if the acetone eluate showed absorptions between 5.5 and 10 ppm (vinylic and aldehyde region) the mixture was further purified by means of preparative thin layer chromatography (silica gel), if necessary preceded by acetylation. If the acetone eluate did not show appreciable NMR-absorption at 5.5—10 ppm, the result was considered negative.

In a few cases (*Empetrum, Myoporum*) the vinylic regions of the spectra were obscured by multiple absorptions, probably from aromatic esters, and further separation after acetylation did not reveal any iridoids in the complex mixtures. These cases, however, deserve further investigation. It should be pointed out that — although we regard this method as convenient and also comparatively sensitive, as an iridoid content as low as 0.01 per cent of the fresh weight can normally be detected — compounds with vicinal phenolic OH-groups are presumably strongly adsorbed to the alumina and thereby lost. Examples of substances not detected by this procedure are oleuropein and esters of caffeic acid. Acids such as monotropein are eluted slowly from alumina.

Secologanin was separated as its tetraacetate and identified by the NMR-spectrum (JENSEN et al. 1973 c).

Table 10 shows the results obtained. Numbers following the names of species where given refer to the numbers in the catalogue of plants grown in the Botanical Gardens of Copenhagen. Voucher numbers are given in the next column. Voucher specimens without collectors' names are to be deposited in the Botanical Museum of the University of Copenhagen (C).

NOTES ON INVESTIGATIONS OF SPECIES

Roridula dentata L. — 4.5 g of herbarium material was available for investigation, and from this was isolated 7 mg of a glycoside; NMR-spectrum: 7.70 ppm (*s*, H-3), 5.22 ppm (*d*, J=3.5 Hz, H-1) and 1.15 ppm (*d*, J=7 Hz, 10-CH_3). After chromatography acetylation yielded ca. 3 mg of a tetraacetate; NMR-spectrum: 7.36 ppm (*s*, H-3), 2.0—2.1 ppm (4×OAc) and 1.27 ppm (*d*, J=7 Hz, 10-CH_3). In both spectra additional absorptions indicating the presence of an iridoid glucoside were observed, though without a signal indicating the common methyl ester group.

Stylidium adnatum R. BR. — A mixture of iridoid glucosides was obtained. One of the fractions after acetylation and further chromatography yielded a nonaacetate, probably of a dimeric iridoid glucoside. The NMR-spectrum of this compound resembles that of monotropein methyl ester acetate in several respects.

Sarracenia purpurea L. and *Darlingtonia californica* TORR. — Morroniside in the pure state was obtained from each of these species. It was identified by its NMR-spectrum (JENSEN and NIELSEN 1974).

Retzia capensis THUNB. — 9 g of herbarium material was available for investigation. After extensive chromatography it gave a fraction (5 mg), the NMR-spectrum of which indicated the presence of an iridoid (absorption at 7.48 ppm). Further attempts to characterize the compound were not successful.

Knautia arvensis (L.) COULT. — The main component of the acetone eluate resulting from this plant was methyl glucoside. It was identified by its NMR-spectrum which apart from absorptions from the glucose moiety, showed distinguishable signals at 4.38 ppm (*d*, J=7.5 Hz, H-1) and 3.57 ppm (*s*, OCH_3). The spectrum was identical with that of the authentic compound.

Dipsacus sylvestris HUDS. — This plant gave a complex mixture of iridoid glucosides, characterized by absorptions in the NMR-spectrum at 7.40—7.65 ppm. Chromatography, first of the glucosidic mixture, and then of the acetate, gave a pentaacetate as the main

Table 10. Taxa investigated in the present study. — * Material was supplied by The Royal Botanic Gardens, Kew, England.

		Botanical Garden No.	Herbarium No.	Presence of Iridoids	Comments
Piperales					
Saururaceae	*Houttuynia cordata* THUNB.	1825/1	48—74	—	
Euphorbiales					
Euphorbiaceae	*Mercurialis perennis* L.		86—74	—	
Violales					
Flacourtiaceae	*Azara microphylla* HOOK. FIL.	5075/2	34—74	—	
	Idesia polycarpa MAXIM.	5079B/1	47—74	—	
Trochodendrales					
Trochodendraceae	*Trochodendron aralioides* SIEB. & ZUCC.	4744/1	12—74	—	
Tetracentraceae	*Tetracentron sinense*	P1970—135		—	
Eupteleaceae	*Euptelea polyandra* SIEB. & ZUCC.	1850B/1	6—74	—	
Cercidiphyllaceae	*Cercidiphyllum japonicum* SIEB. & ZUCC.	5742B/1	45—74	—	
Campanulales					
Campanulaceae	*Campanula* sp.		73—74	—	
	Laurentia petraea (F. MUELL.) E. WIMM.	3060/3	75—74	—	
Lobeliaceae	*Lobelia laxiflora* H. B. & K.	3058/20	76—74	—	
Cunoniales					
Cunoniaceae	*Cunonia capensis* L.	Kew*	85—74	—	
Bruniaceae	*Staavia glutinosa* DAHL		DAHLGREN & STRID 2013 (LD)	—	
Saxifragales					
Crassulaceae	*Sedum telephium* L.		21—74	—	
Gunneraceae	*Gunnera chilensis* LAM.	6139C/1	11—74	—	
Nepenthales					
Nepenthaceae	*Nepenthes*×*mixta*	P1964—268		—	
Droserales					
Droseraceae	*Drosera rotundifolia* L.		144a—72	—	
	Drosophyllum lusitanicum LINK		DAHLGREN & LASSEN 22: 3 (LD)	—	
Parnassiaceae	*Parnassia palustris* L.		72—74	—	
Ericales					
Actinidiaceae	*Actinidia arguta* (SIEB. & ZUCC.) MIQ.	4749B/2	49—74	—	
Clethraceae	*Clethra arborea* AIT.	4320/2	29—74		
Roridulaceae	*Roridula dentata* L.		DAHLGREN & STRID 3183 (LD)	+	unknown, see text

		Botanical Garden No.	Herbarium No.	Presence of Iridoids	Comments
Empetraceae	*Empetrum nigrum* L.		144b—72	—	
Grubbiaceae	*Grubbia rosmarinifolia* THUNB.		DAHLGREN & STRID 2439 (LD)	—	
Cornales					
Diapensiaceae	*Diapensia lapponica* L.		61—74	—	
Stylidiaceae	*Stylidium adnatum* R. BR.	3093/1	27—74	+	unknown, see text
Hydrangeaceae	*Hydrangea heteromalla* D. DON.		67—74	+	loganin and secologanin
Sarraceniales					
Sarraceniaceae	*Sarracenia purpurea* L.	5021/1		+	morroniside, see text
	Darlingtonia californica TORR.	5023C/1		+	morroniside
Ebenales					
Styracaceae	*Styrax japonicum* SIEB. & ZUCC.	4257/4	9—74	—	
Gentianales					
Retziaceae	*Retzia capensis* THUNB.		DAHLGREN & STRID 3515 (LD)	+	unknown, see text
Menyanthaceae	*Villarsia ovata* (L. FIL.) VENT.		DAHLGREN & STRID 3887 (LD)	+	secologanin
Dipsacales					
Dipsacaceae	*Knautia arvensis* (L.) COULT.		16—74	—	methyl glucoside
	Dipsacus sylvestris HUDS.		17—74	+	methyl glucoside and der. of secologanin, see text
	Scabiosa columbaria L.		20—74	+	methyl glucoside, and secologanin, se text
Calyceraceae	*Acicarpha tribuloides* JUSS.	3036/1	46—74	+	secologanin
Morinaceae	*Morina longifolia* WALL.	2190/2	13—74	—	
Goodeniales					
Goodeniaceae	*Selliera radicans* CAV.	3042/1	34—72	+	secologanin
	Scaevola suaveolens R. BR.	3038/3	26—74	+	secologanin present, see text
Solanales					
Cuscutaceae	*Cuscuta epithymum* (L.) L.		22—74	—	
Boraginaceae	*Cordia alba* ROEM. & SCHULT.	3738/6	32—74	—	
Scrophulariales					
Scrophulariaceae	*Digitalis purpurea* L.	3915/6	44—74	—	cornoside, see text
Myoporaceae	*Myoporum laetum* FORST. FIL.	3735/5	28—74	—	
	Eremophila maculata (KERR) F. MUELL.	3735/2	31—74	—	prunasin, see text

component. The NMR-spectrum of this compound was partly superimposable upon that of secologanin tetraacetate, partly upon that of loganin pentaacetate, except for a doublet (J=2.5 Hz) at 6.04 ppm. From the integral values it was deduced that the glucoside contains one molecule of glucose and one each of the secologanin and loganin aglucones, except for the lack of one methyl ester group. The absorption at 6.04 ppm, not seen at this frequency in the free glucoside, must be assigned to H-1 in an acetylated aglucone moiety. Assuming the same configuration as in the parent glucosides loganin and secologanin, this absorption is assigned to H-1 of loganin aglucone because of the small coupling constant. Tentatively, we suggest that the structure of the compound is secologanic acid esterified to C-7 of the aglucone of loganin.

Scabiosa columbaria L. — The presence of iridoids was demonstrated by NMR-absorptions at 7.40—7.70 ppm. Secologanin (or derivatives), which was a main component, was characterized by the aldehyde signal at 9.65 ppm. No attempts were made at further characterization.

Scaevola suaveolens R. Br. — NMR-absorptions at 7.47 and 7.62 ppm indicated that iridoids were present. The absorptions at 7.62 and at 9.65 ppm indicated that secologanin was a minor constituent. No further characterization was attempted.

Digitalis purpurea L. — No iridoids could be detected in this plant. By comparison with the NMR-spectrum of the authentic compound, the main glucoside present proved to be the Cornus quinol glucoside, here named cornoside, found in several species of *Cornus* (Jensen et al. 1973 d) and in some species of *Forsythia* (Jensen and Nielsen unpublished).

Eremophila maculata (Kerr) F. Muell. — Prunasin was isolated in a small amount and identified by its NMR-spectrum. It was converted to a mixture of prunasin and sambunigrin tetraacetates by acetylation (Jensen and Nielsen 1973).

The work will be continued in order to identify the remaining unknown compounds.

APPENDIX II. ON THE SYSTEMATIC POSITION OF CERTAIN FAMILIES CONTAINING IRIDOIDS

Sarraceniaceae

In some other systems Sarraceniaceae has been placed together with Nepenthaceae and Cephalotaceae because of the similar pitcher-like leaves, a character that is known to have developed by convergence along different lines of evolution. A position often recently proposed for the family (or for the order Sarraceniales) is next to Papaverales. It is interesting that Kerner (1891) placed Sarraceniaceae in Sclerophyllae (=Ericales), a place which, as we shall see, agrees rather well with the evidence presented below. On morphological and embryological grounds Sarraceniales was placed next to Ericales and Cornales by one of the present authors (Dahlgren) in 1974. The presence of a seco-iridoid in *Sarracenia* as well as *Darlingtonia* supports a position close to Cornales.

Apart from the presence of iridoids there are a great number of characters in Sarraceniaceae that together point to affinity with the Ericales-Cornales alliance. Morphologically and embryologically Sarraceniaceae perhaps most closely resembles certain members of Ericales. In particular they have a number of characters in common with Pyrolaceae:

Alternate leaves; absence of stipules; anomocytic stomata; vessels with scalariform perforation; 5-merous flowers with 10 or more stamens; pollen grains shed at the binucleate stage; similar pollen morphology; numerous anatropous, unitegmic, tenuinucellate ovules; Polygonum type of embryo sac; cellular endosperm formation; loculicidal capsule; small seeds with thin testa often extended to form a process or wing; small embryo formed according to the Caryophyllad pattern; fleshy endosperm; presence of anthocyanins and tannins of the condensed type and of kaempferol, cyanidin and caffeic acid in the extracts of leaves. The presence of iridoids is also common to both, but they are of different types in the two families, which may indicate that Sarraceniaceae is closer to Cornales than to Ericales.

By virtue of the pitcher-leaves, the scattered vascular bundles in the stem and the more numerous stamens we preliminarily propose treating Sarraceniaceae as a separate order. This we place adjacent to Ericales and Cornales.

Roridulaceae

The presence of an iridoid (though in low concentration) in the leaves of *Roridula dentata* in combination with a number of morphological characters warrants placing the genus in or next to Ericales.

The genus has been placed in Rosales (s.lat.) in several of the classic systems (Engler, Wettstein, Skottsberg, Pulle, etc.), in which Saxifragaceae and a number of supposedly related families were also usu-

ally included. In recent years the genus has usually been treated separately as the family Roridulaceae or together with *Byblis* in Byblidaceae, and in various works placed near Ochnaceae, Saxifragaceae, Pittosporaceae or Droseraceae. It was placed in Clethraceae by HALLIER (1812). In a study of the embryological characters of *Roridula gorgonias*, VANI HARDEV (1972 pp. 339—351) compared the genus with *Byblis* and discovered a number of differences that warranted placing the two genera at least in different families, both of which were well separated from Droseraceae.

Roridula (2 spp.) is found in South Africa. The tentacular glands, which superficially though not in detail resemble those of Byblidaceae and Droseraceae, produce a balsam-like secretion and are thus not proteolytic and not insectivorous in the true sense.

The following characters should be considered in combination: Shrubby habit; alternate, exstipulate leaves; vessels with scalariform perforation; tentacular glands with balsam-like secretion; paniculate, raceme-like inflorescence; actinomorphous, hypogynous, 5-merous flowers with persistent sepals and imbricate petals; 5 free stamens with massive connective nectaries; tetrasporangiate anthers dehiscing by apical pores; 3-colporate, single pollen grains released at the binucleate stage; the 3-carpellate and 3-locular pistil with its funnel-shaped style apex; the ovary with numerous, pendulous, anatropous, unitegmic and tenuinucellate ovules; the Polygonum type of embryo sac; the cellular endosperm, the micropylar part of which tends to behave as a haustorium; and the loculicidal capsule with several seeds with well-developed endosperm and a small embryo. Moreover, the plants are rich in tannins and crystals of calcium oxalate. Unlike *Sarracenia* (see above), the seeds have a thick testa and the embryogeny conforms to the Solanad type.

The presence of iridoids agrees well with this combination of characters, which supports placing *Roridula* in Ericales or in its vicinity. Many features of Byblidaceae also favour a position in this order, but further investigation is desirable. The two families should be placed at some distance from each other, however, and the secreting glands in them at least in part seem to have developed by convergence.

Stylidiaceae

Group I iridoids were found in *Stylidium* in this family. Tannins and leucoanthocyanins are known to occur in Stylidiaceae (HEGNAUER 1973 p. 471). This among other things, argues strongly against placing the family in or next to Campanulales or Asterales, though in one conspicuous chemical character there is agreement with the latter orders, i.e. in the presence of inulin.

Some morphological characteristics of Stylidiaceae are as follows:

The 5-lobate or 2-lipped corolla; only 2 or 3 stamens usually more or less fused with their filaments to the style; the bilocular ovary with several to numerous ovules, which are unitegmic and tenuinucellate; and the capsular fruit. Endosperm formation is cellular, and terminal endosperm haustoria have been recorded. In addition, there are glandular hairs in Stylidiaceae, but not laticiferous ducts, two characters in which this family differs from Campanulaceae and Lobeliaceae.

This combination of characters (except the presence of inulin and the few stamens) is also found within Cornales (sensu DAHLGREN 1975). The position in this order also agrees principally with that in the system of THORNE 1968, where Stylidiaceae is placed in the suborder Saxifragineae in Rosales where several families (i.e. chiefly those with one integument) of our Cornales were included.

Goodeniaceae

The fact that the genera *Scaevola* and *Selliera* of this family contain seco-iridoids (see also HEGNAUER 1966 a p. 213), contrary to the taxa of Campanulaceae and Lobeliaceae investigated, actualizes the question as to whether Goodeniaceae is at all closely related with the two families mentioned.

Goodeniaceae was treated by HUTCHINSON (1963), together with the scarcely distinct Brunoniaceae, and with Stylidiaceae, in the order Goodeniales, placed near Campanulales. In ENGLER's Syllabus WAGENITZ (1964) placed these three families in Campanulales, and also THORNE (1968 p. 61) made a similar arrangement, but excluded Stylidiaceae, which was placed in his Rosales (see above).

Goodeniaceae (incl. Brunoniaceae) is characterized by absence of latex in the vegetative parts; exstipulate, usually alternate leaves; zygomorphous, hypo- to epigynous flowers in a racemose inflorescence; 5 usually small calyx lobes and 5 petals which generally form an apically 5-lobate tongue or ray; 5 stamens with free filaments and free or more or less connate anthers; and a unilocular ovule with 2 or more ovules. The pollen grains are usually 3-colporate and released in the binucleate stage.

Comparing Goodeniaceae with other groups, one will find some conspicuous *differences*.

(1) from Asterales (=Asteraceae) in presence of iridoids, binucleate pollen grains, presence of a pollen cup on the style, well-developed calyx, and usually more than one seed free from the pericarp. — But it may have similar pollen grains and inulin in the vegetative parts, the petals are united to a tongue, the anthers are often connate and introrse, and endosperm haustoria are lacking as in Asteraceae.

(2) from Campanulales s. str. (see DAHLGREN 1975) in the presence of iridoids, absence of laticiferous ducts, presence of sclerenchymatous idioblasts and glandular hairs, presence of a pollen cup, different pollen grains (according to ERDTMAN 1952), absence of endosperm haustoria (VIJAYARAGHAVAN & MALIK 1972 p. 251) and lack of polyembryony. The testa, moreover, is 7—14 layered (1—4 layered in Campanulales s. str.). — But Goodeniaceae *has* inulin in the vegetative parts, petals of similar appearance, and sometimes similar, connate, introrse anthers as in Lobeliaceae.

(3) from e.g. Gentianaceae, Gentianales, in the zygomorphous, usually epigynous corolla, absence of internal phloem, presence of cellular endosperm (mostly ab initio nuclear in the chlorophyll-bearing genera of Gentianaceae). — But it *has* the iridoids in common, and it lacks laticiferous ducts as does Gentianaceae; inulin is also occasionally present in Gentianaceae, and in Gentianales (Apocynaceae etc.) one will find various stylar heads, possibly parallel structures to the pollen cup in Goodeniaceae. Moreover, in the probably related Menyanthaceae, there are sclerenchymatous idioblasts and cellular endosperm as in Goodeniaceae.

The mentioned groups, which at first might seem to be closely related to Goodeniaceae, thus exhibit some striking differences. Remaining, possibly closely related groups are the Cornales, Dipsacales and Scrophulariales, in the former two of which seco-iridoids are present, just as in Goodeniaceae. Examination of these groups similarly reveal a number of differences.

It may be concluded that Goodeniaceae (incl. Brunoniaceae) has a distinct position and may deserve being treated as a separate order. Its distinctness from Campanulales was demonstrated by VIJAYARAGHAVAN & MALIK (1972), who mainly on embryological grounds suggested its treatment as an order, Goodeniales, with its place next to Campanulales. Goodeniaceae seems to agree quite as well with orders like Gentianales, Dipsacales and Cornales, however, and the presence of seco-iridoids support a position rather in this vicinity.

Calyceraceae

Calyceraceae in most recent botanical literature is placed close to Campanulaceae, Lobeliaceae and Asteraceae. Because mainly of the pendulous ovule and certain embryological peculiarities it was excluded from this group by TAKHTAJAN (1969 p. 233) and placed in a separate order, Calycerales. CRONQUIST (1968 p. 309) placed Calyceraceae in Dipsacales, where it was considered by TAKHTAJAN to be somewhat out of place because of the alternate leaves, the lack of glandular hairs, the Asteraceae-like inflorescences and the somewhat different, binucleate pollen grains (the pollen grains are trinucleate in Dipsacales).

The presence of simple seco-iridoids is not in accord with a position in or close to Campanulales or Asterales, but agrees well with the conditions found in orders of Gentiananae. Calyceraceae agrees with Dipsacales in having unilocular ovules with one pendulous ovule, but admittedly is somewhat out of place here by the traits mentioned by TAKHTAJAN. Awaiting further detailed investigations, we prefer to follow CRONQUIST (1968) and THORNE (1968) in placing Calyceraceae as a peripheral member of Dipsacales.

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Additional Note: KOOIMAN in Acta Bot. Neerl. 23: 677—679 (1974), has reported the occurrence of loganin in four genera of Loasaceae, viz. *Cajophora, Loasa, Mentzelia* and *Blumenbachia*. This, he claims, supports a relationship between Loasaceae and the families of Gentianales and Scrophulariales sensu TAKHTAJAN.

Current Topics

The Distribution of Characters within an Angiosperm System

I. Some Embryological Characters

Rolf Dahlgren

DAHLGREN, R. 1975 07 08. Current topics. The distribution of characters within an angiosperm system. I. Some embryological characters. — Bot. Notiser 128: 181—197. Lund. ISSN 0006-8195.

Distribution in the angiosperm system of the following characters is presented: (1) unitegmic versus bitegmic and (2) tenuinucellate versus crassinucellate ovules, (3) ab initio cellular versus nuclear and helobial endosperm, and (4) binucleate versus trinucleate pollen grains.

For each of these, one particular state is virtually predominant in various constellations of orders or superorders in the system. Great importance can at times be laid upon these characters in cases where families with an uncertain taxonomic position are referred to one such major group in which there is absolute dominance of a particular state. In other orders or superorders in the system there may be great inconsistency in the character concerned, which will thus be of less taxonomic importance. The groups that are variable in one of the characters may not be variable at all in another of the characters. Correlation between the distributions of some of the characters concerned is discussed.

Unitegmic ovules, tenuinucellate ovules, ab initio nuclear endosperm and trinucleate pollen grains are probably secondary states. In many cases it is of crucial importance to decide whether convergence or common origin is responsible for the similarity between taxonomic groups with these secondary features.

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In this and forthcoming articles a survey of the distribution of certain characters within the angiosperm system will be presented. The system is that appearing on pp. 119—147 in this issue of Botaniska Notiser, and to which the reader is referred for further information.

The orders to the left of the broken line in Figs. 1—4 represent the monocotyledons, those to the right the dicotyledons. In some recent reports the order Caryophyllales stands out as an isolated group. As its connections with other orders are most uncertain a broken line has also been drawn between this order and the rest of the dicotyledons.

Superorders are often mentioned in the text but are not indicated by names in the diagrams (Figs. 1—4). The system with its superorders and orders is therefore presented in Table 1.

The presence of a given character in an order or some of its families is denoted by shading. Where there are several alternatives different shading has been used (dots, hatching, etc.).

Each family in the order has its fixed position in the diagram. When a family differs from the others in the order in two different characters it appears as a shaded or unshaded spot in the same position in the diagrams for these characters.

Table 1. Orders and superorders of the angiosperm system used (according to DAHLGREN 1975).

DICOTYLEDONEAE

Magnolianae: Magnoliales, Laurales, Aristolochiales, Piperales, Illiciales. — *Rafflesianae:* Rafflesiales. — *Ranunculanae:* Nelumbonales, Ranunculales, Papaverales. — *Nymphaeanae:* Nymphaeales. — *Rutanae:* Rutales, Polygalales, Sapindales, Juglandales, Myricales, Leitneriales, Geraniales, Balsaminales. — *Aralianae:* Araliales, Pittosporales. — *Asteranae:* Asterales. — *Dillenianae:* Dilleniales, Cistales, Malvales, Urticales, Euphorbiales. — *Thymelaeanae:* Thymelaeales. — *Violanae:* Violales, Tamaricales, Salicales, Capparales. — *Celastranae:* Celastrales, Santalales, Rhamnales. — *Solananae:* Solanales. — *Campanulanae:* Campanulales. — *Hamamelidanae:* Trochodendrales, Hamamelidales, Casuarinales, Betulales, Balanopales, Cunoniales. — *Rosanae:* Rosales, Fabales. — *Proteanae:* Proteales. — *Myrtanae:* Myrtales, Elaeagnales, Trapales, Haloragales. — *Saxifraganae:* Saxifragales, Podostemales, Gunnerales. — *Balanophoranae:* Balanophorales. — *Primulanae:* Primulales, Ebenales. — *Theanae:* Theales, Nepenthales, Droserales. — *Cornanae:* Ericales, Sarraceniales, Eucommiales, Cornales. — *Gentiananae:* Dipsacales, Oleales, Goodeniales, Gentianales. — *Loasanae:* Loasales. — *Lamianae:* Scrophulariales, Hippuridales, Hydrostachyales, Lamiales. — *Caryophyllanae:* Caryophyllales.

MONOCOTYLEDONEAE

Alismatanae: Hydrocharitales, Alismatales, Zosterales, Najadales. — *Lilianae:* Dioscoreales, Stemonales, Asparagales, Taccales, Haemodorales, Liliales, Triuridales, Burmanniales, Orchidales, Bromeliales. — *Typhanae:* Typhales. — *Zingiberanae:* Zingiberales. — *Commelinanae:* Commelinales, Eriocaulales, Juncales, Cyperales, Centrolepidales, Poales. — *Arecanae:* Arecales, Pandanales, Cyclanthales. — *Aranae:* Arales.

Information on the occurrence of certain characters in many (or most) families is often difficult to find. It is usually widely scattered in the literature, and knowledge is sometimes very restricted. The four characters presented here have been surveyed by other botanists relatively recently though in combination with other systems and elucidated from other angles.

The diagrams are to be studied in conjunction with the text, keeping in mind the limited basis of information available. In particular it should be pointed out that there is often little or no information on small exotic families.

Three of the aims of the present and forthcoming articles are:

(1) to show the general distribution of a number of characters in the angiosperms

(2) to provide a basis for a discussion on whether the characters have evolved along many lines of evolution or only a few, possibly one single line

(3) when many characters are compared in the future by means of the diagrams, to use the information thus obtained as a basis for improving the system.

DISTRIBUTION OF UNITEGMIC VERSUS BITEGMIC OVULES

The systematic importance of the number of integuments in an ovule has long been recognized in taxonomic literature. It has sometimes been almost completely neglected in system making, sometimes strongly emphasized, with resulting oversimplification.

An extensive survey of the number of integuments and other embryological characters in the angiosperms was made by WUNDERLICH in 1959, and integument and nucellus characters in dicotyledons have recently been discussed by PHILIPSON (1974). The survey presented here has made use of information especially from these articles and from DAVIS 1966.

In Fig. 1 the number of integuments has been shown in the diagram representing the angiosperm system. Information is often only available for one or a few species in each family. To accept this as being representative of the family as a whole is a gross generalization. The number of integuments is usually taken to be known in most families, but in actual

fact there is often a considerable lack of information on this character, and the literature is sometimes contradictory (e.g. for Byblidaceae).

The bitegmic ovules are considered to represent the primary state, an assumption that has practically never been questioned. In particular, the multilayered integuments found in orders here placed in Magnolianae are generally regarded as the most primitive.

Bitegmic ovules are predominant in the monocotyledons, and in the **dicotyledons** they are overwhelmingly dominant in the following superorders (exceptions within some of these are given below): Caryophyllanae, Magnolianae, Nymphaeanae, Rutanae, Dillenianae, Violanae, Thymelaeanae, Theanae, Primulanae, Plumbaginanae, Myrtanae, Rosanae and Proteanae.

In the same way, there are several superorders where the ovules are exclusively unitegmic: Cornanae, Gentiananae, Loasanae, Lamianae, Solananae, Campanulanae, Asteranae and Aralianae.

Unitegmic ovules, however, occur in a number of isolated families within orders with otherwise predominantly bitegmic ovules, pointing to independent lines of evolution. It should be kept in mind that the unitegmic state may have arisen by reduction from the bitegmic state or by fusion.

In Caryophyllales, unitegmic ovules have been reported in a few genera only of Nyctaginaceae. — In Piperales, *Peperomia* has unitegmic ovules, and in Laurales there is a (dubious) record of one integument in *Siparuna,* Monimiaceae. — Of particular interest is Rafflesiales. *Mitrastemon* in Rafflesiaceae has unitegmic ovules but ab initio cellular endosperm, *Pilostyles* bitegmic ovules and nuclear endosperm and in *Rafflesia* the outer integument is strongly reduced and the endosperm nuclear ab initio. (If cellular endosperm and bitegmic ovules are considered primitive features, the situation must be regarded as somewhat complicated in this family.) In the other family in Rafflesiales, Hydnoraceae, the ovules are unitegmic.

In Nymphaeales, the ovules are unitegmic in Ceratophyllaceae only. — In Ranunculales, Circaeasteraceae, some genera of Menispermaceae, and several genera of Ranunculaceae (chiefly those with one-seeded nutlets) also have unitegmic ovules. — In Rutales unitegmic ovules have been reported in Surianaceae (*Suriana*), Burseraceae (*Commiphora, Santiria*) and some species of Meliaceae. — In Sapindales we likewise find unitegmic ovules in *Pistacia* (Anacardiaceae) and Sabiaceae, and in the possibly closely related orders Juglandales and Myricales the ovules are consistently unitegmic. — Similarly in Fagales in the superorder Hamamelidanae, the ovules are consistently unitegmic in Betulaceae, in Corylaceae except *Carpinus* and in the genus *Nothofagus* in Fagaceae. The ovules are also unitegmic in Balanopales. Whether the orders of "amentifers" are closely related or not is still a moot point (here they are placed in principle according to THORNE 1968).

Other orders where bitegmic ovules are predominant include restricted unitegmic-ovuled members. These are, for example, Bruniaceae (Cunoniales), several important genera in Rosaceae (Rosales), Symplocaceae and single genera of Theaceae (Theales), species of *Eugenia* and *Syzygium* in Myrtaceae (Myrtales), most members of Salicales, Limnanthaceae and some Salvadoraceae (Capparales), Aegiceratataceae (Primulales), Sapotaceae and *Halesia* in Styracaceae (Ebenales), and Aquifoliaceae and Avicenniaceae (Celastrales). In the parasitic orders Balanophorales and Santalales we find unitegmic or usually ategmic ovules (in Olacaceae in Santalales even from bitegmic to ategmic ovules). Moreover, the ovules are often completely undifferentiated in these orders.

The sporadic occurrence of unitegmic ovules in the **monocotyledons** does not

appear to make any substantial contribution to the knowledge of phylogeny or interrelationships. Unitegmic ovules occur, for example, in some species of *Aponogeton* (Aponogetonaceae in Hydrocharitales), in a few genera of Orchidaceae (Orchidales) and in some genera of Amaryllidaceae (Asparagales) and Poaceae (Poales). In *Crinum* (Amaryllidaceae) and *Melocanna* (Poaceae) there are even some cases of ategmic ovules.

There is no doubt that the distribution of unitegmic ovules in the dicotyledons, in particular in combination with other characters, supplies information of great systematic importance. Within large complexes such as Cornanae—Gentiananae—Lamianae—Loasanae, Aralianae—Asteranae and Campanulanae—Solananae (which may be closely related to Aralianae—Asteranae), the unitegmic state may well have developed early in the phylogeny and thus become widely distributed in the course of subsequent evolution and differentiation.

In practically all of the above-mentioned superorders unitegmic ovules are also tenuinucellate, suggesting a close connection here between the two characters. Moreover, in several of these superorders the unitegmic ovules are found in combination with ab initio cellular endosperm. These facts are often quoted as evidence for a close connection between the groups. Each of these three characters is distributed independently, however, and although they are frequently found in combination this is by no means always the case.

Another interesting point of coincidence has been demonstrated by JENSEN & al. 1975, viz. that iridoids are restricted to almost hundred per cent to groups with unitegmic (and generally tenuinucellate) ovules, although occurring in far from all of them. For example they do not occur in Solananae, Campanulanae, Asteranae and Aralianae.

In the other groups with unitegmic ovules mentioned above the unitegmic state may have developed independently along different lines, in some cases perhaps in later stages of the phylogeny. The isolated occurrence in some of these groups may therefore be of restricted taxonomic importance.

DISTRIBUTION OF TENUINUCELLATE VERSUS CRASSINUCELLATE OVULES

In many groups of angiosperms the development of the nucellus stands in direct relationship to the number of integuments and the type of endosperm formation and should be discussed in connection with these features.

Truly crassinucellate ovules are by definition characterized by the presence of parietal cells formed by division of the archesporial cells. In tenuinucellate ovules the archesporial cells function directly as megaspore mother cells. Pseudocrassinucellate ovules will be defined and discussed at the end of this section.

The tenuinucellate versus crassinucellate state has long been used as a taxonomically important character, and then often considered in combination with the number of integuments. The importance of the character was stressed, for example, by WARMING in 1878 and DAHLGREN 1927. It also plays an important part in the interpretation and evaluation of endosperm types in WUNDERLICH 1959. The occurrence of tenuinucellate ovules in dicotyledons was surveyed by PHILIPSON as late as 1974.

In the present treatment I shall largely make use of data presented in the last two of these works and in DAVIS 1966. Unfortunately there is some vagueness in the definition of the concept "tenuinucellate ovule". The above-mentioned authors do not agree, for example, in the classification of the ovules in Theales. Thus Theaceae and Ochnaceae were classified as crassinucellate by WUNDERLICH and as tenuinucellate by DAVIS. As parietal cells are not formed they are here classified as tenuinucellate.

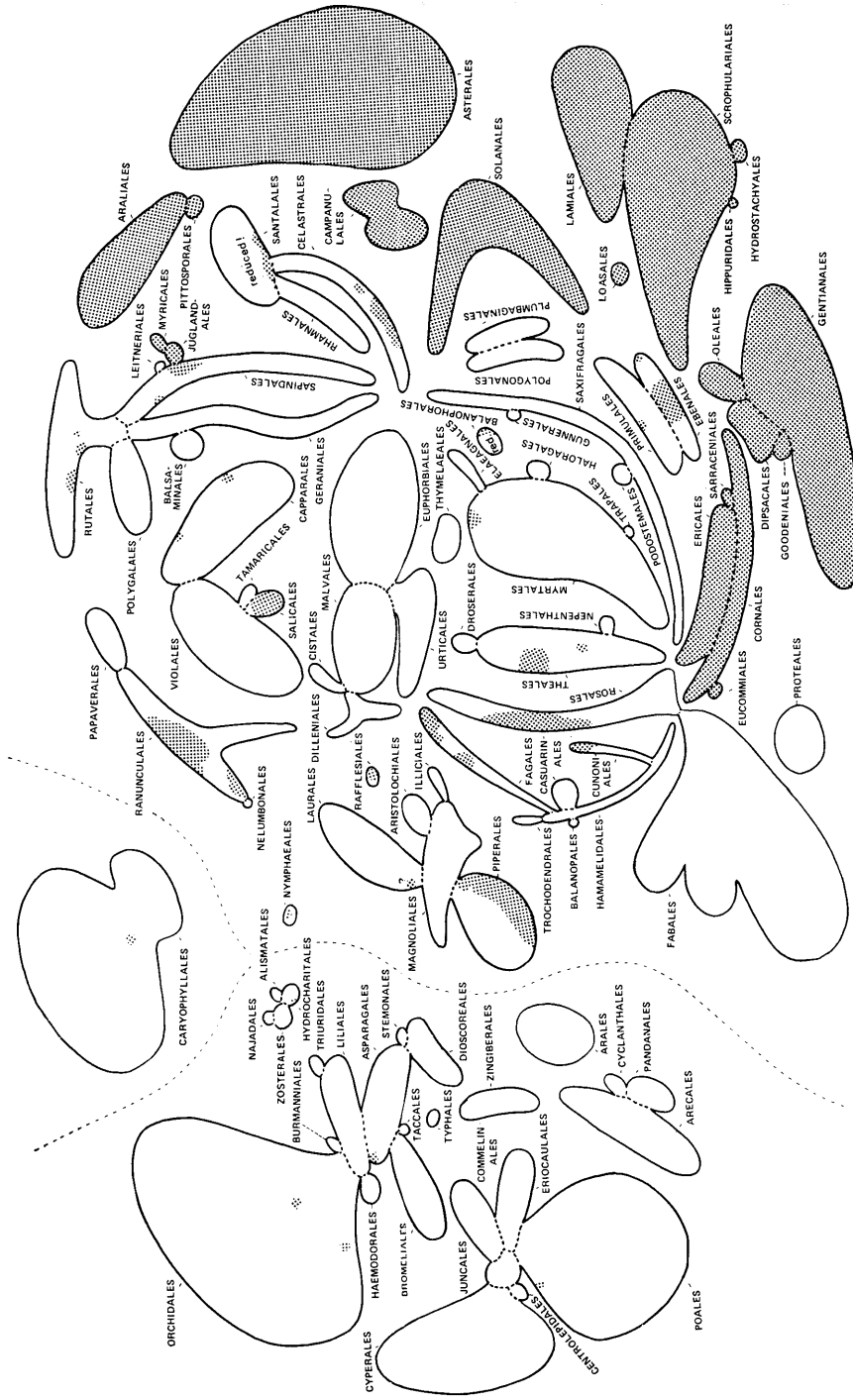

Fig. 1. Distribution of unitegmic (shaded) and bitegmic ovules in the orders of angiosperms. In Santalales and Balanophorales the ovule is greatly reduced and there is no integument at all. (N.B. Balanopales should also be shaded.)

The distribution of tenuinucellate ovules in angiosperms is shown in Fig. 2 (hatching). Broad generalizations have been made, as the sometimes rather few cases known in some families have been taken as being representative. Future investigations may therefore modify details of the picture.

This character varies considerably in a number of families, e.g. in Brassicaceae, Linaceae, Convolvulaceae and Boraginaceae, and sometimes also in one and the same genus, for instance in *Brassica* and *Linum* where primary parietal cells may be present or not.

While there are relatively few groups with unitegmic ovules in the **monocotyledons**, tenuinucellate ovules are commoner. They occur, for example, in practically all members of Orchidales and Eriocaulales, in Xyridaceae (Commelinales), some genera of Araceae, some mainly saprophytic groups (Burmanniales and Triuridales) and in certain members of Asparagales and Liliales such as Ruscaceae and many members of Liliaceae. In many of these cases the tenuinucellate state seems to be simply an expression of the diminutive size of the ovules. Except in Araceae and possibly some member of Burmanniales, tenuinucellate ovules and ab initio cellular endosperm do not occur together (which they do in large groups of the dicotyledons), and there is probably no group with tenuinucellate ovules having a single integument.

In the **dicotyledons**, the ovules are tenuinucellate in all or most families and genera in the superorders Rafflesianae, Theanae, Primulanae, Cornanae, Gentianae, Lamianae, Loasanae, Solananae, Campanulanae, Asteranae and Aralianae, as seen in Fig. 2.

In Rafflesiales the tenuinucellate state may have developed in connection with reduction of the ovules, a first stage, perhaps, in a reduction of the ovules such as found in the similarly parasitic group Balanophorales. In the families in Santalales and Balanophorales the ovules are usually much more reduced and should likewise be classified as tenuinucellate.

In Theales the ovules are tenuinucellate except in Stachyuraceae and Elatinaceae included with hesitation in the order. Parnassiaceae and some Droseraceae (both in Droserales) have tenuinucellate ovules, but the ovules are crassinucellate in other members of Droseraceae and in Nepenthaceae, the latter family making up most of Nepenthales.

Other exceptions from the tenuinucellate state in the above superorders are: Aegiceratacеae (Primulales) and several families in Cornales, viz. Garryaceae, Alangiaceae, Davidiaceae, Nyssaceae, and some or most Icacinaceae, Escalloniaceae, Cornaceae and Sambucaceae (*Viburnum*). The last four families include transition forms between crassinucellate and tenuinucellate ovules. In Solanales there are crassinucellate (or pseudocrassinucellate) ovules at least in some Ehretiaceae and Convolvulaceae, and in Araliales in most genera of Araliaceae studied, but in Apiaceae (and in the related Pittosporales) the ovules are usually tenuinucellate. In the other superorders mentioned above the ovules are nearly always tenuinucellate.

Crassinucellate (in Ranunculales also pseudocrassinucellate) ovules characterize most or all members of Magnolianae, Nymphaeanae, Ranunculanae, Rutanae, Violanae, Dillenianae, Hamamelidanae, Rosanae, Proteanae, Myrtanae and Saxifraganae. The following noteworthy exceptions in these superorders can be mentioned:

In the more primitive orders, *Houttuynia* in Saururaceae (Piperales) and *Circaeaster* (Circaeasteraceae, Ranunculales) have tenuinucellate ovules.

In Thymelaeales, Dichapetalaceae differs from Thymelaeaceae in having tenui-

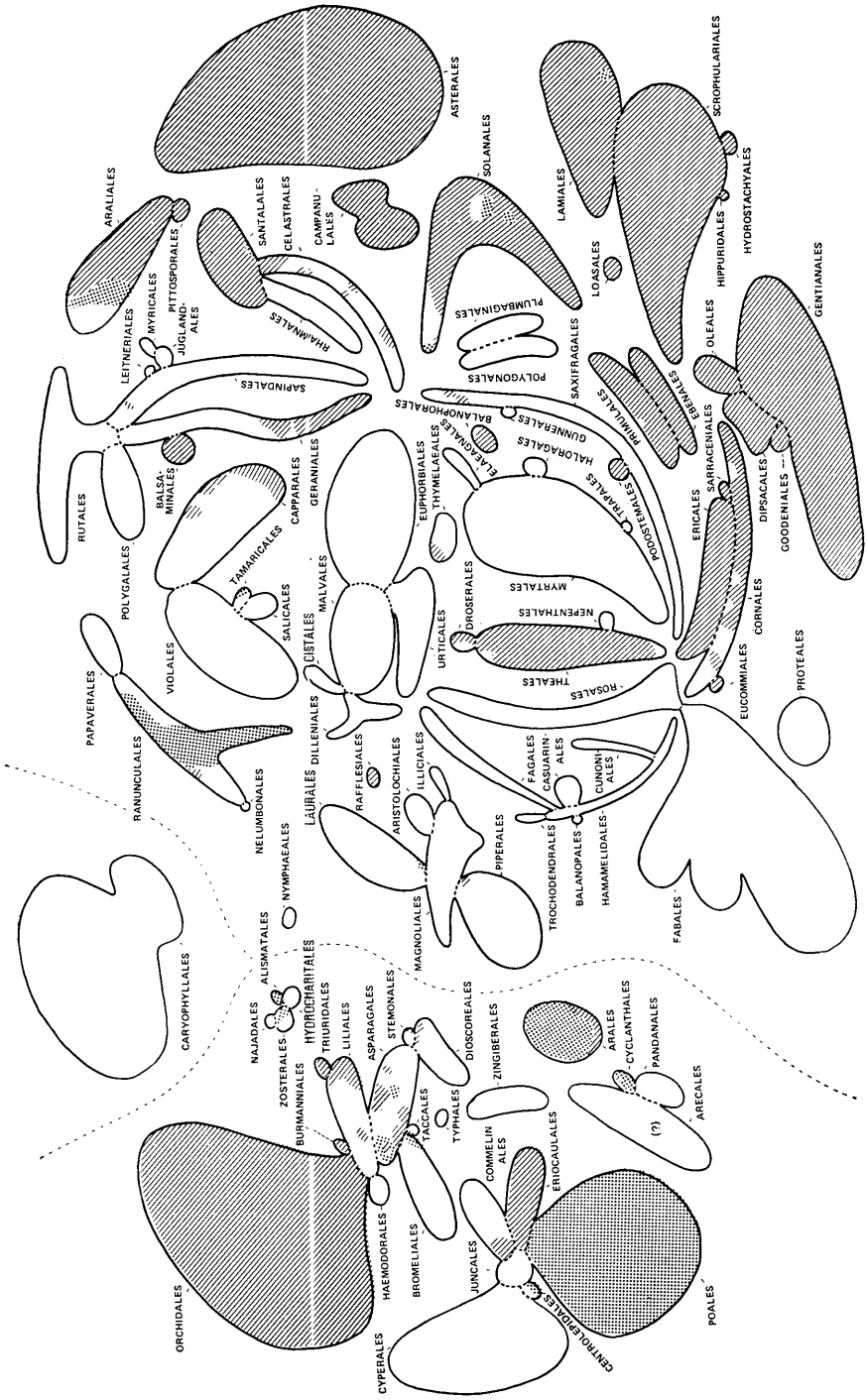

Fig. 2. Distribution of tenuinucellate (hatching), pseudocrassinucellate (shaded with dots) and crassinucellate ovules in orders of the angiosperm system.

nucellate ovules. In Podostemales, where endosperm does not develop at all, the ovules are likewise tenuinucellate, and in Saxifragales tenuinucellate ovules are known to occur in Vahliaceae and Fouquieriaceae.

In Tropaeolaceae, Limnanthaceae and some genera of Brassicaceae (Capparales), Balsaminaceae (Balsaminales), as well as some genera of Oxalidaceae (though not Averrhoaceae) and Linaceae (Geraniales) the ovules are tenuinucellate, Oxalidaceae and Linaceae being variable as regards development of parietal cells. In Celastrales, Stackhousiaceae, Avicenniaceae, some species of *Ilex* in Aquifoliaceae, and, for example, species of *Euonymus* and *Gymnosporia* in Celastraceae are likewise known to have tenuinucellate ovules. In Rhamnales the ovules are known to be crassinucellate, and in Santalales tenuinucellate. These three orders comprise Celastranae, which is thus a heterogeneous superorder in this respect.

The pattern of distribution of tenuinucellate ovules is most interesting when compared with that of unitegmic ovules, and with that of ab initio cellular endosperm.

Tenuinucellate ovules with two integuments occur chiefly in the following groups: most members of Theanae and Primulanae and many of Celastrales, all Podostemales and Balsaminales, Oxalidaceae and some genera of Linaceae (Geraniales), Tropaeolaceae and members of Resedaceae and Brassicaceae (Capparales), Vahliaceae and Fouquieriaceae (here placed in Saxifragales), some Olacaceae (Santalales), some Rafflesiaceae (Rafflesiales), and *Houttuynia* in Saururaceae (Piperales).

These groups doubtless comprise a heterogeneous assemblage, several of them having no obvious relationship with one another. Families in some orders, however, show certain affinities with one another, viz. Capparales, Geraniales and Balsaminales.

In most other groups of dicotyledons, i.e. in the "Sympetalae", the unitegmic ovules are also tenuinucellate. This phenomenon is so consistent that there is reason to suppose that the two characters have here developed at a very early stage in a few or perhaps only one main evolutionary line. No functional connection between the two characters is apparent.

The tenuinucellate state and ab initio cellular endosperm often occur together, i.e. chiefly in the superorders Cornanae, Gentiananae (except most of Gentianales), Lamianae and Loasanae. Further, in Ebenaceae and Styracaceae (Ebenales), in about half of the members of Solanales, in Campanulales and Santalales, in Avicenniaceae and some Aquifoliaceae (Celastrales), and in numerous scattered genera with ab initio cellular endosperm in Asterales. To these should also be added *Houttuynia* in Saururaceae (Piperales) and members of Marcgraviaceae (Theales).

Tenuinucellate ovules with ab initio nuclear endosperm occur in certain groups. Examples of this are: most families of Theales and Droserales, Primulales, Sapotaceae (Ebenales), most Gentianales, some members of Celastraceae (Celastrales), and many in Solanales, in particular most genera of Boraginaceae, Hydrophyllaceae, Polemoniaceae, Cuscutaceae and Convolvulaceae. Also most genera of Apiaceae (Araliales), Pittosporaceae (Pittosporales) and many genera with ab initio nuclear endosperm distributed in most tribes of Asteraceae (Asterales). They are also found in Tropaeolaceae, Limnanthaceae and genera of Resedaceae and Brassicaceae in Capparales, in Oxalidaceae (Geraniales), and finally in *Circaeaster* (Ranunculales) and *Mitrastemon* (Rafflesiales).

Although there are many groups where tenuinucellate ovules and ab initio cellular endosperm occur together, there are also certain tenuinucellate orders where endosperm has become predominantly nuclear ab initio. This will be dealt with later in connection with the different types of endosperm.

On the other hand the dicotyledons with cellular endosperm formation, with some exceptions, are usually tenuinucellate. The exceptions are: most families within Magnolianae and some possibly related groups, for example Nelumbonales, Lardizabalaceae in Ranunculales, Nymphaeales and Trochodendrales, the last two possibly more remotely related to Magnolianae. Further exceptions are Saxifragales, Gunnerales and members of Haloragales, Celastrales and Cornales.

In the dicotyledons with cellular endosperm formation the ovules are usually also unitegmic or even ategmic. There are some exceptions to this which include some of the groups just mentioned.

Pseudocrassinucellar Ovules

In truly tenuinucellate ovules parietal cells are not formed and the megaspore mother cell lies directly beneath the epidermis of the nucellus. Crassinucellate ovules in a broad sense are characterized by well-developed parietal tissue composed of one or several layers of cells. Where parietal tissue is formed from a primary parietal cell cut off from the archesporium the ovule is classified as truly crassinucellate, but where primary parietal cells are not formed and the enlargement of the nucellus takes place by periclinal divisions of the epidermis the term "pseudocrassinucellate" is often used. The truly crassinucellate and pseudocrassinucellate types thus differ histogenetically.

There are various groups where the ovules are pseudocrassinucellate. They are shown in Fig. 2 by shading (dots). Many of them are **monocotyledons**. Here belong certain members of Alismatanae, in particular members of Alismatales and Zosterales (except Potamogetonaceae), most members of Poales, several genera studied in, for example, Araceae (Arales), further most Cyclanthales (but according to available literature not in other Arecanae, which needs perhaps further verification). Finally there are pseudocrassinucellate ovules in Velloziaceae (Bromeliales) and certain members of Asparagales, such as Hypoxidaceae and some Amaryllidaceae.

Of **dicotyledons** reported to have pseudocrassinucellate ovules the following should be mentioned: members of Calycanthaceae (Laurales), Podophyllaceae and several genera of Ranunculaceae (Ranunculales), Frankeniaceae (Tamaricales), some genera of Olacaceae (Santalales), Cobaeaceae and some members of Ehretiaceae and Boraginaceae (Solanales), a few genera in Lamiaceae (Lamiales), and finally certain genera of Apiaceae (Araliales). These obviously do not form a phylogenetically connivent group.

DISTRIBUTION OF AB INITIO CELLULAR ENDOSPERM VERSUS NUCLEAR AND HELOBIAL ENDOSPERM

The taxonomic value of the different types of endosperm formation has been discussed by WUNDERLICH (1959). In particular the fact that nucellus volume and endosperm type often stand in relationship to each other has led certain botanists to conclude that a poorly developed nucellus favours the development of ab initio cellular endosperm, whereas in a well-developed nucellus cell-wall formation is delayed in the early stages. Tenuinucellate ovules, where ab initio cellular endosperm predominates, occur notably in sympetalous groups which are generally taken to be "advanced", and as a consequence ab initio nuclear endosperm has often been considered the more primitive type. However, apart from many sympetalous groups, ab initio cellular endosperm is also found in the majority of the ("primitive") superorder Magnolianae, which increases the scope of the problem.

The circumstances and problems connected with this were tackled by WUNDERLICH, in 1959, who examined the embryological characters and their distribution in the angiosperms. The present account is based chiefly on information obtained from her article and from DAVIS 1966, as well as from recent articles such as that by SWAMY & KRISHNAMURTHY 1973.

Certain general trends can be seen in Fig. 3. First, there are a few groups obviously not closely related where endosperm formation does not take place at all or is arrested in the primary stages. These are Orchidales, Podostemales and Trapales.

In the **monocotyledons**, endosperm formation is either nuclear or helobial (intermediate) with the important exception of members of Arales and possibly some isolated species of *Thismia* in Thismiaceae (Burmanniales), in which the

endosperm is cellular ab initio. In other members of the latter order endosperm is helobial.

Exclusively or predominantly nuclear endosperm formation is found in Arecales, Poales, Cyperales, Commelinales and Dioscoreales, and has also been reported in the few species of Pandanales, Centrolepidales, Stemonales, Taccales and Triuridales that have been embryologically investigated. In the remaining orders the helobial type of endosperm formation appears to be either predominant or to occur parallel to the nuclear type.

Whether the distribution of endosperm types in the families of Asparagales and Liliales is of phylogenetic significance or not is doubtful. In the rather limited material studied it seems that ab initio nuclear endosperm is predominant in Liliales, an order in which the helobial type is known in Melanthiaceae at least. In Asparagales the pattern is more complicated. Nuclear endosperm formation is known, for example, in the three probably closely related families Smilacaceae, Convallariaceae and Asparagaceae and also in Tecophileaceae, whereas the helobial type is known in members of certain other families such as Agavaceae, Amaryllidaceae, Haemodoraceae and Hypoxidaceae.

Zingiberales is likewise heterogeneous with regard to endosperm formation, the helobial type being reported in Zingiberaceae and Costaceae, the nuclear type in Musaceae, Heliconiaceae, Cannaceae and Marantaceae. In Alismatanae ("Helobiae") the helobial type is probably predominant but the nuclear type is known in some genera of Alismataceae and in Juncaginaceae and Najadaceae.

The helobial or intermediate type of endosperm formation is known only in isolated families of **dicotyledons**. Of these families only some show obvious affinities. One of them, viz. Cabombaceae (Nymphaeales), resembles in particular the monocotyledonous order Hydrocharitales, helobial endosperm having been reported in *Cabomba* and *Brasenia* (SCHNARF 1931). These two genera seem to show greater affinities with Hydrocharitales than do the other members of Nymphaeales where endosperm is generally cellular ab initio (and where ellagitannins have been recorded).

Helobial or intermediate endosperm is also known in members of Saxifragaceae, Ribesiaceae, Linaceae (*Linum* spp.), some members of Boraginaceae and Solanaceae (*Hyoscyamus*), Balsaminaceae, and several Acanthaceae (in the last two families in connection with the formation of aggressive haustoria). In most or all of these families the intermediate endosperm type seems to have developed independently and represents a transition from the ab initio cellular type to the nuclear type, though in the first two families mentioned the helobial endosperm could have developed along a single line of evolution.

The most conspicuous feature in the distribution of types of endosperm formation is the preponderence of the ab initio cellular type in the orders of Magnolianae, in which are found the greatest number of features considered to be primitive. Cellular endosperm formation is also found in a number of "intermediate" orders with some "primitive" features, viz. those in Saxifraganae and Cornanae, and finally in orders of the relatively "advanced" superorders Gentiananae, Lamianae, Loasanae, Solananae, Celastranae, and Campanulanae, and also in a great many Asteranae, but not at all in Aralianae! In this system some families with ab initio nuclear endosperm have been placed together in Cunoniales. In Saxifragales and Cornales, on the other hand, the endosperm is chiefly but not always cellular. However there are several points of doubt as to relationships in this part of the system.

Cellular endosperm formation also occurs within a number of isolated genera

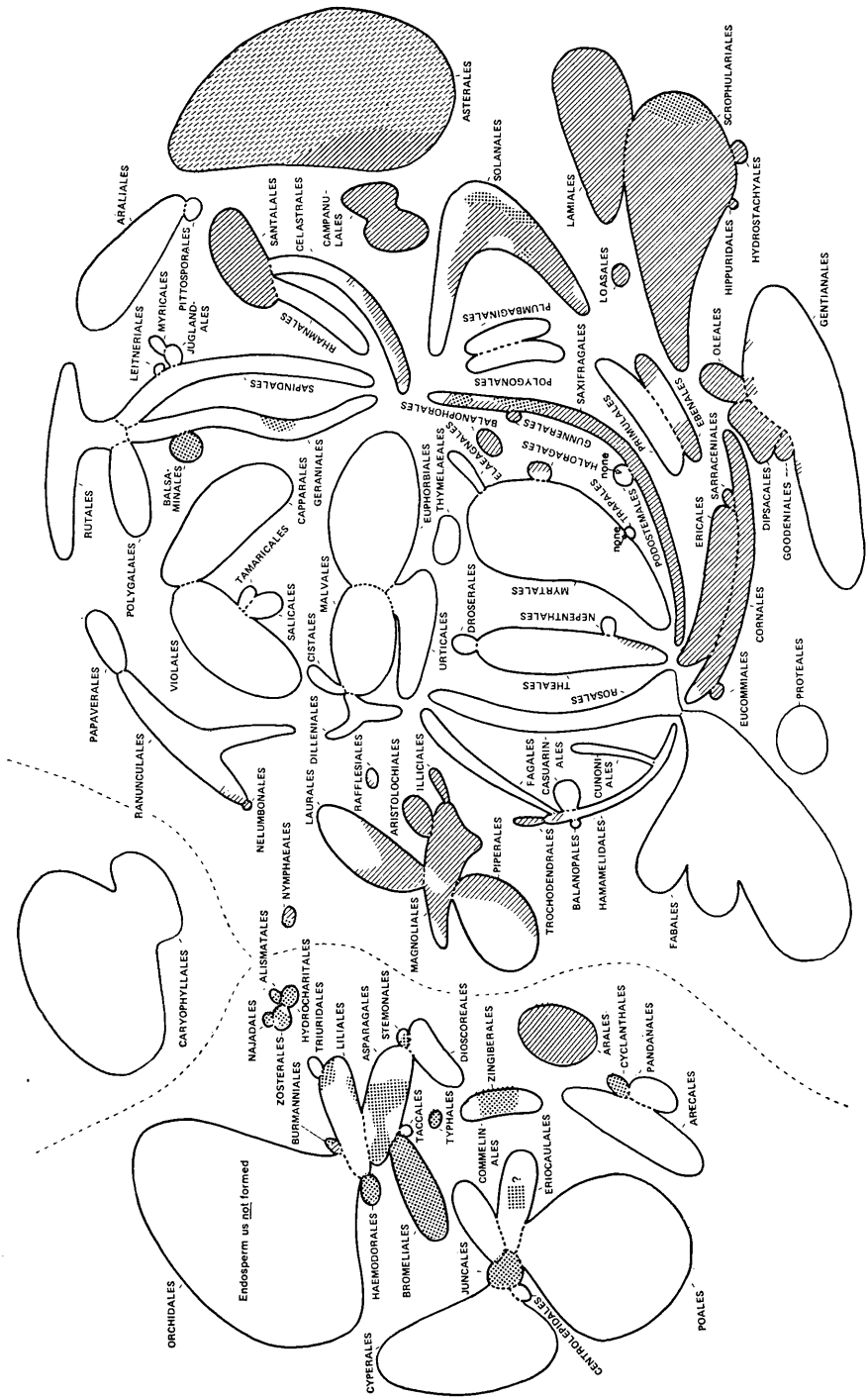

Fig. 3. Distribution of ab initio cellular (hatching), intermediate ("helobial" in a broad sense; shaded with dots) and nuclear endosperm. The great variation of endosperm in Asterales is indicated by hatching with broken lines. — Endosperm is not formed at all in Orchidales. Trapales and Podostemales.

or families outside the superorders mentioned, in orders in which the endosperm is otherwise nuclear ab initio. Although the cellular type dominates in Magnolianae, nuclear endosperm is known in some of the families, e.g. Winteraceae (*Drimys*) and Myristicaceae (*Myristica*) (both in Magnoliales), in several of the genera studied in Lauraceae (Laurales) and in *Piper* (Piperales). Aristolochiaceae conforms to the typical cellular type which is also in agreement with its chemical contents, its kind of sieve tube plastids (of Annonaceous type), etc., indicating a close relationship with Annonaceae (Magnoliales) for example.

In the orders Nymphaeales (except Cabombaceae) and Nelumbonales the endosperm is cellular ab initio, which also applies to *Decaisnea* in Lardizabalaceae and *Circaeaster* in Circaeasteraceae (both Ranunculales) and in *Mitrastemon* (Rafflesiales).

Apart from most of the groups mentioned cellular endosperm formation in crassinucellate ovules is also found, however, in *Trochodendron* and *Cercidiphyllum* (Trochodendrales) at least and some genus in Hamamelidaceae (Hamamelidales). Further in Gunnerales, most taxa of Saxifragales, and some families in Cornales. All these groups differ chemically to a great extent from Magnolianae and Ranunculanae. In Saxifragales endosperm formation is usually cellular, but in many Saxifragaceae and in Ribesiaceae it is intermediate, and in Greyiaceae, Francoaceae and Brexiaceae it is reported to be nuclear. The type of endosperm formation in Tremandraceae is not known. Many characteristics of Saxifragales and Hamamelidales approach those of Cornanae, where cellular endosperm formation is likewise predominant, but often in tenuinucellate and always in unitegmic ovules. Within the Cornales, nuclear endosperm formation is known in *Garrya* and *Alangium* (though cellular endosperm formation is also recorded in the latter genus).

It is of particular interest that the endosperm formation is cellular in Balanophorales, just as in some Rafflesiales and all Gunnerales and Santalales. It has sometimes been proposed that these two last orders are closely related to Balanophorales.

There is close connection between the orders of Cornanae, in particular Cornales, on the one hand and Oleales, Dipsacales and Goodeniales on the other. In all these orders the endosperm is almost exclusively cellular ab initio. There is much evidence in support of placing Gentianales here too. Within this order cellular endosperm formation is found in the possibly rather primitive families Buddlejaceae and Menyanthaceae (each of which deviates in different respects from the other families of the order), and in some parasitic genera of Gentianaceae. In the other (main) groups of Gentianales endosperm formation is nuclear ab initio.

In all Lamianae, Loasanae and Campanulanae cellular endosperm formation is combined with unitegmic and crassinucellate ovules (except for a few pseudocrassinucellate Lamiaceae). In Solanales endosperm formation varies greatly, however. It is cellular in most of the genera in Solanaceae, Nolanaceae and Ehretiaceae that have been studied and in some "primitive" members of Boraginaceae. In most of the other genera of Boraginaceae and in Convolvulaceae, Cuscutaceae, Polemoniaceae and Hydrophyllaceae that have been studied it is nuclear.

The most variable family as regards this character is without doubt Asteraceae, where both the cellular and nuclear types of endosperm formation occur within most tribes. Seen against the background of the relative consistency found in the rest of the system this variation is highly remarkable.

In Santalales endosperm formation seems to be cellular according to available reports, as is also the case in Aquifoliaceae, Avicenniaceae and some Buxaceae

and Celastraceae in Celastrales. In other members of this order and in the taxa that have been investigated in Rhamnales the endosperm is nuclear ab initio.

In Ebenales, the endosperm formation recorded is cellular in Ebenaceae and Styracaceae, but nuclear in Sapotaceae. The heterogeneity of Celastrales and Ebenales is also reflected in other characters, and the orders are presumably unnatural.

In the remaining chief superorders, Caryophyllanae, Rutanae, Violanae, Dillenianae, Thymelaeanae, Plumbaginanae, Theanae, Myrtanae, Rosanae, Proteanae and Aralianae the endosperm formation is consistently nuclear or usually so (in a few families sometimes intermediate, see above). Few but notable exceptions are Marcgraviaceae in Theales (which, moreover, has tenuinucellate ovules and small micropylar endosperm haustoria) and at least some Haloragaceae (Haloragales).

The type of endosperm formation is doubtless of great taxonomic significance especially when considered together with number of integuments, development of nucellus and occurrence of endosperm haustoria, as in WUNDERLICH 1959. According to her the bitegmic crassinucellate ovule with ab initio cellular endosperm is probably the original state. A transition to nuclear endosperm formation has probably occurred at an early stage within certain evolutionary lines, particularly in groups where the ovules remained crassinucellate. Within a few other evolutionary lines where the ovules soon became tenuinucellate endosperm formation remained cellular. A later transition to the nuclear type seems also to have occurred in several of these families, for example within Gentianales, Solanales and Asterales. As pointed out by WUNDERLICH, the endosperm haustoria with free nuclei might well have represented a first step towards the nuclear endosperm in some lines of evolution. A further stage in the evolution towards nuclear endosperm formation might be the intermediate (including the "helobial") type. The types of endosperm formation in genera of Acanthaceae (Scrophulariales) in particular may be examples of such intermediate states.

Applied to the monocotyledons this hypothesis would place Arales in a unique, primitive position with regard to endosperm formation. Orders within Alismatanae and also Asparagales, Juncales, etc. with helobial endosperm formation would be intermediate, and those with ab initio cellular endosperm would be the most advanced. If this were the case, it should be remembered that primitiveness in one set of characters is not necessarily combined with primitiveness in other characters.

DISTRIBUTION OF POLLEN GRAINS RELEASED AT THE TRINUCLEATE VERSUS THE BINUCLEATE STAGE

The data on this character is taken mainly from BREWBAKER 1967, who studied approximately 2,000 species of angiosperms. The number of nuclei in the pollen grains may be regarded as a matter of stage only, i.e. whether the mitotic division of the generative cell has yet divided into two sperm cells. In spite of this the character shows a distinctive pattern of distribution in the angiosperms and contributes aspects on phylogeny. It is also connected with physiological and genetical properties (e.g. with types of self-incompatibility).

The terms bi- and tri*nucleate* are used here rather than two- or three-*celled*, as the walls of the sperm cells are not or hardly visible under an ordinary microscope.

The distribution of bi- and trinucleate pollen grains in angiosperms and the systematic conclusions that may be drawn from this were discussed by BREWBAKER. In the present account will be dealt mainly with distribution in the particular system of angiosperms used here.

The sometimes rather few data available

have been taken as representative of the families in the respective orders and form the basis of Fig. 4. This is a very broad generalization. In fact most smaller families are known only from the characteristics in one or a few species. In large orders this is usually compensated for by records from many families so that a considerable number of taxa are known for many orders. Homo- and heterogeneity respectively will therefore generally be revealed.

The binucleate state is usually considered to be more "primitive" than the trinucleate and there is no evidence to contradict this assumption. It seems that groups known by early fossils also tend to have binucleate pollen grains.

In the **monocotyledons** trinucleate pollen grains occur chiefly in three types of plants: (1) in groups with reduced wind-pollinated flowers such as Poales, Juncales, most of Cyperales and Eriocaulales; (2) in groups adapted to aquatic habitats, for example all Alismatanae, the family Lemnaceae, and some genera of Araceae; and (3) in chlorophylless saprophytic groups such as Triuridales and some Burmanniales.

The trinucleate pollen type has probably not developed as the result of any of these adaptations but it is rather a fortuitous developed in each of these rather homogeneous groups of plants. Poales and Arecales have several important features in common which have been stressed particularly in recent literature, but they are different in regard to number of nuclei in the pollen grains. The marked dominance of trinucleate pollen grains in the Alismatanae is not found in the few members of Nymphaeales so far investigated, though the two groups have otherwise many important traits in common.

In the **dicotyledons**, the pattern differs somewhat from that in the monocotyledons. There seems to be no general tendency among aquatic groups such as Nymphaeales, Podostemales and Trapales to produce trinucleate pollen grains, but they do occur, for example, in Lentibulariaceae and Myriophyllum (Scrophulariales and Haloragales respectively). Nor do the wind-pollinated trees ("Amentiferae" s.lat.) distributed in various orders in this system in general have trinucleate pollen grains.

Certain orders are reported to have consistently trinucleate pollen grains, viz.: Caryophyllales, Plumbaginales, Polygonales, Araliales, Pittosporales and Asterales, and they are predominant, for example, in Thymelaeales (except Dichapetalaceae) and Dipsacales (except Calyceraceae). In these cases the character is obviously of great taxonomical significance, though not all these orders are related to one another.

The fact that trinucleate pollen grains are found in both Caryophyllales and Plumbaginales—Polygonales has sometimes been pointed out when placing these groups close together in the system, but certain differences in other characters make a close relationship doubtful. The agreement between Araliales, Pittosporales and Asterales as regards this character is however supported by numerous chemical and morphological similarities. In this case the trinucleate pollen grains seem to point to close relationship. Several families in Cornales (Icacinaceae, Escalloniaceae, Adoxaceae and Sambucaceae), which likewise have trinucleate pollen grains, are also similar in many chemical and morphological characters to Dipsacales and together with Gentianales and Oleales they all seem to form another natural group.

Remarkably enough, most families of Gentianales, Oleales, Lamiales and Campanulales are heterogeneous in the present character, some genera having trinucleate pollen grains, others binucleate.

In Rutales the binucleate pollen grains are predominant, but trinucleate pollen

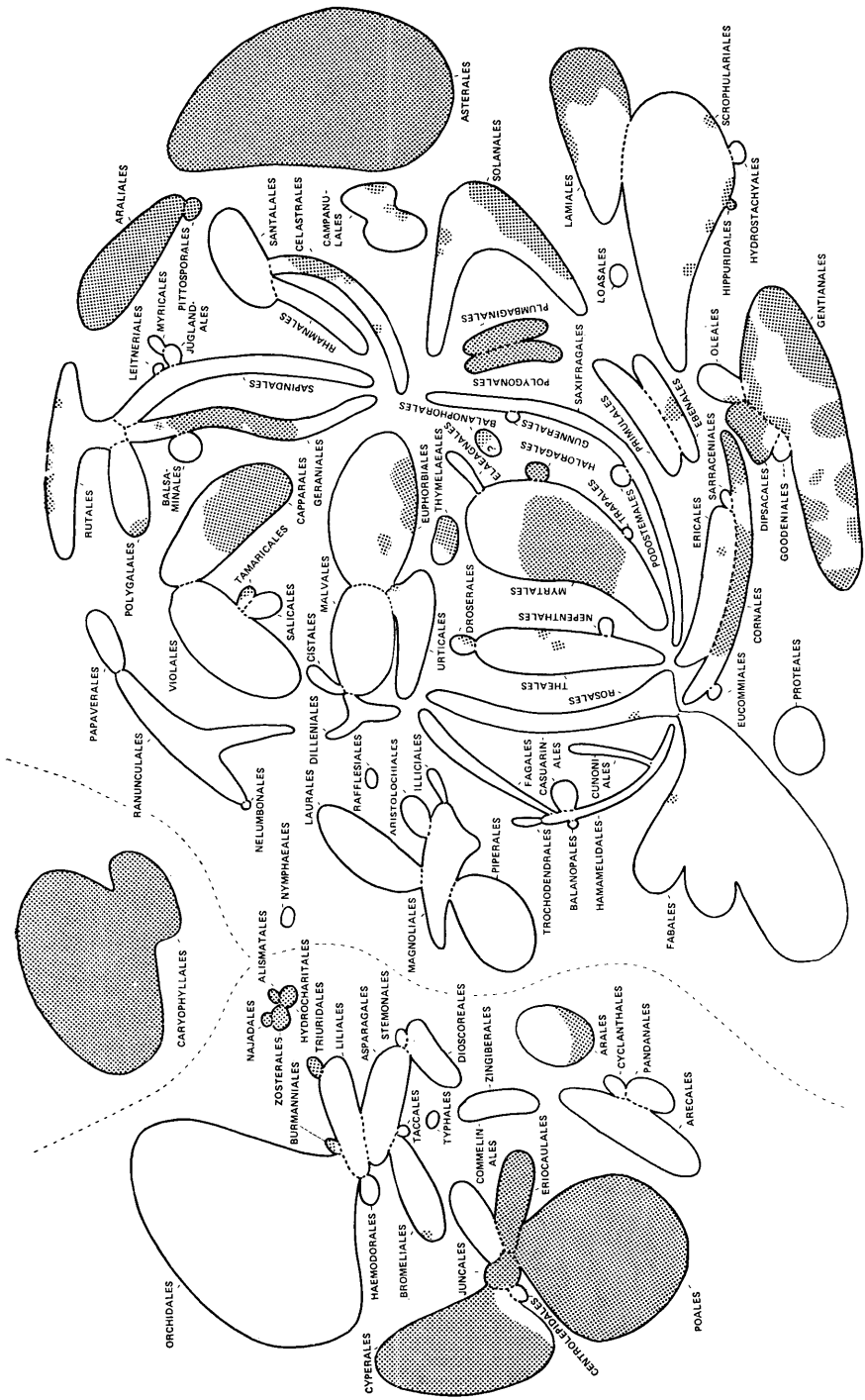

Fig. 4. Distribution of pollen grains released at the trinucleate stage (shaded) and in the binucleate stage in the orders of the angiosperm system.

grains have been recorded in some genera of Rutaceae, in Cneoraceae, and in at least one genus of Meliaceae. In Polygalales, Polygalaceae is heterogeneous, *Securidaca* and *Salomonia* having binucleate pollen grains and species of *Polygala* and *Monnina* trinucleate pollen grains. In Geraniales, trinucleate pollen grains are the commonest, but in Oxalidaceae at least and most genera of Zygophyllaceae studied (except *Tribulus*) the pollen grains are binucleate.

Other heterogeneous families where there are certain genera with trinucleate others with binucleate pollen grains are Euphorbiaceae (Euphorbiales), Ulmaceae (Urticales), Droseraceae (Droserales), Lecythidaceae (Theales), Mimosaceae (Fabales), Ericaceae (Ericales), Vitaceae (Rhamnales), Staphyleaceae and Celastraceae (Celastrales) and Sapotaceae (Ebenales). In some of these families we have only a single record or few records of trinucleate pollen grains. In the other families of the orders the pollen grains seem to be chiefly or exclusively binucleate. It is interesting to note that *Ulmus* differs from other genera of Urticales studied in having trinucleate pollen grains, as it is also known to have a different type of sieve tube plastids and a tetrasporangiate embryo sac.

Further, Brassicaceae deviates notably from other families in Capparales in having, as far as is known, trinucleate pollen grains only (a fact which prompts further studies in border genera between Brassicaceae and Capparaceae). In Tamaricales, Frankeniaceae is likewise reported to differ from Tamaricaceae in having trinucleate pollen grains. The genera of Melastomataceae studied also differ from all other known taxa of Myrtales in having trinucleate pollen grains. Melianthaceae, here provisionally placed in Rosales, is said to have trinucleate pollen grains by contrast to the rest of this order.

Most genera of Boraginaceae studied (except Heliotropium) as well as Cuscutaceae, both in Solanales, have trinucleate pollen grains, but they are binucleate in the remaining families of the order (among them is Ehretiaceae). In Scrophulariales the character is somewhat variable, but binucleate pollen grains are predominant. Trinucleate pollen grains are known in Lentibulariaceae, Martyniaceae, some Plantaginaceae and a few genera of Acanthaceae. The pollen grains are also trinucleate in the monotypic *Hippuris* (Hippuridales).

As regards Balanophoraceae reports differ somewhat. According to DAVIS (1966) the pollen grains are trinucleate when shed, but in the genera studied by BREWBAKER (1967) there were two nuclei only.

As is mentioned above it is a generally accepted fact that grains in the primitive angiosperms were released at the binucleate stage. Obviously a transition to trinucleate grains (i.e. division of the generative nucleus at an earlier stage) has taken place in many independent groups that are only remotely related or not at all. Thus they appear to be scattered over many orders in the system, and in some orders they are limited to certain families or even to certain genera. In other groups there are consistently either trinucleate or binucleate pollen grains which are thus of great taxonomic value.

Trinucleate pollen grains are of particular significance in groups such as Poales, Caryophyllales and Asterales and seem to be entirely lacking in orders such as Magnoliales, Laurales and Violales. Orders where variation is great and the character is of little taxonomic importance are, for example, Gentianales, Oleales, Campanulales and Euphorbiales.

It is sometimes stated in the literature that bi- and trinucleate pollen grains do not occur within the same genus. This does indeed seem to be rare but BREWBAKER (1967) has recorded the occurrence of both types in several genera: *Burmannia* (Burmanniaceae, Burmanniales), *Lobelia* (Lobeliaceae, Campanulales), *Ipomaea* (Convolvulaceae,

Solanales), *Drosera* (Droseraceae, Droserales), *Euphorbia* (Euphorbiaceae, Euphorbiales), three genera of Lamiaceae (Lamiales), *Calliandra* (Mimosaceae, Fabales), *Plantago* (Plantaginaceae, Scrophulariales), and *Ruta* (Rutaceae, Rutales).

The important recently discovered connection between bi- and trinucleate pollen grains and types of self-incompatibility system (see BREWBAKER 1957) opens up further possibilities. Particularly in the dicotyledonous taxa the groups with binucleate pollen grains tend to have the gametophytic type of self-incompatibility, and those with trinucleate pollen grains the sporophytic type (see further, e.g., in PANDEY 1960, and LUNDQUIST & al. 1973).

In Lamiaceae KOOIMAN (1972) has also demonstrated the correlation between binucleate and tricolpate pollen grains and between trinucleate and hexacolpate pollen grains (the former being found in taxa containing iridoid compounds).

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Botanical Literature

TRALAU, H. 1974: Bibliography and Index to Palaeobotany and Palynology 1950—1970. Two volumes: Bibliography (358 pp.) and Index (261 pp.). — Stockholm 1974. Distributed by the Swedish Museum of Natural History, S-104 05 Stockholm 50, Sweden. — Price (both parts) as a direct order: Sw. Kr. 300:—; booksellers price: c. Sw. Kr. 450:—.

This is the second great service index of this kind undertaken by Dr TRALAU, Section for Palaeobotany at the Swedish Museum of Natural History. The fourth part of the other, Index Holmensis, has just been published.

The present work is in two volumes, the Bibliography and the Index. The Bibliography contains about 30,000 references arranged in alphabetic order of authors. The author(s) with initials, year of publication, title of the article or book, title of series (standard abbreviations) and volume, number of pages and number of illustrations are given. A work thus should be easy to trace through most leading libraries.

Each reference in the Bibliography is preceded by a code consisting of the first six letters of the author's name followed by numerals indicating the year of publication and, at the end, three letters generally representing the article or book.

The Index volume consists of a key-word index where the title or part of the title of each reference is presented, the key-word, printed in *italics,* being placed in the centre of the column. Thus, with the help of key words it is possible to trace references, the codes of which are found on the right. These codes lead to the full references in the Bibliography volume. The procedure, which I have personally practised many times, is simple and effective. A short guide showing how to use the Index most effectively is given in the preface. (TRALAU's Index demonstrates the importance of preparing an adequate title for an article. It should be short and contain the relevant key words.)

The fields of palaeobotany and palynology have developed tremenduously during the twenty years covered by TRALAU's Index, and tracing a refence in these fields has often been time-consuming and troublesome. Here is an indispensible tool that will save much time and energy. The index may also help to avoid a considerable amount of unnecessary double research and create a basis for contacts, the importance of which cannot be overemphasized.

The Bibliography and Index to Palaeobotany and Palynology is the result of more than twelve years work by Dr TRALAU. According to him it is not absolutely complete, but this does not detract from its great value. It is a must for all institutes using palaeobotanical and palynological data.

ROLF DAHLGREN

DEGELIUS, G.: The Lichen Genus Collema with Special Reference to the Extra-European Species. — Symbolae Botanicae Upsalienses 20:2. Uppsala (Almqvist & Wiksell) 1974. 215 pp. 65 maps and figures in text. Price Sw. Kr. 60:— (wrappers).

Relatively few universal monographs on lichen genera have been published since W. NYLANDER's Synopsis Lichenum (1858—1860), which was originally intended to cover all genera and species of lichens known from the whole world but which was never completed. Keeping to the ma-

crolichens the following works can be mentioned: *Cladonia* (WAINIO 1887—1897), *Roccella* and allied genera (DARBISHIRE 1898), *Usnea* (MOTYKA 1936—1938), *Neuropogon* (LAMB 1939), *Anaptychia* (KUROKAWA 1962), *Parmelia* (HALE 1965, to be completed in the near future) and *Dirinaria* (AWASTHI 1974).

In 1954 Dr G. DEGELIUS (then of Uppsala, now of the Institute of Systematic Botany Göteborg) published a monograph on "The Genus *Collema* in Europe". The present volume treats the non-European species and also includes many additions to the vast material published in 1954. The completion of this magnificent work is a great event in the history of lichenology.

The 1954 issue is a large volume (499 pp., numerous distribution maps and illustrations) dealing with the 35 species of *Collema* known from Europe. Each species is described in great detail with extensive chapters on nomenclature, distribution and habitat ecology, etc. A general chapter on external and internal morphology gives much new information, expecially on the nature of lichen symbiosis. These results were founded on comprehensive culture experiments with various *Collema* species and their phycobiont *Nostoc*.

The present work, which covers the whole genus, is a smaller volume than its predecessor. The total number of species is recorded as 77, 42 of which do not occur in Europe. All 35 European species appear again with additional information on interesting new localities and on species that have been distributed in exsiccata since 1954.

16 new species and 3 infraspecific taxa are described here. Numerous species and other previously established taxa have been degraded to synonyms and many species to varieties.

The author's species concept is fairly broad and is founded exclusively on morphological characters. He has the advantage of having seen almost all species in nature. Variation within each species and characters distinguishing the species are discussed in great detail.

As in the previous volume chemistry is hardly mentioned. The only chemical reaction specified is "gelatine I+ or I–" in the *Nostoc*-cells. In fact, very few lichen substances are known in *Collema*. "Lichen acids" have often been used in lichen taxonomy, sometimes to distinguish "species" without any relation to morphological differences. As they do not occur at all in *Collema* the author has not been faced with the problem of judging the taxonomic value of the "chemical strains".

Subgeneric divisions recognized under the Code of Nomenclature (subgenera or sections) have not been used, but the species have been arranged in 22 "natural groups".

"The total number of extra-European *Collema* samples examined by me in herbaria may be at least 3 500" — a short note that indicates in a nut-shell the more than twenty years of meticulous work that lies behind the publication of this volume. Seldom has botanical taxonomy known a more diligent and careful worker than Dr DEGELIUS. His survey of material both from nature and herbaria and of the extensive literature is unsurpassed. His magnum opus will remain a classic and should serve as a model for monographic works on other lichen genera.

OVE ALMBORN

TIBELL, L.: The Caliciales of Boreal North America. — Symbolae Botanicae Upsalienses 21:2. Uppsala (Almqvist & Wiksell) 1975. 128 pp. 39 maps and figures in text. Price Sw. Kr. 40:— (wrappers).

The Caliciales have been studied by a fair number of lichenologists, at least in Europe, but their views on the species concept and nomenclature differ widely. The need for a monographic treatment of this group is urgent.

Mr LEIF TIBELL, Institute of Systematic Botany, Uppsala, has previously published some reports on Caliciales, especially on the genus *Cyphelium*. The present volume, which is his thesis for the Ph.D. degree, deals mainly with the genera and species of Caliciales occurring in North America. This study is largely founded on material collected by the author during a six-week field trip in the USA and Canada. Identification keys and diagnoses of 52 species are presented. The distribution, both zonal and geographical, has also been noted for the species. In several cases comparisons are made with the distribution and ecology of the same species in Europe, and many additions to the European ranges are presented. 25 species are new to North America.

Two new species are described (one from Canada, the other from Sweden), and some epithets have been recombined. Several lectotypes have been selected and many valuable comments are made on problems of taxonomy and nomenclature. It is evident, however, that a full treatment of certain species will have to await further revision.

In some species, mainly *Calicium,* spore ontogeny and ornamentation have been studied by means of Transmission and Scanning Electron Microscopy. Spore ornamentation has been found to constitute a very valuable specific character. These observations, rather outstanding in the lichenology of today, are illustrated by a number of photographs of extremely high quality.

The present work is an important step towards a monograph on this interesting group of lichens.

OVE ALMBORN

Appeal for Support for the INDEX HOLMENSIS Project

The INDEX HOLMENSIS is an index of plant distribution maps with a world-wide coverage. It is the only international bibliography of distribution maps of vascular plants.

So far we have published four volumes, viz. Volume I covering vascular cryptogams, Volume II containing Monocotyledoneae A—I, Volume III Monocotyledoneae J—Z and finally Volume IV covering Dicotyledoneae A—B, in all more than 1,000 pages. We intend to continue publishing one volume a year. The total number of distribution maps so far published is estimated to about 400,000, all of which will finally be listed in the index or its supplement. Although the main work is at present being done at the Swedish Museum of Natural History in Stockholm the indexing work is served by an international editorial board. Members of this board to some extent vouch for the completeness of the files for their particular area.

Still, the number of distribution maps published annually is growing rapidly owing to the increased importance that is being accorded the geographic complex of plant taxa. Consequently, not only are there extensive areas all over the world where the entire flora has been systematically mapped, but maps have become a common feature of monographs in different fields, for instance in economic botany, palaeobotany, vegetational history, palynology, etc.

In order to keep the files for the INDEX HOLMENSIS and the projected supplementary volumes up to date we ask our fellow botanists to send us information on their published distribution maps and/or to send reprints of their publications. Needless to say, we shall also continue to supply colleagues, on request, with all information on distribution maps so far not published in the INDEX HOLMENSIS.

All correspondence should be addressed to: Dr HANS TRALAU, The Swedish Museum of Natural History, S-104 05 Stockholm, Sweden.

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Drawings of Scandinavian Plants 103–104

Epilobium L. Sect. Epilobium

Alf Oredsson and Sven Snogerup

OREDSSON, A. & SNOGERUP, S. 1975 10 10. Drawings of Scandinavian Plants 103—104. Epilobium L. Sect. Epilobium. — Bot. Notiser 128: 203—207. Lund. ISSN 0006-8195.

Drawings and descriptions are given for *E. palustre* L. and *E. davuricum* FISCH. ex HORNEM.

Alf Oredsson and Sven Snogerup, Department of Plant Taxonomy, University of Lund, Ö. Vallgatan 18—20, S-223 61 Lund, Sweden.

103. **Epilobium palustre** L. 1753

Perennial herb, (5—)15—40(—80) cm high. Stem either simple, or branched in upper part, or in tall specimens richly branched from the base, producing one to several (1—)2—7(—10)-flowered inflorescences. Middle internodes usually 2—6 cm, but in specimens growing in dry places and littoral specimens often more condensed, upper internodes of small specimens usually shorter than the leaves. Stolons epigean, but usually spreading in a moss cover or in other dense vegetation, 2—15(—30) cm long, usually only c. 0.5 mm thick, either white to reddish or green when developed on the surface of earth or vegetation, with small, widely spaced leaves or the green ones rarely with leaves up to 15 mm long, glabrous. Perennating turions formed at the end of the long stolons or on very short ones from the stem base, fleshy, up to 10 mm long and 5 mm broad, with very broad, blunt, scale-like leaves. Short, few-leaved shoots formed in most of those leaf axils not supporting branches or flowers.

Stem terete, near the base usually 1—3 mm thick, with short and inconspicuous ridges below the midrib of leaves, in northern forms rarely also below leaf margins. Subglabrous to moderately hairy, in upper part evenly, in lower part mainly in broad rows below leaf margins, some northern specimens more uniformly hairy throughout. Hairs 0.1—0.3 mm, longer ones curved, short ones patent and at least partly glandular.

Most leaves opposite, only uppermost ones alternate, nonpetiolate or petiole less than 5 mm, bases of lower cauline leaves uniting around the stem but never decurrent. Basal leaves smaller than the cauline ones, spathulate or short-petiolate, obovate to elliptical. Rarely, in plants developing from winter buds, some of the first leaves thick, scale-like. Middle cauline leaves (10—)20—40(—85) mm long, (2—)5—10(—15) mm broad, narrowly to very narrowly ovate or narrowly lanceolate, obtuse or tapering to an obtuse apex or in some tall southern forms acute, subentire or serrate with few, low and broad teeth. Upper leaves shorter, narrower, often more markedly petiolate, usually subentire. Indumentum of leaves like that of the stem, sparse to moderate, denser on upper leaves, usually denser on midribs and margins. Leaves of some coastal ecotypes more densely and uniformly hairy.

Bracts ± large, leafy. Pedicels in bud and early flower nodding, in fruit erect to erecto-patent. Buds ellipsoidal, blunt. Sepals 3—6 mm, connate to 1—2 mm at base, lanceolate to narrowly ovate, obtuse, green but often with reddish mar-


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Fig. 104. *Epilobium davuricum* FISCH. ex HORNEM. — A: Habit, ×1/3. — B: Basal rosette, ×1/2. — C: Stem nodes, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem part with leaf, ×2.5. — G: Buds, ×1. — H: Flower, ×1. — J: Apical part of capsules, ×2.5. — K: Style, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.

gins, sparsely to moderately hairy, especially towards the base. Petals 5—8.5 (—10) mm, notched to 0.8—2 mm, pinkish-violet to pinkish-white, rarely white. Anthers 0.6—0.8 mm, long filaments 3.5—5.5 mm, short filaments 2—3 mm, usually c. 2/3 as long as the long ones. Style equalling or slightly longer than the long stamens, stigma capitate.

Capsule stalk (5—)15—40(—50) mm.

Fig. 103. *Epilobium palustre* L. — A: Habit, ×1/3. — B: Stolons and winter buds, ×1/2. — C: Stem node, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem part with leaf, ×2.5. — G: Bud, ×1. — H: Flower, ×1. — J: Apical part of capsules, ×2.5. — K: Styles, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.

Capsule (30—)50—60(—75) mm, moderately hairy, denser along the ribs, hairs 0.15—0.4 mm, short ones patent and usually glandular, long ones curved to appressed. Seeds narrowly obovoidal, ± flattened on one side, 1.25—1.8(—2.1) mm long, 0.4—0.55 mm broad, tapering to an obtuse lower end, neck 0.05—0.15(—0.25) mm, surface densely covered with 0.01—0.02 mm long papillae oriented into inconspicuous rows, chalazal hairs 50—60 (—70), 7.5—11 mm long. Flower homogamous.

E. palustre occurs in all sorts of wet places, also in standing or running water, on poor as well as rich soils. It has a circumpolar, temperate to arctic distribution. In Europe it is found as far south as the mountains of the N Mediterranean.

E. palustre is common throughout Scandinavia, occurring up to 1300 m in the southern mountains. It is represented by several very different but intergrading ecotypes in the great variety of biotopes occupied.

Known hybrids: with *E. adenocaulon, alsinifolium, anagallidifolium, collinum, davuricum, glandulosum, hirsutum, hornemanni, lactiflorum, montanum, obscurum, parviflorum, roseum,* and *tetragonum.*

104. **Epilobium davuricum** Fischer ex Hornemann 1819

Perennial herb, (7—)15—30(—40) cm high. Stem either simple, or rarely with one or a few short branches above, thus producing one or rarely a few, 1—5(—7)-flowered inflorescences. Middle and upper internodes usually longer than the leaves. Stolons lacking, dense, short-leaved rosettes developing in the axils of the basal leaves, rarely some of them prolonged up to 3 cm. Shoots in middle leaf axils lacking or rudimentary.

Stem terete, near the base 0.5—1.5 mm thick, usually with weak ridges or lines, in upper and middle part mainly below the midribs of leaves, in basal part also from margins of opposite leaf pairs. Stem sparsely to moderately hairy, either evenly or denser along the ridges, hairs 0.15—0.3 mm, longer ones curved, short ones patent and at least partly glandular.

Basal leaves forming a dense rosette, except in some first-year specimens, lower cauline leaves opposite, middle and upper ones usually alternate, the uppermost one usually odd, all usually with a short but distinct petiole 0—2(—5) mm long. Bases of opposite leaves uniting around the stem but never decurrent. Basal rosette leaves narrowly obovate to elliptical or ovate, 5—15 mm long, glabrous. Middle cauline leaves (5—)10—25(—40) mm long, 1—3 mm broad, lanceolate or narrowly lanceolate to linear, obtuse or tapering to a blunt apex, subentire or with few, often irregular, short teeth. Upper leaves narrower, often shorter and less distinctly petiolate. Indumentum of leaves like that of the stem, though often slightly shorter, sparse, denser on midribs and margins.

Bracts leafy, often placed up to 5(—10) mm up on the pedicel. Pedicels in bud and flower nodding, in fruit erect. Buds broadly ellipsoidal to sphaeroidal, blunt or acutish. Sepals 3—5 mm, connate to 0.9—1.8 mm at base, lanceolate, obtuse, green or often ± reddish, subglabrous or sparsely hairy especially in the basal part, upper margin glandular, slightly fringed, reddish. Petals (3.2—)4—5(—7.5) mm, notched to 0.5—1 mm, white or rarely pinkish-white. Anthers 0.45—0.5 mm, long filaments 2.4—2.8 mm, short filaments 1.4—1.8 mm, usually c. 2/3 as long as the long ones. Style about equalling the long stamens, stigma capitate.

Capsule stalk (10—)15—30(—40) mm. Capsule 30—45(—50) mm, sparsely to moderately hairy, especially on the ribs, hairs 0.1—0.25 mm, like those of the stem. Seeds narrowly obovoidal, ± flattened on one side, 1.3—1.5(—1.7) mm long, 0.5—0.6 mm broad, tapering to an obtuse lower end, neck 0.15—0.3 mm, usually distinctly narrower than the rest of the seed and whitish, surface densely cov-

ered with papillae c. 0.01 mm long in inconspicuous rows, chalazal hairs 60—70, 7.5—11 mm long. Flower homogamous.

E. davuricum is calciphilous, and occurs in different sorts of wet places, especially along streams and on open ground. It has a circumpolar, arctic to subarctic distribution without any great gaps.

In Scandinavia *E. davuricum* occurs mainly in the mountains, up to 1400 m in the south, to 500 m in the north. It is also found scattered in the lowlands of N Finland S to c. 63° N and of Sweden and Norway to c. 60° N.

Known hybrids: with *E. palustre* and *lactiflorum*.

This species and the preceding are no doubt very closely related. They were recently subjected to a detailed investigation in part of their northern range by KYTÖVUORI (1969).

LITERATURE CITED

KYTÖVUORI, I. 1969. Epilobium davuricum Fisch. (Onagraceae) in eastern Fennoscandia compared with E. palustre L. A morphological, ecological and distributional study. — Ann. Bot. Fenn. 6: 35—58.

Karyotype Analysis and Taxonomic Comments on Irises from SW and C Asia

Mats Gustafsson and Per Wendelbo

GUSTAFSSON, M. & WENDELBO, P. 1975 10 10. Karyotype analysis and taxonomic comments on irises from SW and C Asia. — Bot. Notiser 128: 208—226. Lund. ISSN 0006-8195.

Karyotype analysis has been carried out on 21 taxa of genus *Iris*, originating from SW and C Asia. Chromosome numbers of 10 taxa have not been reported previously, viz. *I. afghanica* 2n=22, *I. heweri* 2n=22, *I. barnumae* ssp. *demawendica* 2n=20, *I. iberica* ssp. *lycotis* 2n=20, *I. pamphylica* 2n=20, *I. aitchisonii* 2n=34, *I. cycloglossa* 2n=28, *I. maracandica* 2n=20, *I. microglossa* 2n=30 and *I. xanthochlora* 2n=14+1 B. The pattern of variation within subgenus *Iris* sect. *Hexapogon* and subgenus *Scorpiris* is discussed. In subgenus *Scorpiris* both morphological and cytological variation is extensive, while variation within sect. *Hexapogon* is comparatively narrow. In species of subgenus *Iris*, sect. *Iris* the karyotypes are relatively symmetrical, while asymmetrical karyotypes are found in sect. *Hexapogon*. One new combination has been made, *I. maracandica* (VVED.) WENDELBO.

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This study mainly comprises karyotype analyses with taxonomic comments on species indigenous to the Irano-Turanian floristic province. Special attention has been paid to variation within subgenus *Iris* sect. *Hexapogon* (BUNGE) BAKER and subgenus *Scorpiris* SPACH (for systematic treatments see FEDTSCHENKO 1935, VVEDENSKY 1963, WENDELBO & MATHEW 1975). Both groups have their centres of evolution in this province. Within *Scorpiris* a pronounced morphological variation is found in Afghanistan—Tadjikistan and the species mostly have very narrow geographical areas of distribution. In Afghanistan there are 17 species, 12 of which are endemic to that country and immediate adjacent parts of surrounding countries. Fourteen species are distributed in Tadjikistan of which 5 are endemic. The section *Hexapogon* is divided into two apparently closely related subsections. Subsect. *Hexapogon* is mainly Central Asiatic and most species are found in NE Afghanistan—Tadjikistan. Subsect. *Oncocyclus* (SIEMSS.) BENTH. has its main area in SW Asia, from Israel—Lebanon to E Turkey and NW Iran. Both subsections show comparatively little variation in morphological characters, but especially in *Oncocyclus* the colour patterns of the perigone are extremely variable. Taxonomically this latter group is confusing and the specific concept varies much between different treatments.

Little information is available as regards the intra- and interspecific cytological variation of Asian irises. Although chro-

mosome numbers of numerous species have been reported (for references see FEDOROV 1969), mostly single individuals representing one or two populations of each species have been investigated, and much of the material has been cultivated in gardens for a long time and their origin uncertain. Detailed karyotype analyses have only been carried out by MITRA (1956), RANDOLPH & MITRA (1961) and WEYMOUTH & CHAUDHARY (1974).

MATERIAL AND METHODS

The investigation has been carried out on material collected in natural habitats, with certain exceptions (cf. *I. fosterana, I. kopet-daghensis* and *I. maracandica*). Bulbs and rhizomes respectively were transplanted to pots and cultivated in the Botanical Gardens of Göteborg, Sweden. Usually only one or a few specimens of each population have been available. Original collections and voucher specimens are preserved at Kew and Göteborg.

Root tips were pretreated in 2 mM 8-hydroxiquinoline, kept in a refrigerator at 3—5°C over a night and then fixed in Carnoy (3:1). The root tips were hydrolyzed in 1 N HCl at 60°C for 10 minutes, stained in Feulgen for about two hours and then treated in a solution of 10 % pectinase before squashing in 45 % acetic acid. The squash technique used was as in ÖSTERGREN & HENEEN (1962).

The karyotypes are based on at least 10 good metaphase plates of each individual. The karyological nomenclature is as suggested by LEVAN et al. (1965). The karyotypes have been arranged in the following manner. The chromosome pairs are referred to four groups according to their r-values: m (r=1.0—1.7), sm (r=1.7—3.0), st (r=3.0—7.0) and t (r > 7.0). Within each group the pairs have been arranged according to size. The satellited pairs have been placed at the end of the group to which they belong. Chromosome pairs which cannot be distinguished from one another by conventional cytological methods have been placed together.

GUSTAFSSON is responsible for the cytological investigation and WENDELBO for the taxonomic treatment.

SUBGENUS IRIS SECT. IRIS

I. imbricata LINDL. 1845

GENERAL DISTRIBUTION. Caucasus, N Iran.

MATERIAL INVESTIGATED. Iran, province of Ghilan, FERGUSON 115.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=24 (Fig. 1). m-chromosomes: One large pair (r=1.2). sm-chromosomes: One large pair (r=2.1) and one small pair (r=2.3). sm—st-chromosomes: Nine pairs successively decreasing in length (r=2.8—6.3).

PREVIOUS REPORTS. 2n=24 (MITRA 1956, RANDOLPH & MITRA 1961). The karyotype is similar to those reported by MITRA and RANDOLPH & MITRA, except that no satellited st-chromosomes have been observed. The material investigated by MITRA originated from the Elburz Mountains of N Iran, that of RANDOLPH & MITRA from the Caucasus.

SUBGENUS IRIS SECT. HEXAPOGON (Bunge ex Alefeld) Baker 1876

Subsect. Hexapogon

I. afghanica WENDELBO 1972

TAXONOMIC COMMENTS. *I. afghanica* is from a morphological point of view related to *I. korolkowii,* and is confined to a small area just south of the area of the latter species.

GENERAL DISTRIBUTION. Endemic to NE Afghanistan.

MATERIAL INVESTIGATED. Representatives of two populations have been investigated. Population 768 originates from the province of Kataghan, E of Banu, GREY-WILSON/HEWER 768. Population 698 from the same province, east side of the Salang Pass, GREY-WILSON/HEWER 698.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=22 (Fig. 1). The two populations display a similar karyotype. m-chromosomes: One large pair (r=1.1). st-chromosomes: One large pair (r=6.4). t-chromosomes: Nine pairs showing a continuous decrease in length (r=7.1—12.5).

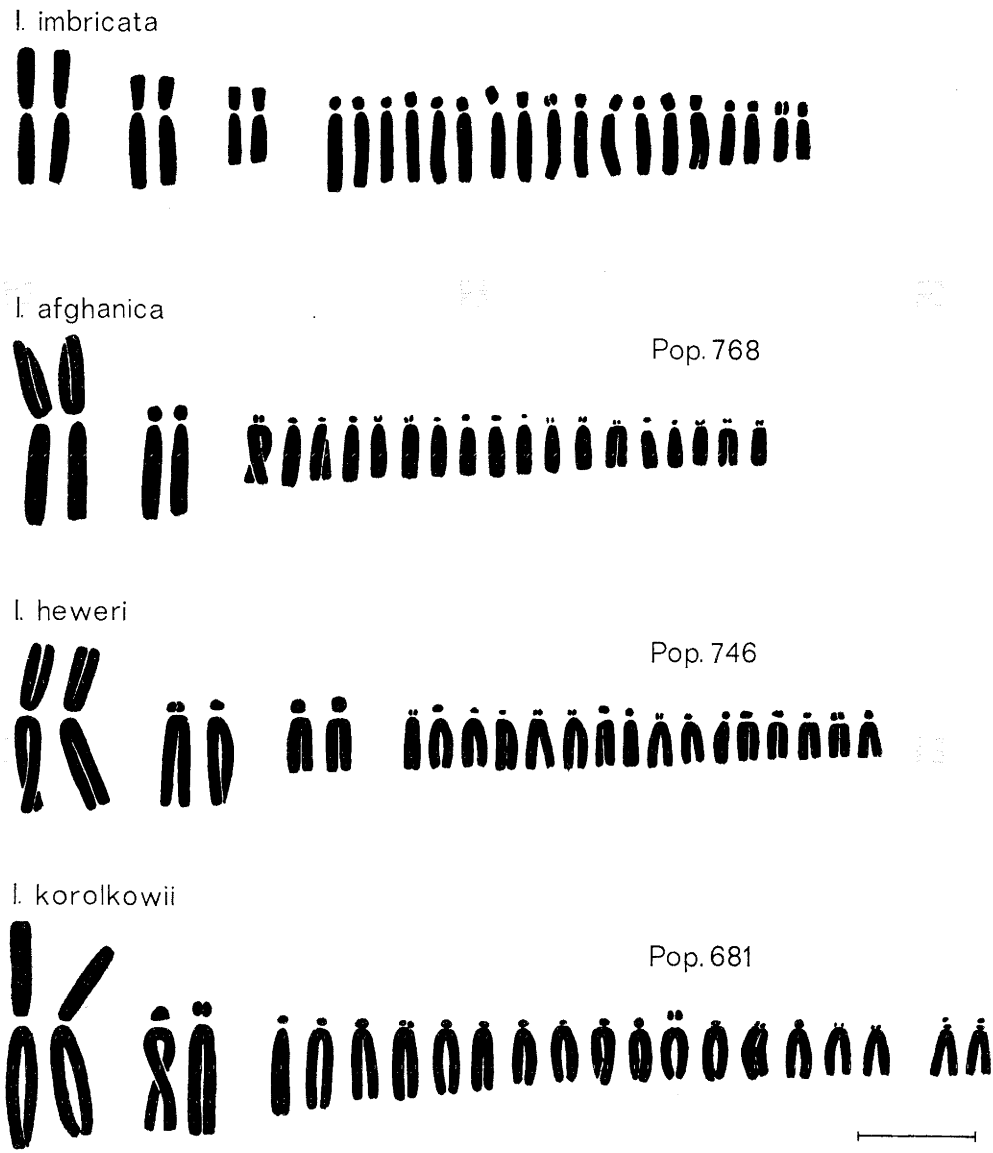

Fig. 1. Karyotypes of *I. imbricata* (2n=24) belonging to sect. *Iris*, and of *I. afghanica*, *I. heweri* and *I. korolkowii* (all having 2n=22) belonging to sect. *Hexapogon* subsect. *Hexapogon*. The scale unit is equal to 5 μ.

I. heweri GREY-WILSON & MATHEW 1974

TAXONOMIC COMMENTS. Morphologically *I. heweri* seems to be most closely related to *I. falcifolia* BUNGE, a species endemic to Soviet Central Asia (cf. FEDTSCHENKO 1935).

GENERAL DISTRIBUTION. Endemic to NE Afghanistan.

MATERIAL INVESTIGATED. Representatives of two populations (746 and 757) collected in the province of Kataghan, E of Khinjan, GREY-WILSON/HEWER 746 and 757.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=22 (Fig. 1). The two populations have a similar karyotype: m-chromosomes: One large pair (r=1.1). st-chromosomes: One large pair (r=6.5) and one small pair (r=3.8). st—t-chromosomes: Eight unidentifiable pairs successively decreasing in length (r=4.3—13.5).

I. korolkowii REGEL 1873

GENERAL DISTRIBUTION. NE Afghanistan to Soviet Central Asia.

MATERIAL INVESTIGATED. Representatives of two populations collected in NE Afghanistan, one (681) in Badakshan, c. 30 km S of Keshm, HEDGE & WENDELBO 9321, the other (918) in Qataghan, FURSE 8207. Population 681 represents the southernmost locality of this comparatively widely distributed species.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=22 (Fig. 1). The karyotypes of the two populations differ somewhat. m-chromosomes: One large pair (r=1.1—1.2). st-chromosomes: One large pair (r=5.7—6.4). st—t-chromosomes: Population 918 has nine unidentifiable pairs (r=6.5—8.6). Population 681 nine pairs (r=5.6—12.0) of which one has a satellite on the short arm.

PREVIOUS REPORTS. 2n=22 (MITRA 1956, ZAKHARYEVA & MAKUSHENKO 1969), 2n=33 (SIMONET 1928, horticultural form), 2n=44 (SIMONET 1928, horticultural form).

The karyotype reported by MITRA corresponds well with those observed by the authors, except that he observed 3 pairs of st-chromosomes with satellites. The origin of the material investigated by MITRA is not known.

Subsect. Oncocyclus (Siemss.) Benth.

I. acutiloba C. A. MEY. ssp. **lineolata** (TRAUTV.) MATHEW & WENDELBO 1975

GENERAL DISTRIBUTION. Caucasus, Iran.

MATERIAL INVESTIGATED. Representatives of two populations from Iran; 659 from Kurdistan, 11 km N of Divandarreh, ARCHIBALD 2170, and 700 from Gorgan, 135 km E of Gonbad-E-Kavus, 1700 m, FURSE 7377. Geographically the two populations are widely separated, population 659 representing the westernmost and 700 the easternmost part of the distributional area.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=20 (Fig. 2). Population 659: t-chromosomes: All ten pairs: Four pairs large, of which one pair seems to have a somewhat longer short arm than the other three pairs, and six small pairs about equal in length. Population 700: Differs from the former population in having only three large pairs, and the difference in size of the short arm is not very pronounced. Besides, one of the large chromosomes has a satellite, the others do not.

PREVIOUS REPORT. 2n=20 (ZAKHARYEVA & MAKUSHENKO 1969).

I. barnumae BAKER & FOSTER ssp. **barnumae** f. **urmiensis** (HOOG) MATHEW & WENDELBO 1975.

I. urmiensis HOOG 1900

TAXONOMIC COMMENTS. This form is a yellow variant of *I. barnumae* ssp. *barnumae*.

GENERAL DISTRIBUTION. NW Iran.

MATERIAL INVESTIGATED. Iran, Kurdistan, ARCHIBALD 3188.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=20 (Fig. 2). All ten pairs

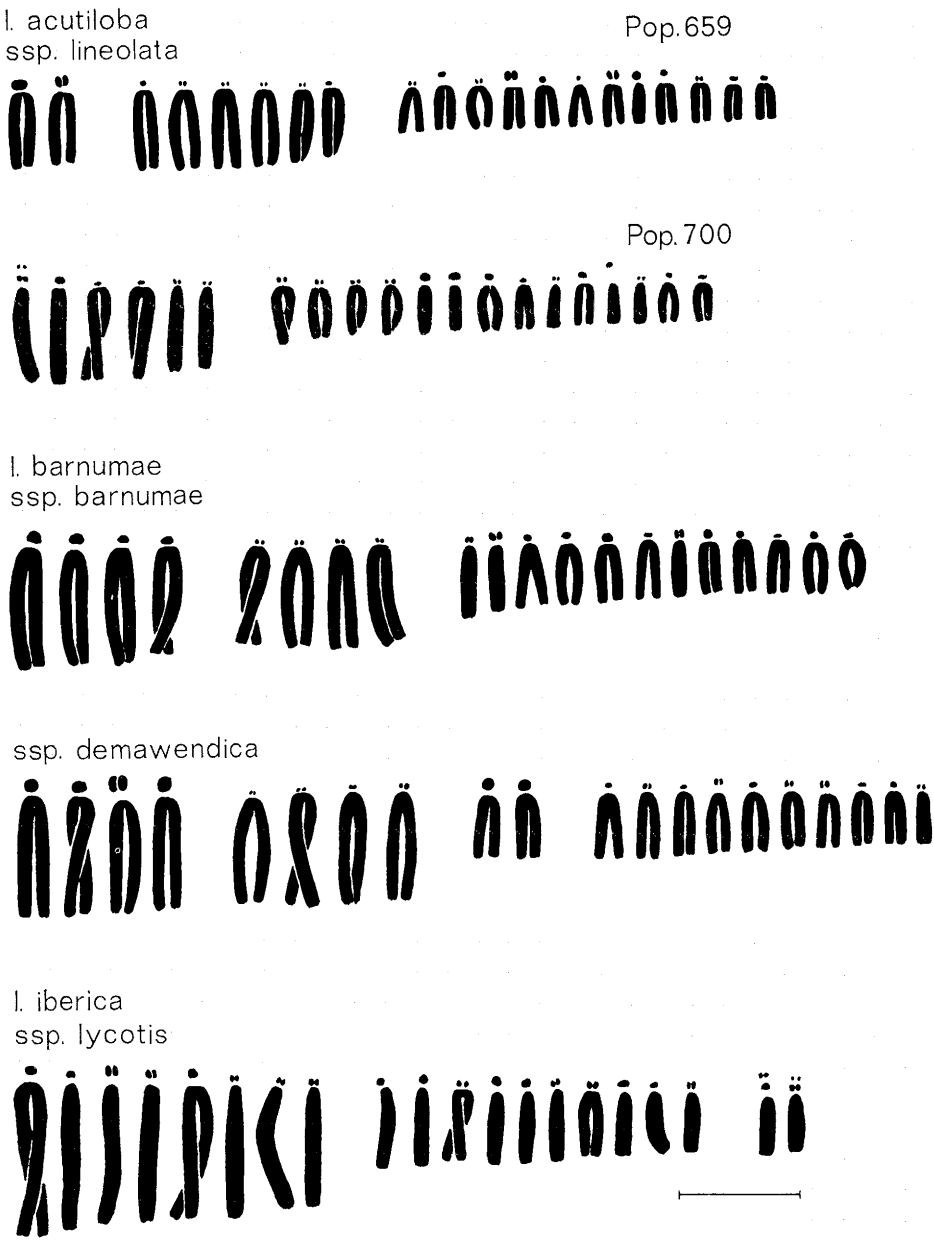

Fig. 2. Karyotypes of four taxa belonging to sect. *Hexapogon* subsect. *Oncocyclus* (all having 2n=20). The scale unit is equal to 5 μ.

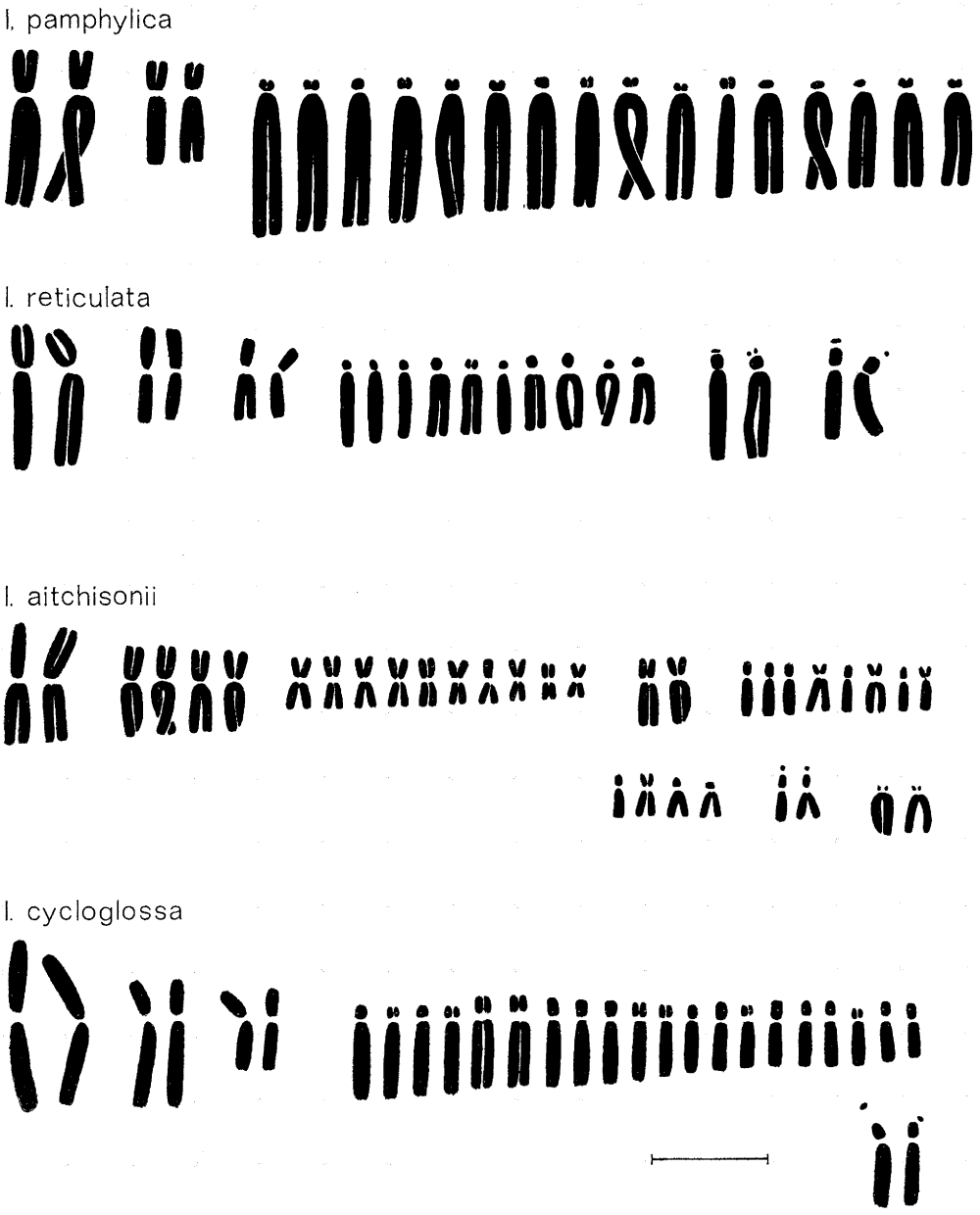

Fig. 3. Karyotypes of *I. pamphylica* (2n=20), *I. reticulata* (2n=20) both belonging to subgenus *Hermodactyloides*, and of *I. aitchisonii* (2n=34) and *I. cycloglossa* (2n=28) belonging to subgenus *Scorpiris*. The scale unit is equal to 5 μ.

are t (r > 7.1), four pairs large, of which two seem to have a somewhat larger short arm than the other two, and six small pairs successively decreasing in length.

PREVIOUS REPORTS. 2n=20 (SIMONET 1932, 1934).

I. barnumae BAKER & FOSTER ssp. **demawendica** (BORNM.) MATHEW & WENDELBO 1975

GENERAL DISTRIBUTION. N Iran.

MATERIAL INVESTIGATED. Elburz Mts, Dizin, 9000 feet. The material was obtained from Kew in 1972.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=20 (Fig. 2). st-chromosomes: One small pair (r=3.9). t-chromosomes: Nine pairs, four pairs large of which two pairs have a somewhat larger short arm than the other two, and five small pairs.

I. iberica HOFFM. ssp. **lycotis** (WORON.) TAKHT. in TAKHT. & FEDOR. 1972

GENERAL DISTRIBUTION. Armenia, NE Iraq, W Iran.

MATERIAL INVESTIGATED. Iran, Bakhtiary, 25 km NW of Shahr Kord, 2700—3000 m, FURSE 1446. The material represents the southernmost part of the distributional area.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=20 (Fig. 2). All ten pairs are t, four pairs large and unidentifiable, six pairs small of which one pair has a satellite on the short arm.

SUBGENUS HERMODACTYLOIDES Spach

I. pamphylica HEDGE 1961

TAXONOMIC COMMENTS. This species is probably most closely related to *I. reticulata* M. B.

GENERAL DISTRIBUTION. Central parts of South Turkey.

MATERIAL INVESTIGATED. Turkey, Isparta, Sübeüler, Kesmeköy, Ahmel UNZOGEN 207.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=20 (Fig. 3). sm-chromosomes: One large pair (r=2.5) and one small pair (r=2.5). t-chromosomes: Eight pairs (r > 10) successively decreasing in length.

I. reticulata M. B. 1808

TAXONOMIC COMMENTS. The material investigated represents a typical dark violet *I. reticulata*. As the occurrence in Afghanistan is far outside the general area of distribution of this species there is reason to believe that the material represents an escape.

GENERAL DISTRIBUTION. E Turkey, Transcaucasus, N and W Iran, NE Iraq.

MATERIAL INVESTIGATED. Afghanistan, Kabul in Paghman, FREITAG s.n.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=20 (Fig. 3). m-chromosomes: One small pair (r=1.2). sm-chromosomes: One large pair (r=2.3) and one small pair (r=1.8). st-chromosomes: Two large pairs with satellites (r=6.3 and 3.8 respectively), and five pairs successively decreasing in length (r=3.8—6.9).

PREVIOUS REPORTS. 2n=20 (DELONE 1928, SIMONET 1928). The karyotype is similar to that drawn by DELONE. In 1959 MITRA & RANDOLPH reported the chromosome numbers 2n=18 for *I. reticulata* "Violet" and 2n=20 for *I. reticulata* "Clarette", both the varieties originating from the firm van Tubergen, Holland. However, this material was obviously of hybrid origin and must be left out of account.

SUBGENUS SCORPIRIS Spach

Juno TRATT. ex ROEM. & SCHULT.
Iris sect. *Juno* (TRATT.) BENTH.
Iris subgenus *Juno* (TRATT.) BAKER.

In his treatment of *Iris,* RODIONENKO (1961) considered this group to be a genus of its own (*Juno*) and most recent reports from Soviet botanists seem to follow him.

I. aitchisonii (BAKER) BOISS. 1882

TAXONOMIC COMMENTS. *I. aitchisonii* may be related to *I. cycloglossa* WENDELBO because of its elongated stem and the winged claw of the outer perigone segments, but the relationship is not very obvious.

GENERAL DISTRIBUTION. W Pakistan to extreme E Afghanistan.

MATERIAL INVESTIGATED. Representatives of one population originating from W Pakistan collected by Dr E. NASIR, Rawalpindi.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=34 (Fig. 3). m-chromosomes: One large pair (r=1.1), two medium-sized pairs (r=1.6) and five small unidentifiable pairs (r=1.1—1.4). sm—st-chromosomes: Seven pairs successively decreasing in length (r=2.4—3.5), and one pair with a satellite on the short arm. t-chromosomes: One small pair (r=11).

I. cycloglossa WENDELBO 1958

TAXONOMIC COMMENTS. This species occupies a somewhat isolated position taxonomically. According to WENDELBO & MATHEW (1975), several characters may be taken as primitive in this otherwise advanced group of *Iris,* and it may therefore be considered the most primitive species of the subgenus.

GENERAL DISTRIBUTION. Endemic to the province of Herat of W Afghanistan.

MATERIAL INVESTIGATED. Near the top of Kotal-e Mir Ali, 1680 m, HEDGE, WENDELBO & EKBERG 7727.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=28 (Fig. 3). m-chromosomes: One large pair (r=1.2). sm-chromosomes: One large (r=2.5) and one medium-sized pair (r=2.0). sm—t-chromosomes: Ten pairs successively decreasing in length (r=2.2—8.0), and one pair of st-chromosomes with a satellite on the short arm.

I. drepanophylla AITCH. & BAKER

TAXONOMIC COMMENTS. *I. drepanophylla* is closely related to *I. kopetdaghensis* (VVED.) WENDELBO & MATHEW and to *I. xanthochlora* WENDELBO.

GENERAL DISTRIBUTION. E Iran, Turkmenistan, Afghanistan.

MATERIAL INVESTIGATED. Representatives of one population from W Afghanistan, the province of Herat, 25.5 miles S of Herat. GREY-WILSON/HEWER 477.

CHROMOSOME NUMBER AND KARYOTYPE. A great number of metaphase plates, derived from several root tips, have been investigated and all have 2n=19 (Fig. 4). m-chromosomes: One large chromosome (r=1.3) apparently without any homologue, and four chromosomes successively decreasing in length (r=1.5, 1.6, 1.6. and 1.1 respectively). st-chromosomes: Five pairs successively decreasing in length (r=3.7—6.9), and one pair of st-chromosomes with a satellite on the short arm (r=4.0). t-chromosomes: One pair (r=8.5).

PREVIOUS REPORT. 2n=20 (BOCHANTSEVA 1966).

I. fosterana AITCH. & BAKER 1888

TAXONOMIC COMMENTS. This species occupies an isolated position and there is no obvious relationship to any other species.

GENERAL DISTRIBUTION. NE Iran, Turkmenistan and W Afghanistan.

MATERIAL INVESTIGATED. Seeds obtained from the Botanical Gardens of Ashkhabad in 1962.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=18 (Fig. 4). m-chromosomes: Five unidentifiable pairs successively decreasing in size (r=1.1—1.3). st-chromosomes: Three pairs (r=4.3—5.5) and one pair with a satellite on the short arm (r=5.0).

PREVIOUS REPORT. 2n=18 (ZAKHARYEVA & MAKUSHENKO 1969).

I. kopetdaghensis (VVED.) MATHEW & WENDELBO 1975

GENERAL DISTRIBUTION. NE Iran, Turkmenistan and Afghanistan.

MATERIAL INVESTIGATED. Seeds obtained from the Botanical Gardens of Ashkhabad in 1962.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=18 (Fig. 4). m-chromosomes: One large pair with satellite on the shortest arm (r=1.1), one medium-sized pair (r=1.2), and three small unidentifiable pairs (r=1.3—1.6). st-chromosomes: Three unidentifiable pairs (r=4.2—5.3), and one pair with a satellite on the short arm (r=3.1).

PREVIOUS REPORTS. 2n=18 (BOCHANTSEVA 1966), 2n=24 (ZAKHARYEVA & MAKUSHENKO 1969).

I. maracandica (VVED.) WENDELBO, comb. nov.

Basionym: *Juno maracandica* VVED. 1963, p. 426.

TAXONOMIC COMMENTS. This species seems to be most closely related to *I. orchioides* CARR., *I. pseudocaucasica* GROSSH. and *I. caucasica* HOFFM.

GENERAL DISTRIBUTION. Tadjikistan.

MATERIAL INVESTIGATED. Seeds obtained from the Botanical Gardens of Tashkent in 1962.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=20 (Fig. 4). m-chromosomes: One large pair (r=1.1), and three small pairs successively decreasing in length (r=1.1—1.4). sm-chromosomes: One large pair (r=2.7) and one small pair (r=2.0). st-chromosomes: One small pair (r=5.3), and two pairs with satellites on the short arm, of which one pair is large (r=5.4) and one small (r=5.0). t-chromosomes: One large pair (r=8.0).

I. microglossa WENDELBO 1958

TAXONOMIC COMMENTS. *I. microglossa* belongs to the species which have non-arillate seeds and a winged claw to the outer perigone segments (cf. p. 222). It is, however, a very characteristic plant which cannot directly be related to any of the other species of this group.

GENERAL DISTRIBUTION. Endemic to NE Afghanistan.

MATERIAL INVESTIGATED. The province of Kataghan, the north side of the Salang Pass, c. 2000 m, EKBERG & WENDELBO. The same locality as HEDGE, WENDELBO & EKBERG 7560.

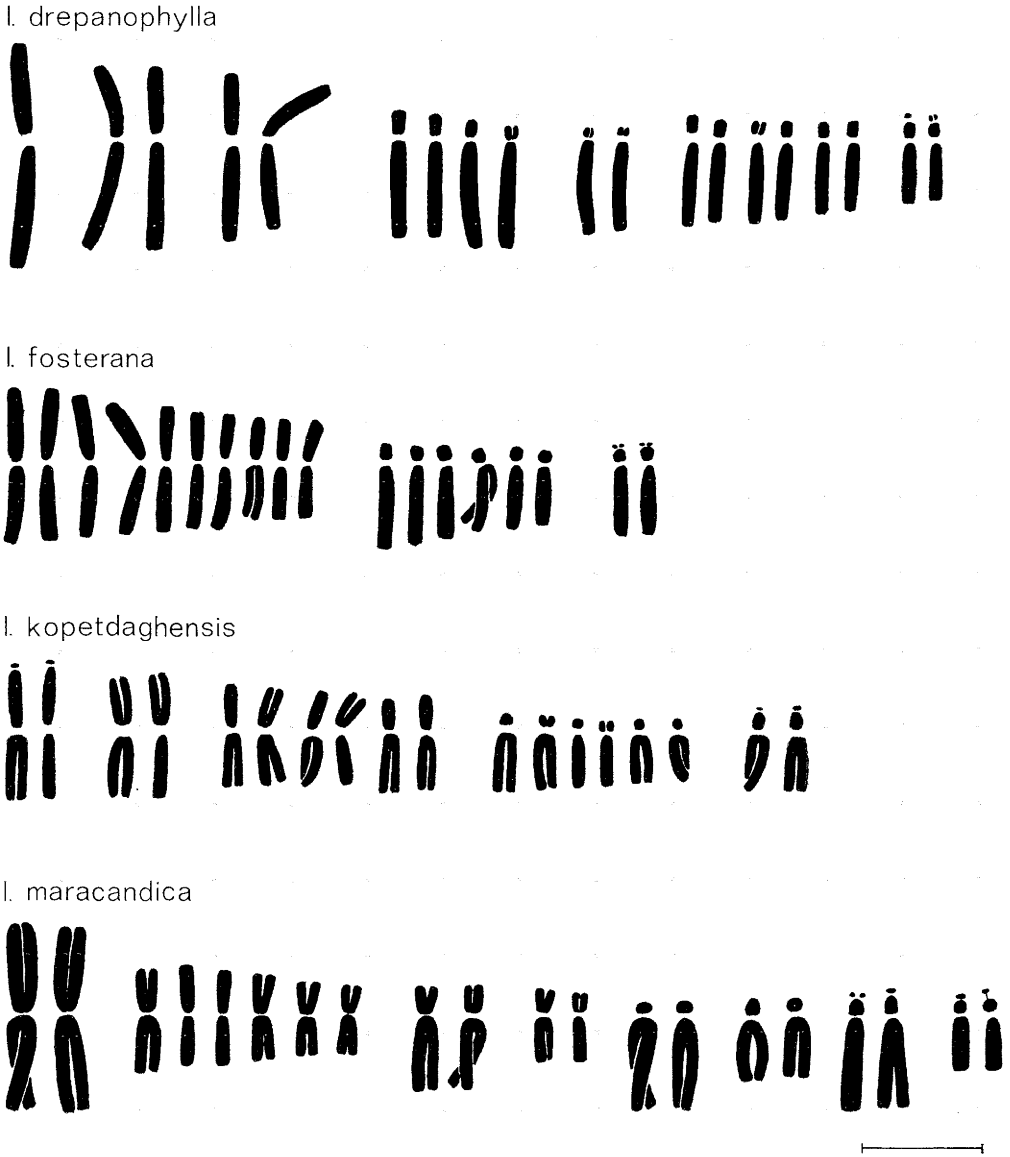

Fig. 4. Karyotypes of four species of subgenus *Scorpiris*, *I. drepanophylla* (2n=19), *I. fosterana* (2n=18), *I. kopetdaghensis* (2n=18) and *I. maracandica* (2n=20). The scale unit is equal to 5 μ.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=30 (Fig. 5). m-chromosomes: One large pair (r=1.5), and six pairs of small chromosomes about equal in length (r=1.1—1.3). sm—st-chromosomes: Eight pairs successively decreasing in length (r=2.8—6.5).

I. persica L. 1753

TAXONOMIC COMMENTS. *I. persica* is a very variable species, with a relatively large area of distribution, and both the taxonomy and nomenclature are rather confused. The material investigated belongs to the taxon described as *I. stenophylla* HAUSSKN. & SIEHE ex BAKER 1900.

GENERAL DISTRIBUTION. Turkey to N Iraq, Syria.

MATERIAL INVESTIGATED. S Turkey, W of Konya, RUNEMARK & WENDELBO 98 B.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=24 (Fig. 5). m-chromosomes: One large pair (r=1.6) and one medium-sized pair (r=1.1). sm—st-chromosomes: Ten pairs (r=2.3—6.9) of which two pairs are large, five pairs medium-sized and three pairs small.

PREVIOUS REPORTS. 2n=26 (SIMONET 1932, 1934, RANDOLPH 1934).

I. rosenbachiana REGEL 1884

TAXONOMIC COMMENTS. *I. rosenbachiana* is probably conspecific with *Juno nicolai* VVED. For further information see discussion in WENDELBO & MATHEW 1975.

GENERAL DISTRIBUTION. The U.S.S.R., Tadjikistan to NE Afghanistan.

MATERIAL INVESTIGATED. Seeds obtained from the Botanical Gardens of Tashkent in 1968. Determination controlled on flowering individuals in Göteborg.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=20 (Fig. 5). m-chromosomes: One large pair (r=1.5), one medium-sized pair (r=1.3), and one small pair (r=1.2). sm-chromosomes: Six unidentifiable pairs (r=1.7—2.2), and one large pair with a satellite on the short arm (r=2.4).

PREVIOUS REPORT. 2n=22 was determined for *Juno nicolai* VVED. by ZAKHARYEVA & MAKUSHENKO 1969.

I. xanthochlora WENDELBO 1969

TAXONOMIC COMMENTS. This species is closely related to *I. drepanophylla* and *I. kopetdaghensis*. It is confined to a small area just to the east of the distributional area of *I. kopetdaghensis*.

GENERAL DISTRIBUTION. Endemic to NE Afghanistan.

MATERIAL INVESTIGATED. The province of Kataghan, the north side of the Salang Pass, 2600 m, EKBERG & WENDELBO, the same locality as pressed material HEDGE, WENDELBO & EKBERG 8568.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=14 + 1B (Fig. 5). m-chromosomes: One large pair with a satellite on the short arm (r=1.5). m—sm-chromosomes: Four pairs successively decreasing in length (r=1.2—2.1). st-chromosomes: One pair with a small satellite and another pair with a minute satellite on the short arm (r=5.5 and 4.8 respectively). B-chromosome: 1.

DISCUSSION

Variation Within Subsect. Hexapogon

The species of this subsection are characterized by having 2 rarely 3 flowers, with falls and usually standards bearded by unicellular hairs, and by arillate seeds. Despite this rather strict morphological definition of the subsection the number of species included varies with different authors. Particularly, the taxonomic position of *I. humilis* GEORGI (=*I. flavissima* PALL., and *I. arenaria* WALDST. & KIT.), *I. falcifolia* BUNGE and *I. longiscapa* LEDEB. has been a matter for discussion. According to FEDTSCHENKO (1935) these species belong to sect. *Pogoniris* BAKER

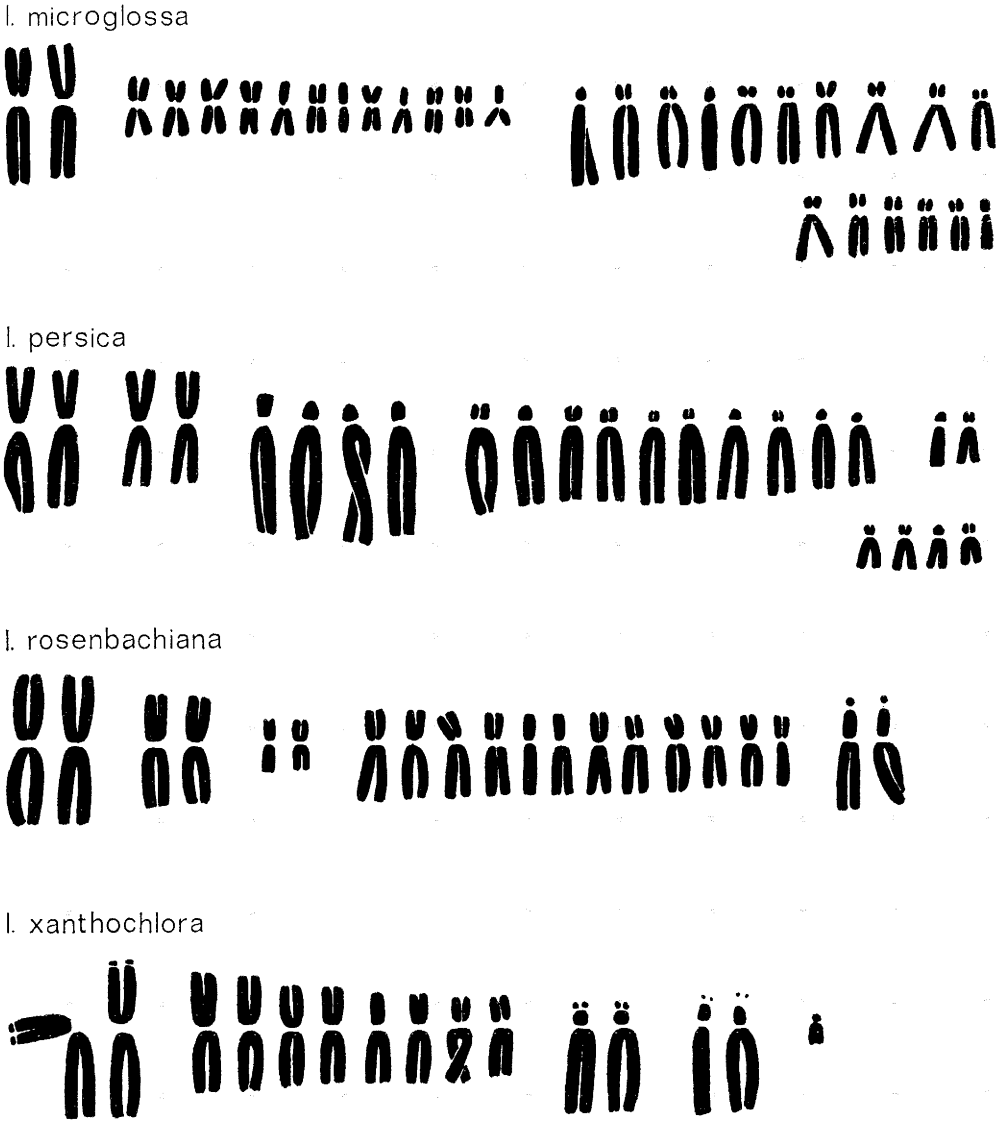

Fig. 5. Karyotypes of four species of subgenus *Scorpiris*, *I. microglossa* (2n=30), *I. persica* (2n=24), *I. rosenbachiana* (2n=20) and *I. xanthochlora* (2n=14+1 B). The scale unit is equal to 5 μ.

(now sect. *Iris*), but according to LAWRENCE (1953) they belong to subsect. *Hexapogon*.

The chromosomal differentiation is summarized in Table 1. *I. afghanica, I. heweri* and *I. korolkowii* seem to be closely related, they are all diploid (2n=22) and the chromosome complement comprises one pair of m-chromosomes, one pair of large st-chromosomes and nine pairs of st—t-

Table 1. A summary of karyotypes of species within sect. *Hexapogon* subsect. *Hexapogon*. Nomenclature of centromere position see p. 209; sat and non sat indicate chromosomes with and without satellites respectively.

Species	Number and type of chromosomes				2n	Author	Origin
	m	sm	st—t				
			non sat	sat			
I. afghanica WENDELBO	2	—	20	—	22	GUSTAFSSON & WENDELBO	Afghanistan
I. heweri GREY-WILSON & MATHEW	2	—	20	—	22	"	"
I. korolkowii REGEL	2	—	14	6	22	MITRA 1956	Unknown cultivated
I. korolkowii REGEL	2	—	18	2	22	GUSTAFSSON & WENDELBO	Afghanistan
I. korolkowii REGEL	2	—	20	—	22	"	"
I. hoogiana DYKES	4	—	34	6	44	MITRA 1956	Unknown cultivated
I. stolonifera MAXIM.	4	—	38	2	44	"	"
I. longiscapa LEDEB.	—	2	16	—	18	RANDOLPH & MITRA 1961	Turkmenistan

chromosomes. However, intra- as well as interspecific differences exist, although they are of a low magnitude. In *I. heweri* one pair of st-chromosomes has a relatively long short arm not observed in the other species. In *I. korolkowii* the number of pairs of satellited st-chromosomes varies from none to three. The two pairs of marker chromosomes seem to be similar in all the species (Fig. 6), except for population 918 of *I. korolkowii*. In this population structural changes have occurred in the m-chromosomes as well as in the st-chromosomes. Possibly a translocation is involved, but information from meiosis is needed before any conclusions can be drawn. The tetraploid species (2n=44) *I. hoogiana* DYKES and *I. stolonifera* MAXIM. show a close affinity to the other three species. The different types of chromosomes observed in *I. afghanica, I. heweri* and *I. korolkowii* seem to occur in quadruplicate (MITRA 1956). *I. hoogiana* only differs from *I. stolonifera* in having one pair of satellited m-chromosomes.

The karyotype of *I. humilis* differs from the previous species in having one small pair of m-chromosomes and two pairs of sm-chromosomes. This karyotype shows a close similarity to those observed within sect. *Iris*. Although some morphological traits, for instance arillate seeds, indicate affinity to species of subsect. *Hexapogon, I. humilis* and allied taxa are probably better accommodated in sect. *Iris*.

The karyotype and chromosome number of *I. longiscapa* deviate from the other species. It has 2n=18 and one small pair of sm-chromosomes and eight pairs of st—t-chromosomes (RANDOLPH & MITRA 1961).

The appearance of the karyotypes indicates that *I. afghanica, I. heweri, I. korolkowii, I. hoogiana* and *I. stolonifera* form a fairly uniform group distinguished from *I. longiscapa*. This difference is supported by other diversities, for instance

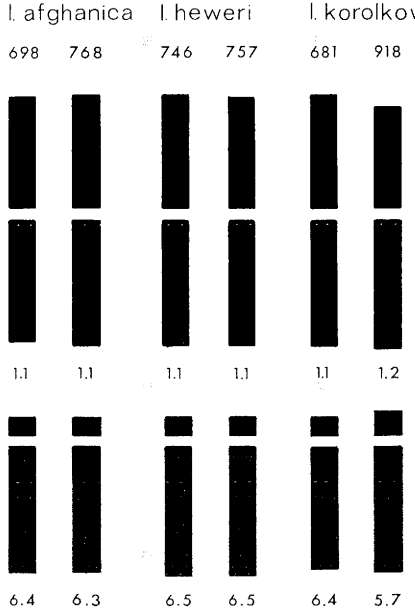

Fig. 6. Variation in two marker chromosomes in *I. afghanica* (populations 698 and 768), *I. heweri* (populations 746 and 757) and *I. korolkowii* (populations 681 and 918). The figures indicate r-values.

in habitat. *I. longiscapa* and the closely related *I. falcifolia* (not yet cytologically investigated) inhabit arid biotopes such as clayey deserts, rocks and sandy places. The other species grow at higher altitudes under less arid conditions. Despite these differences *I. longiscapa* and *I. falcifolia* probably belong to subsect. *Hexapogon*, but further information on morphological variation and cytology is highly desirable.

Variation Within Subsect. Oncocyclus

The number of species varies between 20 and 35 according to the author. The distinguishing characteristics of some of the species are insignificant and do not extend beyond differences in the colouration of the perigone segments. There are two main centra of evolution, one in Transcaucasus—NW Iran and one in Lebanon, Syria— SE Turkey.

The chromosome number of about 31 taxa has hitherto been determined (for references see FEDOROV 1969, and WEYMOUTH & CHAUDHARY 1974). All taxa have 2n=20 except *I. lupina* FOSTER (probably conspecific with *I. sari* SCHOTT in BAKER), which has the deviating number 2n=21 (SIMONET 1934). In all the species the chromosome complement seems to be exclusively represented by st—t-chromosomes. Four chromosome pairs are usually large, the other six medium-sized to small. The only deviation is population 700 of *I. acutiloba* ssp. *lineolata*, which has three large pairs instead of four. The number of pairs with a satellite varies from none to three and heterozygosity for satellites is known in some taxa, for instance in *I. susiana* L., *I. lortetii* BARB. (MITRA 1956) and in *I. acutiloba*. Very little is known about the degree of intraspecific variation as usually only a few individuals of single populations have been investigated. However, differences exist at least in *I. acutiloba* ssp. *lineolata*. In contradiction to WEYMOUTH & CHAUDHARY the present authors consider the interspecific differences to be small. It is necessary to investigate meiosis in artificially produced hybrids before any conclusions concerning relationships can be drawn.

Variation Within Subgenus Scorpiris

Scorpiris is distinguished from all other *Iris* groups in having the combination of bulb and canaliculate leaves. The pattern of morphological variation within *Scorpiris* is rather complicated and most of the species described are endemic to very small areas. The variation is most pronounced in characters such as development of stem, shape of outer and inner perigone segments, form of stylar branches, colour of flower and presence or

absence of aril on the seeds. At present the phylogenetic relationship is not quite clear, but three sections have been distinguished.

Sect. *Juno* is characterized by a bulb consisting of storage leaves, non-tuberculate pollen grains and non-arillate seeds. It comprises about 27 species distributed in SW and C Asia except the Mediterranean parts. To this section belong *I. aitchisonii, I. cycloglossa, I. fosterana, I. maracandica, I. microglossa* and *I. persica.*

Sect. *Physocaulon* (RODION.) MATHEW & WENDELBO is characterized by a bulb consisting of a swollen and persistent stem base and with few storage leaves only, non-tuberculate pollen grains and arillate seeds. It comprises about 11 species distributed in the central parts of Asia, for example *I. drepanophylla, I. kopetdaghensis, I. rosenbachiana* and *I. xanthochlora.*

Sect. *Acanthospora* RODION. (under the genus *Juno*). The bulb consists of storage leaves, pollen grains are tuberculate and it has non-arillate seeds. It comprises two species only, *I. planifolia* (MILLER) FIORI & PAOL. (syn. *I. alata* POIR.) and *I. palestina* BOISS. which are both Mediterranean in distribution. It is uncertain as to whether they deserve a section of their own or not.

The chromosome numbers of the species investigated within the different sections are summarized in Table 2. In sect. *Juno* 18 species have so far been investigated and the chromosome number varies considerably from 2n=18 (*I. caucasica* and *I. fosterana*) to 2n=50 (*I. albomarginata*). However about one half of the species have the chromosome number 2n=22. The aneuploid number 2n=21 has been observed within *I. willmottiana* M. FOSTER (SIMONET 1952). Intraspecific variation has been recorded within *I. caucasica* (2n=18, SIMONET 1932; 2n=22, BOCHANTSEVA 1966), within *I. orchioides* (2n=22, SIMONET 1930; RANDOLPH & MITRA 1956; 2n=30, BOCHANTSEVA 1966) and within *I. persica* (2n=24, present authors; 2n=26, SIMONET 1932; RANDOLPH 1934). In sect. *Physocaulon* the chromosome number of 4 species out of 11 has been determined and varies between 2n=14 (*I. xanthochlora*) and 2n=24 (*I. kopetdaghensis*). An aneuploid chromosome number has been observed in *I. drepanophylla* (2n=19; present authors). Intraspecific variation has been recorded within *I. kopetdaghensis* (2n=18, BOCHANTSEVA 1966; present authors; 2n=24, ZAKHARYEVA & MAKUSHENKO 1969) and in *I. rosenbachiana* (2n=20, present authors; 2n=22, ZAKHARYEVA & MAKUSHENKO 1969). In sect. *Acanthospora* the only species investigated, *I. planifolia,* has 2n=24 (SIMONET 1932). Thus, sections *Juno* and *Physocaulon* at least show a considerable variation in chromosome number, apparently without any relationship to the morphological variation.

The karyotypes, which are summarized in Table 3, show a similar pattern of variation. There seems to be little or no correlation between appearance of karyotype and morphological similarity. The karyotype of *I. rosenbachiana* most closely resembles that of *I. aitchisonii,* although the chromosome numbers differ and there are small differences in the karyotypes, but they represent different sections. The karyotype of *I. fosterana* most closely resembles that of *I. kopetdaghensis,* but they, too, belong to different sections. *I. kopetdaghensis* is undoubtedly related to *I. xanthochlora.* The karyotypes are similar, but the chromosome numbers differ.

Hybridization is reported to occur in sect. *Juno,* mainly between species with the same chromosome number (*I. narbuti* × *orchioides, I. narbuti* × *subdecolorata, I. bucharica* × *vicaria,* all having 2n=22, cf. FEDTSCHENKO 1935), but also between species with differing chromosome numbers (*I. narbuti,* 2n=22 × *maracandica,* 2n=20). Moreover, vegetatively vigorous plants of hybrid origin have been used for ornamental purposes, for example *I. warlsind* (*I. sindjarensis* × *warleyensis*) produced by the firm van Tubergen, Holland.

Table 2. Distribution of chromosome numbers in three sections of subgenus *Scorpiris*. a indicates the number of populations investigated and b the number of species investigated. Intraspecific variation has been observed in three species of sect. *Juno* and in two species of sect. *Physocaulon*, see page 222.

Section	2n												a	b
	14	18	19	20	21	22	24	26	28	30	34	50		
Juno	—	2	—	1	1	10	2	1	1	1	1	1	21	18
Physocaulon ...	1	1	1	1	—	1	1	—	—	—	—	—	6	4
Acanthospora ..	—	—	—	—	—	—	1	—	—	—	—	—	1	1

Obviously, the interspecific cytological differentiation as regards chromosome number and karyotype is not sufficiently large to prevent hybridization and the establishment of hybrid derivatives. Vegetative propagation of bulbs probably makes it possible for hybrids and plants with aneuploid chromosome numbers to become established in natural habitats.

The great morphological and cytological variation and differentiation within subgenus *Scorpiris* indicates that this group is in an active stage of evolution.

Chromosome Evolution Within the Genus Iris

The pattern of morphological variation seems to be similar in *Scorpiris, Hexapogon* and *Oncocyclus,* i.e. there is strong local differentiation. By contrast, the pattern of cytological variation differs entirely in *Scorpiris* and *Oncocyclus. Scorpiris* shows a wide variation in chromosome number and in the appearance of the karyotypes. All the species in subsect. *Oncocyclus* have the same chromosome number (2n=20) and the karyotypes of

Table 3. Karyotype differentiation within subgenus *Scorpiris*. The number of pairs belonging to each group is not noted, as transitions from m to sm, and sm to st-chromosomes are present. Nomenclature of centromere position see p. 209. sat and non sat indicate chromosomes with and without satellites respectively. The lengths of the chromosomes are abbreviated as follows: la=large, me=medium-sized, sm-small.

Species	Number and type of chromosome									
	2n	m			sm		st		t	
		non sat		sat	non sat	sat	non sat	sat	non sat	
		la	me—sm	la	la—sm	la—sm	la—sm	la—sm	la—sm	
I. aitchisonii	34	+	+	—	+	+	+	—	+	
I. cycloglossa	28	+	—	—	+	—	+	+	+	
I. drepanophylla	19	+	—	—	—	—	+	+	+	
I. fosterana	18	+	+	—	—	—	+	+	—	
I. kopetdaghensis	18	—	+	+	—	—	+	+	—	
I. maracandica	20	+	+	—	+	—	+	+	+	
I. microglossa	30	+	+	—	+	—	+	—	—	
I. persica	24	+	+	—	+	—	+	—	—	
I. rosenbachiana	20	+	+	—	+	+	—	—	—	
I. xanthochlora	14+1B	—	+	+	+	—	—	+	—	

species from the Middle East and Asia respectively seem to be similar. In subsect. *Hexapogon* the variation is approximately intermediate, a certain amount of variation is obvious in the chromosome number as well as in the karyotype, but it is not at all as pronounced as in *Scorpiris*.

Karyotypes of species of *Scorpiris* differ from those of species of *Hexapogon* and *Oncocyclus*. In all species of *Scorpiris* there is one pair of large m-chromosomes while the number of sm and st-chromosomes varies. Telocentric chromosomes seem to be rare in this group. All species of *Hexapogon*, except *I. longiscapa*, have one or two pairs of large m-chromosomes and of large st-chromosomes. In *Oncocyclus* all ten pairs are st—t-chromosomes, m—sm-chromosomes have not been observed at all. It is rather remarkable that this asymmetrical karyotype is found in all *Oncocyclus* species, as complements with a high proportion of stable t-chromosomes are rare in higher plants. The most extreme karyotypes in this respect have been observed in *Welwitschia mirabilis* (KHOSHOO & AHUJA 1963) and in *Tradescantia micrantha* (JONES & COLDEN 1968) where all the chromosomes are telocentric. In addition, a large proportion of st—t-chromosomes has been found in the genera *Ginkgo* (LEE 1954), *Podocarpus* (HAIR & BEUZENBERG 1958), *Tripogandra* (JONES & COLDEN 1968) and *Goniolimon* (RUNEMARK 1974). Telocentric chromosomes may arise in two ways, by misdivision in the centromeric region of biarmed chromosomes, or by structural changes such as shifts, pericentric inversions and translocations. In subsect. *Oncocyclus* it seems less probable that the t-chromosomes have arisen by centromeric misdivision as at least five must have occurred. Moreover, the successive transition from st to t-chromosomes in *Oncocyclus* and the presence of such chromosomes in other *Iris*-groups indicate that they have arisen by some types of chromosomal rearrangements.

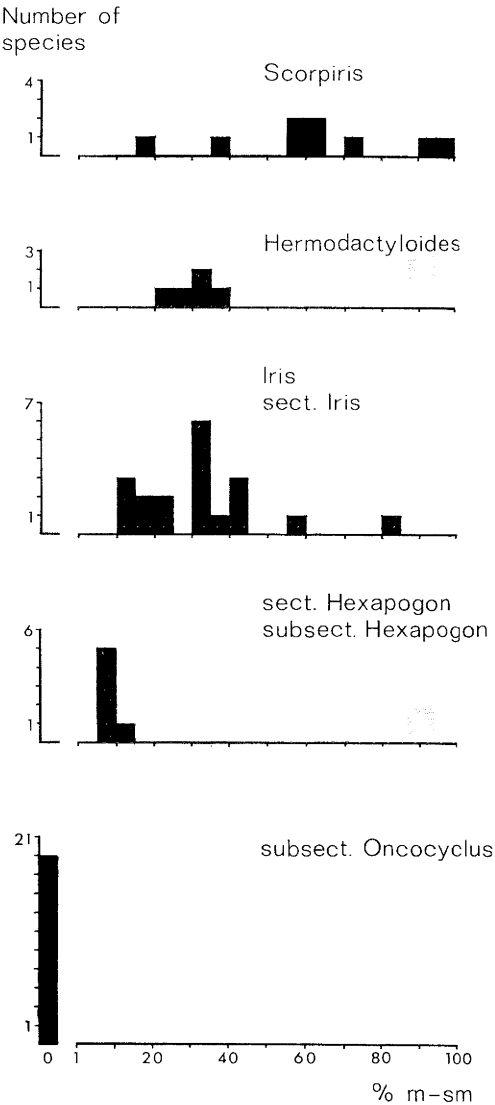

Fig. 7. The relative proportion of m—sm-chromosomes in species of subgenera *Scorpiris*, *Hermodactyloides* and *Iris*.

The relationship between plant phylogeny and symmetrical-asymmetrical karyotypes has been extensively discussed. It is generally considered that asymmetrical karyotypes have evolved from sym-

metrical ones (for references see SWANSON 1965, STEBBINS 1971), but reversals of this trend may occur (see JONES 1970). The relative proportion of m and sm-chromosomes in species of *Iris* subgenera *Scorpiris, Hermodactyloides* and *Iris* is summarized in Fig. 7. In *Scorpiris* the proportion of m—sm-chromosomes varies between 15 and 100 %, and in *Hermodactyloides* from 20 to 40 %. In subgenus *Iris* the frequency varies with the group. Species of sect. *Iris* show a variation from 10 to 85 %, subsect. *Hexapogon* from 5 to 15 %, and in subsect. *Oncocyclus* no m—sm-chromosomes are present at all. Thus *Iris* species belonging to sect. *Iris,* like those of *Scorpiris* and *Hermodactyloides,* show a more or less symmetrical karyotype, while the asymmetrical karyotype is most pronounced in subsect. *Oncocyclus.* In *Iris,* a too limited amount of information is available for certain conclusions concerning the direction of chromosome evolution. But species of subsect. *Oncocyclus* show some advanced morphological features in addition to the asymmetrical karyotype, for instance reduced number of flowers and arillate seeds.

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A Study of Cachrys Populations in Israel and Its Application to Generic Delimitation

Ilana Herrnstadt and Chaia C. Heyn

HERRNSTADT, I. & HEYN, C. C. 1975 10 10. A study of Cachrys populations in Israel and its application to generic delimitation. — Bot. Notiser 128: 227—234. Lund. ISSN 0006-8195.

Sixteen local populations referred to either *Cachrys* L. or *Prangos* LINDL. (Umbelliferae) were studied in their natural habitats. In seven of these, 2n=66 (or n=33) was found. The characters examined included the suberization and wing development of fruit and other fruit and leaf characters. As a rule considerable intra- and interpopulational variation occurs in the majority of the characters including those used for generic delimitation. A study of fruit ontogenesis showed that the relative extent of suberized tissue and wing development may undergo considerable change during the maturation of the fruit. No correlation was found between any trend in fruit variation and the variation of leaf lobes. It is proposed to accept the pattern of continuous variation as being sufficient proof for including *Cachrys* L. and *Prangos* LINDL. in a single genus, and the plants from the populations investigated in a single species. For nomenclatural reasons this species must be called *Cachrys ferulacea* (L.) CALEST.

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The problematic status of *Cachrys* L. and *Prangos* LINDL. (Umbelliferae) has been previously discussed by us (HERRNSTADT & HEYN 1974). Though several authors, including the present ones, consider that the above genera comprise a single genus, no detailed reason for this has so far been published.

This study is an attempt to approach the problem of the generic delimitation of *Cachrys* and *Prangos* by examining populations of plants described as belonging to one of the genera in Israel.

The extent of the confusion prevailing between *Cachrys* and *Prangos* is reflected in the names of the species recorded from the region investigated: BOISSIER (1872) described *Cachrys goniocarpa* from "circa Asdod (=Ashdod) et Ramlah (=Ramla)". POST (1932) also recorded the same species from Mt Carmel, Sharon, Esdraelon (=Yizre'el Valley) and Safad, *Prangos asperula* from Gaza, the Galilee and Jerusalem and *P. asperula* var. *leiopetala* (POST 1896) from Gaza. As the diagnostic characters for these three taxa he used the degree of the development of ridges on the fruit and the pubescence of petal surface. RECHINGER (1952) also records *C. goniocarpa* and adds two varieties to *P. asperula*: var. *stenoptera* BOISS. (Distr. Safed, Safad, Zefat — all refer to the same locality in different transcriptions) and var. *judaica* SAM. (from the Judean Mts — "el Kubab"). The characters used to define these taxa are again the extent of ridge development as well as the length and breadth of fruit (as compared with the length of pedicels). MOUTERDE (1953) added *C. goniocarpa* var. *asperifolia* as growing in the region concerned (having scabrid leaves in contrast with the smooth-leaved typical variety). ZOHARY (1972),

Table 1. *Cachrys* populations studied.

	Population number and locality	Organs investigated: Leaves	Organs investigated: Fruit
	N Negev		
1	10 km W of Arad ..	+	+
2	Lahav (single plant)		+
3	Shoval (single plant)	+	
4	Qiryat Gat	+	+
	Shefela		
5	6 km N of Mashmia	+	+
6	Bet Hashmonai		+
7	Gilboa, N slopes	+	+
8	Lower Galilee, Migdal Ha'Emeq	+	+
9	Belvoir	+	+
10	Yizre'el Valley, Daverat	+	+
	Lower Galilee		
11	Kafr Kanna	+	+
12	Biq'at Bet Netofa ...	+	+
13	Golan Heights, Mevo Hamma	+	+
	Upper Galilee		
14	btw. Rosh Pinna & Zefat	+	+
15	Meron Junction	+	+
16	Har Almon		+

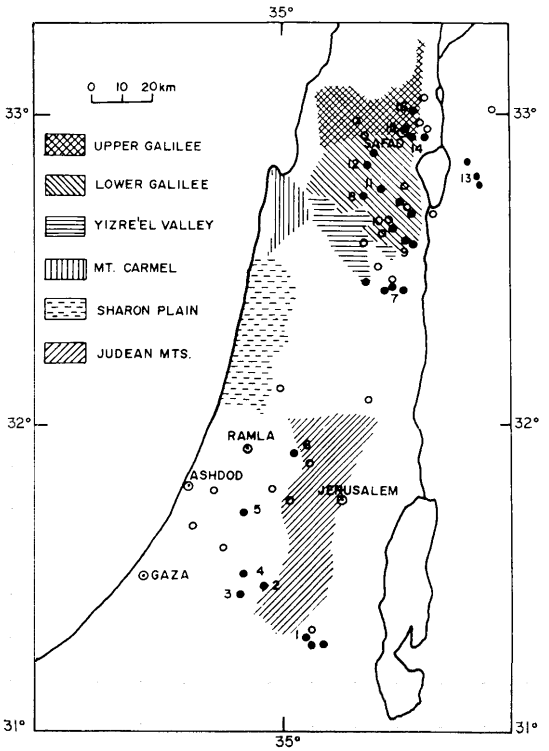


Fig. 1. Distribution of *Cachrys ferulacea* in Israel. Previous records from literature: regions — differentially shaded; localities — named. Dots represent single plants or populations investigated in this study (numbers correspond to those in Table 1); circles represent herbarium specimens.

who considers *Prangos* and *Cachrys* a single genus, records the following taxa: *P. asperula* as a very rare plant of the S Judean Desert and *P. goniocarpa* with a rare typical variety and the more widespread var. *stenoptera* with narrowly winged fruits. (See Fig. 1 for the above localities.)

MATERIAL AND METHODS

Plants of "*Cachrys*" and "*Prangos*" are fairly widespread in Israel and usually grow in small populations, at 150—500(— 800) m above sea level on diverse soils. They are tumble-weeds of fallow fields occurring mostly along the border of the Mediterranean and Irano-Turanian regions.

Sixteen populations were studied in their natural habitats (cf. Table 1 and Fig. 1). In each population about 5—15 plants were examined in the field; additional material was collected for documentation and further studies. Special attention was paid to individual plants with characters deviating from the normal. Most localities were visited twice a year, once in the early spring for a study of vegetative parts and flowers and again in summer for a study of fruits. As far as possible the same individuals were examined within each population for 3 consecutive years (1968—1971).

The following characters were investigated: size and shape of fruit (length/breadth), development of suberized mesocarp, fruit surface (obsoletely ribbed, distinctly ridged or

Fig. 2. Inter- and intrapopulational variation in fruit shape of *Cachrys ferulacea*; fruits in horizontal rows are from one population (numbers correspond to those in Table 1).

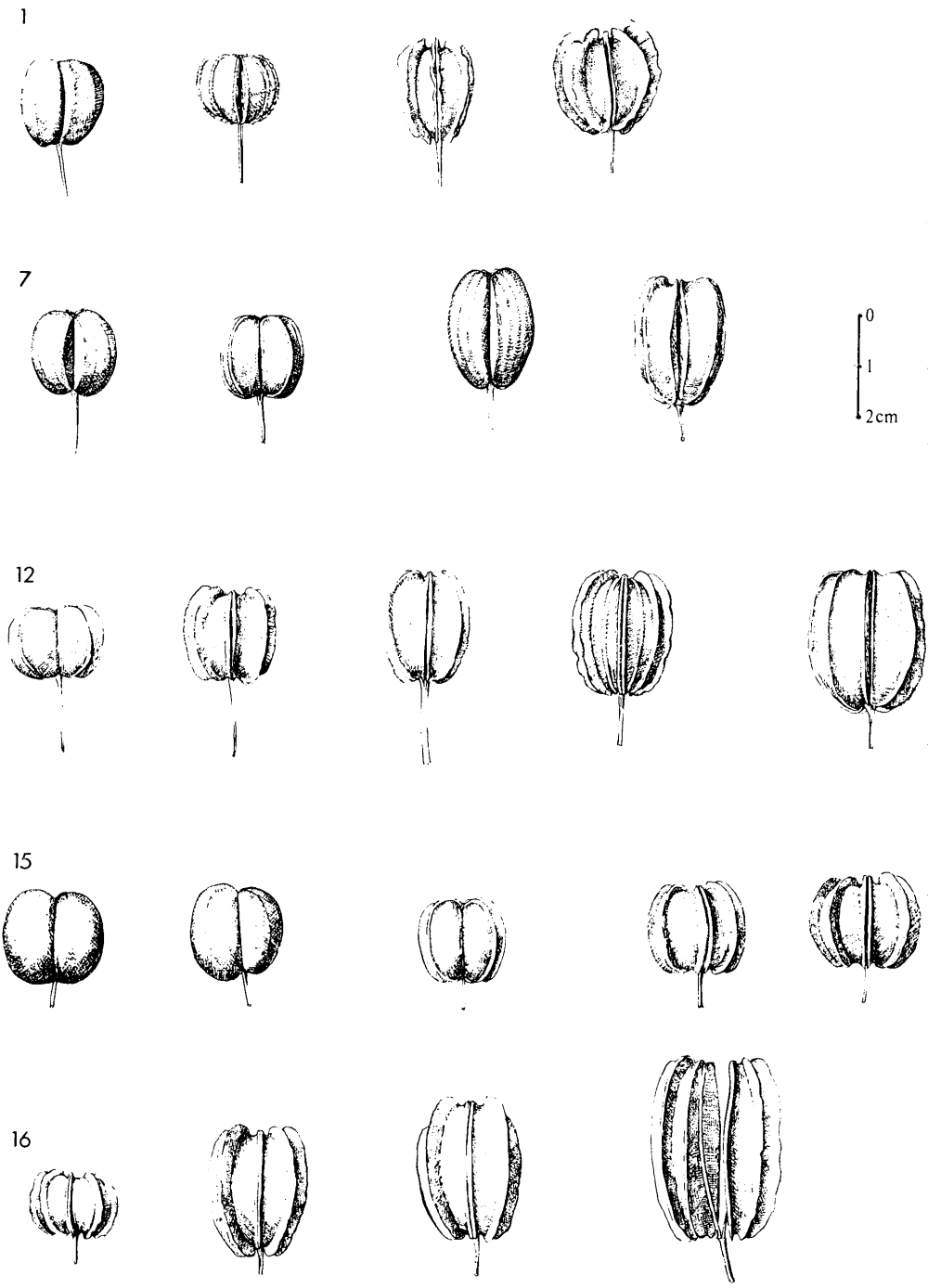


Fig. 2.

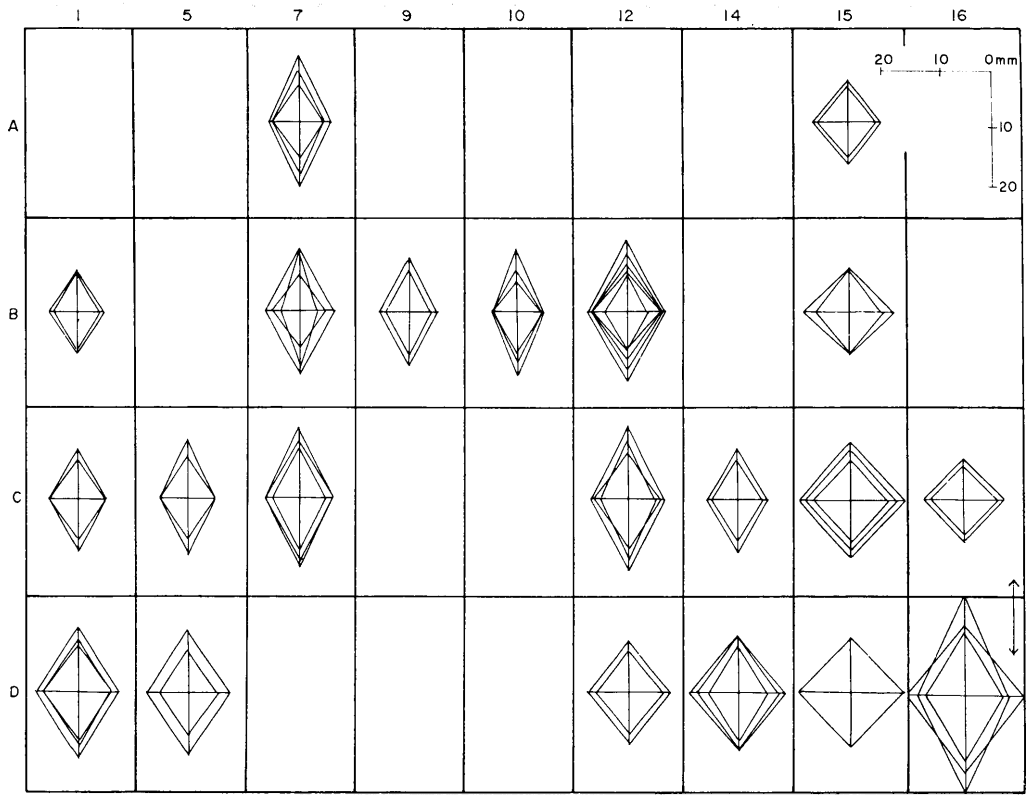


Fig. 3. Diagrammatic representation of inter- and intrapopulational variation in fruit shape of *Cachrys ferulacea*. Each vertical row represents one population (numbers as in Table 1); each horizontal row shows the extent of wing development. (A: Fruit smooth. B: With prominent ridges. C: With wings up to 1.5 mm wide. D: With wings 2—4 mm wide.) — In each square one to several fruits are represented by rhombs (horizontal diagonal shows width, vertical shows length).

winged), the length of the fruit in relation to the length of the pedicel; the size and indumentum of terminal leaf lobes.

Chromosomes were studied in seven populations. In four, mitotic metaphase was investigated in roots of seedlings pre-treated with paradichlorobenzene; squashes were made in 2 % aceto-orcein. In three populations meiosis in PMCs was studied in 2 % aceto carmine smears.

RESULTS

FRUIT. Many of the characters examined were found to be extremely variable within populations and between populations (Figs. 2 and 3).

In general populations differ greatly from one another in the size, shape and ridge development of the fruit. Also, whereas some populations are homogeneous in fruit shape (populations 7, 9, 10, 15), length (5, 9, 14, 15), ridge development (5, 9, 10, 14, 16) and suberization (5, 9, 10, 11, 14), others show remarkable heterogeneity of shape (1, 5, 12, 14, 16), length (1, 7, 10, 12, 16), ridge development (1, 7, 12, 15) and suberization (1, 7, 12, 15, 16).

Table 2. Range of variability of fruits in single plants. Each population is represented by one plant (as a rule the more variable plants were chosen in field studies). All measurements in mm.

Population number	Fruit length	Fruit, length/width ratio of extreme values	Width of ridges of fruit
1	15—22	1.8—2.1	0.25—1.5
2	10.5—17	1.1—1.6	0.25—0.75
4	10—16.5	1.2—1.4	0—0.25
6	11.5—21	1.6—1.9	0.25—0.75
7	16—25.5	2.0—2.3	0—0.75
8	(12) 16—21	1.5—1.6 (1.7)	0.25
9	15—25	1.6—2.6	0
10	14.5—19	1.8—2.2	0—0.25
11	12.5—23	1.2—1.4	0—0.5
12	13—19	1.2—2.0	0.25—0.5
13	17—22	1.6—1.8	0.5—1
14	13—20.5	1.3—1.5	0.25—1
15	11.5—19	1.2—1.5	0
15	12—25	1.1—1.4	0.75—2
16	20—36	1.9—2.1	0.5—2

The variation in fruit shape in single plants was studied in each population (usually over 100 fruits per plant). The characters measured were length, breadth and ridge development. Fruits of single plants show considerable variation in all characters mentioned and may represent the range of variability existing in the population as a whole (Table 2).

The relative amount of suberized tissue and the size of ridges or wings (=ridges over 1 mm wide) as compared with the whole fruit may gradually change during fruit ontogenesis and may reach a different degree of development in mature fruit (Fig. 4 A—C). Sometimes wings of the young fruit are somewhat undulate, straightening later (this may be the source of the records of *C. asperula* Boiss. from Israel).

The ratio fruit/peduncle was as a rule found to be most inconstant and therefore an unreliable character.

LEAVES. The size of leaves, of leaf segments and lobes is variable within and between populations. Some examples of the variation of leaf segments and lobes may be seen in Fig. 5. Fig. 6 is a diagrammatic representation of the length and width of leaf lobes of some plants within each of the populations studied.

Scabridity of leaves and other parts (assessed by the number of papillae per square unit) was found to be fairly constant within each population but varied greatly between populations.

CHROMOSOMES. The same chromosome number was found in seven populations examined: 2n=66 (populations 6, 10, 12, 16) (Fig. 4 D); n=33 (populations 9, 14, 15). Karyotypes seem to be identical according to a preliminary study.

CONCLUSIONS AND DISCUSSION

The characters studied by us are mainly those used for defining the genera *Cachrys* and *Prangos*, i. e., in the former, wingless strongly suberized fruit, in the latter, winged and only slightly suberized fruit. However, these characters were found to exhibit a wide range of variability in and between populations and no correlation between this variability and the variation

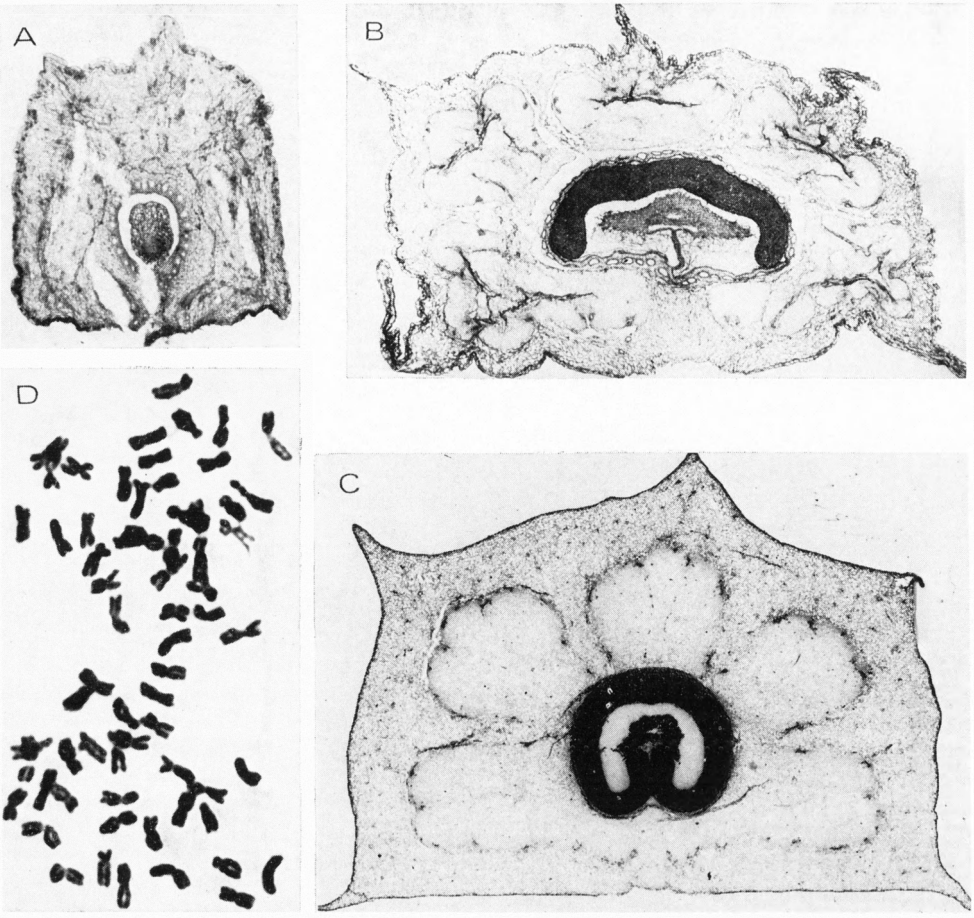
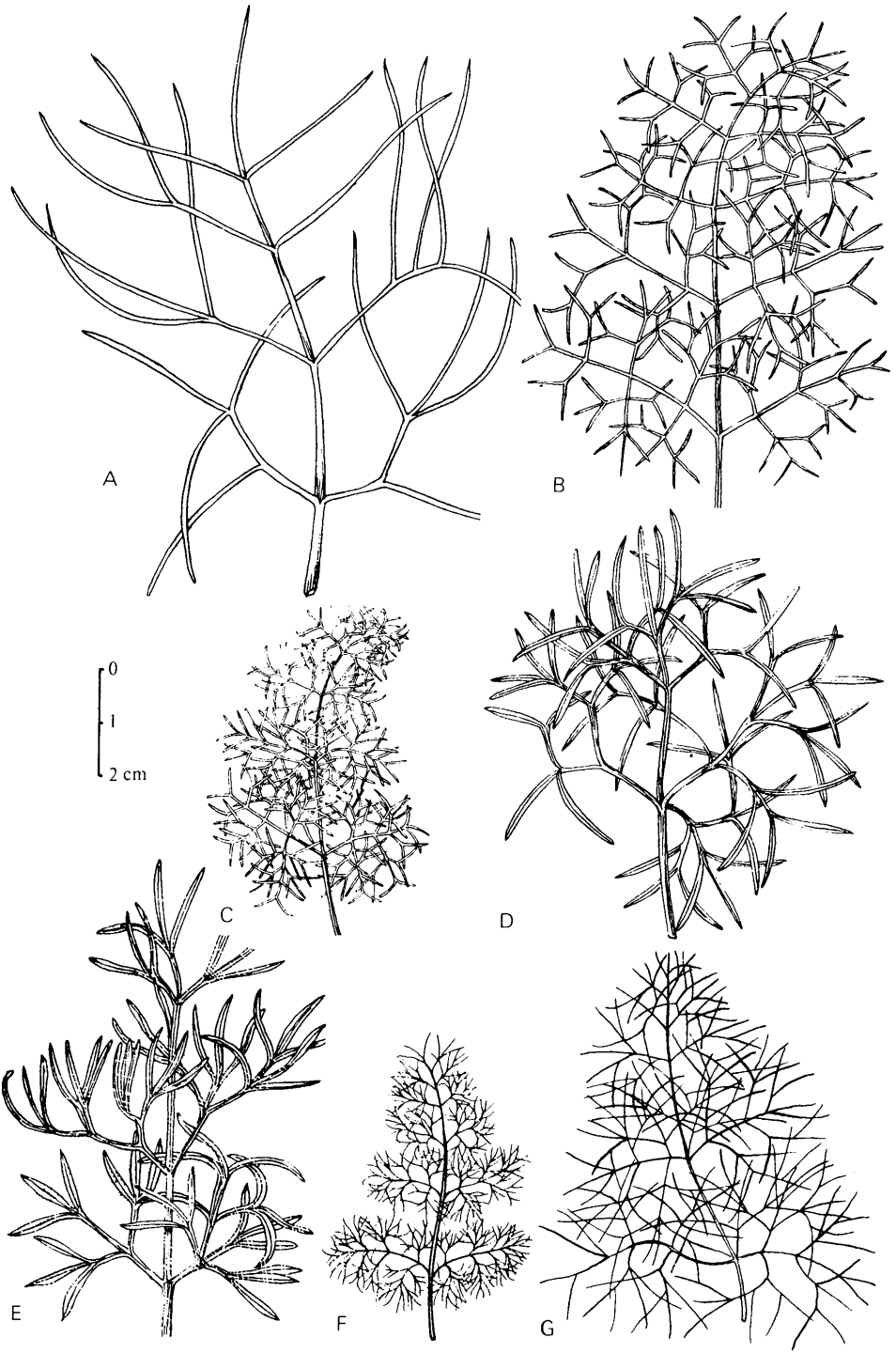


Fig. 4. A—C: Fruit ontogenesis in *Cachrys ferulacea* (cross-sections of one mericarp). A: × 19. B: × 9.5. C: × 7.5. — D: Chromosomes of metaphase plate in root tip mitosis. ca. × 1350. — A—C: population 5. D: population 10; numbers correspond to those in Table 1.

in length and breadth of leaf lobes could be observed. The fruit characters studied intergrade, they occur in diverse combinations within single populations and vary to some extent even between individual fruits of single plants. Therefore it does not seem reasonable to separate the two genera on the basis of these characters and because of priority the thus extended genus must be named *Cachrys* L. (cf. GRUENBERG-FERTIG et al. 1973).

Even more, because of the continuous variation in characters it seems that all plants examined must be regarded as part

Fig. 5. *Cachrys ferulacea*. Inter- and intrapopulational variation in leaf segments and lobes. — A, B: Population 7; C, D: Population 9; E, F: Population 1; G: Population 12. Numbers correspond to those in Table 1.


A
B
0
1
2 cm
C
D
E
F
G

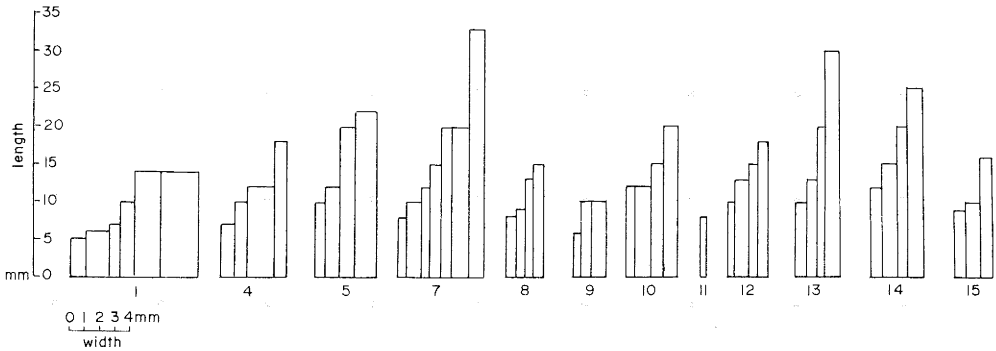


Fig. 6. *Cachrys ferulacea.* Diagrammatic representation of the variation in size of leaf lobes in and between populations; each column represents the longest terminal leaf lobe of one plant (population numbers correspond to those in Table 1).

of one species with a wide range of variation. (Such variation might be explained to some extent by the hexaploid level of the plants.) The earliest name available for this taxon is *C. ferulacea* (L.) CALEST. This species has a wide range of distribution — from Italy eastwards to Iran, Armenia and the Caucasus and throughout the eastern Mediterranean. All other species of "*Cachrys*" and "*Prangos*" previously recorded from Israel are to be referred to *C. ferulacea* and to be considered synonymous with it.

ACKNOWLEDGEMENTS

Thanks are due to Mrs E. HUBER for the drawings and to Mrs R. FRENKEL for the map and the diagrams.

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Asystasia laticapsula (Acanthaceae), a Widely Used but Previously Invalid Name

Per-Olof Karlström

KARLSTRÖM, P.-O. 1975 10 10. Asystasia laticapsula (Acanthaceae), a widely used but previously invalid name. — Bot. Notiser 128: 235—238. Lund. ISSN 0006-8195.

Asystasia laticapsula is described from tropical East Africa. The somatic chromosome number found is 2n=26.

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Asystasia laticapsula C. B. CL. ex KARLSTRÖM, sp. nov.

Herba perennis, usque ad 40 cm alta, basi decumbens, partes floriferae erectae. Planta omnis pilis multicellulosis uniseriatis praedita. *Folia* oblonga, pilosa, pili plerumque 8—10-cellulis praediti; lamina 3—7 cm longa, 1—2 cm lata, apice obtusa—subacuta, basi attenuata; petioli usque ad 3 mm longi, plerumque circiter 2 mm longi. *Inflorescentiae* axillares, racemosis instructae, usque ad 20 cm longae (pedunculo incluso), plerumque 6—8-floribus ornatae; bracteae minutae, lineares, usque ad 3 mm longae; pedicelli circiter 2 mm longi, ad basin bracteolis linearibus, circiter 2 mm longis, praediti. *Calyx* 5-partitus, pilis uniseriatis, cellulosis (4 cellulae) obtectus; segmenta calycis linearia, 8—13 mm longa, 1 mm lata. *Corolla* alba, lobus inferior prope faucem maculis violaceis ornatus; tubus circiter 15 mm longus, ad basin 2—3 mm latus, ad faucem gradatim dilatatus usque ad circiter 5 mm. *Stamina* 4; filamenta basi per paria usque 0,5 mm connata, breviora 4 mm longa, altiora 5 mm longa; antherae 3 mm longae. Granulae pollinis 3 poris instructae, 50—53 µm × 30—32 µm. *Ovarium* pilis uniseriatis obtectum; basis styli aeque pilosa. *Capsula* circiter 2 cm longa, pilis multicellulosis uniseriatis et pilis glandulosis instructa. *Semina* 4, 3—4 mm diametro, compressa, rugosa.

Perennial herb up to 40 cm high, decumbent at base, flowering parts erect. The whole plant covered with many-celled, uniseriate hairs. Leaves oblong with generally 8—10-celled, uniseriate hairs; laminae 3—7 cm long, 1—2 cm wide, obtuse to subacute at apex, narrowed at base into the very short petiole (Fig. 2 D); petioles up to 3 mm long, usually about 2 mm. Cystoliths common in stems and leaves, solitary, rounded or somewhat elongated, blunt at both ends. Inflorescences axillary, racemose, loose, up to 20 cm long (the lower flowerless part included), mostly 6—8-flowered; lower flowers remote. Bracts minute, linear, up to 3 mm long (Fig. 2 B). Pedicels about 2 mm long, with two linear bractlets about 2 mm long, near the base. Calyx divided to the base, segments 5, linear, 8—13 mm long, 1 mm wide, covered with 4-celled, uniseriate hairs (Fig. 2 B). Corolla white, lower lip with violet markings near the throat (Fig. 1 A, B); tube about 15 mm long, 2—3 mm wide near the base, expanding to about 5 mm at the throat. Stamens 4; filaments basally united in pairs (Fig. 2 E), shorter ones 4 mm long, longer ones 5 mm long; anthers 3 mm long. Pollen grains 3-porate, prolate, 50—53 µm×30—32 µm. Style base and ovary covered with uniseriate hairs (Fig. 2 C); ovary 2-celled with 2 ovules in each cell. Capsule 4-seeded, about 2 cm long (Fig. 2 F), with many-celled, uniseriate hairs and stalked glandular hairs. Seeds 3—4 mm in diameter, compressed, rugose (Fig. 2 G).

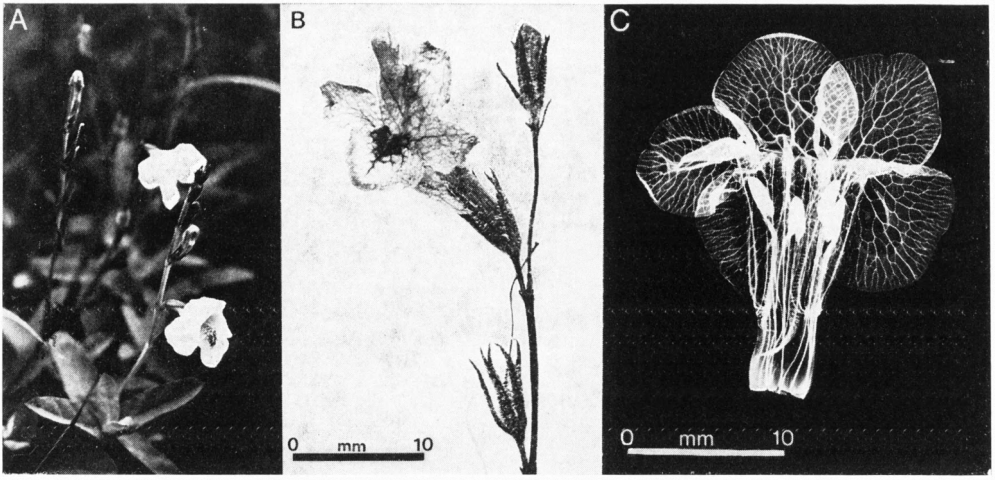

Fig. 1. *Asystasia laticapsula*. — A: Flowering specimen. Photo: P.-O. KARLSTRÖM, Ruiru, 16 km NE Nairobi 13.V. 1971. — B: Part of inflorescence (BALLY 356 a). Photo: D. NILSSON. — C: Corolla, showing the attachment of the stamens (KARLSTRÖM 371). Photo: D. NILSSON.

CHROMOSOME NUMBER. 2n=26. Counts were made in six cells, all from one plant.

TYPE COLLECTION. Kenya, "British East Africa", near Nairobi 1903 A. WHYTE s.n. (K; two sheets, one of which is the holotype).

FURTHER COLLECTIONS STUDIED. Kenya. ARCHER 204 (K), BALLY 356 a (K), BOGDAN 838 (K), ELLIOTT s.n. (K, mounted on the same sheet as one of WHYTE's specimens), GILLET 18108 (K), HINDORF 823 (K), KARLSTRÖM 306, 352, 356, 371 (GB), NAPIER 426 (K), NAPPER & ABDALLAH 1896 (K), STRID 4029 (GB), VERDCOURT 506 (K), VERDCOURT & POLHILL 3163 (K).

Asystasia laticapsula is a commonly used name for a species from tropical East Africa characterized among other things by oblong, hairy leaves, white corolla, and the lower lip of the corolla with violet markings near the throat. The specific epithet originates from a specimen collected by ALEXANDER WHYTE near Nairobi in 1903 and labelled "Asystasia laticapsula sp. nov. C. B. Cl. ms 17 Aug. 1901". (The date is probably incorrect, since another specimen collected by WHYTE near Nairobi in 1903 is labelled "Asystasia laticapsula sp. nov. C. B. Cl. ms 17 Aug. 1905".) The label bears the annotation "Close to A. coromandeliana Nees. Capsule broader, more hairy. Corolla smaller. Leaves more oblong and hairy". In a recently published flora of upland Kenya (AGNEW 1974) the species described above is included, and there is also a drawing of the species. The species is cited as "*Asystasia laticapsula* C. B. CL.". However CLARKE never published a description of the species. In order not to cause confusion I have chosen to use the specific epithet *laticapsula* since many botanists do so for the species described above.

All specimens studied originate from Kenya. According to Dr R. WINGFIELD, the university of Dar es Salaam, Tanzania, who is working on the "*Asystasia gangetica*" group in East Africa, *A. laticapsula* probably occurs throughout Tanzania above 550 m and probably in all surrounding countries (pers. comm.).

Fig. 2. *Asystasia laticapsula.* — A: Specimen grown under greenhouse conditions and taken from the same population as the specimen in Fig. 2 D. — B: Detail of inflorescence showing calyx, bracts and bractlets (KARLSTRÖM 356). — C: Gynoecium with hairy style base and ovary (KARLSTRÖM 371). — D: Specimen collected in the field in Kenya (KARLSTRÖM 371). — E: Corolla opened (corolla from the same specimen as in Fig. 2 A). — F: Ripe capsule (KARLSTRÖM 352). — G: Seed (KARLSTRÖM 352).

Specimens were collected by me in different grassland localities in Kenya during the period Dec. 1970—Jan. 1971 and in May 1971. The cuttings collected were grown at the Department of Systematic Botany, University of Göteborg. Compared with the collected specimens, these plants often had leaves that were more markedly oblong, had longer and wider laminae and longer petioles (Fig. 2 A). This is probably due to the favourable conditions in the greenhouse.

Cystoliths are common in the stems and leaves of *A. laticapsula*. They are solitary, rounded or somewhat elongated, blunt at both ends. This is in agreement with HOBEIN (1884), who studied the cystoliths in several species of the Acanthaceae, including some species of *Asystasia*.

Asystasia incl. *A. laticapsula* has been studied embryologically by KARLSTRÖM (1974).

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I am much indebted to Professor GUNNAR HARLING for the critical reading of the manuscript and to Dr UNO ELIASSON for fruitful discussions on taxonomy and terminology. The Latin diagnosis was written by Dr EMIN TENGSTRÖM. I greatly appreciate his kindness and help.

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Cytological Studies in the Macaronesian Genus Argyranthemum (Compositae: Anthemideae)

Christopher John Humphries

HUMPHRIES, C. J. 1975 10 10. Cytological studies in the Macaronesian genus Argyranthemum (Compositae: Anthemideae). — Bot. Notiser 128: 239—255. Lund. ISSN 0006-8195.

Seventeen species of *Argyranthemum* WEBB ex SCHULTZ BIP. from the Canary Islands and the Salvage Islands have been investigated cytologically. All taxa are diploid (x=9), except for a cultivated population of the natural hybrid *A. frutescens* (L. FIL.) SCHULTZ BIP. × *A. coronopifolium* (WILLD.) WEBB ex SCHULTZ BIP., which has a range of chromosome numbers between the diploid and tetraploid levels. Chromosome counts have been determined in 72 populations.

A general survey of chromosome morphology at mitosis is presented. Twenty-eight populations representing 12 species have been studied in detail and variation in two pairs of marker chromosomes is given. Differences are in no way correlated with recognised taxa but do vary significantly between populations. Details of pairing behaviour at meiosis are also given and chiasma frequency variation is discussed in the light of its adaptive significance.

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Since 1969 the author has been studying relationships in *Argyranthemum* WEBB ex SCHULTZ BIP., a woody perennial genus allied to *Chrysanthemum* L. s.str., endemic to the Macaronesian archipelagos of Madeira, the Salvage Islands and the Canary Islands.

The purpose of the work is partly to provide a taxonomic revision of the genus (HUMPHRIES 1973, 1975 in press), but principally to study problems of variation and evolution at the population level in one of the largest Macaronesian endemic genera. For this type of investigation, chromosome studies and crossing experiments have provided a wealth of valuable information for interpretation of the evolutionary situation in *Argyranthemum*.

This publication is the first of two papers on problems of adaptation in *Argyranthemum* and part of a wider study on the systematics of the Compositae: Anthemideae. In the present paper a general survey of chromosome number, chromosome morphology at mitosis, and pairing behaviour at meiosis in cultivated and natural populations of seventeen species of *Argyranthemum* will be given.

MATERIAL

The genus *Argyranthemum* consists of twenty-two allopatric species appearing in all of the principal vegetation zones of the northern Macaronesian archipelagos, except the Azores (HUMPHRIES 1973, 1975 in press). Apart from two relatively widespread species, *A. frutescens,* a polymorphic coastal and lowland species found on the islands of Tenerife, Gran Canaria and Gomera and *A. adauctum* (LINK) C. J. HUMPHRIES an upland species found in the pine forests and highlands of Gran Canaria, Tenerife and Hierro, the remaining species occur as distinct, isolated population groups on individual islands. The taxonomy and nomenclature follows that of HUMPHRIES (1975 in press).

The cultivated material was raised primarily from seed collected in the Canary Islands by Dr D. BRAMWELL and myself during the spring of 1971. Seed was also provided by Dr D. BRAMWELL, the late Dr E. R. SVENTENIUS, Mr G. KUNKEL and Miss LIV BORGEN from collections made by them during 1969, 1970 and 1971. Chromosome numbers have been determined in all populations and marker chromosomes from at least one or two populations of each taxon have been examined in detail. Pairing behaviour at meiosis has been studied in buds fixed in the field during 1971.

PREPARATORY TECHNIQUES

Mitotic preparations were made from root-tips of 3—12-month-old plants using monobromonaphtalene for pre-treatment, Feulgen and acetic orcein as stains. Meiotic preparations were stained with acetic orcein without prior fixation. Slides were made permanent by using the 'Arcton' (CF_2Cl_2) gas method.

CHROMOSOME MEASUREMENTS

For karyotype studies 10 good mitotic preparations showing about the same degree of chromosome contraction were selected from each plant. Usually 4—5 plants were studied in any one population. Drawings were made with the aid of a Zeiss camera lucida at a magnification of × 1600. Measurements were taken from the drawings, and the diagrams in Fig. 1 represent the karyotypes examined in detail. Photographs in Figs. 2 and 3 were taken on a Zeiss photomicroscope. The populations studied were all from Canary Islands taxa, apart from one sample of *Argyranthemum thalassophilum* from the Salvage Islands. No data for Maderian plants are available.

The definition of chromosome type is based upon the scheme devised by LEVAN et al. (1965), whereby the centromeric position is determined by calculating the r-index.

To show variation between populations, the ordinary r-index (long arm/short arm) and the l-index (haploid complement/length of the chromosome) were calculated for two marker chromosomes. The chromosomes with satellites (SAT-chromosomes) numbers 13, 14, 15 and 16 (Fig. 1) were easily identified and used for statistical calculations. The length of the satellite, but not of its connecting thread was added to the length of the short arm.

SOURCES OF ERROR IN THE DETERMINATION OF ARM RATIOS

During the preparation of root tip squashes for comparative studies at mitosis there are many occasions when artifacts may occur both mechanically and through the influence of chemical treatments (SYBENGA 1959, BOTHMER 1970, BENTZER et al. 1971), notably in the use of pre-treatment drugs for chromosome contraction. Mechanical difficulties usually arise from uneven squashing, causing stretching or constrictions of chromosome segments and poor separation of chromosomes causing overlapping, twisting and apparent shortening by vertical rises within the cell (LEWITSKY 1931, SYBENGA 1959, SIMAK 1962, BOTHMER 1970).

There are several reports on information regarding chemically induced contraction during the course of mitosis. SASAKI (1961) observed that long mammalian chromosomes for example, varied more in relative length than short ones under colchicine pre-treatments and thus had a distinct tendency for centralisation of the centromere in highly differentiated karyotypes. In groups with symmetrical karyotypes, such as *Argyranthemum* this effect is likely to be small and can be disregarded (BOTHMER 1970). BENTZER et al. (1971) indicated that the same applies with long chromosome arms versus short ones. SYBENGA (1959), working on the cereal grass *Secale,* observed that similar effects were achieved with a variety of different pre-treatments including 8-hydroxyquinoline and monobromonaphthalene.

In *Argyranthemum* identification of individual chromosomes is the worst problem so far encountered. In m-chromosomes with low r-values and no secondary constriction confusion between non-homologous arms and reversal of homologous chromosomes is unavoidable when the significant difference between overall arm lengths is less than 12—20 % (SIMAK 1962, MATERN & SIMAK 1968, BOTHMER 1970).

Table 1. Chromosome number reports in *Argyranthemum*.

Species	Present determinations		References for previous determinations
	Somatic 2n=18	Gametic n=9	
frutescens			
subsp. *frutescens*	×	×	Shimotomai 1937, Dowrick 1952, Tahara 1915, Harling 1951, Larsen 1960, Bramwell et al. 1971
subsp. *succulentum* ..		×	Larsen 1960, Borgen 1969, Bramwell et al. 1971
subsp. *gracilescens* ..	×	×	Borgen 1969, Bramwell et al. 1971
subsp. *parviflorum* ..	×	×	Larsen 1960
subsp. *foeniculaceum* .	×	×	Larsen 1960
subsp. *canariae*	×	×	
subsp. *pumilum*		×	
haouarytheum	×	×	Harling 1951, Bramwell et al. 1971
foeniculaceum	×	×	Larsen 1960, Borgen 1969, Bramwell et al. 1971
gracile	×	×	Harling 1951, Larsen 1960, Borgen 1969
tenerifae	×	×	Harling 1951, Linder & Lambert 1965 Larsen 1958, 1960, Borgen 1969, 1970, Bramwell et al. 1971
maderense	×	×	Larsen 1958, 1960, Borgen 1970
winteri		×	
lidii		×	
thalassophilum	×	×	
callichrysum	×	×	Bramwell et al. 1971, Borgen 1974
coronopifolium	×	×	Larsen 1960, Bramwell et al. 1971
broussonetii			
subsp. *broussonetii* ..	×	×	Larsen 1958, 1960, Borgen 1970
hierrense	×	×	
webbii		×	
filifolium	×	×	Shimotomai 1937, Dowrick 1952, Borgen 1970
escarrei		×	
adauctum			
subsp. *canariense* ...	×	×	Larsen 1960, Borgen 1969, Bramwell et al. 1971
subsp. *gracile*	×	×	Larsen 1960
subsp. *jacobaeifolium*		×	Borgen 1970
subsp. *dugourii*		×	
subsp. *adauctum*		×	Larsen 1960
subsp. *erythrocarpon* .		×	

In *Argyranthemum* virtually the whole karyotype consists of m-chromosomes (with r-values around 1) and the total complement has less than a 20 % difference between the largest and smallest chromosomes at any stage during contraction. Closer study of the whole karyotype is therefore impossible and detailed arm-ratio analysis has been restricted to the two pairs of chromosomes with secondary constrictions (Fig. 1; nos. 13—14, 15—16), the only ones to be positively identified in any preparation without fear of misidentification or reversal. Idiogram analysis to compare different taxa has not been carried out due to the difficulties outlined above, but samples of each examined species are presented to give an idea of the variation throughout the genus.

RESULTS

Chromosome Numbers

All species of *Argyranthemum* hitherto investigated from natural populations are diploid, with a basic number of x=9 and a somatic chromosome number of 2n=18 (TAHARA 1915, HARLING 1951, LARSEN 1958, 1960, BORGEN 1969, 1970, 1974). Table 1 shows the chromosome numbers determined by previous authors and the new counts resulting from this study.

During the course of this work new counts have been made for 6 species, 2 subspecies of *A. frutescens,* and 2 subspecies of *A. adauctum* and confirmed at least once in 10 of the remaining 16 species.

Sterile triploids have been reported for garden populations of *A. frutescens* (TAHARA 1915, DOWRICK 1952), a plant commonly known as the 'Paris Marguerite'. In the present study diploids have been found in all field population samples, but in F_2 and later generations cultivated from seed collected from a single population occurring in the wild of the hybrid between *A. coronopifolium* and *A. frutescens* subsp. *frutescens.* In this, the only example of natural interspecific hybridisation within the genus, plants with somatic numbers ranging from 18 to 36 were detected (HUMPHRIES 1973). It seems possible that disturbances during meiosis have given rise to unbalanced gametes in the hybrid plants, in turn giving rise to aneuploids, triploids and tetraploids. Moreover, individuals normally having 18 chromosomes in the complement have numbers of 19, 24, 27, 35, 36, and 37 in some root-tip cells. The triploid is shown in Fig. 2 A.

Chromosome Morphology

In *Argyranthemum* there is little apparent structural differentiation of the karyotype between the various species. The chromosomes are more or less symmetrically metacentric (m) or submetacentric (sm) (Fig. 1, 2 B, C). There is a small but continuous transition from the largest to the smallest chromosomes, and there are no chromosomes conspicuously larger or smaller than the others. In most cases the only chromosomes that can be identified with certainty are the SAT-pairs 13—14, 15—16 (Fig. 1). One exception is a pair of subterminal (st) chromosomes detected in *A. hierrense* (Fig. 1 N).

Most previous cytological reports of chromosome morphology in the Canary Islands species have mentioned the ocurrence of none, or only one pair of satellite chromosomes (DOWRICK 1952, LARSEN 1958, 1960, BORGEN 1969, 1970, 1974). This is not borne out by my results. Only the Salvage Islands species *A. thalassophilum,* reported here for the first time (Fig. 1 K), has been seen to have one pair of satellite chromosomes and in all other species two pairs are present.

The short arm and satellites of the non-homologous chromosome-pairs (13—14, 15—16) can usually be separated from one another as the long arm is consistently longer in chromosomes 13—14. Thus, a much higher r-value is obtained. In both pairs of chromosomes with secondary constrictions the satellites consist of a small distal body connected to the short arm by a thin thread. In chromosomes 15—16 the satellite is sometimes larger than the non-homologous satellites of chromosomes 13—14 and in good preparations of early metaphase with little contraction in the connecting thread, an interstitial body comparable to the 'tandem satellites' described by JONES & JOPLING (1972) can be seen (Fig. 2 B).

Chromosome Variation

To investigate the possibility of interpopulational chromosomal differences, 28 populations belonging to 12 different species were examined in respect of the r-index and l-index for the chromosome pair 15—16. Similar data were also obtained for the chromosome pair 13—14 in 21 populations of 6 different species.

Fig. 1. Karyotypes from root-tip mitoses in different species of *Argyranthemum*. — A: *A. frutescens* subsp. *frutescens* (70247). — B: *A. frutescens* subsp. *gracilescens* (71020). — C: *A. frutescens* subsp. *parviflorum* (71012). — D: *A. frutescens* subsp. *canariae* (71039). — E: *A. frutescens* subsp. *foeniculaceum* (71022). — F: *A. haouarytheum* (70266). — G: *A. foeniculaceum* (70036). — H: *A. gracile* (70227). — I: *A. maderense* (70076). — J: *A. callichrysum* (70284). — K: *A. thalassophilum* (71010). — L: *A. broussonetii* subsp. *broussonetii* (71030). — M: *A. coronopifolium* (70236). — N: *A. hierrense* (71006). — O: *A. filifolium* (71008). — P: *A. adauctum* subsp. *canariense* (71039). — Scale 10 µ.

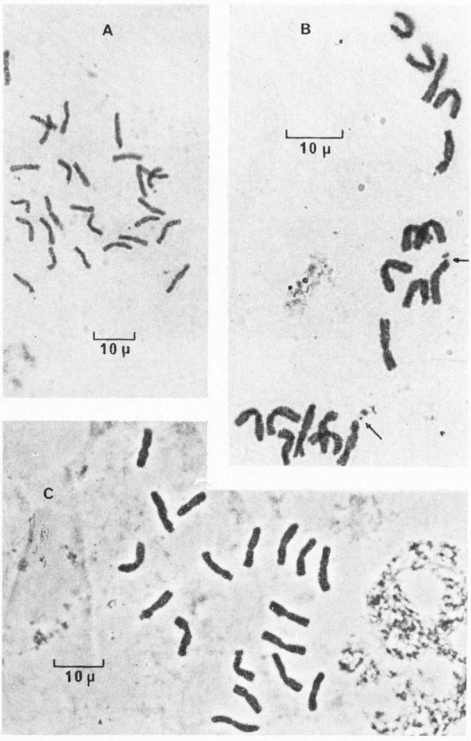

Fig. 2. Metaphases of root-tip mitoses in *Argyranthemum*. — A: Cultivated triploid progeny of the natural hybrid *A. frutescens*× *A. coronopifolium* (population 70237). — B: *A. frutescens* subsp. *frutescens* (population 70247). — C: *A. frutescens* subsp. *gracilescens* (population 71020). — Arrows refer to "tandem satellites" (see p. 242).

The data are presented in Table 2 and the t-values obtained by comparing mean values and standard deviations for homologous chromosomes measurements are presented in Figs. 3—6. In many cases it appears that the differences are statistically significant, from which several conclusions can be drawn:

1. There is a wider and more independent range of variation in the chromosome pair 15—16 for both the relative arm-length (r-index) and relative chromosome-length (l-index) than in chromosomes 13—14.

2. Variation in relative arm-length is greater than in relative chromosome-length for the same chromosome.

3. Populations 71013, 70223, 71021, 71039, 70224, 71030, 70238, 70240, 70236 and 70219 appear to be the most distinctive populations.

4. There tends to be greater variation between populations of different species than between populations of the same species. Thus, the ten populations of *A. frutescens* show fewer significant differences, than for example occur between the other populations listed in Figs. 3—6, which belong to different species.

Meiosis

Diakinesis and metaphase I were studied in 51 populations belonging to 15 species of Canary Islands *Argyranthemum*. The haploid number was invariably n=9 and several new counts confirming this chromosome number have been determined in the following taxa: *A. frutescens* subsp. *canariae*, *A. adauctum* subsp. *dugourii* and subsp. *erythrocarpon*, *A. winteri*, *A. lidii*, *A. hierrense*, *A. webbii* and *A. escarrei* (Table 1).

In most populations chromosome pairing is normal, with 9 bivalents being formed (Table 3). The chiasma position can be terminal, subterminal or median (Fig. 7 A, C).

Variation in Chiasma Frequency

There is good reason to suppose that adjustments in chiasma frequency at meiosis may have a direct adaptive significance (Rees & Ahmad 1963, Jones & Rees 1966, Crowley 1969, Rees & Dale 1974) as there is a strong correlation between chiasma position and genetic recombination (Darlington 1939). One expects, therefore, to find variation in chiasma frequency within and between populations of the same and different species exposed to different kinds of selection in different habitats as recombination

Table 2. r-index (relative arm length) and l-index (relative chromosome length) values for the homologous chromosome pairs 13—14 and 15—16 in twelve species of *Argyranthemum*. Means ± standard deviations.

Population number	Species	Chrom. 13—14		Chrom. 15—16	
		r-index	l-index	r-index	l-index
	frutescens				
70247	subsp. *frutescens*	2.46±0.54	9.4 ±0.95	1.98±0.5	9.98±0.2
70282	„	2.40±0.3	8.6 ±1.2	2.4 ±0.5	10.2 ±0.6
71013	„	2.78±0.5	8.85±0.86	2.6 ±0.57	9.95±0.4
70223	„	2.96±0.57	9.76±0.6	2.68±0.59	9.9 ±1.1
71031	subsp. *gracilescens*	3.36±0.95	8.92±0.89	2.29±0.67	9.48±0.96
71020	„	2.5 ±0.70	9.4 ±0.67	1.86±0.2	9.7 ±1.1
71021	„	2.75±0.3	9.1 ±0.28	2.74±0.2	10.2 ±0.1
71012	subsp. *parviflorum*	2.26±0.15	9.56±0.58	1.9 ±0.4	10.6 ±1.2
71022	subsp. *foeniculaceum* ...	2.74±0.38	8.78±1.26	2.26±0.28	10.46±0.9
71039	subsp. *canariae*	3.29±0.78	9.96±2.26	2.3 ±0.2	9.86±1.78
70266	*haouarytheum*	2.96±0.54	9.02±1.14	2.12±0.67	10.5 ±1.25
70267	„	2.74±0.6	8.66±1.3	1.64±0.39	10.84±0.74
70228	„	2.32±0.68	9.55±0.6	2.09±0.5	10.2 ±1.29
70036	*foeniculaceum*	—	—	1.72±0.59	8.95±0.87
70227	*gracile*	—	—	7.74±0.4	8.98±1.22
70076	*maderense*	—	—	1.8 ±0.38	8.3 ±0.58
71010	*thalassophilum*	—	—	2.4 ±0.7	8.95±1.57
70240	*callichrysum*	2.18±0.54	9.46±1.35	2.28±0.38	8.82±0.87
70284	„	2.19±0.66	9.67±1.3	2.55±0.58	9.28±1.13
70236	*coronopifolium*	2.5 ±0.7	9.82±1.8	2.46±0.85	9.14±0.7
70219	„	2.1 ±0.27	9.85±0.84	2.11±0.4	8.13±0.5
	broussonetii				
71030	subsp. *broussonetii*	2.63±0.69	10.0 ±1.1	3.05±0.4	9.58±0.54
70238	„	3.04±0.75	9.95±1.8	3.68±0.88	8.3 ±1.04
71042	„	2.18±0.79	10.24±1.5	1.85±0.4	8.95±1.25
71005	*hierrense*	—	—	1.57±0.36	9.17±1.57
71006	„	—	—	2.0 ±0.7	8.85±0.33
71008	*filifolium*	—	—	1.7 ±0.17	9.23±0.32
	adauctum				
70224	subsp. *canariense*	2.0 ±0.1	8.3 ±0.1	2.4 ±0.1	8.3 ±0.1

at meiosis in outbreeders is a major source of heritable variation. The survey has shown that indeed significant differences can be found and Table 3 gives a list of the chiasma frequencies for the populations studied in *Argyranthemum*. The results indicate that there is a wider range of chiasma frequencies for populations of widespread variable species (e.g. *A. frutescens* and *A. adauctum)* than for distinctive, less variable 'narrow' endemics of restricted distributions (e.g. *A. filifolium, A. lidii* and *A. escarrei*).

In virtually every plant in which meiosis was studied in detail the pollen mother cells showed a regular formation of bivalents at prophase and metaphase I. However, a single interchange has been detected in two populations of *Argyranthemum* (Table 3). Quadrivalents occur in 25 % of cells examined in plants from a large population of *A. frutescens* subsp. *frutescens* collected at Santa Ursula on Tenerife (Fig. 7 B) and a similar percentage of interchange heterozygotes was found in a large population of *A. adauctum*

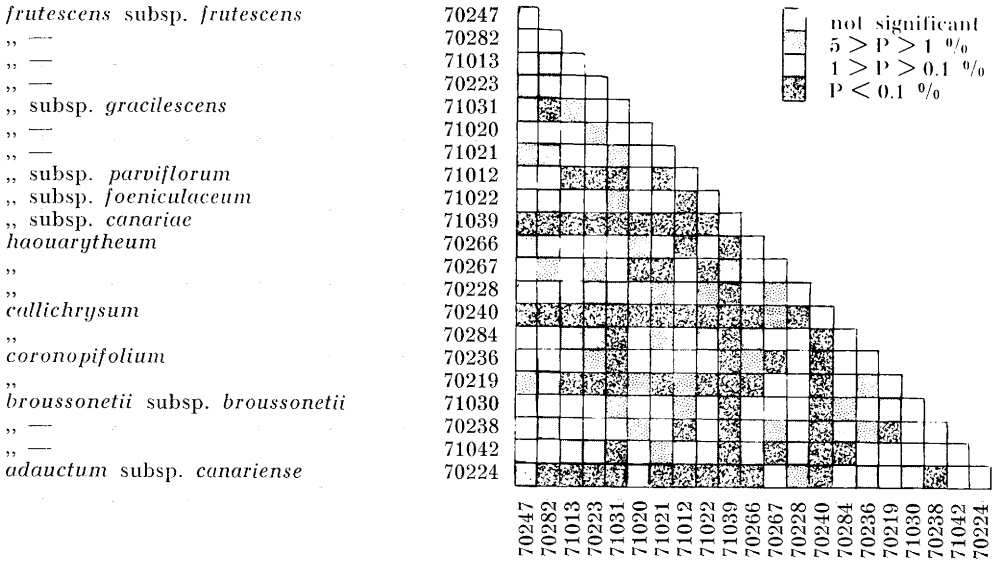

Fig. 3. Significant t-values obtained by comparing arm indices (r-index) for chromosomes no. 13—14 in 21 populations from 6 species of *Argyranthemum*.

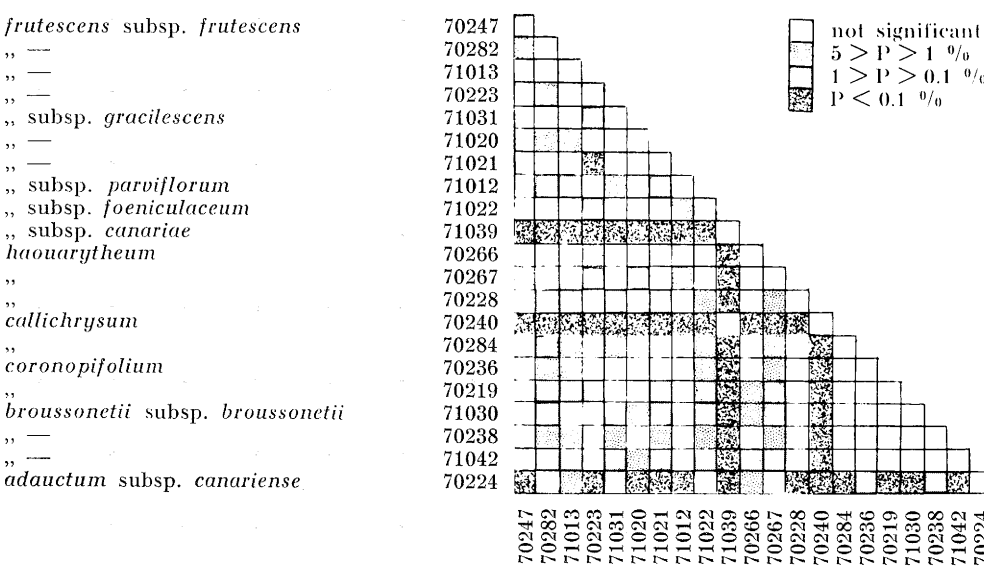

Fig. 4. Significant t-values obtained by comparing length indices (l-index) for chromosomes no. 13—14 in 21 populations from 6 species of *Argyranthemum*.

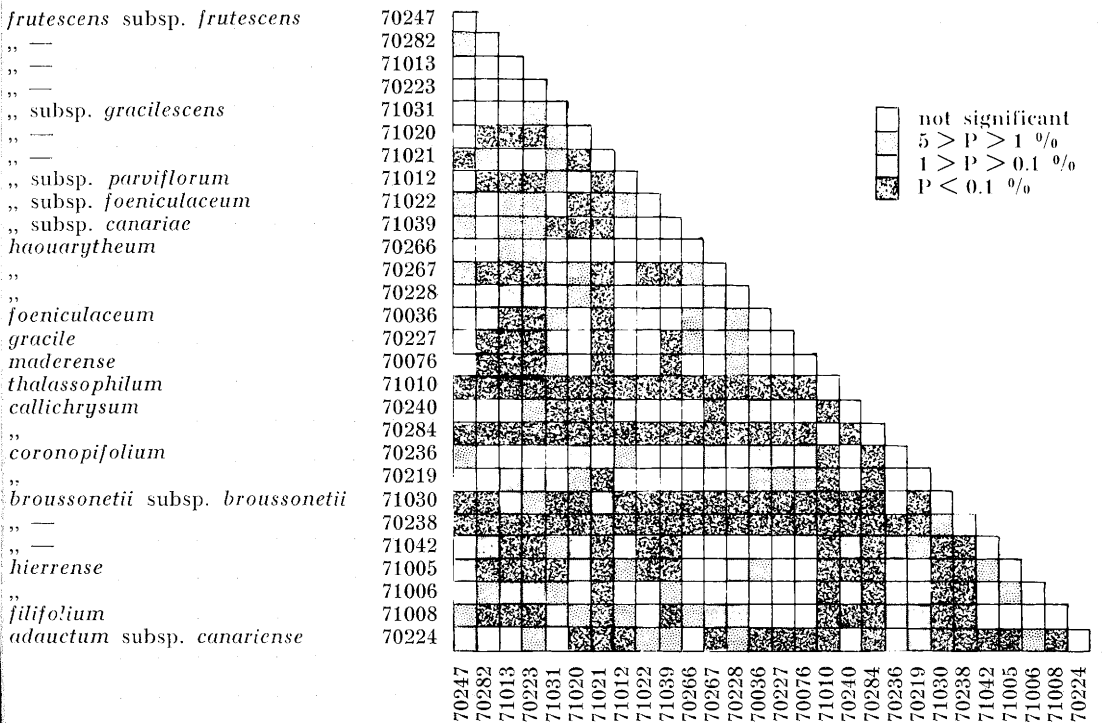

Fig. 5. Significant t-values obtained by comparing arm indices (r-index) for chromosomes 15—16 in 28 populations from 12 species of *Argyranthemum*.

subsp. *canariense* collected at Rincon de Teneguida on Gran Canaria. In both cases, the cells with quadrivalents had a reduced chiasma frequency but there was little overall effect on the recombination index (haploid chromosome number/number of chiasmata) for the whole population.

DISCUSSION

Chromosome Numbers

About 400 out of the approximate estimate of 1400 species of the Anthemideae are known cytologically with respect to chromosome numbers (Table 4). The basic number is invariably x=9 and variations from the diploid 2n=18 are known mostly in polyploid series and occasional aneuploids. There is a wide range of polyploid numbers in the tribal complex from the 2x (2n=18) to the 22x (2n=198) levels (DOWRICK 1952), the specific frequencies of which are shown in Table 4.

Although the Anthemideae are widely distributed throughout the temperate northern hemisphere and South Africa with few taxa outside these areas polyploid variation is restricted to two or three genera and closely associated with particular eco-geographical conditions and regional diversity. Undoubtedly, the widest range of variation is found in the genus *Leucanthemum*, with a centre of distribution in the central and southern European mountains and the western Mediterranean mountains of Morocco. In North Africa all members of the genus appear to be

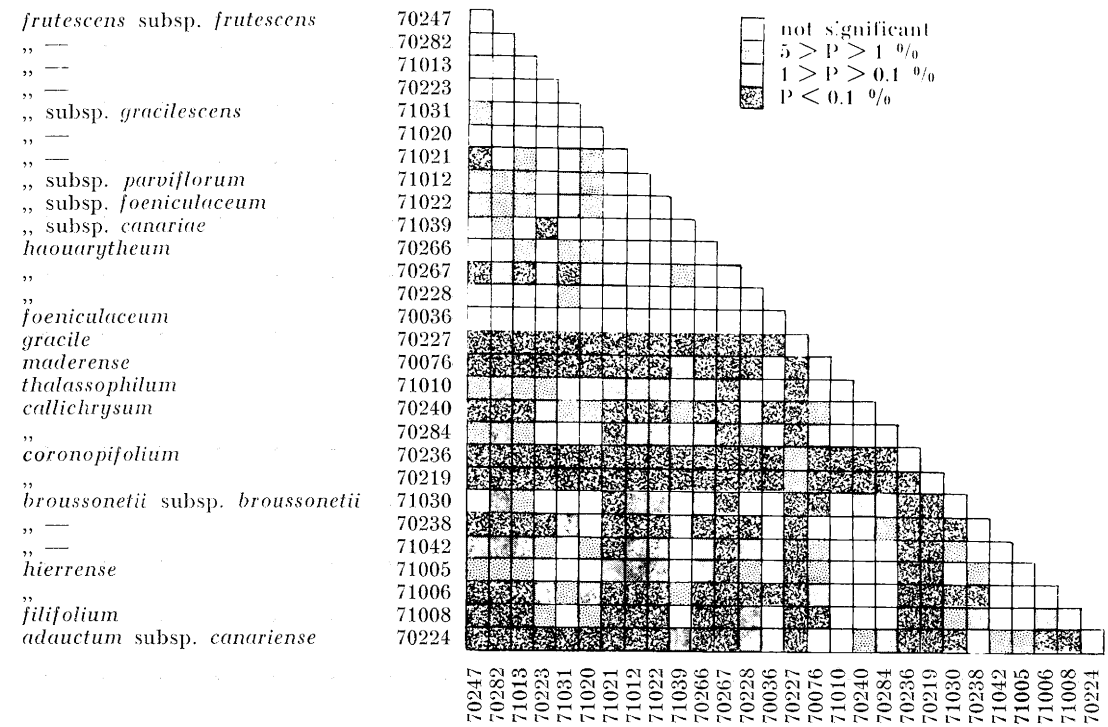

Fig. 6. Significant t-values obtained by comparing length indices (l-index) for chromosomes 15—16 in 28 populations from 12 species of *Argyranthemum*.

diploid but in Europe species exhibit a wide range of numbers between the diploid (2n=18) and decaploid (2n=90) levels (Baksay 1956, 1957, Böcher & Larsen 1957, Favarger 1959, Favarger & Villard 1965, Polatschek 1966, Villard 1970, Papeš 1972). The polyploid endemic species of *Dendranthema* of eastern China and Japan are also well known cytologically. In this region about 30 species have been examined and shown to have a range of ploidy levels between the diploid (2n=18) and the dodecaploid (2n=108) (Shimotomai 1932, 1933, 1937 a, b, 1938, Shimotomai & Takemoto 1939, Shimotomai et al. 1956, 1957, 1958, 1960, Tanaka 1959 a, b, c, Shimuzu 1962). Few high chromosome counts exist for genera in other areas of Anthemidean diversity and available reports seem to indicate that most taxa are either diploid (2n=18) or tetraploid (2n=36) (see Bolkovskikh et al. 1969, Moore 1973). In Macaronesia all taxa of the Chrysantheminae so far examined are diploid, apart from a single tetraploid population of *Tanacetum ptarmiciaeflorum* reported from Gran Canaria by Larsen (1960).

Chromosome Morphology

There have been numerous well documented examples of karyotype evolution (Babcock 1947, Lewitsky 1931, Smith 1964, Stebbins 1950). Stebbins (1971) showed that it is often quite possible to determine the morphological sequence of karyotype evolution by using the following

Table 3. Chiasma frequencies, mean number of chiasmata ($\bar{x}$), recombination indices (R. I.), and pairing configurations of chromosomes at diakinesis and metaphase I in field collections of 15 species of *Argyranthemum*. — N: number of cells studied.

Population	Species	Per cent chiasmata						$\bar{x}$	R.I.	Configuration	N
		14	15	16	17	18	19				
	frutescens										
3461	subsp. *frutescens*	—	—	—	10	90	—	17.9	1.99	9II	195
3275	„	—	12	—	24	64	—	17.5	1.94	9II	300
3282	„	—	—	—	25	75	—	17.9	1.99	9II	119
70282	„	—	—	40	15	15	30	20.1	2.24	9II (75 %) 1IV+7II (25 %)	700
DB320	„	—	—	—	—	50	50	18.5	2.08	9II	50
70223	„	—	—	—	20	60	—	18.2	2.03	9II	76
3376	subsp. *succulentum* ..	—	—	—	85	15	—	17.9	1.99	9II	80
70227	subsp. *gracilescens* ..	—	—	50	20	30	—	16.8	1.66	9II	142
70265	„	—	—	20	20	10	50	18.0	2.00	9II	225
3179	„	—	—	—	15	85	—	17.9	1.99	9II	133
3208	„	—	—	—	—	100	—	18.0	2.00	9II	175
3360	subsp. *parviflorum* ..	—	—	—	45	55	—	17.5	1.94	9II	40
3363	„	—	—	—	80	20	—	17.3	1.92	9II	138
3348	subsp. *foeniculaceum*	—	—	—	33	67	—	17.8	1.98	9II	150
3352	„	—	—	10	45	45	—	17.4	1.93	9II	124
3001	subsp. *canariae*	—	—	—	85	15	—	17.9	1.99	9II	254
3002	„	—	—	—	—	100	—	18.0	2.00	9II	250
3417	*haouarytheum*	—	—	—	25	75	—	17.9	1.99	9II	170
3429	„	—	—	—	15	75	10	18.0	2.00	9II	166
70036	*foeniculaceum*	—	—	30	40	30	—	17.0	1.88	9II	355
3262	„	—	—	—	—	100	—	18.0	2.00	9II	125
71017	„	—	—	—	—	100	—	18.0	2.00	9II	107
3252	*gracile*	—	—	—	15	85	—	17.9	1.99	9II	195
3260	„	—	—	10	—	90	—	17.9	1.99	9II	70
DB265	*tenerifae*	—	—	—	10	75	15	18.1	2.01	9II	65
71019	*winteri*	—	—	—	—	100	—	18.0	2.00	9II	13
3152	*lidii*	—	—	—	—	100	—	18.0	2.00	9II	23
70240	*callichrysum*	15	—	15	40	30	—	16.7	1.63	9II	44
70236	*coronopifolium*	—	—	—	—	100	—	18.0	2.00	9II	32
3382	*broussonetii*	—	—	—	10	90	—	17.9	1.99	9II	230
3364	„	—	—	—	40	60	—	17.6	1.95	9II	20
3323	*hierrense*	—	—	—	60	40	—	17.4	1.93	9II	12
3409	*webbii*	—	—	—	—	100	—	18.0	2.00	9II	72
3060	*filifolium*	—	—	—	40	60	—	17.6	1.95	9II	90
3081	„	—	—	—	—	100	—	18.0	2.00	9II	45
3077	*escarrei*	—	—	—	—	100	—	18.0	2.00	9II	45
	adauctum										
70224	subsp. *canariense* ...	20	40	30	10	—	—	15.3	1.70	9II	133
3007	„	8.5	58	25	8.5	—	—	14.8	1.60	9II	140
3008	„	—	—	—	30	70	—	17.6	1.95	9II	30
3009	„	—	10	20	40	20	10	17.0	1.88	9II (77 %) 1IV+7II (23 %)	165
3013	subsp. *gracile*	—	—	—	10	80	10	17.6	1.95	9II	112
3012	„	—	—	—	30	70	—	17.6	1.95	9II	64
3014	„	—	—	—	12.5	77.5	10	18.0	2.00	9II	340
3034	„	—	—	—	—	100	—	18.0	2.00	9II	25
3046	„	—	—	—	—	100	—	18.0	2.00	9II	34
3110	„	—	—	—	30	70	—	17.5	1.94	9II	24
3111	subsp. *jacobaeifolium*	—	—	—	10	90	—	17.9	1.99	9II	17
3386	subsp. *dugourii*	—	—	—	—	100	—	18.0	2.00	9II	90
3186	subsp. *adauctum*	—	—	5	30	60	5	17.6	1.95	9II	42
3190	„	—	—	—	25	75	—	17.7	1.96	9II	18
3309	subsp. *erythrocarpon*	—	—	—	10	90	—	17.9	1.99	9II	20

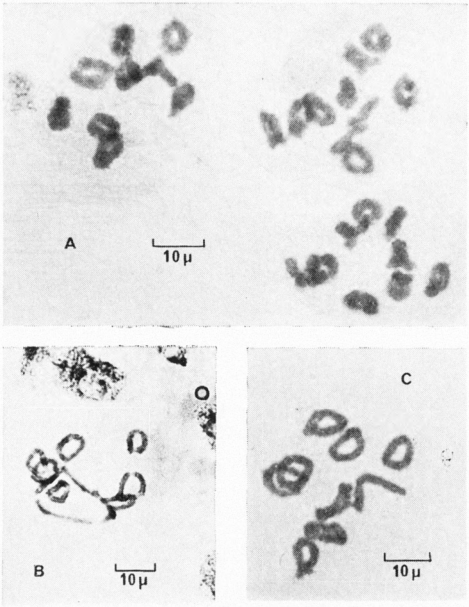

Fig. 7. A: Meiotic metaphase bivalents in *Argyranthemum tenerifae* (population DB265), showing variation in chiasma position. — B: A single terminal reciprocal translocation in chromosomes of *Argyranthemum frutescens* subsp. *frutescens* (population 70282). — C: Metaphase bivalents in *Argyranthemum filifolium* (population 3060).

criteria: (a) differences in the absolute size of chromosomes; (b) differences in centromere position (symmetry v. asymmetry); (c) differences in relative chromosome size; (d) differences in the basic number; and (e) differences in the number and position of satellites. In many plant groups, however, where there are only slight changes in the appearance of chromosomes, the significance of cytological differentiation can be very difficult to assess directly from morphological observation (Bothmer 1970, Jones 1970, Jones & Jopling 1972, Morley 1972).

The chromosomal variation in *Argyranthemum*, for example, has been shown to be due to slight differences in chromosome size and centromeric position. However, there is no discernible morphological sequence which can be interpreted as an evolutionary sequence, from one species to the next. Minute differences do occur but they may be of the same magnitude between different populations within a species as between different species in the genus. Thus, in a genus in which all taxa have a basically similar karyotype, adaptive gene sequences are presumably brought about by genic or slight structural cytological changes. These may be affected mechanically by erosion at the tips of chromosome arms (*A. hierrense*), by loss of satellites (*A. thalassophilum*), or by the translocation of small terminal segments which can only be detected at meiosis (*A. canariense* and *A. frutescens*). These processes may become rapidly fixed in a population by an outcrossing breeding system. Populations of *Argyranthemum* are normally strongly ecologically isolated from one another and hybrids between them rarely become established (Humphries 1973). There are always some phenotypic differences between adjacent populations which can be interpreted as the direct result of minute structural or genic changes.

Significant statistical differences in the karyotype between populations do tend

Table 4. Frequency of different chromosome numbers within the Anthemideae. Compiled from Bolkovskikh et al. 1969 and Moore 1973.

2n	18	27	36	54	72	90	108	198	Intraspecific polyploids	Aneuploids
No. of species	252	5	75	28	8	6	1	1	65	36

to be greater for populations of different species than for populations of the same species. However, it must be pointed out that such differences are not always necessarily significant cytologically. Normally there is no well defined specific variation which can be detected at mitosis except perhaps for *A. hierrense,* which has a single pair of subterminal (st) chromosomes, and *A. thalassophilum* which has only one pair of satellite (SAT) chromosomes.

Meiosis and the Breeding System

Studies of pairing behaviour at meiosis in natural populations of different species of *Argyranthemum* indicates that there is some genetic and cytological control of population variability. The principle effect of significant differences in chiasma frequency and hence adjustments in the degree of recombination is the regulation of extent and flow of variability within populations. DARLINGTON (1939) and MATHER (1943) postulated on theoretical grounds that a restriction of recombination to reduce variability, i.e. a low chiasma frequency, would be desirable for survival among short-lived ephemeral and annual plants. However, recently the totally opposite situation has been suggested for the agriculturally important grasses *Lolium, Festuca* and *Secale.* Investigations on these grasses by REES & AHMAD (1963), SUN & REES (1964), JONES & REES (1966), CROWLEY (1969) and REES & DALE (1974) have shown that a low chiasma frequency can be correlated with the perennial habit, and a high chiasma frequency predominates in annual populations. REES & AHMAD (1963) and CROWLEY (1969) suggest that the high chiasma frequencies in short-lived populations may compensate for reduced variability, although recently REES & DALE (1974), working on the assumption that chiasma frequencies are heritable in populations of different origins, argue that high chiasma frequencies are not the result of low genetic variability but are instead the cause of it. All species of *Argyranthemum* are perennial with some individuals known to survive to the age of ten or fifteen years (HUMPHRIES 1973) and so the observed variations in chiasma frequency cannot be explained in terms of an adaptation correlated with longevity. Species represented by a few populations and individuals with low overall variability (HUMPHRIES 1973), such as the Gran Canarian endemics *A. filifolium* and *A. lidii,* have an overall relatively high chiasma frequency when compared with more widespread taxa. Variable species such as *A. adauctum* and *A. frutescens,* both found in a number of different ecological conditions on three of the western Canary Islands, have much lower observed chiasma frequencies. The high chiasma frequency of the specialised endemic is presumably best explained as a compensatory device for depleted variability and in the more variable taxa as a conservation maintenance system preserving well adapted genotypes. Indeed the presence of a single translocation in the chromosomes of just two populations of *A. frutescens* and *A. adauctum* underlines the adaptive value of complex heterozygosity for survival in the Chrysantheminae (RANA & JAIN 1965, PARIA & PRADHAM 1972).

An added complication to this interpretation stems from the nature of the breeding system. Although all species of *Argyranthemum* so far examined show obvious characteristics for outbreeding, with heterogamous radiate capitula, exhibiting centripetalous floral maturation, they can also be self-compatible (HUMPHRIES 1973). Individuals can be found in most of the vegetation zones of the Macaronesian islands and it is highly likely that in pioneer situations self-fertilization will be the principal breeding system, rather than the exception. One would expect therefore in these situations for an increase in chiasma frequency as a response to increased homozygosity in the inbreeding plants. In conclusion it must be said that

there must be many factors which can effect the variability of populations and the ways in which they respond to different selective pressures. However, despite the lack of critical quantitative data on the precise modes of genetic flexibility and variability in *Argyranthemum,* it seems that variation in chiasma frequency is an effective method of controlling genetic and hence phenotypic expression in a diploid genus with species of a similar genomic constitution.

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APPENDIX

List of material investigated

Collecting data for population samples are as follows, and unless otherwise specified, collecting and cultivation numbers are those of HUMPHRIES and BRAMWELL, collected jointly in 1971.

Argyranthemum frutescens (L. FIL.) SCHULTZ BIP. subsp. *frutescens*: 70223, Tenerife, Teno, 1969, BRAMWELL; 70247, 70282, 71013, Tenerife, Santa Cruz, 1969, BRAMWELL; DB320, Tenerife, Casas de Teno Bajo, 25 m, 25.10. 1968, BRAMWELL; 3275, same locality, 5.4. 1971; 3282, Tenerife, El Fraile, 50 m, 5.4. 1971; 3461 Igueste de San Andrés, 200 m, 18.4. 1971.

A. frutescens subsp. *succulentum* C. J. HUMPHRIES: 3376, Tenerife, Playa del Roque, Taganana, 20 m, 9.4. 1971.

A. frutescens subsp. *gracilescens* (CHRIST.) C. J. HUMPHRIES: 71031 & 3178, Tenerife, between Sobradillo & Bco. Grande, 2.4. 1971; 70227 & 70265, Tenerife, Candelaria, 4.11. 1968, BRAMWELL; 3208, Tenerife, Bco. de Tamadaya, 600 m, 3.4. 1971.

A. frutescens subsp. *foeniculaceum* PITARD & PROUST: 71022 & 3348, Gomera, Bco. de Vallehermoso nr. El Puerto, 6.4. 1971; 3352, Gomera, 3 km W of Agulo nr. Las Rosas 500 m, 3.4. 1971.

A. frutescens subsp. *canariae* (CHRIST.) C. J. HUMPHRIES: 71039, Gran Canaria, nr. Banaderos, 15.3. 1970, BORGEN; 3001, Gran Canaria, San Felipé, 50 m, 17.3. 1971; 3002, same locality, 200 m, 17.3. 1971.

A. frutescens subsp. *pumilum* C. J. HUMPHRIES: 3155, 3169, Gran Canaria, Bco. Laya del Risco, 23.3. 1971.

A. haouarytheum C. J. HUMPHRIES & D. BRAMWELL: 70228, La Palma, La Cumbrecita, 9.6. 1969, BRAMWELL; 70266, La Palma, Pinar de Fuencaliente, 50 m, 9.6. 1969, BRAMWELL; 70267 & 3429, La Palma, Casa de Cumbrecita, 15.4. 1971; 3414, La Palma Heliño, between Fuencaliente and Los Llanos, 15.4. 1971, BRAMWELL; 3417, La Palma, Roque de Teneguia, 150 m, 15.4. 1971.

A. foeniculaceum (WILLD.) WEBB ex SCHULTZ BIP.: 70036, Tenerife, SVENTENIUS; DB390, Tenerife, Hoya de Malpais, 450 m, 1969, BRAMWELL; 71017, Tenerife, 1971, cult. ex Tafira Botanic Garden; 3262, Tenerife, El Retamar, 4.4 1971; 3469, Tenerife, Bco. del Masca, 19.4. 1971.

A. gracile SCHULTZ BIP.: 70227, Tenerife, Adeje, 11. 1968, BRAMWELL; 70288, Tenerife, Guimar, ex Jardin de Acclimatacion; 3252, Tenerife, Valle Seco, 600 m, 4.4. 1971; 3260, Tenerife, Tamaimo, Riscos de Malpais, 4.4. 1971.

A. tenerifae C. J. HUMPHRIES: DB265, Tenerife, Las Cañadas, El Portillo, 2000 m, 1969, BRAMWELL.

A. maderense (D. DON) C. J. HUMPHRIES: 70076, Lanzarote, Famara, 1969, BORGEN; DB1655, same locality, 300 m, 15.5. 1969, BRAMWELL.

A. winteri (SVENT.) C. J. HUMPHRIES: 71019, Fuerteventura, Handia (typus leg. SVENTENIUS) 1971, coll. ex Tafira Botanic Garden.

A. lidii C. J. HUMPHRIES: 3152, Gran Canaria, Anden verde between Agaëte and San Nicolas, 600 m, (typus).

A. thalassophilum (SVENT.) C. J. HUMPHRIES: 71010, Salvage Islands, Pico Grande, (SVENTENIUS) coll. ex Tafira Botanic Garden.

A. callichrysum (SVENT.) C. J. HUMPHRIES: 70240, Gomera, between Agando & Iguelero, 27.7. 1969, BRAMWELL; 70284, Gomera, Valle Exito, Cañada de Horchilla, Iguelero, SVENTENIUS.

A. coronopifolium (WILLD.) C. J. HUMPHRIES: 70219 and 70236, Tenerife, Buenavista, El Fraile, 6. 1969, BRAMWELL.

A. broussonetii (PERS.) C. J. HUMPHRIES subsp. *broussonetii:* 70238, Tenerife, Cumbre de Taganana, El Bailedero, 21.5. 1969, BRAMWELL; 71030 & 3382, Roque del Agua, 9.4. 1971; 71042, Tenerife, Monte Mercedes, 450 m, 24.3. 1970, BORGEN; 3364, Tenerife, Azano, 9.4. 1971.

A. hierrense C. J. HUMPHRIES: 71005, Hierro, Cuesta de Sabinosa, 150 m, 8.4. 1971; 71006, Hierro, Roques de Salmar, 9.4. 1971; 3323, Hierro, NW of Sabinosa, 9.4. 1971.

A. webbii SCHULTZ BIP.: 3409, La Palma, Bco. del Agua, 14.4. 1971.

A. filifolium (SCHULTZ BIP.) C. J. HUMPHRIES: 71008 & 3060, Gran Canaria, Arguiniguin, 250 m 21.3. 1971; 3081, Gran Canaria, 7 km N of Mogan, 21.3. 1971.

A. escarrei (SVENT.) C. J. HUMPHRIES: 3077, Gran Canaria, Bco. de Tasarte, 600 m, 21.3. 1971.

A. adauctum (LINK) C. J. HUMPHRIES subsp. *adauctum*: 3186, Tenerife, Mirador Ortuno 2.4. 1971; 3190, Tenerife Los Raices, Monte De Esperanza, 2.4. 1971.

A. adauctum subsp. *canariense* (SCHULTZ BIP.) C. J. HUMPHRIES: 70224, Gran Canaria, Lentiscal, 400 m, KUNKEL; 3008, Gran Canaria, 2 km S of San Mateo, 650 m, 17.3. 1971; 3009, Gran Canaria Rincon de Tenteniguada, 600 m, 19.3. 1971.

A. adauctum subsp. *gracile* (SCHULTZ BIP.) C. J. HUMPHRIES: 3012, Gran Canaria, Temisas, 900 m, 19.3. 1971; 3013, Gran Canaria, 1 km S of Santa Lucia de Tirajana, 19.3. 1971; 3014, Gran Canaria, San Bartolomé, 750—800 m, 19.3. 1971; 3034, Gran Canaria, 3 km N of Paso de la Plata, 19.3. 1971; 3046, Gran Canaria, below Fataga, 200 m, 21.3.

1971; 3110, Gran Canaria, Pinos de Tamadaba, 25.3. 1971.

A. adauctum subsp. *jacobaeifolium* (SCHULTZ BIP.) C. J. HUMPHRIES; 3111, Gran Canaria, 1350 m, Pine forest, 25.3. 1971.

A. adauctum subsp. *dugourii* (BOLLE) C. J. HUMPHRIES: 3386, Tenerife, El Retamar, 2300 m, 10.4. 1971.

A. adauctum subsp. *erythrocarpon* (SVENT.) C. J. HUMPHRIES: 3309, Hierro, La Frontera, 850 m, 7.3. 1971.

On the Size and Microstructure of Pollen Grains of Quercus robur and Q. petraea (Fagaceae)

Ulf Olsson

OLSSON, U. 1975 10 10. On the size and microstructure of pollen grains of Quercus robur and Q. petraea (Fagaceae). — Bot. Notiser 128: 256—264. Lund. ISSN 0006-8195.

The tricolpate pollen grains of *Q. petraea* and *Q. robur* are very similar in the structure of the exine and intine. All types described are to be found within all the species. The pollen dimensions (P, E) of polar and equatorial axes are greater in *Q. petraea* than in *Q. robur* but intraspecific variation is greater than interspecific. A wide or skewed distribution of the values of E sometimes exceeding the extremes of either species is indicative of the hybrid nature of an oak. This is also shown to be valid for two oaks with aberrant leaves (*Q. petraea* ×*robur* nm. *mespilifolia*).

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INTRODUCTION

Quercus petraea (MATTUSCHKA) LIEBL. and *Q. robur* L., subgenus *Lepidobalanus* (ENDL.) OERSTED have a wide distribution in Europe. The optimum ecological demands as regards habitat differ with the species (FRIES 1865, WEIMARCK 1947 a). However, the sessile and pedunculate oaks do exist as sympatric species resulting in hybrids and introgressive populations (COUSENS 1962, 1963, 1965; CARLISLE & BROWN 1965). This is also confirmed by the author, who has examined the population structure of oak woods in southern Sweden (OLSSON 1975 a).

The object of this investigation is to compare variation in pollen morphology in *Q. petraea* and *Q. robur* as well as in oaks which are presumed to be the spontaneous hybrid progeny of these species. In addition the characteristics of pollen grains of two oaks with aberrant leaf forms are noted (cf. OLSSON 1975 b).

The pollen morphology of *Q. petraea* and *Q. robur* has been described by ČERNJAVSKY (1935), ERDTMAN (1943), ERDTMAN et al. (1961), VAN CAMPO & ELHAI (1956), MONOSZON (1954, 1962) and PRAGLOWSKY (1962) who all used conventional light microscopy. VAN DER SPOEL-WALVIUS (1963) presents a description based on phase contrast microscopy. The *Quercus* species studied by him are subdivided into two groups on the basis of their pollen morphology. Thus *Q. petraea, Q. robur* and *Q. pubescens* WILLD. constitute one type according to the taxonomic subdivision made by SCHWARZ (1936—1939). This is also confirmed by SMIT (1973) in a scanning electron microscopic study of *Quercus* pollen grains. He combines six species to form a *robur* — *petraea* group but makes no attempt to subdivide this group further. PILCHER (1968) states "that the variation seen in the pollen of a single tree is so great that the differentiation of the two species in fossil material seems to be impossible". In another scanning electron microscopic examination of recent pollen grains DUPONT & DUPONT (1972) confirm this statement and note moreover the greater variability of *Q. robur* grains.

According to the present study of the exine and intine structures all types observed are to be found in *both* species. There is a statistically significant difference between the species as regards the length of the polar and equatorial pollen axes: the grains of the sessile oak are on the average larger, but the intraspecific variation may be the same as or greater than the interspecific one. Yet the distribution of these characters is of great value in detecting introgressive individuals. In a previous experimental study of *Linaria vulgaris* (L.) MILLER and *L. repens* (L.) MILLER the author has shown that, after repeated crossings, plants of the first filial generations in particular have a frequency distribution of biometric pollen values (P, E, P/E) which is markedly divergent from what is normal for either of the parent species (OLSSON 1975 c). The results of corresponding analyses of oak pollen support the assumed occurrence of hybrid individuals. These are presumed to be introgressives on the results of other morphological studies (OLSSON 1975 a).

MATERIAL AND METHODS

Light microscopy (LM) and scanning electron microscopy (SEM) have been used to study pollen grains of *Q. robur* and *Q. petraea* from localities in Bohuslän and Skåne in southern Sweden. Apart from pollen grains of the oaks mentioned the pollen types of two oaks with subentire leaves (*Q. petraea*× *robur* nm. *mespilifolia* (WALLR.) WEIM.) are described (vouchers, see Appendix).

Preparation Techniques

LM

The slides have been prepared by the Palynological Laboratory, Solna, Sweden and by the author following the method of acetolysis introduced by ERDTMAN (1960).

SEM

The instrument used was a Cambridge Stereoscan Mark II microscope (30 kV accelerating voltage; the specimen stage placed at 30—45° to the beam; Department of Zoology, University of Lund). The pollen grains were mounted on wax-coated (OLSSON 1975 c) specimen stubs, subsequently shadowed with gold/palladium (40/60). A couple of these preparations of pollen grains from the oak species concerned were treated with short beams of ruby laser radiation in order to get ruptured grains for the study of inner structures. This technique is described in a separate paper (OLSSON 1975 d).

RESULTS

Quercus petraea (MATTUSCHKA) LIEBL.

Pollen grains radially symmetrical, isopolar, 3-colpate, spheroidal-subprolate, 28×27 µ (cf. Table 1, $\bar{x}$ /P/, $\bar{x}$ /E/). Amb rounded triangular. Colpi rather narrow. Apocolpium about 9 µ. Exine 1.6—1.9 µ thick, stratification usually verrucose. Verruca often have microverrucae (Fig. 2 A, E). Other types may be found, such as semipsilate-pitted (Fig. 2 I a) or more or less verrucose-ornate (Fig. 2 I b, M). Inner side of intine striate-reticulate (Figs. 3, 4).

Quercus robur L.

Pollen grains radially symmetrical, isopolar, 3-colpate, spheroidal-subprolate, 27×26 µ (cf. Table 1). Exine, amb, colpi and apocolpium as in *Q. petraea*. However, of the verrucae types observed (Fig. 1 A, E, I, M), semipsilate-pitted areas with microverrucae between groups of larger verrucose processes are a more usual type of exine structure than that found in *Q. petraea*. Intine structure as in *Q. petraea* (illustrated in OLSSON 1975 d).

Introgressives

Structural and sculptural elements as in the parent species. The relative frequency distribution of different stratification types has not been considered. However, a comparison of P, E and P/E for the species and their spontaneous hybrid offspring is presented below.

Biometry

Survey of pollen samples from *Q. petraea, Q. robur,* their introgressives and

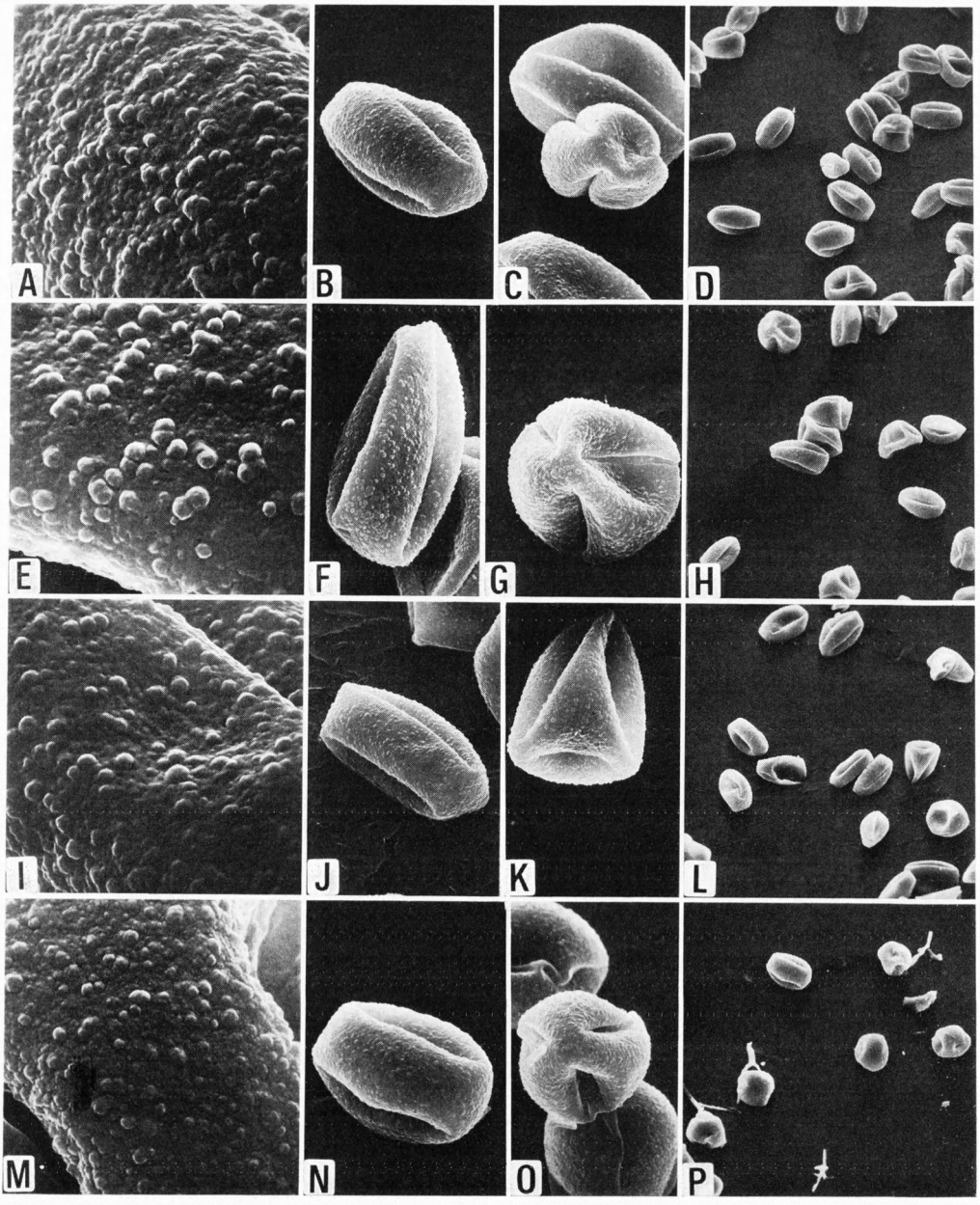

Fig. 1. *Quercus robur*. SE micrographs of pollen grains. — B, F, J, N: Lateral view of pollen grains showing the mesocolpium area (x 2,400). — A, E, I, M: Details of mesocolpium area, representative of the entire exine, showing the unevenly distributed verrucae of varying shapes. Between the groups of verrucae one can find areas of a semipsilate nature with very small processes and perforations (E, I), (x 12,000). — C, G, K, O: Pollen grains in polar view. Because of shrinkage the actual shape of the colpi is difficult to interpret (x 2,400). — D, H, L, P: Surveys of pollen grains from four oaks (x 600).

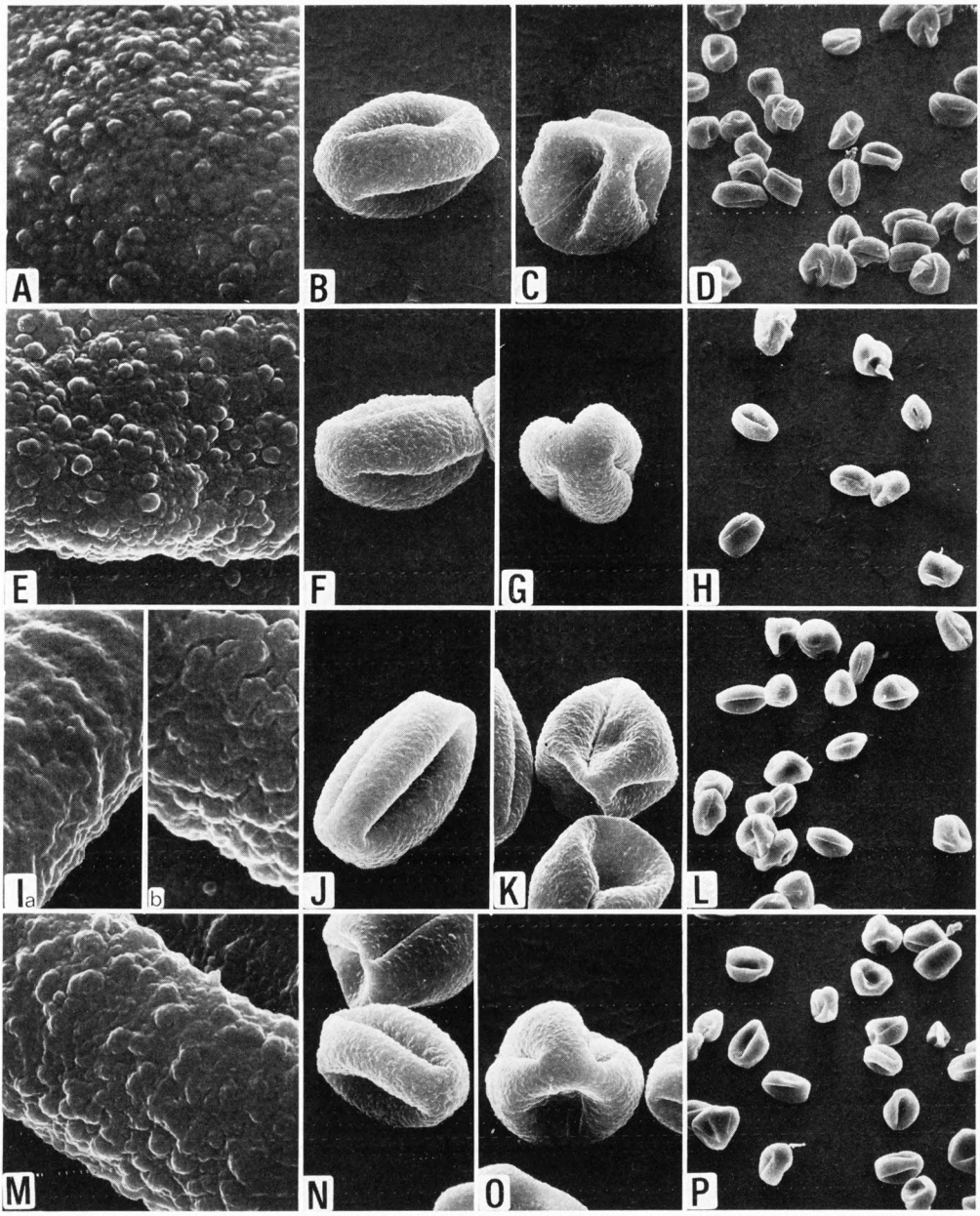

Fig. 2. *Quercus petraea.* SE micrographs of pollen grains. — B, F, J, N: Lateral view of pollen grains showing the mesocolpium area (x 2,400). — A, E, I a and b, M: Details of the mesocolpium area. Apart from the most representative types of verrucae in A and E one can find exine sculpturing as in I b and M showing verrucae interlacing to form winding ridges. Note the almost psilate surface of I a (x 12,000). — C, G, K, O: Pollen grains in polar view (x 2,400). — D, H, L, P: Surveys of pollen grains from four oaks (x 600).

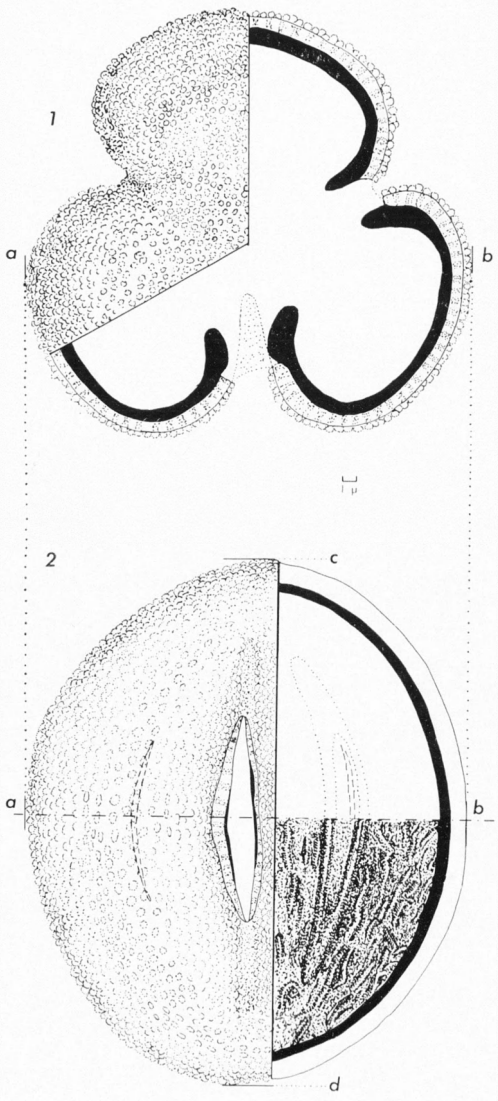

Fig. 3. *Quercus petraea* and *Q. robur*. — Palynogram showing the arrangement and shape of colpi of the tricolpate pollen grain. The structure of the inner surface of the intine is also shown. The cross-section a—b in polar view (1) coincides with the equator of the lateral view (2). The actual shape of the verrucae is not shown.

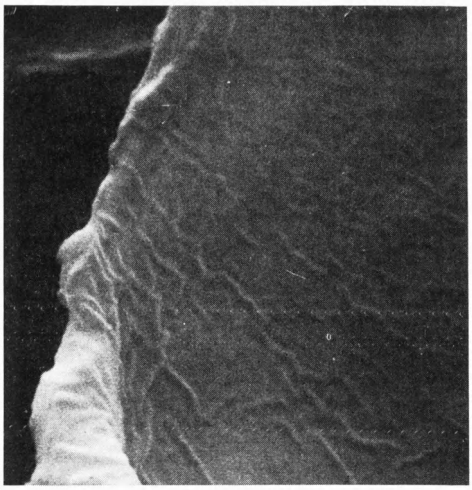

Fig. 4. *Quercus petraea*. — Pollen grain fractured by ruby laser beams. SE micrograph of the inner surface of the intine showing striate-reticulate ornamentation (x 12,000).

two trees with aberrant leaf forms have been the subject of a biometric analysis of the frequency distribution of the values of the length of the polar axis (P), the equatorial axis (E) and their quotient (P/E). Samples of each species were chosen from trees with high male fertility (i.e. as a rule > 90 % stainable pollen) from populations which have been found to be representative for the species. In the same way introgressives have been taken from oak populations which are composed of many hybrid individuals (Olsson 1975 a).

The differences in mean values of E and P observed between the species are statistically significant (Table 1). The cumulative distribution curves of Fig. 5 show the overlapping range of values (E) of both species compared. Obviously, although the differences in mean values between the species are statistically significant, these data cannot be used for taxonomical conclusions at species level.

Corresponding pollen data for a sample of oaks from an introgressive population exhibit skewed or bi- to polymodal distri-

Table 1. *Quercus petraea, Q. robur* and their spontaneous introgressives including *Q. petraea*×*robur* nm. *mespilifolia*. — Pollen biometry; statistical data. — E: Length of equatorial axis (μ). — P: Length of polar axis (μ). — n: Number of pollen grains. — $\bar{x}$: Mean value. — $\bar{x}_d$: Difference between mean values. — SD: Standard deviation. — P. Levels of significance in per cent. — The representatives of nm. *mespilifolia* have the voucher nos 480101 (Gullarp) and 480201 (Högsma).

	Character	Taxon	n	$\bar{x}$	SD	$\bar{x}_d$	P (%)
Quercus petraea (Qp) ..... and *Q. robur* (Qr) with ⩾ 90 per cent stainable pollen	E	Qp	250	27.26	2.72	1.37	P < 0.1
		Qr	350	25.89	2.45		
	P	Qp	200	28.41	2.31	1.64	P < 0.1
		Qr	200	26.77	2.73		
	P/E	Qp	200	1.08	0.11	0.04	0.1 < P < 1
		Qr	200	1.11	0.13		

	Character	Voucher	n	$\bar{x}$	SD	Stainable pollen (%)
Introgressives	E	480101	50	28.89	2.58	94
		480201	50	31.67	2.54	92
		QX01	50	23.62	5.41	24
		QX05	50	26.94	3.59	48
		QX09	50	26.30	3.76	64
	P	480101	50	34.16	2.09	
		480201	50	40.36	3.09	
		QX01	50	29.18	3.65	
		QX05	50	28.11	2.84	
		QX09	50	30.21	2.83	
	P/E	480101	50	1.19	0.12	
		480201	50	1.31	0.14	
		QX01	50	1.30	0.27	
		QX05	50	1.07	0.12	
		QX09	50	1.17	0.17	

bution curves (not illustrated). The wide distribution is also reflected in the high values for standard deviation or quartile deviation (Tables 1, 2). This indicates the hybrid nature of the individual in question. Indeed the occurrence of a wide amplitude of, for example, pollen diameter (E) better indicates the hybrid nature of a plant than does a low percentage of stainable pollen grains alone (cf. OLSSON 1975 c).

The aberrant oaks examined from northern Skåne (Högsma, Gullarp) have previously been studied by SYLVÉN (1934), WEIMARCK (1947 b) and others, who stressed the problems in connection with the origin of these oaks with subentire leaves. In another paper (OLSSON 1975 b) the author has shown that the oaks may be the hybrid offspring of *Q. petraea* and *Q. robur,* as WEIMARCK (1947 b) also concluded.

Both representatives of "mespilifolia" oaks have markedly large pollen grains, in the Högsma oak even larger than in *Q.*

Table 2. *Quercus petraea, Q. robur* and introgressives including *Q. petraea×robur* nm. *mespilifolia.* — Pollen data, viz. male fertility as percentage of stainable pollen grains, quartile deviation of pollen diameter (μ) (equatorial axis, E; n=50), and number of leaf and fruit characters indicating hybrid or introgressive nature.

Taxon	Voucher	Per cent stainable pollen	Quartile deviation of E	Number of intermediate characters
Quercus robur	QO13	96	0.96	0
	QO09	96	1.13	0
	QO01	95	1.32	0
	QO12	95	1.36	0
	QO08	94	1.56	0
	QO15	93	1.24	0
	QN15	90	1.49	0
	QO04	55	1.16	(1)
	QO02	48	2.26	0
Introgressives	QX01	24	2.41	3
	QX05	48	2.02	1
	QX09	64	2.31	1
	QY11	59	2.03	1
	QY22	57	2.69	2
Q. petraea×robur nm. *mespilifolia*	480101	94	1.90	1
	480201	92	1.46	2
Q. petraea	QB07	71	1.78	0
	QA02	81	2.35	(1)
	QB10	91	2.20	0
	QB18	91	2.20	0
	QB19	94	2.07	0
	QA08	96	1.58	0
	QB11	99	1.05	0

petraea (Fig. 5). This is indicative of the hybrid nature of these oaks and thus supports the previous results.

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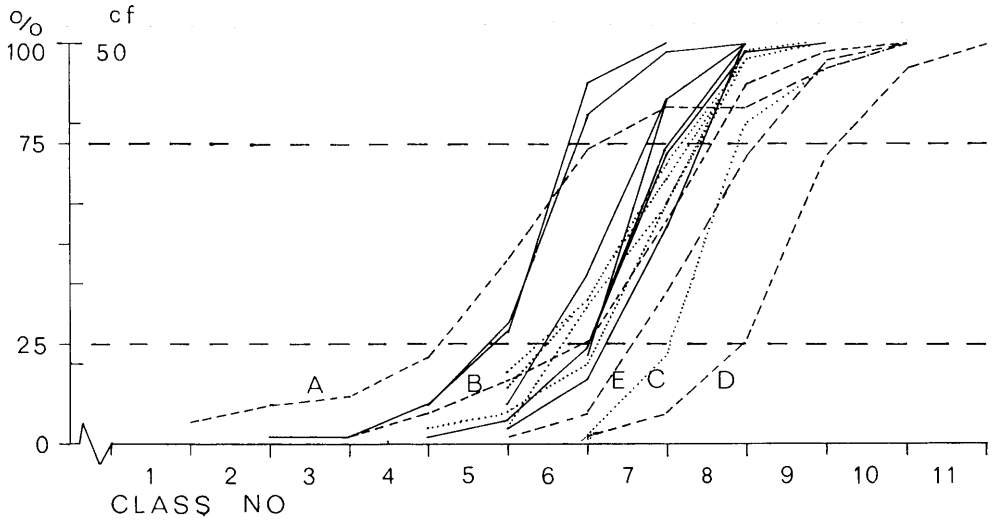

Fig. 5. *Quercus petraea*, *Q. robur* and their spontaneous introgressives including *Q. petraea* ×*robur* nm. *mespilifolia*. — Cumulative distribution curves of pollen data (E, equatorial axis) of pollen samples from single trees. Heavy lines=*Q. robur*. Dots=*Q. petraea*. Broken lines=Introgressives. All representatives of the species have a percentage of stainable pollen grains exceeding 90 %. C represents a sessile oak with especially high pollen stainability (99 %). The material is divided into eleven classes. The class width is 2.44 µ. The lower limit of class no. 1 is 10.98 µ. — A. Introgressive oak (QX01). — B. Ditto (QX05). — C. (QB11, see above). — D. *Q. petraea*×*robur* nm. *mespilifolia* (Högsma). — E. Ditto (Gullarp).

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APPENDIX

Code to collections of natural oak populations used in this investigation.

Q. petraea. QA02, QA08: Hjärsås (Skåne); QB07, QB10, QB11, QB18, QB19: Sundsvik (Bohuslän).

Q. robur. QO01, QO02, QO04, QO08, QO09, QO12, QO13, QO15: Veberöd (Skåne); QN15: Hemlinge, Glimåkra (Skåne).

Hybrid populations. Introgressives: QX01, QX05, QX09: Tjurkö (Blekinge); QY11, QY22: Verkö (Blekinge). The *mespilifolia* types: 480101: Gullarp, Osby (Skåne); 480201: Högsma (Skåne).

Oaks With Subentire Leaves from Skåne, Sweden. A New Critical Attempt to Explain Their Origin

Ulf Olsson

OLSSON, U. 1975 00 00. Oaks with subentire leaves from Skåne, Sweden. A new critical attempt to explain their origin. — Bot. Notiser 128: 265—274. Lund. ISSN 0006-8195.

Of the known occurrences of oaks with entire or subentire leaves belonging to the form series between *Quercus petraea* (MATTUSCHKA) LIEBL. and *Q. robur* L., two trees from northern Skåne have been studied in detail. The results of morphological investigations of these oaks compared with corresponding investigations of *Q. petraea* and *Q. robur* afford a certain amount of evidence that these oaks with subentire leaves are hybrids between *Q. petraea* and *Q. robur*.

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INTRODUCTION

In Scandinavia, oaks with entire leaves, described as forms of *Q. petraea* or *Q. robur*, have been observed exclusively in Sweden (WEIMARCK 1947). In the remaining parts of Europe many forms or varieties have been described, some of which are discussed below.

Two oaks with aberrant leaf forms at Högsma and Gullarp in NE Skåne (Sweden) have been studied over a period of years. Morphological variation, observations on fruit-setting and percentage stainable pollen are presented and compared with corresponding observations on *Q. petraea* and *Q. robur* in their Swedish range.

The "Högsma" oak was discovered in 1868 and then named *Q. sessiliflora* var. *subintegrifolia* (PERSSON 1885). The "Gullarp" oak is younger. On account of its entire leaves this oak was protected in 1943 (GERTZ 1944). The Högsma oak is also protected. Both oaks have long been interpreted as forms of *Q. petraea* (HYLANDER 1941; GERTZ 1945). HYLANDER distinguishes two types with subentire leaves: *Q. petraea* f. *mespilifolia* (WALLR.) SCHWARZ and *Q. petraea* f. *subintegrifolia* (J. PERS.) HYL. The Högsma oak is the type tree of the latter form. The Gullarp oak may also belong to this form. WEIMARCK (1947) combines the oaks with subentire leaves into one hybrid form, *Q. petraea*×*robur* f. *mespilifolia* (WALLR.) WEIM., later called *Q. petraea*×*robur* nm. *mespilifolia* (WEIMARCK 1963). This view (WEIMARCK) is in part supported by the results of this investigation.

RESULTS

Plant Habit

The general morphology of sessile and pedunculate oaks has been summarized earlier (OLSSON 1974, 1975 a). The original shoot type of oaks is a monopodium. The tendency to drop annual shoots or larger twigs in the autumn (especially by *Q. robur*) may modify the shape of the crown so that it resembles that of a tree with sympodial branching (JONES 1959). In addition the Högsma oak is characterized by a bunched crown. The Gullarp oak resembles *petraea* in crown habit.

Table 1. *Quercus petraea×robur* nm. *mespilifolia*. Some morphological data.

Character	Oak at Högsma	Oak at Gullarp
Petiole length	22.7 ±0.7 mm	15.3 ±0.5
Peduncle length to first bract	7.7 ±0.6 mm	2.3 ±0.3
Width to length ratio of acorn	1.27 ±0.03	1.36 ±0.03

Special crown forms such as those found in pendulous and fastigiate oaks are inherited in a simple Mendelian manner (OPPERMANN 1932, PYATNITSKII 1947). The almost "corymbous" crown of the Högsma oak may be a heritable oak form. About three per cent of the trees of *Q. robur* examined have corymbous crowns. None of these oaks, however, has subentire leaves.

Buds

Buds are more or less like those of *Q. robur*. Terminal and lateral buds of fruiting shoots of these trees resemble "typical" buds of *Q. robur* and *Q. petraea* (Fig. 4). The buds illustrated from specific individuals are regarded as representative as they agree with earlier results of morphological analyses of *petraea*- and *robur*- oaks (OLSSON 1974, 1975 a). There is no pronounced difference between these buds, indeed, the bud characters are very variable. One can find *Q. petraea* trees with large acute buds.

Leaves

The Högsma oak tends to have leaves that are more elliptical than in the other taxa. However, leaf shape cannot be used as a distinguishing character in the taxonomic analysis. The leaf bases are cuneate of *petraea*-type. In the case of lobed leaves that can appear on epicormics, the leaves look like true *Q. petraea* leaves, except that the lobes are acute or almost acuminate. New foliage consisting of lobed leaves was seen in 1969 on the Gullarp oak after the foliage had been completely destroyed by caterpillars (Figs. 2 B, 3 A—C).

The length of the petiole is a good distinguishing character. In *Q. petraea* the petiole is about twice as long as in *Q. robur*. The petioles of the Högsma oak are extremely long, longer than those of the Gullarp oak which exceed those of *Q. petraea*.

Flowers and Fruiting

The Gullarp oak resembles *Q. petraea* in flower and fruit characters. The Högsma oak usually has longer catkins, but one can find almost "sessile" and very long catkins side by side on the same shoot (Fig. 5 A). The acorns of both subentire-leaved oaks resemble the fruits of sessile oaks, but the acorns of the Gullarp oak in all samples hitherto obtained have constricted tops, indicating non-maturity (Figs. 5 C, 7).

Male Fertility and Fruit-Setting

The Högsma oak has about 92 per cent stainable pollen, the Gullarp oak 94 per cent, but this alone is not indicative of hybridity. Both oaks, however, have on the average larger pollen grains than the putative parent species (see OLSSON

Fig. 1. *Quercus petraea×robur* nm. *mespilifolia*. The Högsma oak. — A. Fruiting shoot. — B. Flowering shoot. — C. Detail of male catkin; b bract of male flower. — D. Clustered female inflorescences.

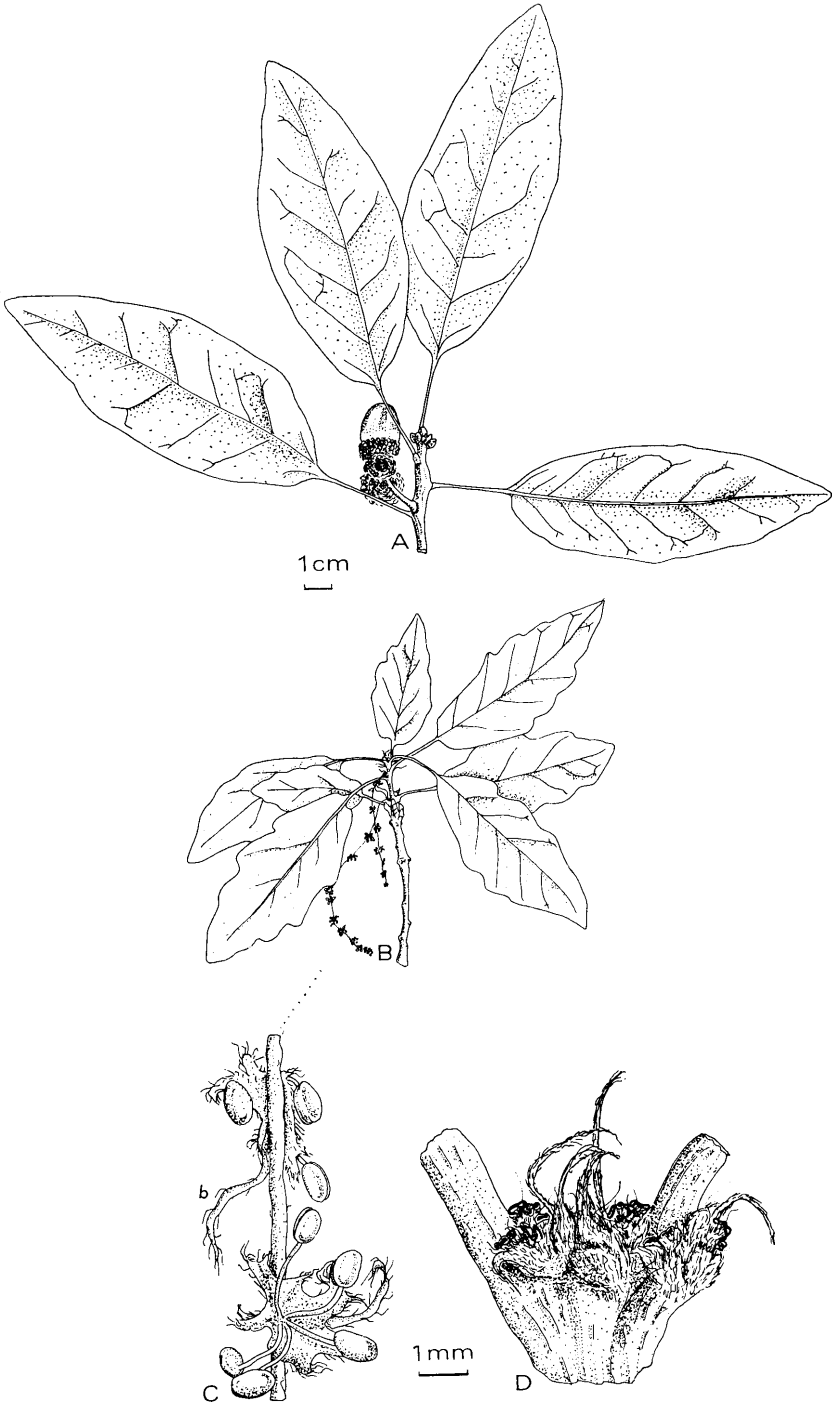
A
1cm
B
b
C
1mm
D

Fig. 2. *Quercus petraea*×*robur* nm. *mespilifolia*. The Gullarp oak. — A. Fruiting shoot. — B. Epicormic shoot. — C. Flowering shoot. — D. Detail of male catkin; b bract of male flower. — E. Female catkin.

1975 b) where the variation in size and microstructure is reported. Cryptic structural hybridity may be the cause of the unexpectedly high percentage of stainable pollen (OLSSON 1975 a). The acorn growth of the oaks in Skåne in 1971 was very good. Even young trees bore fruit, which is unusual. Both the Högsma oak and the Gullarp oak also yielded acorns which have been described earlier. Yet the fruit-setting in these trees was very low compared with "normal" oaks in the same localities. This may be a good indication of the hybrid origin of these oaks with subentire leaf margins.

Progeny of the Högsma Oak

Twenty acorns from the Högsma oak and Gullarp oak respectively collected in 1971 were put into pots in the greenhouse in Lund (March 1972). At the same time the same number of acorns from typical *Q. petraea* and *Q. robur* were also sown. The seedlings of *Q. robur* (19 in number) and of *Q. petraea* (13) had normally lobed leaves. Three acorns only of the Högsma oak germinated, but in all seedlings the leaf margins were more or less entire. None of "Gullarp" acorns germinated. The persistent character of almost non-lobular leaves of the few seedlings from the Högsma oak may indicate that this leaf form is hereditary.

Some of the younger oaks in the vicinity of the Högsma oak may be the progeny of this oak. They have divergent leaf shapes. In one case the leaves are very little lobed (Fig. 6 B).

CONCLUSIONS AND DISCUSSION

The morphological analysis of the oaks with subentire leaves (Högsma, Gullarp)

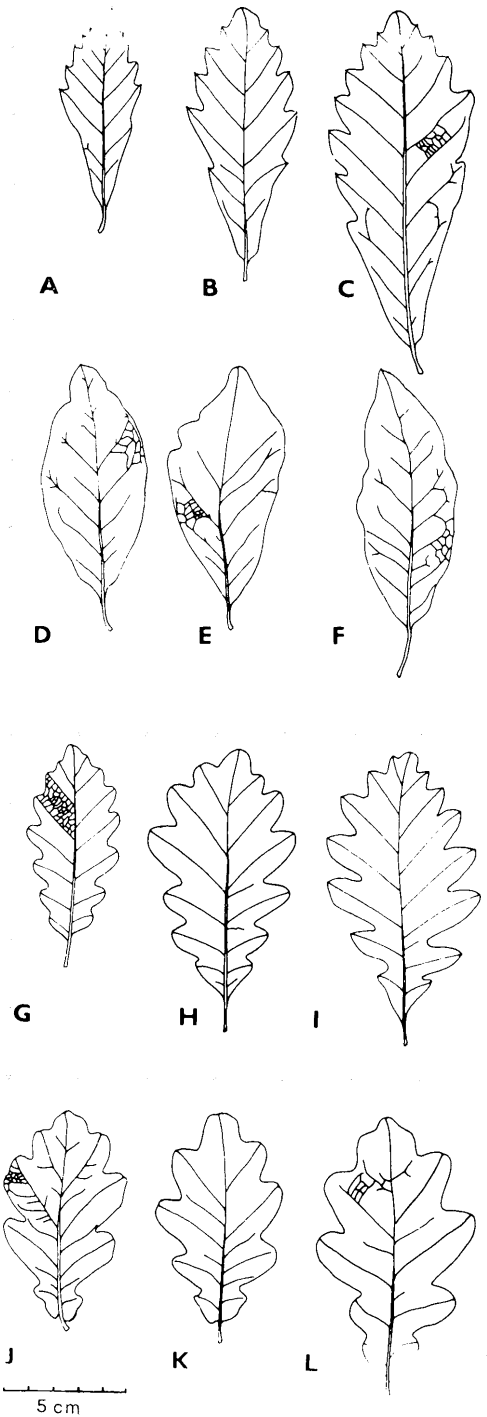

Fig. 3. Leaf types of oaks with subentire leaves (A—F) compared with typical leaves of *Quercus petraea* (G—I) and *Q. robur* (J—L). A—C show leaves from epicormics of the Gullarp oak.

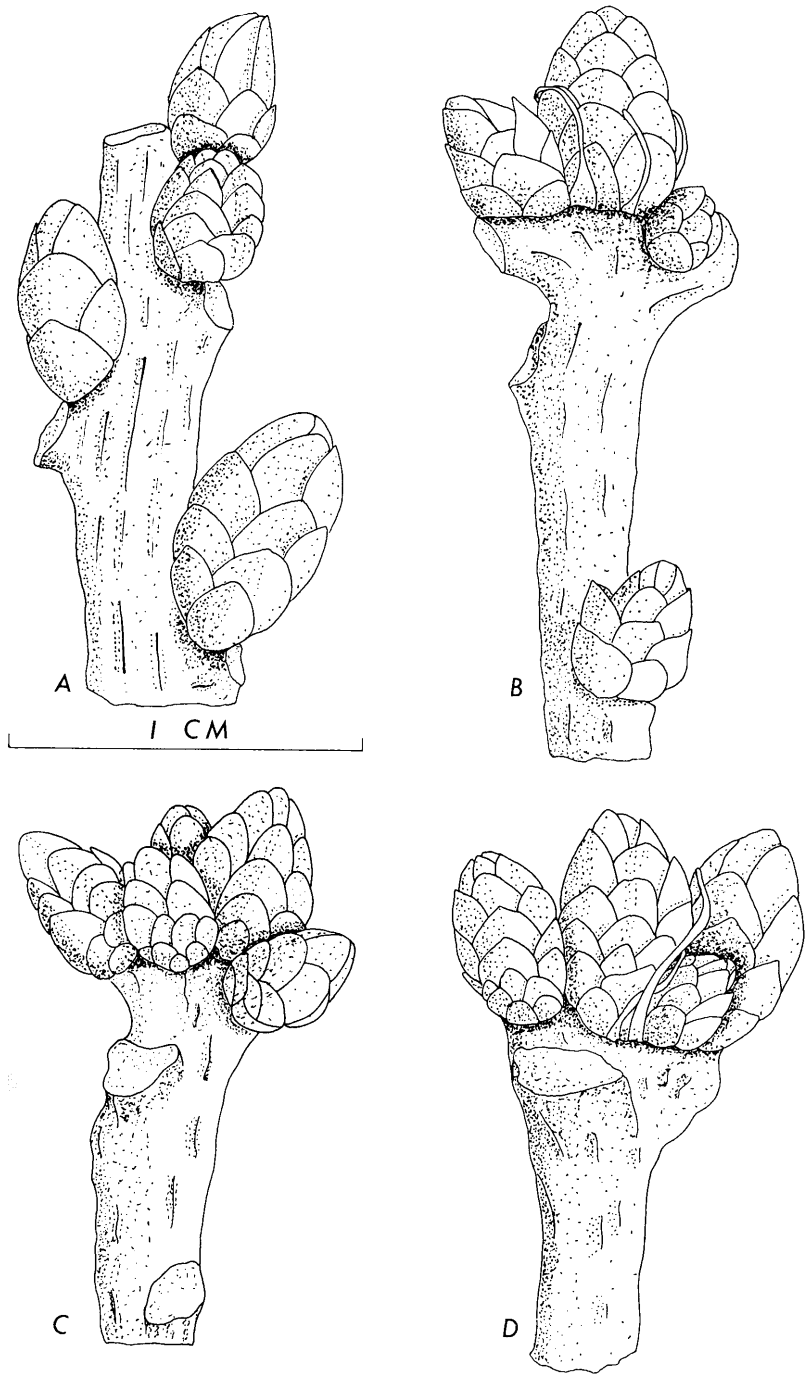

Fig. 4. Terminal buds of fruiting twigs (October) from oaks regarded as representative. — A. *Quercus robur*. — B. *Q. petraea*. — C. The Högsma oak. — D. The Gullarp oak.

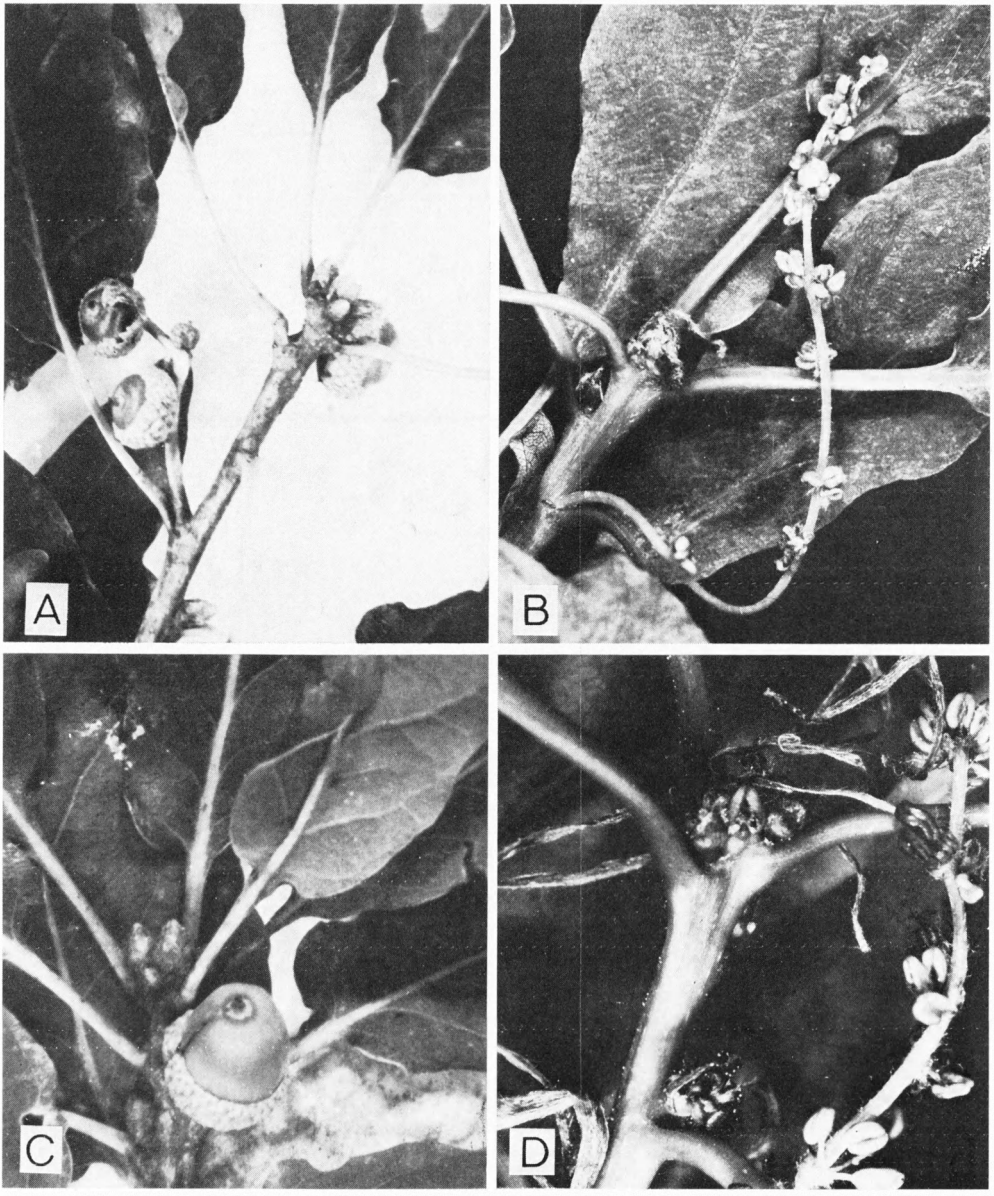

Fig. 5. Fruiting and flowering shoots from the Högsma oak (A, B) and the Gullarp oak (C, D). Note the varying length of the female peduncles on the same shoot and the small undeveloped acorns in A (Högsma). The acorns from the Gullarp oak (C) are usually small and conical with a somewhat constricted zone near the top and a lateral "suture" of ectocarpous folds. In D is shown the sessile female inflorescence. — A (×0.6), B (×2), C (×1.5), D (×3).

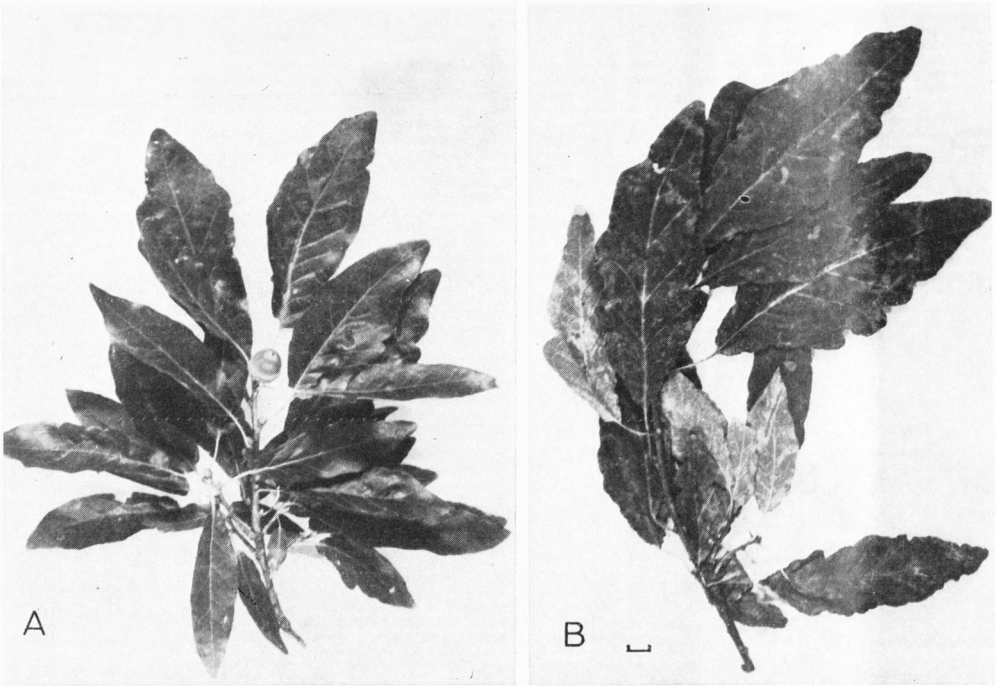

Fig. 6. A twig from the Högsma oak (A) compared with another twig (B) from an oak c. 6 m high, in the vicinity of the Högsma oak. The leaves are rounded-acute at the top and base and have very few lobes. The tree may be a spontaneous progeny of the Högsma oak. Collected 1971. — A (×0.3), B (scale=1 cm).

does not give a clear indication of hybrid origin. This is true of the leaf characters in particular. Precautions must be taken in comparing the leaf characters of the Högsma and Gullarp oaks and the oak species investigated, as the possibility cannot be excluded that a pleiotropic effect at the leaf primordium stage can also have been the cause of other changes as well as that of entire leaf margins. Moreover an exceptional leaf shape with almost no lobes does not permit of an adequate comparison between spontaneous hybrids and parental species with regard to certain characters such as leaf outline, lobation and venation which will make it difficult to use some indices for comparison.

Some *Q. petraea*×*robur* probably represent crosses between the primary hybrid and one of its parents. GESCHWIND (1876), PYATNITSKII (1939) and DENGLER (1941) have shown that the primary hybrid between *Q. robur* and *Q. petraea* displays hybrid vigour expressed, for instance, in an abundance of new shoots with large leaves. GESCHWIND's crossings of *Q. robur* (male) and *Q. petraea* (female) produced a hybrid which had entire leaves. He writes: . . . "Das Blatt, grösser als das von Q. sessiliflora Sm., aber kleiner als das von Q. pedunculata, zeigt die Unregelmässigkeit der Form von letzterer Species, ist l a n g g e s t i e l t, ganzrandig, am Rande wellenförmig, sonst ei-lanzettförmig, kahl, entbehrt der characteristischen Einbuchtungen des Eichenblattes gänzlich und ähnelt oft mehr jenem von Castanea vesca, Gärtn.". Furthermore he

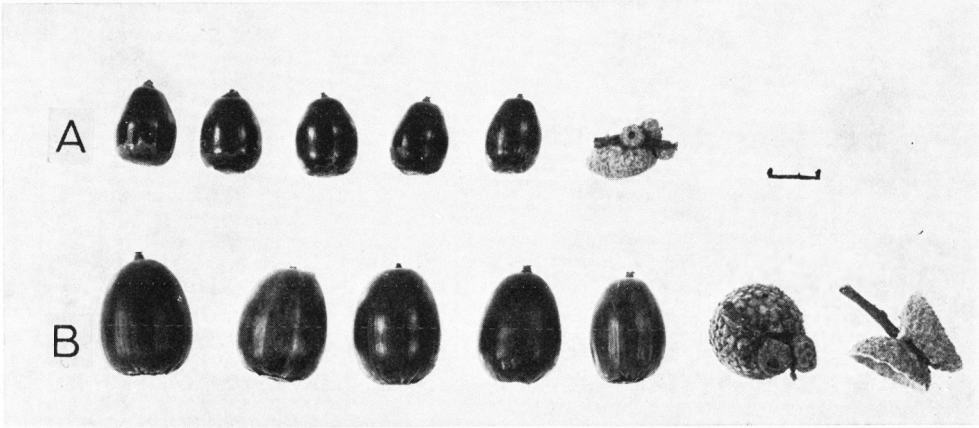

Fig. 7. A series of acorns with catkins from the Gullarp oak (A) and the Högsma oak (B) showing relative size and shape. — Scale=1 cm.

states that the male flowers have well-developed pollen and that the female catkins are short and have fewer flowers than those of *Q. petraea*. He obtained four hybrids, all with different types of leaves. This is important and may indicate that the parent trees were not truly specific but heterozygous and possibly introgressive. It is remarkable how well the description of one of the artifically produced hybrids agrees with the Högsma and Gullarp oaks regarding leaf characters, pollen and fruit-setting.

The strongest indications of hybridity (*Q. robur*×*Q. petraea*) in the Högsma oak are the relatively low frequency of flowers and normal acorns, and in the Gullarp oak there is a low frequency of flowering with presumably no normal acorns. In spite of insufficient indications of hybridity in parts of the investigation there is still reason to believe that the Högsma oak and the Gullarp oak are crossing products of *Q. petraea* and *Q. robur*.

TAXONOMY

In the early 1800's entire- and subentire-leaved oaks from different parts of Europe were described. The first oaks observed were given the rank of species: (1) *Q. sublobata* KIT. (see SCHULTES 1814 p. 619, KITAIBEL 1863 p. 355); (2) *Q. mespilifolia* WALLROTH 1822; (3) *Q. louettei* PETZOLD & KIRCHNER 1864 p. 531. Many botanists and authors of floras have called attention to these aberrant oaks. However, the taxonomic interpretation of the oaks has changed. Most later writers are inclined to describe the entire-leaved type as a forma or varietas of *Q. petraea* (MATTUSCHKA) LIEBL. (syn. *Q. sessiliflora* SALISB., *Q. sessilis* EHRH.): (4) *Q. sessiliflora* SALISB. var. *subintegrifolia* J. PERSSON 1885; (5) *Q. sessilis* EHRH. var. *schidlayana* DOMIN 1937.

The author confirms the opinion of WEIMARCK (1947, 1963) that the subentire-leaved oaks at Högsma and Gullarp may belong to the hybrid *Q. petraea*×*robur*. The correct name will be *Q. petraea* (MATTUSCHKA) LIEBL. ×*robur* L. nm. *mespilifolia* (WALLR.) WEIM. 1963. (syn. *Q. sessiliflora* SALISB. var. *subintegrifolia* J. PERS. — the Högsma oak; *Q. petraea*× *robur* f. *mespilifolia* (WALLR.) WEIM. 1947. — the Högsma and Gullarp oaks; Other names than these synonyms (cf.

1—5 above) are assigned to entire-leaved oaks, but do not apply to the trees at Högsma and Gullarp.)

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Botanical Literature

AHMADJIAN, V. and HALE, M. E. (eds.): The Lichens. — Academic Press, New York and London, 1973. XIV+697 pp., 62 plates, 296 figures. Price £ 19.50 (cloth).

The present volume is a comprehensive and up-to-date survey of various fields within lichenology. It is a companion to the five-volume treatise "The Fungi" edited by G. C. AINSWORTH, F. K. SPARROW and A. S. SUSSMAN and published by Academic Press between 1965 and 1973. The high standard of the print and of the illustrations known from the latter work is also met with in "The Lichens". Most figures are original or reproduced from recent literature. This should be noted as a decided improvement as some similar works issued in the 1960's have borrowed illustrations from SCHWENDENER, BORNET and other 19th century lichenologists.

"The Lichens" is a multi-authored treatise produced by no less than 23 authors from various parts of the world. Hence it is self-evident that the way of presenting the material differs fairly widely from one chapter to another. In some cases we meet with detailed surveys including several previously unpublished data. Other chapters are rather brief summaries, but the mostly comprehensive lists of references will facilitate the reader's further studies.

The volume is organized into 5 major parts, viz. "Structure and Development", "Physiology of the Intact Thallus", "Environmental Response and Effects", "Secondary Metabolic Products" and "Symbiont Interactions".

The introductory chapter "Anatomy, Morphology, and Development" by H. M. JAHNS is a most valuable account illustrated with excellent figures mainly taken from HENSSEN and JAHNS, "Lichenes" (cf. review below). M. A. LETRUIT-GALINOU gives useful information, often from recent research, on "Sexual Reproduction". It is evident, however, that several problems, for example the fertilization of the ascogone by spermatia and role of the apogamy, are still under discussion. Brief chapters on "Systematic Evaluation of Morphological Characters" and "Lichen Propagules" are presented by J. POELT and F. BRIAN PYATT respectively. An informative and critical chapter on "Fine Structure" by E. PEVELING has been illustrated with electron micrographs and SEM photographs of very high quality.

Part II deals with "Physiology of the Intact Thallus" including chapters on "Absorption and Accumulation of Mineral Elements and Radioactive Nucleides" (Y. TUOMINEN and T. JAAKOLA), "Pedogenetic Significance of the Lichens" (J. K. SYERS and I. K. ISKANDAR), "Photosynthesis and Carbohydrate Movement" (D. H. S. RICHARDSON) and "Nitrogen Metabolism" (J. W. MILLBANK and K. A. KERSHAW).

Part III "Environmental Response and Effects" discusses "Response to Extreme Environments" (L. KAPPEN), "Water Relations" (O. B. BLUM), "Substrate Ecology" (I. M. BRODO), "Lichens and Air Pollution" (O. L. GILBERT) and "Growth" (M. E. HALE).

Some aspects of "Secondary Metabolic Products" are treated in Part IV, viz. "Nature of Lichen Substances" (S. HUNECK), "Biosynthesis of Lichen Substances" (K. MOSBACH) and "Antibiotics in Lichens" (K. O. VARTIA).

Part V is concerned with "Symbiont Interactions". V. AHMADJIAN gives a very brief survey of his research on "Resynthesis of Lichens". "Evolutionary Aspects of Symbiosis" are presented in a somewhat philosophical article by G. D. SCOTT.

For reasons difficult to understand three concluding chapters have been entitled "Appendices", viz. "Classification" (J.

POELT), "Identification and Isolation of Lichen Substances" (J. SANTESSON) and "Methods of Isolating and Culturing Lichen Symbionts and Thalli" (V. AHMADJIAN). POELT briefly discusses previous lichen systems and outlines, in a very fragmentary manner, a new system "based partly on my own preliminary studies of ascus structure". He rightly emphasizes the difficulties in integrating the lichenized fungi in any accepted fungal system. "Lichen systematists have hardly ever been really familiar with the corresponding fungal groups, and mycologists have had enough difficulties with their own groups without bringing in the lichenized fungi."

The "complete authoritative coverage" of lichenology stated on the cover of this book is somewhat of an exaggeration. Certain topics are not treated at all, for example lichen sociology and geographical distribution and there are others that could have been dealt with in greater detail. Nevertheless, "The Lichens" is a mine of information both for the student and the advanced lichenologist.

OVE ALMBORN

HENSSEN, A. and JAHNS, H. M.: Lichenes. Eine Einführung in die Flechtenkunde. — Georg Thieme Verlag, Stuttgart, 1974. XII+467 pp., 142 figures, 8 plates. Price DM. 19.80 (flexible paper cover).

The notable new interest in lichens during the last two decades has resulted in several floras, monographs and handbooks covering more or less wide fields of "general lichenology". As nearly forty years have elapsed since such a textbook was issued in the German language, the present work by Dr AINO HENSSEN (Marburg) and Dr HANS M. JAHNS (Groningen, now Frankfurt am Main) is especially welcome.

The authors have modestly called their book "An Introduction to Lichenology". They have, however, admirably succeeded in condensing a surprising number of facts into a comprehensive volume no bigger than a pocket book, and at a very reasonable price.

A brief introductory survey of the history of lichenology is followed by far more elaborate chapters on the morphology of the lichens, especially the organs of reproduction. These parts are of extreme value as both authors have carried out very important investigations on this topic. Several new results are published here for the first time, often with original drawings and photographs.

The physiology of the lichens is treated in a concise chapter. Lichen chemistry is dealt with by a specialist, Dr JOHAN SANTESSON, Uppsala. This subject, introduced more than a hundred years ago for diagnostic purposes, has developed immensely during the last few decades and has become an important source of information for the understanding of the metabolism of lichens. Symbiosis, parasitism and related problems are briefly discussed, as well as synthesis in vitro between mycobionts and phycobionts. There are also short accounts of growth, diaspores, ecology (including sociology and the effects of air pollution), distribution and economic importance.

Nomenclature and classification are treated in some detail. A new lichen system is presented, differing essentially from ZAHLBRUCKNER's classical arrangement and also from the system proposed by J. POELT (cf. review above). HENSSEN and JAHNS have founded their taxonomy on modern views on the ontogeny of the fruitbodies of the non-lichenized ascomycetes. Much attention has been paid to ascolocular or ascohymenial development, bitunicate or unitunicate asci, etc. As experts in this field it is not unreasonable that the authors have laid stress upon taxonomic characters derived from ontogeny. Though the place of some families is described as tentative so far, the reviewer believes that the main features of the future lichen system will much resemble the taxonomy outlined by HENSSEN and JAHNS.

An extensive list of references to literature and another of lichenological terms conclude this well-organized volume. No effort will be made here to compare it with the major work reviewed above, "The Lichens", but it seems highly probable that a translation of "Lichenes" into English would be appreciated in many parts of the world.

OVE ALMBORN

TRALAU, H. (ed.) 1974. Index Holmensis, IV. A World Index of Plant Distribution Maps. Dicotyledoneae A—B. — Scientific Publishers Ltd., Zürich.

Three volumes of Index Holmensis have been published previously, viz. Vol. I: Vascular cryptogams and gymnosperms; Vol. II: Monocotyledoneae A—I; and Vol. III: Monocotyledoneae J—Z. The last two were reviewed in Bot. Notiser 125 p. 199. The fourth volume, Dicotyledoneae A—B, which has now appeared is especially welcome as it promises a full continuation of the Index for the rest of the higher plants.

An innovation for Vol. IV is that in addition distributions of plant species incorporated in vegetation maps have been included in the Index (but only where Latin names of the species concerned are given). This extends the coverage of the Index considerably and adds much useful information.

The present volume, like the previous one, contains a tremendous amount of information. *Astragalus,* a genus of c. 1,600 species, contributes references of maps extending over approx. 65 columns. Important tree genera such as *Betula, Alnus,* and *Acacia* are also included, with numerous columns of reference each, which should be of immeasurable importance to forest ecologists all over the world.

It is hardly necessary to repeat that I consider Index Holmensis to be of great importance. It should be found in any biological institute or library with effective research and service respectively. The Index provides information that is of primary importance to ecologists in the fields of botany as well as zoology, and to systematists, horticulturalists and plant geographers. It can also be used to trace literature supplying information on other aspects of the species concerned.

As the number of maps being published is rapidly increasing Dr TRALAU appeals for assistance in collecting information on new maps published, and in getting reprints of publications with distribution maps (see Bot. Notiser 128 p. 201 and Taxon 24 p. 142). This is a matter of utmost urgency. There are numerous maps printed in publications that are difficult to obtain and that in addition may have mixed contents.

Index Holmensis is an undertaking that is deserving of all support. It is without doubt an investment that is a means of saving time and money for the research worker.

ROLF DAHLGREN

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Drawings of Scandinavian Plants 105–108

Epilobium L. Sect. Epilobium

Alf Oredsson and Sven Snogerup

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Drawings and descriptions are given for *E. alsinifolium* VILL., *E. hornemannii* REICHENB., *E. lactiflorum* HAUSSKN. and *E. anagallidifolium* LAM.

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The four species nos. 105—108 are without doubt closely related. They all occur mainly in the arctic areas, in the mountain chain and by springs and cold streams in the northern lowlands. The group is recognized by a usually simple inflorescence, two lines of hairs on the stem and the lack of or scarcity of eglandular hairs on the capsules.

There are some fully fertile populations that are difficult to determine but most of the material can without any difficulty be referred to one of the species. Some of the extreme measurements in our descriptions may refer to introgressive populations but we have avoided specimens which are obviously intermediate in several characters. The nature and significance of hybridization in the group is in need of further experimental investigation. Morphological variation in populations from the northern part of Scandinavia has been treated in detail by KYTÖVUORI (1972).

In the case of the seed surface structure, there is an apparent contradiction between the descriptions given by KYTÖVUORI (1972) and those by SKVORTSOV and RUSANOVITCH (1974) and BERGGREN (1974) founded on scanning electron microscopy. In reality, the fresh seeds have papillae, but these collapse on hard drying. The preparation technique for scanning microscopy will cause all or most papillae to collapse, resulting in a pitted structure.

105. **Epilobium alsinifolium** VILLARS 1779

Perennial herb, (10—)15—30(—50) cm high, often forming dense stands. Stem more branching than in related species, sometimes forming adventitious stems or green, epigean runners from the basal nodes, usually with more or less stunted branches in the axils of middle cauline leaves, producing one (1—)2—5(—8)-flowered inflorescence or sometimes also a few smaller lateral ones. Stolons formed from basal nodes, subterranean or occurring deep down in floating vegetation, 2—10 cm long, 1—2 mm thick, pale, with long internodes and scale-like leaves 2—5 mm long. Turions formed at the ends of the stolons, compact, c. 10 mm long and 5 mm thick, with blunt, fleshy leaves.

Stem 1—3(—4) mm thick, terete, at least in the basal part with 4 weak ridges or lines below midribs and leaf margins. Two rows of hairs below the leaf margins, rarely also more uniformly hairy in upper part, hairs 0.1—0.3 mm, usually all recurved, rarely also some glandular, erect ones on upper part.

Most leaves opposite, usually only upper

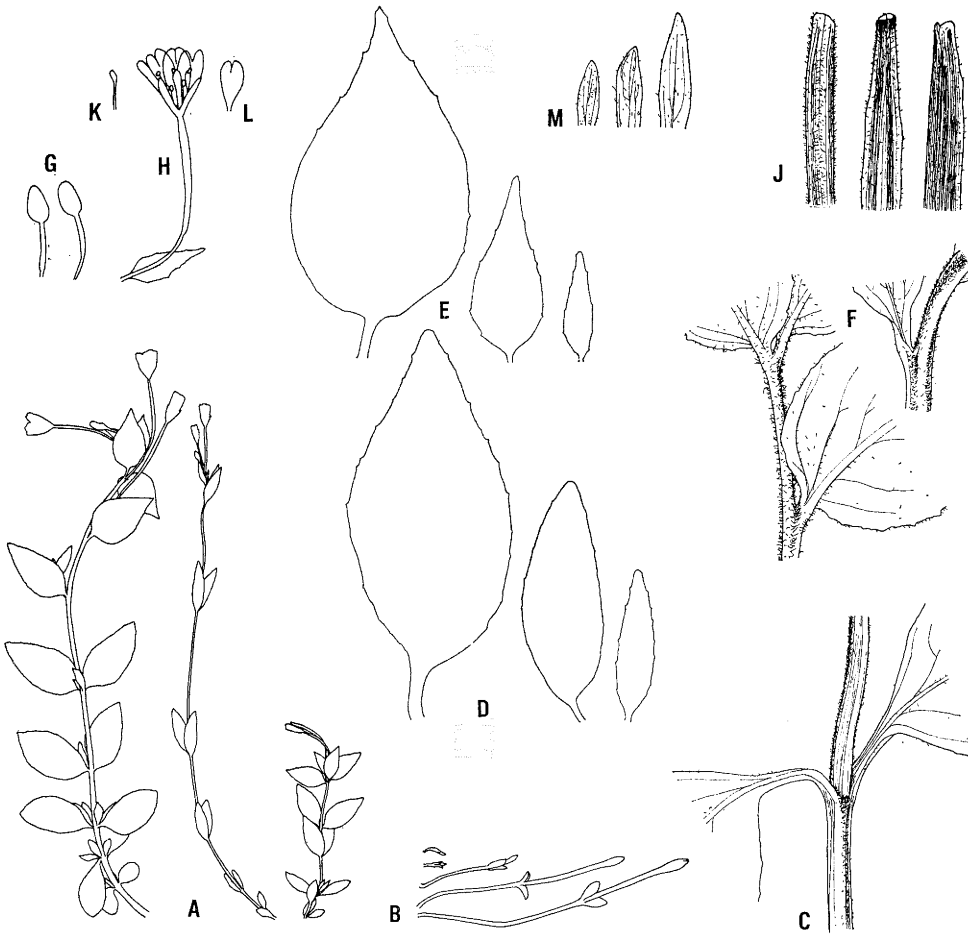

Fig. 105. *Epilobium alsinifolium* VILL. — A: Habit, ×1/3. — B: Stolons, ×1/2. — C: Stem node, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem parts with leaves, ×2.5. — G: Buds, ×1. — H: Flower, ×1. — J: Apical part of capsules, ×2.5. — K: Style, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.

bracts alternate, all petiolate, petiole 0.5—3(—7) mm, longest in lower and middle parts, leaf bases united around the stem but never decurrent. Basal leaves smaller, on the lowest part of the stem in mud or dense vegetation often scale-like, higher up obovate to elliptical, obtuse. Middle and upper leaves (10—)20—35(—60) mm long, (5—)10—18(—25) mm broad, all ovate or rarely some of the lower ones elliptical, middle ones tapering to an obtuse apex, upper ones acute, serrate with small, usually up to 0.3 mm high teeth evenly distributed or denser towards apex. Bracts broader than in related species, even the upper ones large, often concealing the buds. Leaves subglabrous, sparsely hairy only on adaxial side of midrib, hairs like those of the stem. Inflorescense almost erect even when young, though often bent in dried material. Pedicels erect to erecto-patent in all stages. Buds ovoidal to ellips-

oidal, blunt or with a minute mucro. Sepals (4.5—)6—7(—7.5) mm, connate to 0.8—2 mm at base, narrowly ovate, acute or rarely obtuse, reddish or rarely pure green, sparsely glandular-hairy. Petals (6—)9—12(—13) mm, notched to 1—1.5 mm, reddish-violet, very rarely purplish-pink or white. Anthers 0.7—0.9 mm, long filaments (4.5—)5—6.5 mm, short filaments (3.5—)4—4.5 mm. Style equalling or shorter than the long stamens, stigma capitate.

Capsule stalk (10—)15—30(—50) mm. Capsule 40—60(—70) mm, young ovary rather densely glandular-hairy, with a few eglandular hairs on the ridges, hairs like those of the stem, ripe capsules usually subglabrous. Seeds narrowly obovoidal, with one markedly flattened side, (1.1—)1.4—1.8 mm long, (0.35—)0.45—0.55 mm broad, with an acutely tapering base and a blunt apex, neck (0.05—)0.1—0.15 mm, surface with many rows of low papillae, chalazal hairs 50—60, 4.5—7 mm long. Flower homogamous.

E. alsinifolium occurs almost exclusively by springs and along watercourses, often in water, rarely in other wet places. It is commonest below the timberline, in the north it is found up to 700 m, to c. 1300 m in the S part of the mountain chain. It is at least slightly calcicole.

E. alsinifolium is an European endemic occurring on most mountains except in the extreme south. In Scandinavia it occurs in the entire mountain chain, in the arctic and subarctic parts and with scattered localities in the lowlands of Sweden southwards to c. 61° N and in Finland to 64° N.

Known hybrids: with *E. hornemannii*, *lactiflorum* and *palustre*.

106. **Epilobium hornemannii** Reichenbach 1824

Perennial herb, (10—)15—30(—40) cm high. Stem usually simple, rarely forming some adventitious stems or creeping branches up to 5 cm long from the lower nodes, usually lacking branches in the axils of cauline leaves, producing one 2—8(—10)-flowered inflorescence or rarely also a few smaller lateral ones. Stolons often lacking, if present green, epigean, usually erect to erecto-patent, 5—20(—50) mm long, c. 1 mm thick, with small, opposite leaves. Turions formed at the end of the stolons as loose rosettes of green leaves 1.5—10 mm long.

Stem 1—2(—3) mm thick, terete, its basal part often pale, with small leaves, at least in its lower part with 4 weak ridges or lines below midribs and leaf margins. Two rows of hairs below the leaf margins, hairs 0.1—0.3 mm, usually all eglandular, incurved, rarely also few to many glandular, erect ones on upper part.

Most leaves opposite, only some upper ones alternate, all petiolate, petioles 1—5(—10) mm, longest in lower and middle leaves, bases uniting around the stem but never decurrent. Basal leaves smaller, obovate to elliptical, often some of the lowest ones scale-like. Middle and upper leaves (10—)20—30(—50) mm long, (5—)8—15(—25) mm broad, all ovate or some of the lower ones elliptical, tapering to an obtuse to acute apex, upper ones always acute. Leaves serrate with teeth usually less than 0.5 mm, denser on upper part of margin or evenly distributed. Leaves subglabrous, usually sparsely hairy only on the adaxial side of the midrib, hairs like those of the stem.

Inflorescence almost erect even when young, though often bent in dried material. Pedicels erect to erecto-patent in all stages. Buds broadly ellipsoidal to subglobose, obtuse. Sepals (3—)4.5—5.5 mm long, connate to c. 1.5 mm, narrowly ovate, acute or obtuse, always reddish, sparsely glandular-hairy. Petals (4.5—)5—7(—8.5) mm, notched to 1—1.5 mm, reddish or pinkish-purple, very rarely white. Anthers 0.4—0.5(—0.85) mm, long filaments 4.5—5 mm, short filaments 3—3.5 mm. Style shorter than the long stamens, stigma capitate.

Fig. 106. *Epilobium hornemannii* REICHENB. — A: Habit, ×1/3. — B: Stolons and winter buds, ×1/2. — C: Stem node, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem part with leaves, ×2.5. — G: Buds, ×1. — H: Flower, ×1. — J: Apical part of capsules, ×2.5. — K: Style, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.

Capsule stalk (10—)15—30(—40) mm. Capsule (35—)40—50(—55) mm, young ovary densely or moderately glandular-hairy, ripe capsules usually subglabrous, hairs 0.1—0.2 mm, erect. Seeds narrowly obovoidal, with one markedly flattened side, 1.0—1.25(—1.4) mm long, 0.35—0.45 mm broad, with an acutely tapering base and a blunt apex, neck 0.05—0.15 mm, surface with many rows of more or less conical papillae, chalazal hairs 45—50, 3.5—5.5 mm long. Flower homogamous.

E. hornemannii grows by springs and watercourses but also in fens and meadows and along ditches, both in the lower alpine zone and in the woodland, up to 1100 m in the north, to 1500 m in the southern mountains.

E. hornemannii has a discontinuous circumpolar distribution. In Scandinavia it is fairly common in the mountains and in the arctic and subarctic parts, with scattered occurrences in the lowlands of Sweden southwards to 60.5° N and in Finland to 63° N.

Known hybrids: with *E. alsinifolium, anagallidifolium, lactiflorum* and *palustre.*

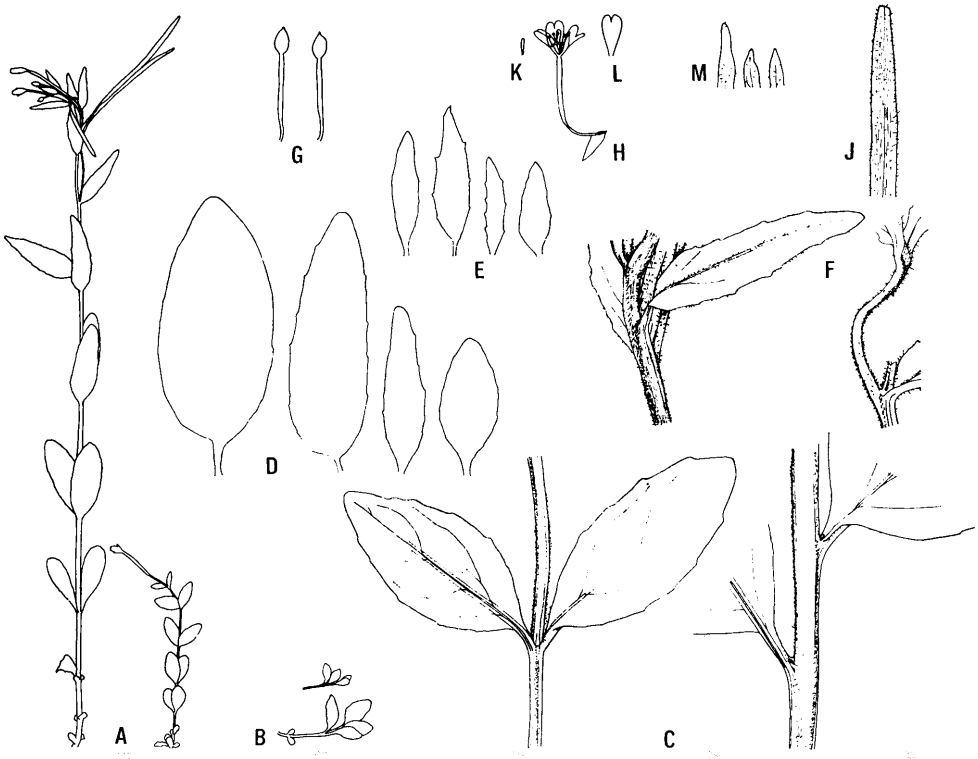

Fig. 107. *Epilobium lactiflorum* HAUSSKN. — A: Habit, ×1/3. — B: Stolons, ×1/2. — C: Stem nodes, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem parts with leaves, ×2.5. — G: Buds, ×1. — H: Flower, ×1. — J: Apical part of capsule, ×2.5. — K: Style, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.

107. **Epilobium lactiflorum** HAUSSKNECHT 1879

Perennial herb, (5—)15—30(—40) cm high. Stem usually simple, without branches in the axils of cauline leaves, producing one (1—)2—6(—8)-flowered inflorescence. Stolons often lacking, if present very short or up to 10 mm long, 0.5—1 mm thick, pale or green, epigean, with a few small, usually scale-like leaves. Turions formed at the ends of stolons or apparently directly in the axils of basal leaves, as loose rosettes of leaves 2—10 mm long. Specimens sometimes apparently branched basally because of the proliferation of several turions from the same old stem base.

Stem 1—2 mm thick, terete, at least in the lower part with 4 weak ridges or lines below midribs and leaf margins. Two rows of hairs below the leaf margins, hairs 0.1—0.3 mm, usually all eglandular, incurved, rarely some erect, glandular ones in the upper part.

Most leaves usually opposite, upper ones alternate, all petiolate, petioles 0.5—4(—8) mm, longest in lower cauline leaves, bases uniting around the stem but never decurrent. Basal leaves smaller, spathulate to obovate or elliptical. Middle and upper leaves (10—)15—35(—40) mm long, (3—)5—12(—15) mm broad, all ovate or often some middle ones elliptical, uppermost ones ovate to narrowly ovate, middle ones usually broadly obtuse, upper ones acute. Bracts smaller than the other leaves, upper ones often very small, not con-

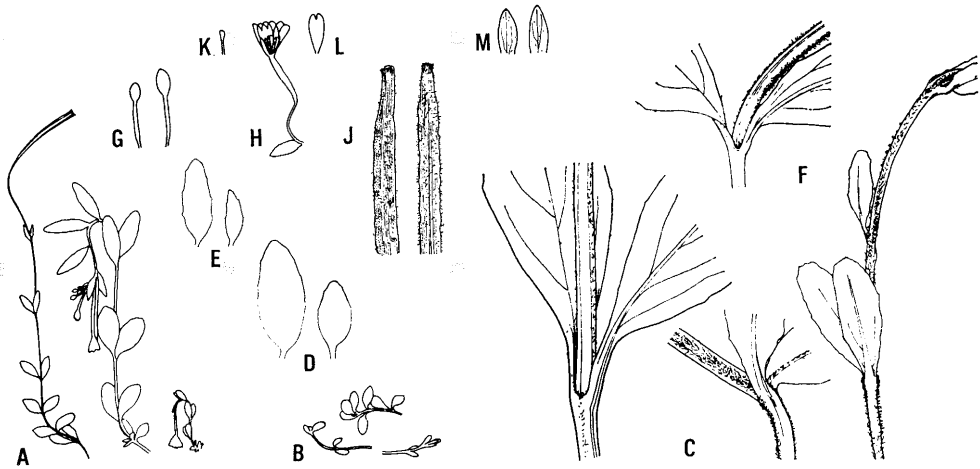

Fig. 108. *Epilobium anagallidifolium* LAM. — A: Habit, ×1/3. — B: Stolons, ×1/2. — C: Stem nodes, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem parts with leaves, ×2.5. — G: Buds, ×1. — H: Flower, ×1. — J: Apical part of capsules, ×2.5. — K: Style, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.

cealing the buds. Lower and middle leaves subentire or serrate with small teeth more numerous in the middle part of the margin or uniformly distributed, upper leaves always serrate. Leaves subglabrous, hairy only on adaxial side of the midrib and on the margin, hairs like those of the stem though smaller.

Inflorescence almost erect even when young, though often bent in dried material. Pedicels erect to erecto-patent in relation to axis in all stages, or often the young capsule ± pendent due to bending of the pedicel. Buds subglobose, with a distinct, blunt tip. Sepals (2.8—)3.5—4.5(—5) mm, connate to 1—1.5 mm, narrowly ovate, acute or rarely obtuse, pure green or more or less reddish, sparsely glandular-hairy. Petals (3—)4.5—5.5(—7) mm, notched to c. 1 mm, white, pinkish-white or rarely pinkish violet. Anthers 0.45—0.55 mm, long filaments 2.5—3.5 mm, short filaments 1.5—2.5 mm. Style equalling or shorter than the long stamens, stigma capitate.

Capsule stalk (10—)15—30(—40) mm. Capsule 35—50(—60) mm, young ovary sparsely to densely glandular-hairy, hairs erect, 0.1—0.2 mm. Seeds narrowly obovoidal with one markedly flattened side, (1—)1.2—1.35(—1.4) mm long, 0.35—0.45 mm broad, with an acutely tapering base and a blunt apex, neck 0.05—0.15 mm, surface with many rows of very flat papillae, thus often apparently smooth, chalazal hairs c. 40, 7—9 mm long. Flower homogamous.

E. lactiflorum occurs in wet meadows and fens, rarely along watercourses. It is found up to 1600 m in the southern part of the mountains, to 900 m in the north.

E. lactiflorum has a discontinuous circumpolar distribution. It is rather common in the mountains and in the arctic parts of Scandinavia, with isolated occurrences in the lowlands southwards to 60.5° N in Sweden, in Finland only occurring in the extreme north.

Known hybrids: with *E. alsinifolium, anagallidifolium, davuricum, hornemannii, montanum* and *palustre*.

108. **Epilobium anagallidifolium** LAMARCK 1786

Perennial herb, (2—)5—15(—20) cm high. Stem unbranched, producing one 1—3-flowered inflorescence. Stolons usually present, epigean, 5—20(—50) mm long, c. 0.5 mm thick, rarely branching, with opposite, widely spaced leaves 2—10 mm long. Turions formed at the end of the stolons as loose rosettes of green leaves 2—10 mm long.

Stem terete, 0.5—1(—1.5) mm thick, in the basal part with 4 low ridges or lines below midribs and leaf margins. Two rows of hairs below leaf margins, especially in the upper part, hairs 0.1—0.3 mm, all eglandular, recurved, or also some erect, glandular ones within the inflorescence.

Basal and middle leaves opposite, upper ones alternate, all petiolate, 0.5—3(—10) mm, longest in the middle leaves, bases uniting around the stem, but never decurrent. Basal leaves smaller, obovate to spathulate. Middle and upper leaves 5—20(—25) mm long, 2—5(—10) mm broad, ovate to elliptic, all obtuse or the upper ones acute, lower ones subentire, upper ones serrate with few, short, irregular teeth. Bracts usually smaller than the middle leaves, not concealing the buds. Basal and middle leaves glabrous to subglabrous, upper ones sparsely hairy on adaxial side of midrib and the margin, hairs usually less than 0.15 mm, mostly eglandular, recurved, rarely also a few erect, glandular ones.

Inflorescence characteristically nodding when young, in fruit strictly erect. Pedicels erect in relation to the axis in all stages. Buds broadly ellipsoidal to ovoidal, obtuse. Sepals 3—4 mm, connate to c. 1 mm, narrowly ovate, acute, reddish, sparsely glandular-hairy. Petals 3.5—6 mm, notched to 0.5—1 mm, reddish or pinkish-purple. Anthers 0.3—0.4(—0.5) mm, long filaments 2.5—3 mm, short filaments 2—2.5 mm. Style equalling or slightly exceeding the long stamens, stigma capitate.

Capsule stalk (6—)20—40(—50) mm. Capsule 20—30(—35) mm, young ovary sparsely hairy, with both glandular hairs and basally some eglandular, incurved ones, hairs 0.1—0.2 mm, ripe capsule subglabrous. Seeds narrowly obovoidal, with one markedly flattened side, 0.8—1.1 mm long, 0.35—0.4(—0.5) mm broad, with an acutely tapering base and a blunt apex, neck c. 0.5 mm, surface with many rows of small, flat papillae, chalazal hairs 40—50, 3—4 mm long. Flower homogamous.

E. anagallidifolium occurs on the banks of watercourses, on wet slopes, meadows and snow-beds. Mainly in the alpine and arctic zones, to 1750 m in the S mountains, to 1100 m in the north.

E. anagallidifolium has an arctic-alpine circumpolar distribution. In Scandinavia it is rather common throughout the mountain chain and in the arctic coastal areas, with only few, scattered localities along watercourses in the northern lowlands.

Known hybrids: with *E. hornemannii, lactiflorum* and *palustre.*

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Interrelationships of the Subfamilies of the Ericaceae and Derivation of the Monotropoideae

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WALLACE, G. D. 1976 02 09. Interrelationships of the subfamilies of the Ericaceae and derivation of the Monotropoideae. — Bot. Notiser 128: 286—298. Lund. ISSN 0006-8195.

The mycoparasitic Monotropoideae and other subfamilies of the Ericaceae were examined to clarify the position of the former in this family. There are few, if any, absolutely distinctive characteristics in any of the subfamilies. Excluding the features associated with mycoparasitism, the Monotropoideae have features found among other members of the Ericaceae. Based on their floral biology, nature of the stamens and particularly anthers, embryology, phytochemistry and other features, the Monotropoideae are most closely allied to the Arbuteae of STEVENS' (1971) Vaccinioideae. STEVENS' concept of the Vaccinioideae (i.e. including Vaccinieae and Arbuteae) is accepted here.

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The aim of this paper is to clarify the taxonomic position of the Monotropoideae with respect to the rest ot the Ericaceae. The possibility of derivation of the subfamily from other groups of the Ericaceae will be discussed. The Monotropoideae and Pyroloideae are usually placed in or near the Ericaceae and close to one another. There remains, then, to be determined how much taxonomic divergence, in this case, is allowable to a subfamily and how much is allowable before a subfamily should be elevated to familial status. A newly erected family would, of course, be closely allied to the family from which it is segregated since the mere act of separation of two taxa should not inherently alter the taxonomic distance which precipitated the division. The greater the number of characteristics common to the Monotropoideae and the other members of the Ericaceae, the closer the two groups should be placed to one another and the less tenable would be a shift to a different status. This assumes the use of taxonomically relevant characters. Many of the earlier classifications of the Monotropoideae were either based upon incomplete information or incorrect interpretations of available data. Rarely has adequate material of all the species been available for study. Even though most classifications have put the Monotropoideae close to the Pyroloideae, there is no particular reason to believe that they were derived from the Pyroloideae. The Pyroloideae may represent quite a different line of the Ericaceae. Comparative data for each of the six subfamilies THORNE (1968) recognized in the Ericaceae are given in Table 1.

The mycotrophic, achlorophyllous species which comprise the Monotropoideae have usually been considered saprophytes. More recent studies (BJÖRKMAN 1960, FURMAN & TRAPPE 1971) have shown evidence of the existence of fungal bridges between the mycotrophs and the host species. This habit could be termed mycoparasitism to differentiate it from other forms of parasitism and to draw attention to the integral role played by the mycor-

rhizae. The 12 species of the Monotropoideae are distributed among 10 genera. This may be compared with the nearly 40 species in three (two to four) genera of the Pyroloideae and the approximately 100 genera and 2,500 species of the rest of the Ericaceae. A description of the Monotropoideae and one for each of the included species has been provided in another paper (WALLACE in press). Any study to determine the relationships of the Monotropoideae must take into account those characteristics related to their mycoparasitic habit. Such features could be expected to be interrelated. There is no reason to doubt that there have been normal evolutionary pressures upon pollination mechanisms and propagule dispersal systems of the Monotropoideae.

There are a few other families in which there are mycoparasites. A rather complete list of the genera, by family, was given in FURMAN and TRAPPE (1971). In each of the families considered, except the Triuridaceae, the majority of the species are chlorophyllous. The mycoparasitic *Epirixanthes* BLUME differs from autotrophic *Salomonia* LOUR., both of the Polygalaceae, only in habit (KENG 1969). The former genus is the only case of mycoparasitism in the Polygalaceae. WILLIS (1973) combined the two genera in *Salomonia*. *Petrosavia* BECC. is the only mycoparasitic genus placed in the Liliaceae by THORNE (1968) and FURMAN and TRAPPE (1971). *Protolirion* RIDL., listed by the latter authors, is synonymous with *Petrosavia*. WILLIS (1973) considered the genus a monotypic family. There are about 200 species among the mycoparasitic genera of the Orchidaceae noted by FURMAN and TRAPPE (1971). They also list six genera of the Gentianaceae which include over 50 mycoparasites. The Triuridaceae is the only family composed entirely of mycoparasitic species. STANT (1970) stated that she would have no objections to placement of *Petrosavia* in the Triuridaceae on the basis of anatomical evidence. This could be a case of convergence of habit. The family Burmanniaceae is interesting in that mycoparasitic species outnumber autotrophic species. There are about 14 genera of mycoparasites and only *Burmannia* has chlorophyllous and achlorophyllous species. In *Burmannia*, JONKER (1938) treated 23 of the 57 species as saprophytic, here termed mycoparasitic. Only the Triuridaceae have apparently diverged too far to be allied with any close autotrophic relatives.

PREVIOUS TAXONOMIC TREATMENT

The members of the Monotropoideae, historically, have been placed in several taxonomic positions close to the Ericaceae. NUTTALL (1818) was one of the first botanists to unify the known genera of the Monotropoideae. He erected a separate family, his "natural order", the Monotropeae (sic). NUTTALL noted the similarities among the seeds of *Monotropa* L., *Hypopithys* SCOP., and *Pterospora* NUTT., the genera he knew and accepted, and those of *Pyrola* L. He considered the form and distribution of the anthers of the three genera sufficiently different, however, to warrant their separation from *Pyrola* as a family. NUTTALL claimed that *Monotropa* had a "monopetalous" corolla that was separate to the base, which appeared then as separate petals. The petals are, in fact, entirely separate in *Monotropa*. DESVAUX (1827) treated the Monotropoideae as a family, the Semicirculaceae, apart from the Ericaceae. *Monotropa hypopithys* L. was the only member of the family. LINDLEY (1836) elevated both the Pyroloideae and Monotropoideae to separate families. His Monotropaceae differed from the Pyrolaceae in that its members had straight styles, longitudinally dehiscent anther sacs, leafless stems, apparently sympetalous corollas, and were parasitic plants. DE CANDOLLE (1839) reasoned the group to be a segregate family, pointing out the lack of terminal pores in anthers and the difference in

Table 1. Comparative data on the Monotropoideae and other subfamilies of the Ericaceae. The subfamilies are those recognized by THORNE (1968). Data are drawn from the descriptions of over 100 genera, many of which were assigned to subfamilies by STEVENS (1971); additional genera were assigned by the author. The Vaccinioideae s. str. indicates my view that the Arbutoideae should be included in the Vaccinioideae as the Arbuteae. Most data on the Monotropoideae were obtained from studies of the group by the author. Data in Table 1 were also obtained from the following sources: ABRAMS 1951, ANDERSON 1959, BAKER & OLIVER 1967, BOLUS, GUTHRIE & BROWN 1909, BULLOCK 1954, BUSH 1967, DAVIS 1966, ERDTMAN 1952, HITCHCOCK, CRONQUIST & OWNBEY 1959. HOOKER 1882, HULTÉN 1968, MACBRIDE 1959, MARLOTH 1932, MEISNER 1863, MUNZ 1974, MUNZ & KECK 1959, OHWI 1965, OLIVER 1877, PALSER 1954, 1958, SLEUMER 1966, SMITH 1932, 1933, STANDLEY & WILLIAMS 1966, STEARN 1972, WEBB 1972, WOOD 1961.

Pyroloideae	Monotropoideae	Arbutoideae	Vaccinioideae s. str.	Rhododendroideae	Ericoideae
DISTRIBUTION					
N temp.: Euras. N & C Am.; W.I.	N temp. or mont. zones of N trop. Am., espec. W Am.; Eur.; E & S As.	N circumpolar; temp. N,C, & S Am.; E & S As. Himal., Malesia; Circumpacific, Tasm., N.Z., Galap. IS, Falk., W As., Eur., Med.	temp. Am. & mont. zones of trop. N, C, & S Am., Andes, W.I.; SE As., N. Gu., Malaya; S Afr., Madag.; Qld., Fiji; some Pac. Is; arctic	N circumpolar; temp. & trop. As. & Am.; S & E As., Himal.; N. Gu. & other Pac. Is; Atl. Eur., Azores; Austr.	S Afr., Madag., trop. Afr.; Med. Eur., some Atl. Is; As. Min., Syria; (Atl. N Am.).
HABIT					
per., herb to slightly woody, evergr. rarely achlorophyllous herbs with creeping rhizomes, terr. Lvs. alt., or whorl.; coriaceous or thin marg. ent. to dent. or ser.; oblan., ellip. or ovate; petiolate; us. glab	per., herb., achlorophyllous herbs; roots creeping to variously clustered. Lvs. absent, axill. appendages are sterile bracts. Inflor. annual & the only above ground parts	per., woody, evergr. (—decid.) erect to prostr. subshrubs to sm. trees, rarely lian.; oft. thin exfol. bark; occas. bog or epiphy. pls. Lvs. alt., opp. or whorl.; coriaceous or thin & decid.; marg. ent., ser. or cren. oft. revol. linear to ovate, ellip.; petiolate, occas. sessile; oft. glab.; winter buds scaled	per., woody, evergr. (—decid.) erect to prostr. shrubs to sm. trees, oft. epiphy., occas. stolonif. Lvs. alt.; oft. small; coriaceous, occas. thin; marg. ent., ser., or cren.; oblan. to ovate etc.; petiolate, occas. sessile; oft. gland. pubes. winter buds scaled	per., woody, evergr. to decid. erect to prostr. shrubs to sm. trees rarely epiphy. Lvs. alt., opp., or whorl.; coriaceous or thin & decid.; marg. ent. to revol.; oval, obovate, ellip., to narrow; petiolate rarely sessile; some gland. pubes.; winter buds scaled	per., woody, evergr., erect to prostr. shrubs. Lvs. us. whorl., rarely opp.; coriaceous; marg. revol. or channeled; back convex; mostly narrow; short petiolate; no winter buds formed
INFLORESCENCE					
racem. to corymb.; one- to several-fl.; bracteate; term.	racem., occas. condensed or scapose; one- to few- or many-fl.; bracteate	racem., panic., or corymb. rarely fascic.; one- to several- or many-fl.; oft. bracteate; term. occas. axil.; rarely perulate	racem., corymb., or panic.; one- to few- (or many-) fl.; some bracteate; us. axil. some term.; some perulate	racem., corymb. or panic., one to several fl.; bracteate; term. occas. axil.; some perulate	variously clust.; oft. one to few fl. per head, racem. or panic.; some bracteate; term., axil., or variable; not perulate

Table 1 (continued).

Pyroloideae	Monotropoideae	Arbutoideae	Vaccinioideae s. str.	Rhododendroideae	Ericoideae
FLOWER					
actino. to zygo.; med.-sized; pedicel.; ebracteolate; bisex.	actino.; med. to sm.; pedicel.; rarely bracteolate; bisex.	actino.; rather sm.; pedicel.; us. bracteolate; bisex. *Pernettya mucronata* funct. dioecious	actino.; oft. sm. to med.; pedicel., oft. articulate; bracteolate; bisex	actino. to zygo.; lg. to sm.; oft pedicel.; us. bisex. *Epigaea* funct. dioecious. us. bracteolate	us. actino.; sm. to larger; us. pedicel.; some bracteolate; bisex.
PERIANTH					
5-merous; calyx of persist. coriaceous, basally unit. sepals; imbric. in bud. Corolla of sep. concave petals; saucer-shaped to shallow campan.; us. decid.	5 (3—6)-merous; calyx of persist. coriaceous or thin, decid. sepals; imbric. in bud. Corolla of sep. or unit. petals; open campan., cylind. or urceo.; decid. or persist.	5, rarely 4—8-merous; calyx of persist. us. coriaceous, us. unit. sepals; Imbric., valv. or quin. in bud; some accrescent in fruit. Corolla of unit. petals; urceo., campan., ovoid or cylind. persist. or decid.	5, seldom 4-merous; calyx occas. winged, of persist. us. coriaceous, unit. sepals; campan. or cup-shaped; occas. adnate to ovary, some angled. Corolla of unit. petals; ovoid, urceo., tub.or campan.; rarely angled; decid. or perist.	5, 4 (6—8)-merous; calyx us. of persist., coriaceous, sep. to unit. sepals; us. imbric. in bud. Corolla of unit. or sep. petals; saucer shaped, campan., rotate, occas. tub. or urceo.; decid. or perist.	4 (3)-merous; calyx us. of persist., coriaceous, unit. occas. sep. sepals; campan. to tub.; oft. one sepal larger; oft. 4-angled. Corolla of unit. (occas. sep.) petals; campan., urceo. or variable; persist. (or decid.)
ANDROECIUM					
stam. 10; us. incl.; hypog. Fil. free or not; glab. or pubes.; oft. incl. to one side of fl.; some dilated at base; gen. flat.	stam. 10 (6) or irreg. more; incl.; hypog.; oft. of alt. uneq. lengths. Fil. free; pubes. or glab.; some dilated at base; terete to flat.	stam. 10, rarely 8; incl.; hypog. rarely basally epi. Fil. free; us. pubes. & dilated at base; terete to flat.; some geniculate	stam. 10 (8) rarely 4, 12; incl.; hypog. or basally epi.; some of alt. uneq. lengths. Fil. free or con.; glab. to pubes.; some dilated at base; terete to flat; some geniculate	stam. 10—(5, 8), rarely 4—25; incl. to exser.; us. hypog.; oft. of alt. uneq.lengths. Fil. free; glab. to cil.; some dilated at base; some incl. to one side	stam. 4, 8, occas. 3—6; us. incl.; us. hypog. Fil. free to variously con.; us. glab.; some geniculate
ANTHER					
oblong, elong.; awnless; dehis. by pores, dist. occas. horned or short-tubed	glob. to linear; rarely awned; dehis. by term. or oblique gaping slits or longi.	oblong to oval; oft. awned; dehis. by pores, occas. slits, these oblique-term.; some with tubules	oblong to oval; occas. awned; dehis. by term. clefts, pores or short slits; tubules present	ellip., oval to linear; awnless; dehis. by term. or lat. longi. slits, or term. pores	oblong to elong.; awned or not; dehis. by slits, term. or lat. pores; sacs free or con.
POLLEN					
tetrads, rarely monads; no "viscin" strands	monads; no "viscin" strands	tetrads; no "viscin" strands	tetrads; no "viscin" strands. *Enkianthus* monad	tetrads; us. "viscin" strands present	tetrads, rarely monads; no "viscin" strands

Table 1 (continued).

Pyroloideae	Monotropoideae	Arbutoideae	Vaccinioideae s. str.	Rhododendroideae	Ericoideae
GYNOECIUM					
ov. sup.; us glab.; 5 loc.; plac. axile may appear pariet. above; style straight or declined to one side, apex upturned; stigma peltate or lob. Nect. pres. or not	ov. sup.; pubes. to glab.; 1, 5, 4 (6) loc.; plac. axile or "intruded" pariet.; style straight, elong. to column., incl.; stigma disc. to funnel-formed. Nect. pres. lob. or low ridges	ov. sup., rarely half infer.; 5 (4—10) loc.; plac. axile, apical or pendulous; style straight, elong., some exser.; stigma minute, simple, truncate or obtuse. Nect. oft. pres.	ov. infer.; 5 (3 or falsely 8—10) loc.; plac. axile or cent. etc.; style filiform, straight, us. incl.; stigma truncate to obtuse. Nect. pres.	ov. sup., rarely emmersed; 4—5 (2—7) loc.; plac. us. axile; style oft. straight, short to long, some declined to one side; stigma cap., glob. or obscur. lobed. Nect. pres.	ov. sup. rarely half infer.; 2—4 (1, 8) loc.; rarely stipitate; plac. oft. cent.; style straight oft. exser.; stigma simple, peltate, rarely 4-fid or cap. Nect. oft.pres.
OVULE					
numer. per loc.; anatrop.; unitegmic; tenuinucellar	numer. per loc.; anatrop.; unitegmic; tenuinucellar	one to numer. per loc.; anatrop. to campy.; unitegmic; tenuinucellar	one to several per loc.; anatrop. to campy.; unitegmic; tenuinucellar	us. numer. per loc.; anatrop.; unitegmic; tenuinucellar	one to several per loc.; us. pendul.; unitegmic; tenuinucellar
FRUIT					
capsular, loc. dehis.; cent. column persist. Seeds minute, spindle-shaped	baccate & indehis. or capsular & loc. dehis., us thin-walled; gen. glob. to elong. Seeds minute, ovoid to spindle-shaped; winged or not	capsular, loc. dehis., some thin-walled or baccate to drupaceous & indehis.; some glob. Seeds small, ovoid to elong., winged or not; variously aggregated nutlets	baccate (or drupaceous), indehis. Seeds small ellips. to lentic. not winged	capsular, sept. dehis.; oft. elong. Seeds minute, ovoid to linear, winged or not	capsular, loc. dehis.; rarely somewhat fleshy; *Calluna* sept. Seeds minute, ellips. rarely lentic.; rarely winged

numbers of perianth segments in terminal versus lateral flowers. He inferred relationships among his Monotropaceae, *Pyrola aphylla* SMITH in REES, and *Cladothamnus* BONG. BENTHAM and HOOKER (1876) elevated the Monotropoideae, but not the Pyroloideae, to familial status. They supposed the Monotropoideae to be root parasites. They also recognized a link among their Monotropeae, Ericaceae, and Pyroloideae through *Pyrola aphylla*. The Monotropaceae of SMALL (1914) were noted to possess simple pollen grains. He judged the members to be saprophytes and that their ovaries were either 1- or 4—6-celled. The baccate fruits of some of the members were still poorly known at that time and SMALL noted that the fruits of some were merely somewhat fleshy. Recently CRONQUIST (1968) also recognized Monotropaceae. He lists lack of chlorophyll, lack of leaves, presence of longitudinally dehiscent anthers, monad pollen, and variable placentation as differentiating characteristics. EICHLER (1875) was the only author to treat the Monotropoideae as a subfamily of the Hypopityaceae (sic). Similarly ROUY (1897) considered the Pyroloideae and Monotropoideae subfamilies of his Monotropaceae. The Monotropoideae was considered a tribe of the Ericaceae by D. DON (1834). He characterized the group as having unilocular anthers, peltate seeds, and as being leafless, parasitic herbs. BAILLON (1891) separated the genera which make up the Monotropoideae into two series, the Monotropées and the Pterosporées which he subordinated to the Ericaceae. The two series were distinguished by whether or not the corolla was sympetalous.

Usually the Monotropoideae is placed as a subfamily of the Pyrolaceae or Ericaceae. DRUDE (1889) put the subfamily into the Pyrolaceae. He noted that the Pyroloideae had reflexed anthers with apical dehiscence at anthesis and pollen in tetrads. His Monotropoideae had erect anthers with united, ring-shaped or hippocrepiform slits and monad pollen. DRUDE's treatment was used by SCHULTZE-MOTEL (1964). LAWRENCE (1951) stated that the Pyrolaceae, in which he included the Monotropoideae and Pyroloideae, differed from the Ericaceae by their herbaceous habit, corolla of distinct petals, and loculicidally dehiscent capsule. There are some exceptions to each of these characteristics. *Chimaphila umbellata* (L.) BART. and *C. maculata* (L.) PURSH are somewhat woody; *Hemitomes* GRAY, *Monotropsis* SCHW. in ELL., *Pterospora,* and *Sarcodes* TORR. have sympetalous corollas; and *Cheilotheca* HOOK. FIL., *Hemitomes, Monotropastrum* H. ANDRES, *Monotropsis, Pityopus* SMALL, and *Pleuricospora* GRAY have baccate fruits. The author has considered the Monotropoideae a subfamily of the Ericaceae in a previous paper (WALLACE in press). This position had also been taken by several earlier authors (HENDERSON 1919, COPELAND 1939, 1941, 1947, THORNE 1968, STEVENS 1971). HENDERSON (1919) allied the Monotropoideae and Pyroloideae to the Ericaceae in a series characterized by increasing saprophytism. This increasing saprophytism was accompanied by anatomical and morphological change. She noted that except for their saprophytism, the supposed differences among the Monotropoideae, Pyroloideae and Ericaceae broke down when viewed carefully. COPELAND (1939) followed JEPSON (1925) in placing the Monotropoideae and Pyroloideae in the Ericaceae, admitting his uncertainty of their true relationships. In two later papers COPELAND (1941, 1947) maintained this position but gave reasons for treating the two subfamilies as tribes of the Arbutoideae of the Ericaceae. THORNE (1968) did not elaborate on his reasons for placement of the Pyroloideae and Monotropoideae in the Ericaceae. STEVENS (1971) stated that in placing the two subfamilies in the Ericaceae he followed COPELAND (1941, 1947) and HENDERSON (1919). He asserted that several characteristics and observations utilized by DRUDE (1889) in

his classification of the groups were incorrect.

DISCUSSION

The subfamily Monotropoideae has usually been considered to be close to the Ericaceae. The question is whether they should be included in the Ericaceae. The following will include a discussion of some of the information provided in Table 1. Other data, whose presentation is not enhanced by a tabular format, and a brief discussion on the acceptability of some of the other subfamilies and their members will be included.

The Pyroloideae and Monotropoideae are restricted to the Northern Hemisphere. The Ericoideae, apparently indigenous only in the Old World, has the Cape Province of Africa as its center of diversity and is infrequently represented outside Africa in comparison. The Rhododendroideae, Vaccinioideae, and Arbutoideae are also probably of northern origin but are widespread in the New and Old Worlds. The center of diversity for the Monotropoideae is western North America. Five genera are restricted to this area and two of the other five are found there. Some of the species are seldom collected.

Many modifications of the Monotropoideae are related to their mycoparasitic habit. These include reduced herbaceous habit, presence of nonphotosynthetic sterile bracts instead of leaves and associated features, and lack of above ground vegetative buds. The only above ground portions of the species are the annual inflorescences. These reproductive structures represent the most noticeable portions, and not surprisingly the major source of taxonomic data of the species. SLEUMER (1966) pointed out that sterile material of any members of the Ericaceae is of little value because the most useful information is to be found in the characteristics of the reproductive structures. WATSON (1965) based some suggested taxonomic alterations within the Ericaceae upon stomatal characters and few other features. Some of his other data do not seem to support changes suggested by his stomatal data, particularly in the case of removal of the Phyllodoceae from the Rhododendroideae (HARBORNE & WILLIAMS 1973, IKUSE 1954).

Floral Biology

Several features utilized in taxonomic delimitations of members of the Ericaceae may be directly related to specialized pollen presentation mechanisms. Awned, shaker-type anthers; narrow orificed, urceolate corollas; and pollen lacking "viscin" (sporopollenin) strands are found primarily in the Ericoideae and Arbutoideae. The constricted mouth of the corolla with awned anthers presented just below its narrowest portion may be selective for particular insects or may spatially restrict entry so pollen will not be wasted. The anthers are disturbed, in their pendulous position, when the insect visitor pushes on the anthers or awns trying to reach the nectar at the base of the flowers. Pollen will normally be shaken out at this time. Autogamy, usually effected in later stages of anthesis, has been described for some species in the Ericaceae with pollen presentation mechanisms of this type (HAGERUP 1954, KERNER VON MARILAUN, 1894—95). The more flaring flowers of the Rhododendroideae have awnless anthers and "viscin" strands among the pollen grains. The pollen thus held in aggregates may become tangled in the feet or other body parts of insects and transferred to the sticky stigma. The comparisons noted in Table 1 reflect characteristics of extant members of the Ericaceae and include data on specialized features of the above types. These specializations may hinder any attempt at erecting a natural arrangement of the Ericaceae. For this reason care must be taken to consider data from many potentially useful features before tentative lines of development are drawn.

Stamens

The range of characters associated with the androecium and anthers of the Monotropoideae may usually be found among the other subfamilies of the Ericaceae as well. Anther dehiscence varies greatly in most of the subfamilies. Monad pollen occurs in five genera of the Ericoideae, one of the Vaccinioideae, one of the Pyroloideae, and all ten genera of the Monotropoideae. Characteristics of anthers are of particular taxonomic value in the Ericaceae. These may exhibit a wide range of forms depending upon the pollen presentation mechanism peculiar to the taxon concerned. The general form of the ericaceous stamen is, however, relatively uniform. MATTHEWS and KNOX (1926) noted that the stamens, of members of the Ericaceae, have a single trace which usually curves from the connective toward the distal portion of the anther, whether or not it is termed the apex or base of the anther. They chose the latter term. In most of the stamens they depicted, the trace was unbranched and generally occupied the most massive or isolated areas of sterile tissue in the anthers. In *Daboecia polifolia* D. DON, as might be expected, the much elongate anther sacs are provided with a trace between them, which MATTHEWS and KNOX termed a subsidiary trace. This strand is found toward the porous end of the anther. This would be consistent with CARLQUIST's (1970) emphasis on the probability that relative size and duration of the stamen determine the amount of vascularization. In many cases in the Ericaceae, the anthers at maturity are positioned with their distal portions directed toward the base of the ovary on the adaxial sides of the staminal filaments. COPELAND (1943) noted that the anthers of the members of the Rhododendroideae were developed in, rather than moved to, the position described above. The anthers of *Erica hirtiflora* CURT. were described by MATTHEWS and TAYLOR (1926) as developing with their distal portion directed toward the base of the ovary. These do not undergo late anther inversion. In this respect they are similar to the anthers of the Rhododendroideae described by COPELAND (1943). This is the most frequently encountered situation among the other members of the Ericaceae. Flowers of some members of the Arbutoideae mentioned by MATTHEWS and KNOX (1926) develop with the distal portions of the anthers directed toward the still closed floral orifice and invert during the latter stages of their development to attain the same positions as the anthers of other Ericaceae. COPELAND (1943) mentioned species of *Pyrola* and *Arctostaphylos* ADANS. whose staminal development would conform to this description.

There are several types of stamens found among the members of the Monotropoideae. *Cheilotheca, Hemitomes, Monotropa hypopithys, Pityopus, Pleuricospora,* and *Sarcodes* have straight filaments topped by erect, linear or hippocrepiform anthers which undergo no movements like those described above. *Allotropa* TORR. & GRAY ex GRAY in NEWBERRY, *Monotropa uniflora* L., *Monotropastrum, Monotropsis,* and *Pterospora* have relatively straight filaments topped by globose or variously shaped anthers, but these are not linear. The distal portions of these anthers are horizontally directed toward the style. During their maturation, the distal portions of the anthers may bend downward slightly, but usually less than 90° from the horizontal, so that it approaches a position more directed toward the floral base. The inversion in these species of the Monotropoideae is not considerable and in some cases may be achieved by the reflection of the stamens allowed by the expansion of the corolla at anthesis. The ovaries of *Allotropa, Monotropa uniflora, Monotropastrum, Monotropsis,* and *Pterospora* are rather globose or oblate spheroidal. In bud, the anthers usually occupy the space in the angle between the apex of the ovary and the straight style. In most

of the other species of the Monotropoideae the ovaries are more elongate and the stamens lie along side of and parallel to the style. This latter condition is found in many members of the Ericaceae in which there is little or no movement of the anther in relation to the mature expanded filament. The movement is more pronounced in some species of the Pyroloideae. In *Moneses* SALISB. the angle through wich the anther must deflex is greater than that encountered in any species of the Monotropoideae. The anthers of *Moneses* are also provided with short tube-like channels. Movement of the maturing anthers atop the filaments may serve to orient the extending awns, possessed by many of the species, to a position where the awns are against the corolla. The slight movement of some of the anthers of the Monotropoideae is all that is required to orient the dehiscence openings of those species. Many species with urceolate corollas do not have anthers which undergo any degree of inversion. These are most frequent among members of the Vaccinioideae. In these, the anthers are provided with elongate dehiscence tubules which would, in most cases, spatially preclude any inversion movements of the anthers. The inversion would be detrimental anyway since the apparent purpose is to align the dehiscence openings of the anthers toward the floral orifice. MATTHEWS and KNOX (1926) further noted that many taxa in the Vaccinioideae have, in addition to the tubules, appendages on either their filaments or anthers. These appendages are of variable position, and would serve to orient the anthers. In the Ericoideae, some species with included stamens but awnless anthers have filaments that are curved to make contact with the corolla and thus provide the necessary support for the orientation of the anthers. STEVENS (1970) reported the presence of curved filaments, which he called geniculate, in several genera of the Andromedeae. These were also noted in a later paper (STEVENS 1971). The stamens and anthers of the Monotropoideae seem to be most closely allied to those of the Arbutoideae. Among the members of the Monotropoideae only *Pterospora* has an urceolate corolla and awned anthers.

Pollen

The distribution of bi- and trinucleate pollen grains among the mycoparasites and other angiosperms is of interest but of uncertain significance. BREWBAKER (1967) included a long list of taxa and their type of pollen. He considered trinucleate pollen grains the advanced type. Binucleate pollen grains predominate in the angiosperms and among mycoparasitic genera. BREWBAKER listed *Neottia* GUET. of the Orchidaceae, *Salomonia* LOUR. of the Polygalaceae, and the Monotropoideae and Pyroloideae of the Ericaceae as having binucleate pollen grains. The Triuridaceae, as well as *Apteria* NUTT. (Burmanniaceae) and two chlorophyllous species of *Burmannia* L., are trinucleate. He listed two mycoparasitic species of *Burmannia* as binucleate. BREWBAKER'S list included relatively few genera of these families so the prevalence of either type of pollen is unknown. This would be necessary for proper comparisons in light of other taxonomic evidence to determine the significance of this type of information. *Enkianthus* LOUR. is the only genus of the Ericaceae known to possess trinucleate pollen grains.

Embryology

All the features associated with the gynoecia of members of the Monotropoideae may be found elsewhere in the Ericaceae. Characteristics of the ovules are almost uniform throughout the Ericaceae. On the basis of her embryological work DAVIS (1966) separated the Monotropaceae and Pyrolaceae from the Ericaceae. For the purpose of this discussion data for her three families will be considered as though it were for a united family, the Ericaceae.

DAVIS noted several embryological characteristics. The ovules are anatropous, unitegmic, and tenuinucellate except in some of her Ericaceae where the ovule may be nearly campylotropous. The archesporial cell functions directly as the megaspore mother cell and cytokinesis accompanies meiosis. Some members of DAVIS's Ericaceae vary in the latter characteristic. The chalazal megaspore of a usually linear tetrad develops into a *Polygonum*-type embryo sac. Endosperm formation is *ab initio* cellular in almost all cases. Embryogeny is of the caryophyllad type in DAVIS's Pyrolaceae and Monotropaceae but of the solanad type in the Ericaceae. The difference may represent a reduction of the embryo from the solanad type in which the basal cell forms a suspensor for two or more cells, to the caryophyllad type in which the basal cell undergoes no further divisions (MAHESHWARI 1950).

Data from GANAPATHY and PALSER (1964) and STUSHNOFF and PALSER (1969) indicate that the embryos of members of the Ericaceae, except for the Pyroloideae and Monotropoideae, are linear and have two short cotyledons. COPELAND (1947) stated that the embryos of the genera he put in the Pyroleae (*Pyrola, Chimaphila* PURSH, and *Moneses*) failed to form any distinct parts. According to JOHANSEN (1950), the mature embryo of *Monotropa hypopithys* consists of about nine cells. TEREKHIN (1963) claimed that the embryo and endosperm in the Pyroleae and Pterosporeae consisted of about 30—40 cells. Embryos of species of the Pyrolaceae (including *Monotropa*) studied by PYYKKÖ (1968) were reportedly undifferentiated and embedded in endosperm. COPELAND (1947) had reported that the embryos absorbed most of the endosperm. The reduction of the embryos of the Monotropoideae and Pyroloideae is in keeping with their reduced stature and habit. It seems likely that in both subfamilies infection by the mycorrhizal fungi occurs soon after the seeds are shed. This may alleviate the necessity for abundant endosperm. MAHESHWARI (1950) provided a list of embryological features common to the Ericales. PALSER (1961) expanded this list. There are some minor exceptions to some of the noted features in her list.

Phytochemistry

HEGNAUER (1966 a) recorded the occurrence of several compounds among the members of the Ericaceae. The diterpenes are the toxic constituent of the Ericaceae. Andromedotoxin, one of these, has been isolated from members of the Rhododendroideae and Arbutoideae but was not found among the few species of the Ericoideae, Vaccinioideae, and Pyroloideae investigated. It was, however, found in *Monotropa uniflora*, the only member of the Monotropoideae investigated. HEGNAUER (1966 b) mentioned the presence of arbutin in *Arbutus* L., *Arctostaphylos, Pyrola,* and *Vaccinium* L. All members of the Pyroloideae and Monotropoideae were said to possess monotropeoside.

Gossypetin was recognized as a useful taxonomic marker by HARBORNE and WILLIAMS (1973). This compound was noted by them primarily in the Rhodoreae and Phyllodoceae of the Rhododendroideae but was also found in *Erica* L. (some species) of the Ericoideae; *Comarostaphylis* ZUCC. of the Arbutoideae; and *Harrimanella, Chamaedaphne* KUNTZE, and *Oxydendrum* DC. of the Vaccinioideae. Hydroquinone was found in all members of the Arbutoideae examined, *Pyrola,* and *Chimaphila* as well as some species of *Pernettya* GAUDICH and *Vaccinium* (HARBORNE & WILLIAMS 1973). They also noted the occurrence of the monomethyl ether of hydroquinone in *Pyrola* and *Vaccinium*. Ursolic acid, β-sitosterol, and p-coumaric acid have been reported from *Monotropa uniflora* by BOBBITT et al. (1966). HEGNAUER (1966 a) reported ursolic acid from each of the other subfamilies of the Ericaceae. He mentioned the occurrence of β-sitosterin in *Befaria*

MUTIS ex L., *Lyonia* REICHB., and *Pyrola*. HARBORNE and WILLIAMS (1973) state that the Pyroloideae and Monotropoideae fit into the Ericaceae based upon their chemistry and suggest that the Vaccinioideae is similar.

The tribes and most of the subfamilies of the Ericaceae are fairly distinct but have been subjected to various taxonomic combinations. For the purposes of this brief discussion of the other subfamilies of the Ericaceae, STEVENS' (1971) classification is the most useful. The presence of gossypetin and pollen grains with "viscin" strands, among the taxa of the Phyllodoceae and Rhodoreae enforce STEVENS' treatment of the Rhododendroideae. The Ericoideae is relatively distinct in most of its features. STEVENS placed the Arbutoideae as a tribe of the Vaccinioideae. His classification has many merits, however, the Arbutoideae is separated in the present work in an attempt to allow comparison of the two groups. I would have to agree with STEVENS (1971), however, and unite the Arbutoideae with the Vaccinioideae. Several characters associated with pollen presentation mechanisms were found to be common between the two groups. These mechanisms were not correlated by STEVENS. Some of the characters which are interrelated include the shape of the corolla, presence or absence of "viscin" strands, presence or absence of anther tubules, and inversion of anthers.

CONCLUSIONS

Data in Table 1 clearly indicate the close relationship of the Monotropoideae to the other members of the Ericaceae. Most features found among the members of the Monotropoideae may be found in some other members of the Ericaceae. The mycoparasitic habit of the subfamily is the most distinguishing feature of the group. Several characteristics are associated with this habit. Among these are reduced habit and embryological features, as well as changes in gross morphology, anatomy, physiology, and pollen presentation mechanisms. The Monotropoideae appear to be most closely allied to the Arbuteae of STEVENS' (1971) Vaccinioideae. In addition to evidence from Table 1 there are other shared characteristics. Anthers of some members of the Monotropoideae undergo a modified form of anther inversion, a feature noted in the Arbuteae and Pyroloideae. The Monotropoideae and Arbuteae possess a similar range of floral characteristics. Chemical evidence also indicates a close relationship among the tribes of the Vaccinioideae and the subfamily Monotropoideae. The case against maintainence of the Pyrolaceae is also apparent from data in Table 1. They, like the Monotropoideae, possess no features unique among Ericaceae, except possibly mycoparasitism.

The Pyroloideae form a rather uniform subfamily which should be placed near the Monotropoideae. The Monotropoideae and Pyroloideae were probably derived from the vaccinioid line, but in both cases the separation was some time ago and extant members have diverged to a great extent. There is no reason to belive that the Monotropoideae were dervided from the Pyroloideae, even though one or more species of *Pyrola* are occasionally leafless and so perhaps mycoparasitic, and *Pyrola secunda* L. has monad pollen. This probably represents similar levels of specialization. The subfamily Arbutoideae is recognized in Table 1 following THORNE (1968). This greatly simplified presentation of the data and provided an opportunity to examine STEVENS' placement of the Arbuteae with the Vaccinioideae. STEVENS' combination does, as expected, seem quite reasonable. THORNE proposes to follow this view in the future (THORNE, pers. comm.). The recognized subfamilies of the Ericaceae would then be as follows: Rhododendroideae, Ericoideae, Vaccinioideae, Pyroloideae, and Monotropoideae. The taxa of each of these are aligned as in STEVENS (1971). WILLIS (1973) tentatively placed *Wittsteinia* F. MUELL. of

STEVENS' Wittsteinioideae in the Epacridaceae. Since no new evidence on the placement of this controversial genus (STEVENS 1971) could be provided, it was not treated in this paper.

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Contribution à l'étude cytotaxonomique de quelques Angiospermes de l'Iran

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ARYAVAND, A. 1976 02 09. Contribution à l'étude cytotaxonomique de quelques angiospermes de l'Iran. — Bot. Notiser 128: 299—311. Lund. ISSN 0006-8195.

Chromosome numbers are given for 41 species of angiosperms from Iran belonging to 33 genera and 12 families. The chromosome numbers of 27 species and six genera (*Lepyrodiclis* FENZL ex ENDL., *Pseudofortuynia* HEDGE, *Robeschia* HOCHST. ex FOURN., *Straussiella* HAUSSKN., *Lepechiniella* M. POP. and *Hymenocrater* FISCH. & MEY.) are published for the first time. The chromosome numbers of three species differ from those given by other authors. Chromosome races have been found in *Arabidopsis pumila* (STEPH.) N. BUSCH, *Primula auriculata* LAM. and *Senecio coronopifolius* DESF.

In *Clypeola aspera* (GRAUER) TURRILL a cytotype with n=13 was found. It probably originated from material with n=14 by means of one unequal translocation.

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Dans le cadre de nos recherches cytotaxonomiques sur la flore de l'Iran (ARYAVAND 1975 a, b), nous présentons dans ce travail les résultats concernant 42 espèces appartenant à 12 familles et 33 genres différents. Pour environ deux tiers de ces taxons les nombres chromosomiques sont rapportés pour la première fois.

MATÉRIEL ET MÉTHODES

La plus grande partie de notre matériel consiste en boutons floraux que nous avons récoltés et fixés sur le terrain en Iran, à l'alcool-acétique (3: 1). Seul le matériel de *Cousinia tenella* ainsi qu'un échantillon de *Lepyrodiclis holosteoides* proviennent de graines reçues respectivement des jardins botaniques de Taschkent et de Versailles. Ces graines ont été cultivées dans le jardin botanique de l'Institut de Botanique de l'Université de Neuchâtel. Les boutons ont été fixés par le Professeur C. FAVARGER. Pour chacun des taxons étudiés, un témoin a été séché; ces témoins seront conservés dans l'herbier de la Faculté des Sciences de l'Université d'Esfahan (Iran). La technique utilisée a été celle des écrasements au carmin acétique. Les familles ont été classées suivant la classification du Syllabus der Pflanzenfamilien de ENGLER-DIELS (DIELS 1936) et dans chaque famille les genres et les espèces sont présentés par ordre alphabétique. Nous n'avons figuré ici que les images cytologiques se rapportant à des plantes qui n'avaient pas encore été étudiées à ce point de vue ou qui présentaient un intérêt particulier.

Tous nos comptages concernant la méiose sont effectués sur les cellules-mères du pollen.

LILIACEAE

Allium ascalonicum L. — n=8

LOCALITÉ. Esfahan: Khunsar, Golestan kuh, 2400 m (74-165).

Ce nombre a été trouvé par plusieurs auteurs chez cette espèce sur des provenances différentes (in BOLKHOSKIKH et al. 1969) et cela indique, pour le moment, que le nombre chromosomique de cette espèce est constant. Les chromosomes ont une taille assez grande.

Allium stamineum BOISS. — 2n=16

LOCALITÉ. Fars: Ali abad-e Kamin, 1600 m (74-206).

Notre résultat concorde avec celui de FEINBRUN (in BOLKHOSKIKH op. cit.) sur du matériel de Palestine. Les chromosomes sont grands. Chacun d'eux mesure environ 13 microns à l'anaphase de la mitose somatique de l'ovaire.

Bellevalia glauca (LINDL.) KUNTH — n=4 (Fig. 1 A)

LOCALITÉ. Esfahan: Damaneh, 2100 m (74-163).

Cette espèce n'a pas fait l'objet d'un comptage chromosomique. Mais le nombre de base x=4 est très fréquent chez le genre *Bellevalia*. PODLECH et BADER (1974) ont trouvé chez *Bellevalia saviczii* WORON. le nombre 2n=24 (hexaploïde) sur un matériel d'Afghanistan. *B. glauca* a été subordonné par BOISSIER (1884) à *B. ciliata* (CYRILL) NEES. Ce dernier taxon possède aussi 2n=8.

Eremurus persicus JAUB. & SPACH — 2n=14 (Fig. 1 B)

LOCALITÉ. Esfahan: Ghameshlou, 2050 m (74-149).

Cette espèce n'a pas été étudiée auparavant à notre connaissance. Mais toutes les espèces du genre *Eremurus* qui ont été étudiées jusqu'à maintenant possèdent le nombre chromosomique 2n=14. Donc au point de vue du nombre chromosomique ce genre semble être très uniforme.

CARYOPHYLLACEAE

Lepyrodiclis holosteoides C. A. MEY. — n=17, 2n=34 (Fig. 2 A)

LOCALITÉS. Esfahan: Nadjaf abad, 1550 m (74-130) — Iran (récolté par le jardin bot. de Versailles) (71-988).

Aucun représentant du genre *Lepyrodiclis* FENZL ex ENDL. n'a fait à notre connaissance l'objet d'un comptage chromosomique. Nous avons étudié deux spécimens différents, l'un récolté directement dans la nature (Nadjaf-Abad à 20 km W d'Esfahan) et l'autre, également originaire de l'Iran, provenant du jardin botanique de Versailles.

Dans les deux cas, nous avons obtenu le nombre n=17. Ce nombre se rencontre également dans certains genres de la famille des Caryophyllacées, comme *Honkenya* EHRH., *Gypsophila* L. et surtout *Cerastium* L. Il existe certaines affinités morphologiques entre ce dernier et le genre *Lepyrodiclis*.

PAPAVERACEAE

Hypecoum pendulum L. — 2n=16 (Fig. 2 B)

LOCALITÉ. Esfahan: Cité Universitaire, 1600 m (74-22).

Cette espèce n'a jamais fait l'objet d'un comptage chromosomique. SMITH (1935—1936) et SUGIURA (1937) (in BOLKHOSKIKH et al. 1969) ont trouvé chez *Hypecoum procumbens* respectivement les nombres 2n=12 et 16?. MĚSICEK et SOJAK (in MOORE 1973) ont compté chez *Hypecoum erectum* L. 2n=16 sur du matériel de

Fig. 1. A: *Bellevalia glauca,* mitose pollinique, n=4. — B: *Eremurus persicus,* mitose somatique de l'ovaire, 2n=14. — C: *Clypeola aspera,* métaphase I, n=13. — D: *Clypeola aspera,* mitose de la racine, 2n=26. — E: *Nonnea caspica,* métaphase I, n=22. — F: *Nonnea persica,* diacinèse, n=16 (14 bivalents et 1 tétravalent). — G: *Cousinia pugionifera,* prophase de la mitose somatique de l'ovaire, 2n=24.


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Mongolie. En plus CHOUKSANOVA (in BOLKHOSKIKH op. cit.) a trouvé chez *Hypecoum trilobum* TRAUTV. 2n=32. Ces résultats montrent que le nombre de base chez le genre *Hypecoum* L. est probablement 8.

Papaver tenuifolium BOISS. — n=7 (Fig. 2 C)

LOCALITÉ. Esfahan: Ghameshlou, 2050 m (74-134).

Cette espèce n'a pas été étudiée auparavant à notre connaissance. Mais dans le genre *Papaver* L., le nombre chromosomique 2n=14 est le plus répandu.

BRASSICACEAE

Arabidopsis pumila (STEPH.) N. BUSCH — n= 8 (Fig. 2 D)

LOCALITÉ. Esfahan: Mt Homayoun shahr, 1700 m (74-56).

MANTON (1932) a compté sur un spécimen du SW de l'Asie le nombre chromosomique 2n=32. Donc, notre échantillon qui provient de la région d'Esfahan (Iran) est un diploïde (n=8). Mais malheureusement MANTON n'a pas indiqué la localité précise de son échantillon. Il faut mentionner que *Arabidopsis wallichii* (HOOK. FIL. & THOMS.) N. BUSCH possède aussi le nombre chromosomique 2n=16 (PODLECH & BADER 1974).

Arabidopsis pumila avec une aire de distribution assez vaste (Russie centrale et méridionale et Asie centrale et austro-occidentale) possède de nombreuses variétés (SCHULTZ 1924). De toute façon, nos observations montrent que cette espèce a au moin deux races chromosomiques, l'une diploïde (Iran: Esfahan) et l'autre tétraploïde (SW Asie).

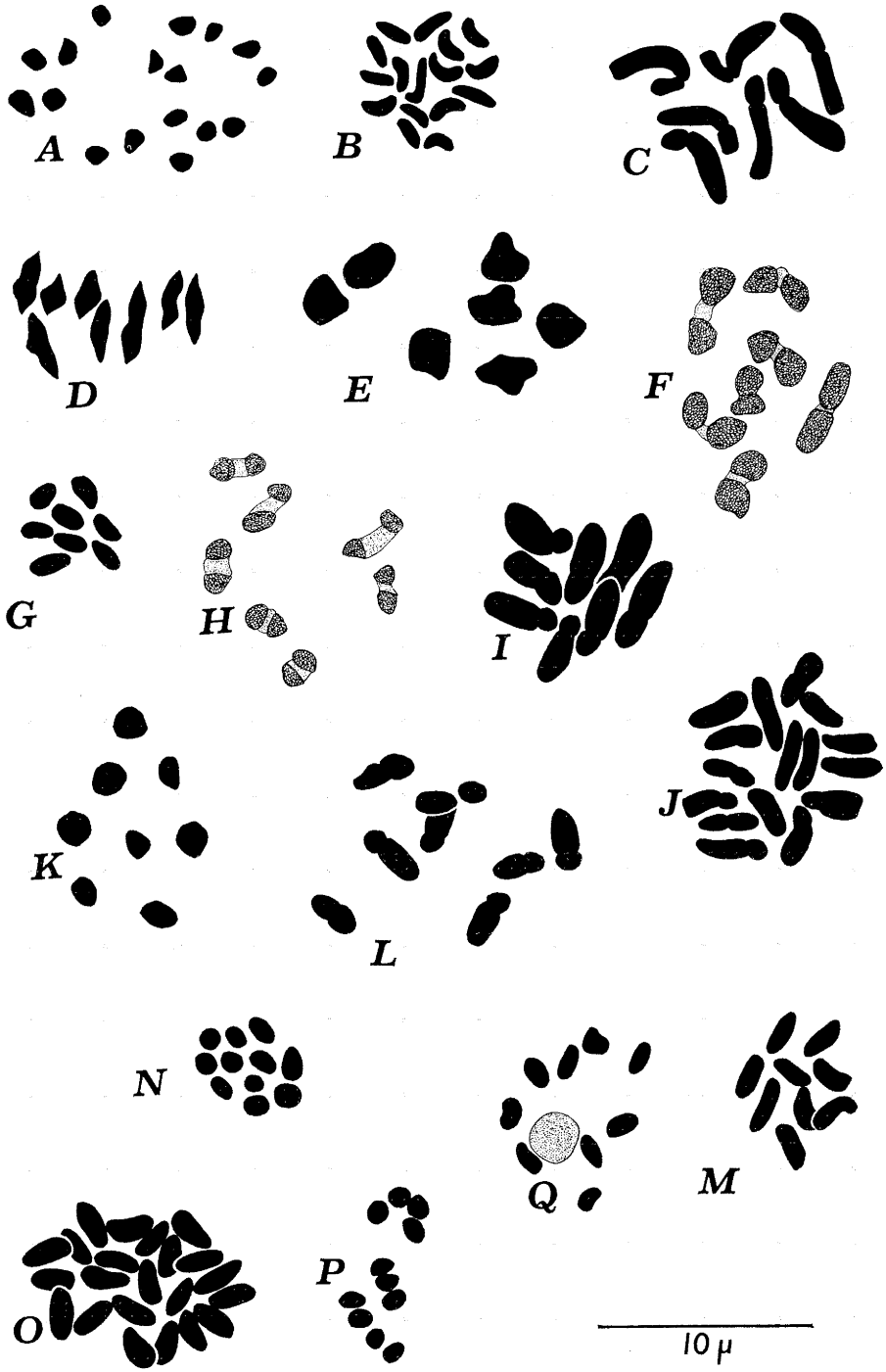
Clypeola aspera (GRAUER) TURRILL — n=13, 2n=26 (Fig. 1 C, D)

LOCALITÉS. Esfahan: Mt Kolah-ghazi, 1800 m (75-534) — Fars: Kazeroun, Komaradj, 1100 m (75-569).

D'après nos recherches antérieures (ARYAVAND 1975 a), il existe chez cette espèce deux nombres chromosomiques différents: n=7 et n=14. Depuis lors, nous avons observé chez deux individus de provenances différentes le nombre chromosomique n=13 et 2n=26. Dans les mitoses somatiques de la racine, on aperçoit 12 chromosomes avec constriction dans la région médiane, 12 chromosomes à constriction submédiane et 2 chromosomes dont la taille est environ deux fois plus grande que celle des autres et possèdant une constriction submédiane. A la métaphase I des cellules-mères de pollen, nous avons observé 12 bivalents de taille normale et 1 bivalent beaucoup plus grand que les autres et en forme d'anneau à deux chiasmas. Il semble bien que le type à n=13 dérive du type à n=14 par fusion de deux chromosomes entre eux à la suite sans doute de translocations inégales (cf. SWANSON 1960 p. 397). Jusqu'à présent nous n'avons pu déceler de différences morphologiques entre les plantes à n=14 et à n=13, mais ce point exigera encore d'autres investigations.

Ce phénomène de fusion des chromosomes n'est pas comparable au phénomène Robertsonien, souvent observé dans le

Fig. 2. A: *Lepyrodiclis holosteoides,* anaphase I, n=17. — B: *Hypecoum pendulum,* mitose somatique de l'ovaire, 2n=16. — C: *Papaver tenuifolium,* mitose pollinique, n=7. — D: *Arabidopsis pumila,* métaphase I, n=8. — E: *Clypeola dichotoma,* anaphase I, n=7. — F: *Pseudofortuynia esfandiarii,* diacinèse, n=7. — G: *Robeschia schimperi,* mitose pollinique, n=8. — H: *Sisymbrium septulatum,* diacinèse, n=7. — I: *Straussiella purpurea,* mitose pollinique, n=8. — J: *Astragalus bachtiaricus,* mitose somatique de l'ovaire, 2n=16. — K: *Astragalus candolleanus,* mitose pollinique, n=8. — L: *Astragalus fragiferus,* mitose pollinique, n=8. — M: *Sophora griffithii* ssp. *hortensis,* mitose pollinique, n=9. — N: *Primula auriculata,* métaphase II, n=11. — O: *Arnebia decumbens,* mitose somatique de l'ovaire, 2n=22. — P: *Lepechiniella persica,* anaphase I, n=11. — Q: *Hymenocrater bituminosus,* anaphase I, n=9.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règne animal et rarement chez les plantes supérieures (KOLLMANN 1969), puisque dans ce cas ce sont des chromosomes télocentriques qui se soudent entre eux pour donner par exemple des chromosomes méta- ou submétacentriques, le nombre total des bras restant identique. Tandis que dans notre cas, il ne s'agit pas de chromosomes télocentriques mais plutôt de chromosomes à constriction médiane ou submédiane ou enfin subterminale qui se soudent entre eux pour donner un nouveau chromosome. Il semble bien cependant que la masse totale de la chromatine reste à peu près identique.

Clypeola dichotoma BOISS. — n=7 (Fig. 2 E)

LOCALITÉ. Esfahan: Mouteh, 2000 m (74-194).

Nous avons compté (ARYAVAND 1975 a) le nombre chromosomique des *Clypeola microcarpa* et *C. aspera* appartenant respectivement aux sections *Jonthlaspi* (ADANS.) DC. et *Bergeretia* DC. L'espèce *C. dichotoma* BOISS. appartient à la section *Pseudanastatica* BOISS. Dans l'état actuel de nos connaissances, le nombre x=8 est particulier à la section *Jonthlaspi* et x=7 aux sections *Bergeretia* et *Pseudanastatica.*

Conringia persica BOISS. — 2n=14

LOCALITÉ. Esfahan: Mt Homayoun shahr, 1700 m (74-55).

Notre résultat concorde avec le comptage effectué par PODLECH et DIETERLE (1969) sur du matériel d'Afghanistan. Ce nombre a été trouvé chez deux autres espèces du genre *Conringia* (cf. BOLKHOSKIKH op. cit.) et on peut dire pour le moment que le nombre de base chez le genre *Conringia* est x=7.

Pseudofortuynia esfandiarii HEDGE — n=7 (Fig. 2 F)

LOCALITÉ. Esfahan: Ghameshlou, 2050 m (74-151).

Pseudofortuynia HEDGE est un genre monotypique, endémique des provinces de Fars et d'Esfahan de l'Iran. Ce genre, découvert récemment par HEDGE (HEDGE & RECHINGER 1968), ne comporte qu'une seule espèce *P. esfandiarii* HEDGE. Notre échantillon provient de la région de Ghameshlou à environ 60 km au NW d'Esfahan. C'est une nouvelle localité pour cette espèce. C'est la première fois qu'un comptage chromosomique a été effectué dans ce genre. D'après HEDGE (HEDGE & RECHINGER op. cit.), le genre *Pseudofortuynia* appartient à la tribu Brassiceae et à la sous-tribu Moricandiinae. Or, dans cette sous-tribu on connaît les nombres chromosomique des trois genres: *Conringia, Moricandia* et *Orychophragmus.* Chez ce dernier genre, le nombre chromosomique de *O. violaceus* (L.) O. E. SCHULZ a été déterminé par MANTON (1932): 2n=24, nombre dont nous ne pouvons pas tirer de conclusion. Comme nous l'avons expliqué plus haut, chez le genre *Conringia,* le nombre de base est 7. Quant au genre *Moricandia,* on connaît à l'heure actuelle, les nombres chromosomiques de quatre espèces. Tous ces comptages, à l'exception d'un comptage effectué par QUÉZEL (1955) sur *M. arvensis* (L.) DC. 2n=24, ont donné comme nombre chromosomique 2n=28 (in BOLKHOSKIKH op. cit. et MOORE 1973). Toutes ces observations montrent que le nombre n=7 de *Pseudofortuynia esfandiarii* HEDGE justifie la situation taxonomique de ce taxon.

Robeschia schimperi (BOISS.) O. E. SCHULZ — n=8 (Fig. 2 G)

LOCALITÉ. Esfahan: Mouteh, 2000 m (74-192).

Le genre *Robeschia* HOCHST. ex FOURN. ne comporte qu'une seule espèce dans le monde: *R. schimperi* (BOISS.) O. E. SCHULZ (SCHULZ 1924). Cette espèce se trouve au Sinai, en Syrie, en Iran et au Pakistan. Cette plante n'a pas été étudiée auparavant à notre connaissance.

Sisymbrium septulatum DC. — n=7, 2n=14 (Fig. 2 H)

LOCALITÉ. Esfahan: Mt Kolah-ghazi, 1800 m (74-67).

Cette espèce, non plus, n'a pas été étudiée auparavant. Mais le nombre 2n=14 est très fréquent chez le genre *Sisymbrium*. Le nombre chromosomique 2n=28 a été trouvé chez *S. irio* L. par PODLECH et DIETERLE (1969) sur du matériel d'Afghanistan, et par AMIN (in LÖVE 1973) sur du matériel d'Egypte.

D'après SCHULZ (1924), notre espèce appartient à la section *Pachypodium* (WEBB & BERTH.) FOURN. dont deux autres représentants (à savoir *S. altissimum* L. et *S. orientale* L.) ont un nombre chromosomique de 2n=14 (in BOLKHOSKIKH op. cit.). Il faut ajouter que la section *Pachypodium* est tout à fait proche de la section *Irio* DC. dont fait partie l'espèce *S. irio* L.

Straussiella purpurea (BGE.) HAUSSKN. — n=8 (Fig. 2 I)

LOCALITÉ. Esfahan: Mouteh, 2000 m (74-186).

C'est à notre avis le premier comptage publié sur le genre *Straussiella* HAUSSKN. *Straussiella purpurea* est une plante vivace, endémique de l'ouest et du centre de l'Iran. Le genre *Straussiella* appartient à la tribu *Alysseae* dans laquelle un certain nombre de genres comme *Alyssum, Fibigia, Clypeola* (pro parte) etc. présentent aussi le nombre chromosomique x=8.

Torularia aculeolata (BOISS.) O. E. SCHULZ — n=7

LOCALITÉ. Esfahan: Mt Homayoun shahr, 1700 m (74-43).

Dans un travail antérieur (ARYAVAND 1975 a), nous avons publié pour la première fois le nombre chromosomique (2n=14) pour cette espèce. Notre comptage sur un spécimen d'une autre localité donne le même resultat.

FABACEAE

Astragalus bachtiaricus BGE. — 2n=16 (Fig. 2 J)

LOCALITÉ. Esfahan: Ghameshlou, 2050 m (74-159).

Cette espèce n'a pas été étudiée auparavant. Mais le nombre 2n=16 est très fréquent chez le genre *Astragalus*.

Astragalus candolleanus BOISS. — n=8 (Fig. 2 K)

LOCALITÉ. Esfahan: Kuf-e Sofeh, 1700 m (74-75).

Cette espèce non plus, n'a jamais fait l'objet d'un comptage chromosomique. Nous avons observé quelques phénomènes anormaux dans la mitose pollinique des échantillons que nous avons étudiés (ARYAVAND, en cours de publication).

Astragalus fragiferus BGE. — n=8 (Fig. 2 L)

LOCALITÉ. Esfahan: Mt Kolah-ghazi, 1800 m (74-88).

Cette espèce n'a pas, non plus, été étudiée auparavant. A la métaphase de la première mitose pollinique le chromosome paranucléolaire présente une constriction assez grande.

Melilotus officinalis (L.) MED. — n=8

LOCALITÉ. Teheran: Ab-e ali, 2400 m (74-277).

Notre résultat concorde avec celui de nombreux auteurs sur des matériels de provenances différentes (cf. BOLKHOSKIKH op. cit. et MOORE 1973). Il faut noter que le nombre chromosomique 2n=32 pour cette espèce (LESINS 1952) correspond à une race artificielle obtenue par l'utilisation de colchicine.

Sophora griffithii STOCHS ssp. **hortensis** (BOISS. & BUHSE) YAKOVL. — n=9 (Fig. 2 M)

LOCALITÉ. Esfahan: Cité Universitaire, 1600 m (74-24).

Ce taxon n'a pas été étudié auparavant.

Mais le nombre x=9 est très fréquent chez le genre *Sophora*. C'est un arbuste ornemental à fleurs jaunes qui a été multiplié ces dernières années à Esfahan.

Vicia sativa L. — 2n=12

LOCALITÉ. Khuzistan: Ahvaz, Hamidyieh, 150 m (74-15).

Beaucoup de comptages chromosomiques ont été effectués sur cette espèce. Trois nombres chromosomiques ont été notés: 2n=10, 12, 14. Le nombre 2n=12 est signalé le plus souvent.

GERANIACEAE

Erodium cicutarium (L.) L'HÉRIT. ex AITON — 2n=40

LOCALITÉ. Esfahan, Mt Kolah-ghazi, 1800 m (74-33).

Cette espèce collective a été beaucoup étudiée par différents auteurs. Les résultats montrent qu'il existe en général deux nombres de base différents x=9 et x=10. Le nombre x=10 est de beaucoup le plus fréquent. La plupart des auteurs semblent être d'accord pour la dérivation du nombre x=9 à partir de x=10. PODLECH et DIETERLE (1969) ont trouvé le nombre 2n=36 sur du matériel d'Afghanistan.

Comme le type à 2n=18 n'a jamais été rencontré jusqu'a l'heure actuelle chez cette espèce, il semble bien que le type à 2n=20 a donné naissance au type 2n=40 et celui-ci, dans certaines régions de l'aire de distribution de l'espèce a donné naissance au type à 2n=36 par un phénomène d'aneuploïdie.

Il faut ajouter que PODLECH et DIETERLE (1969) ont rapporté d'après ROTTGARDT (1956) le nombre 2n=18 pour le var. *immaculatum* et 2n=20 pour le var. *pimpinellifolium*. Il s'agit sans doute d'une erreur typographique car les nombres publiés par ROTTGARDT sont respectivement n=18 et n=20.

ZYGOPHYLLACEAE

Peganum harmala L. — n=12

LOCALITÉ. Esfahan: Mt Kolah-ghazi, 1800 m (74-122).

Si l'on fait abstraction d'une numération assez ancienne de NEGODI (1937 in BOLKHOSKIKH op. cit.): 2n=22, notre comptage est identique aux résultats obtenus par plusieurs auteurs (in BOLKHOSKIKH op. cit. et MOORE 1973) sur des plantes de provenances différentes. Il faut noter que récemment HANLET (in LÖVE 1973) a trouvé une race tétraploïde (n=24) de cette espèce en Mongolie dans des peuplements de *Lasiagrostis*, influencés par l'homme.

PRIMULACEAE

Primula auriculata LAM. — n=11 (Fig. 2 N)

LOCALITÉ. Esfahan: Khunsar, Golestan kuh, 2500 m (74-166).

Le premier comptage effectué chez cette espèce date de 1920 (MARCHAL): 2n=54, résultat qui nous paraît erroné. SOKOLOVSKAJA et STRELKOVA (1940, 1948, in BOLKHOSKIKH op. cit.) ont trouvé 2n=45 sur du matériel du Caucase. TUMAJANOV et BERIDZE (1970) ont compté 2n=44 sur du matériel de l'Ossètie (Géorgie). Enfin KRESS (1969) a compté sur un matériel du jardin botanique de Münich le nombre chromosomique 2n=44. Cette plante avait été récoltée lors d'une expédition anglaise (Bowles-Expedition), et c'est M. le Dr B. MATHEW qui nous a aimablement communiqué l'endroit précis de sa récolte. Il s'agit de la région Khoy, à 2000 m alt. à l'extrême Nord-ouest de l'Iran, à environ 70 km de la frontière de l'URSS.

L'état actuel des connaissances cytologiques sur cette espèce peut se résumer ainsi:

Race tétraploïde
2n=45 (Caucase)
2n=44 (Géorgie)
2n=44 (Khoy, NW de l'Iran)

race diploïde
2n=22 (Golestan kuh, Khunsar, environ à 130 km NW d'Esfahan), le présent auteur.

Au point de vue taxonomique SCHWARZ (1968) divise ce taxon en deux espèces différentes. D'après cet auteur les plantes de l'Iran peuvent être considérées comme étant le *P. auriculata* LAM. (au sens strict), et les spécimens du Caucase, de la Transcaucasie et de l'Asie Mineure comme appartenant à *P. glacialis* ADAM. ex WILLD. Comme, nous venons de l'expliquer, les limites des races chromosomiques ne coïncident pas parfaitement avec la proposition de SCHWARZ. Dans l'état actuel de nos connaissances, nous pouvons dire que la partie sud de l'aire de distribution de cette espéce est occupée par la race primitive diploïde. Cette race diploïde a donné naissance vers le NW à une race tétraploïde qui occupe actuellement le NW de l'Iran et le Caucase et probablement l'Asie Mineure. Une étude biosystématique plus complète serait d'un grand intérêt pour distinguer les limites précises de ces deux races.

BORAGINACEAE

Arnebia decumbens (VENT.) COSS. & KRAL. — n=11, 2n=22 (Fig. 2 O)

LOCALITÉ. Esfahan: Mouteh, 2000 m (74-182).

Notre résultat sur cette espèce ne concorde pas avec les résultats obtenus par MATVEJEVA et TIKANOVA (en cours de publication) (in BOLKHOSKIKH op. cit.). En effet les auteurs russes ont compté le nombre 2n=8 sur un matériel provenant probablement de l'URSS. D'après RIEDL (1967), cette espèce comprend deux sous-espèces dans le territoire couvert par «Flora Iranica». Notre échantillon appartient probablement au ssp. *decumbens,* mais en l'absence de fruits nous ne pouvons pas l'assurer.

Lepechiniella persica (BOISS.) H. RIEDL — n=11 (Fig. 2 P)

LOCALITÉ. Tehran: Plour, 2300 m (74-273).

A notre connaissance, aucun représentant du genre *Lepechiniella* M. POP. n'a fait l'objet d'un comptage chromosomique. *Lepechiniella persica* (BOISS.) H. RIEDL est une espèce vivace, endémique du nord de l'Iran.

Nonnea caspica (WILLD.) G. DON — n=22, 2n=44 (Fig. 1 E)

LOCALITÉ. Esfahan: Cité Universitaire, 1600 m (74-20).

Notre résultat ne concorde pas avec ceux obtenus par PODLECH et BADER (1974) sur cette espèce. En effet les auteurs allemands ont compté 2n=28 sur du matériel de l'Afghanistan. Cette espèce selon RIEDL (op. cit.) possède dans le territoire couvert par «Flora Iranica» quatre sous-espèces différentes. L'avenir dira si la différence de nombre chromosomique coïncide ou non avec les limites de ces sous-espèces.

A noter que VASUDEVAN (à l'impression) a compté n=8 chez un *Nonnea caspica* du Tangmarg (Kashmir). Si la plante a été correctement déterminée, cela signifie qu'il y a des races de cette espèce possédant n=14 et n=8, ce qui permettrait de comprendre l'existence d'un nombre n=22.

Nonnea persica BOISS. — n=16 (Fig. 1 F)

LOCALITÉ. Esfahan: Ghameshlou, 2050 m (74-153).

Cette espèce n'a pas été étudiée auparavant à notre connaissance. Mais plusieurs auteurs ont trouvé le nombre 2n=16 chez *N. rosea* LINK (in BOLKHOSKIKH op. cit.). Il faut noter que *N. persica* appartient à la section *Nonnea*, tandis que *N. rosea* appartient à la section *Orthocaryum* DC.

Il faut ajouter que, à la diacinèse nous avons observé 14 bivalents et 1 tétravalent. La présence d'un tétravalent laisse supposer qu'il s'agit peut-être d'un autotétraploïde.

LAMIACEAE

Eremostachys adenantha JAUB. & SPACH — n=11 (Fig. 3 A)

LOCALITÉ. Esfahan: Mouteh, 2000 m (74-195).

C'est à notre avis le premier comptage publié sur cette espèce. Le nombre chromosomique 2n=22 est déjà connu pour six autres espèces du genre *Eremostachys* (cf. BOLKHOSKIKH op. cit. et MOORE 1973). A la métaphase de la première mitose pollinique un des chromosomes possède un satellite.

Hymenocrater bituminosus FISCH. & MEY. — n=9 (Fig. 2 Q)

LOCALITÉ. Esfahan: Mt Kolah-ghazi, 1800 m (74-81).

Aucun représentant du genre *Hymenocrater* n'a été étudié auparavant à notre connaissance. Le nombre chromosomique n=9 est assez répandu dans la famille des Labiées.

Nepeta racemosa LAM. s. l. — n=18 (Fig. 3 B)

LOCALITÉ. Tehran: Plour, 2300 m (74-274).

Cette espèce n'a pas été étudiée auparavant. Il s'agit probablement d'une espèce tétraploïde avec le nombre de base x=9. Or, ce dernier nombre est très fréquent chez le genre *Nepeta* L.

Nepeta schiraziana BOISS. — n=8 (Fig. 3 C)

LOCALITÉ. Shahr-e Kord: Kuh-rang, 2350 m (74-259).

Cette espèce du genre *Nepeta* n'a pas, non plus, fait l'objet d'un comptage chromosomique. Mais le nombre chromosomique 2n=16 a été trouvé chez *N. teydea* WEBB et BERTH. par plusieurs auteurs (cf. BOLKHOSKIKH op. cit. et MOORE 1973).

SCROPHULARIACEAE

Veronica farinosa HAUSSKN. — 2n=16 (Fig. 3 D)

LOCALITÉ. Esfahan: Damaneh, 2100 m (74-161).

Cette espèce n'a pas été étudié auparavant. Elle appartient au groupe *Orientalis* (RÖMPP 1928). Comme FISCHER (1970), en particulier, l'a montré, le nombre de base dans ce groupe est x=8 avec des taxons diploïdes (comme *V. farinosa* HAUSSKN.), tétraploïdes (comme *V. microcarpa* BOISS.), hexaploïdes (comme *V. multifida* BENTH.) et octoploïdes (*V. elmaliensis* M. FISCHER).

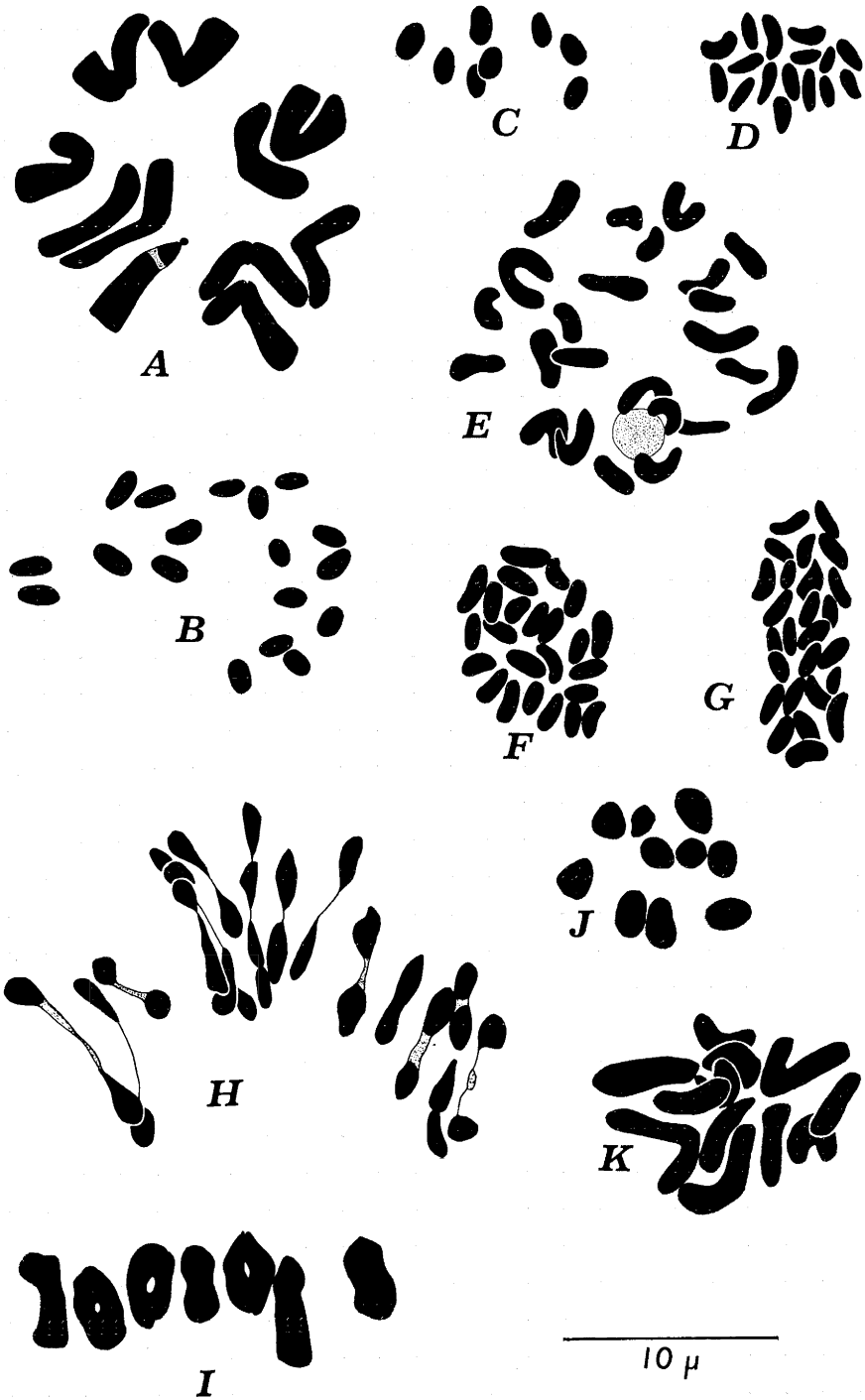
ASTERACEAE

Cousinia congesta BGE. — 2n=24 (Fig. 3 E)

LOCALITÉ. Esfahan: 25 km S Delidjan, 2100 m (74-263).

Notre résultat ne concorde pas avec le comptage effectué par CHOUKSANOVA (non publié, in BOLKHOSKIKH op. cit.) sur du matériel probablement originaire de Turkmenistan. En effet, l'auteur russe a trouvé le nombre chromosomique 2n=26. C'est une espèce vivace de la section *Congestae* BGE. qui se trouve dans le nord de l'Iran, le Turkmenistan et l'Afghanistan.

Fig. 3. A: *Eremostachys adenantha,* mitose pollinique, n=11. — B: *Nepeta racemosa,* anaphase I, n=18. — C: *Nepeta schiraziana,* métaphase II, n=8. — D: *Veronica farinosa,* mitose somatique de l'ovaire, 2n=16. — E: *Cousinia congesta,* prophase de la mitose somatique de l'ovaire, 2n=24. — F: *Cousinia kornhuberi,* mitose somatique de l'ovaire, 2n=24. — G: *Cousinia tenella,* mitose somatique de l'ovaire, 2n=26. — H: *Onopordon heteracanthum,* métaphase I, n=17. — I: *Scorzonera picridioides,* métaphase I, n=7. — J: *Senecio coronopifolius,* anaphase I, n=10. — K: *Tragopogon straussii,* mitose somatique de l'ovaire, 2n=12.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Cousinia kornhuberi HEIMERL — 2n=24 (Fig. 3 F)

LOCALITÉ. Hamadan, Barrage de Shahnaz, 2000 m (74-232).

C'est à notre avis le premier comptage publié sur cette espèce vivace, endémique de la province d'Hamadan située à l'ouest de l'Iran.

Cousinia pugionifera JAUB. & SPACH — 2n=24 (Fig. 1 G)

LOCALITÉ. Esfahan: 10 km N Meymeh, 2100 m (74-245).

Cette espèce non plus n'a pas été étudiée auparavant. C'est une espèce bisannuelle ou vivace de la section *Pugioniferae* BGE., endémique de la région d'Esfahan.

Cousinia tenella FISCH. & C. A. MEY. — 2n=26 (Fig. 3 G)

LOCALITÉ. Récolté par le jardin bot. de Tashkent (74-220).

L'échantillon que nous avons étudié provient du jardin botanique de Taschkent; il a donc probablement été récolté dans le Turkmenistan ou l'Asie centrale. Cette espèce se trouve en Iran dans les provinces Azerbaidjan, Gorgan, Tehran et Khorassan. Ce taxon annuel de la section *Tenellae* BGE. n'a pas fait non plus l'objet d'un comptage chromosomique.

Le genre *Cousinia* est bien représenté dans la flore de l'Iran. Il prend le deuxième rang au point de vue du nombre d'espèces après le genre *Astragalus*. Heureusement, ce genre a été le sujet d'un remarquable volume de la «Flora Iranica» traité avec beaucoup de mérite par le Professeur Dr RECHINGER (1972). Il possède 354 espèces dont la plupart endémiques. Mais au contraire, peu d'études cytotaxonomiques ont été consacrées à ce genre. Les nombres chromosomiques connus jusqu'à présent chez 24 espèces dans l'ensemble du genre sont 2n=18, 20, 24, 26 et 36. Il est encore trop tôt pour avoir une idée générale sur la cytotaxonomie de ce genre. Mais nous espérons continuer son étude cytotaxonomique au fur et à mesure de nos possibilités.

Onopordon heteracanthum C. A. MEY. — n=17 (Fig. 3 H)

LOCALITÉ. Esfahan: Djargouyeh, 1550 m (74-261).

Cette espèce, non plus, n'a jamais fait l'objet d'un comptage chromosomique. Mais, il semble bien que le nombre 2n=34 soit pour le moment le seul nombre chromosomique connu chez le genre *Onopordon*.

Scorzonera picridioides BOISS. — n=7 (Fig. 3 I)

LOCALITÉS. Esfahan: Mt Kolah-ghazi, 1800 m (74-30) — Esfahan: Ghameshlou, 2000 m (74-132).

Cette espèce non plus n'a pas été étudiée auparavant. Mais dans le genre *Scorzonera*, le nombre chromosomique n=7 est le plus répandu.

Senecio coronopifolius DESF. — n=10 (Fig. 3 J)

LOCALITÉ. Luristan: Tangueh Malavi, 850 m (74-13).

Nous avons compté le nombre chromosomique n=10 sur un matériel provenant de Tangueh-Malavi (Luristan), localité située à l'ouest des chaînes de montagnes Zagros.

MEHRA et RAMANANDAN (in LÖVE 1969) ont rapporté pour cette même espèce le nombre n=20 trouvé sur un matériel de Simla (dans l'Himalaya occidental). Donc, il existe probablement chez cette espèce annuelle et polymorphe (BOISSIER 1875), au moins deux races chromosomique différentes; l'une diploïde (n=10) (ouest de l'Iran) et l'autre, tétraploïde (Himalaya occidental). Il serait très intéressant de déterminer les limites géographiques de ces deux races, ainsi que leurs différences morphologiques.

Tragopogon straussii BORNM. — 2n=12 (Fig. 3 K)

LOCALITÉ. Arak: 35 km W de la ville Arak, 2000 m (74-241).

C'est à notre avis le premier comptage publié sur cette espèce. Le nombre chromosomique 2n=12 est le plus fréquent chez le genre *Tragopogon*.

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Notes on Central American Marantaceae II

New Species from Panamá and Costa Rica

Helen Kennedy

KENNEDY, H. 1976 02 09. Notes on Central American Marantaceae II. New Species from Panamá and Costa Rica. — Bot. Notiser 128: 312—322. Lund. ISSN 0006-8195.

Three new species of *Calathea* (Marantaceae) are described: *Calathea portobelensis* and *C. robin-fosteri* from Panamá and *C. similis* from Panamá and Costa Rica. A new record, *Calathea guzmanioides,* previously known only from Colombia is noted for Panamá.

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The Marantaceae is a family of herbaceous monocots, including forest floor species 15 cm high as well as clambering liana-like species of 7—8 m. It is a prominent element in the moist to wet tropics below 1500 m elevation. The majority of species occur in the Neo-tropics, especially near the equator.

As an outgrowth of pollination studies of this family in Central America (KENNEDY 1974) a revision of the Marantaceous flora of Panamá was undertaken. Although the number of species of Marantaceae known from Panamá has significantly increased in the past 5—6 years, it continues to be a rich source of unreported and undescribed species. In his comments on the coverage of families treated in the early parts of WOODSON and SCHERY's Flora of Panama (1945), DRESSLER (1972 p. 184) noted 35 species of Marantaceae as occurring in Panamá, a sizable increase over the 23 species listed in the flora. Since then the number of species known from Panamá in this family has risen to 49. In *Calathea,* the largest and most diverse genus of the family, an additional 23 species have been found since the original treatment, an increase of 164 %. In the family as a whole the percent increase is 110.

Much of the wet forest area near the continental divide and on the Atlantic slope of Panamá remains inadequately explored botanically. This is indicated by the number of new species in the Portobelo area (Colón Province) and in the recently accessible forest along the El Llano-Carti road (km 12—17) in the Cordillera de San Blas. A total of 17 species is known from this latter area of which 7 (6 *Calatheae* and 1 *Ischnosphon*) were new records for Panamá as well as new species. Of the 15 species known from the Río Guanche site (near Portobelo, Colón Prov.), 6 were new records for Panamá, 5 of which were also new species. Out of the 13 species at Cerro Jefe (Panamá Prov.) 5 were new records and 3 new species. Seven species were common to both Cerro Jefe and the Carti road area, 5 species in common between Cerro Jefe and Río Guanche and 5 between the Carti road and Río Guanche. The degree of species overlap between these relatively rich wet forest areas is only about 1/3. Many of these species are known from only a few individuals or small, very localized,

populations. This low population density and sporadic occurrence is most common in species of the wetter forest habitats growing within the forest rather than at an edge or in disturbed situations. Because of the distributional patterns of these species the problem of adequately sampling an area such as the Atlantic slope becomes a challenge indeed, especially considering the lack of roads. Of the 26 species of *Calathea* discovered since 1945 in Panamá, 15 are known from only a single locality within Panamá. Probably a few of these species are indeed narrow endemics. However, more extensive collecting in Panamá, Costa Rica and the Chocó region of Colombia will quite likely show these species to have a wider distribution, though not necessarily a wider habitat tolerance. Six of the 15 Calatheas mentioned above have been collected in Costa Rica and 3 in Colombia. The claviculate bracteoles which are so characteristic of inflorescences in the majority of South American Calatheas, though rare in Central American ones, occur in 8 species from eastern Panamá (east of the Canal Zone) but in none from western Panamá, indicating their South American affinities. With continued exploration of the wet forest areas of Panamá the Marantaceous flora for this area will probably reach 60—70 species.

Calathea portobelensis KENNEDY sp. nov. — Fig. 1

Planta ad 1.1 m alta vulgo ramificans. Petioli supra sulcati, parte superiore ad 2 cm longa callosa supra tomentosa; lamina elliptica supra smaragdina secus parte centrale pallidior. Spicae plures raro solitariae cylindricae, pedunculo ad basim tumido albo demum deflexo; bracteae dilute virides; omnis par florum bracteolis indurato-claviculatis comitatum; corollae albae vel violaceo-suffusae tubo ad 2.6 cm longo.

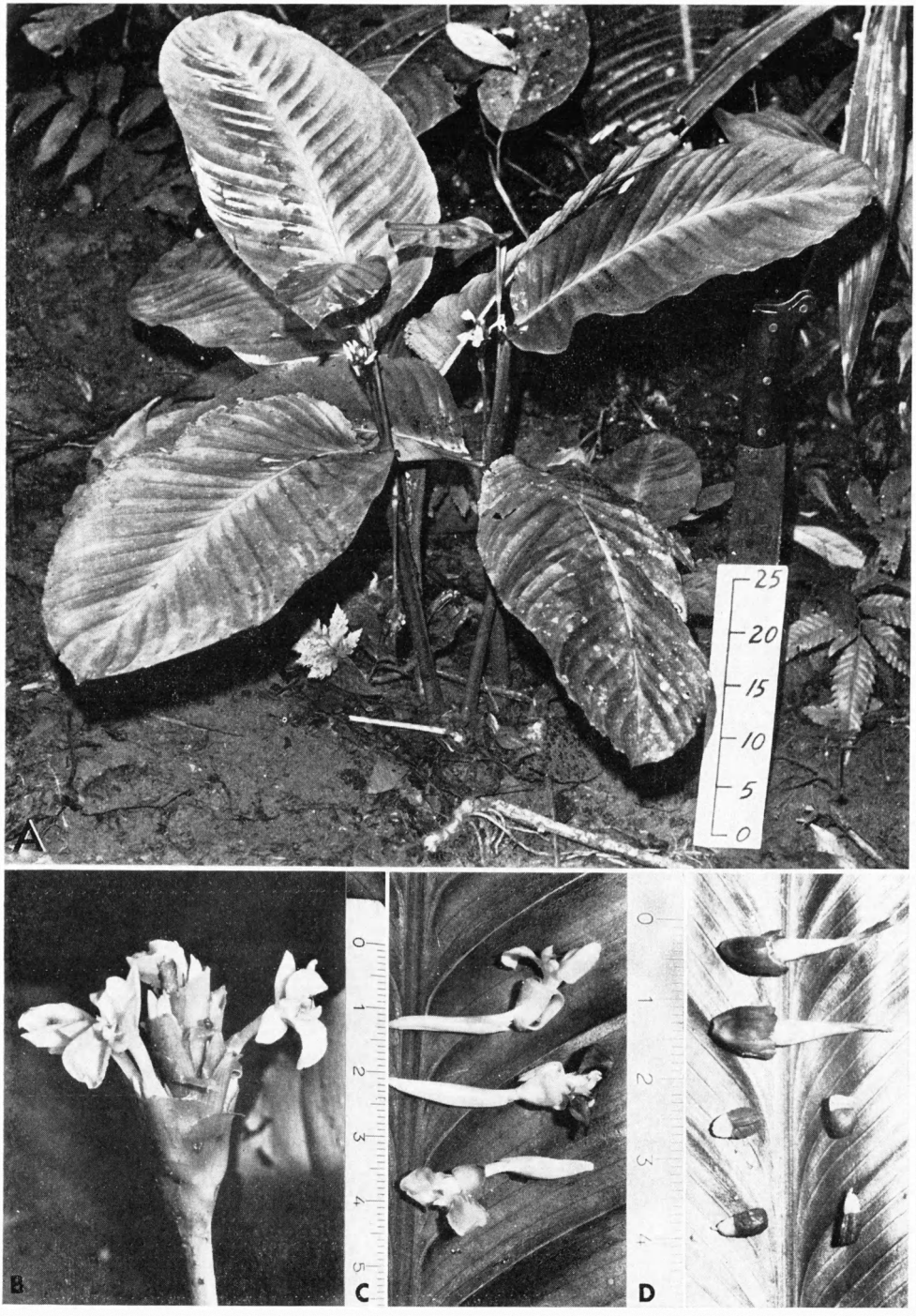
Caulescent herb, 0.4—1.1 m high. An individual plant usually has one or more branch shoots arising in the axils of the lowermost leaves, though generally only one shoot per leaf axil. In older plants branch shoots often arise in the axil of the leaf subtending the inflorescence. Rhizome ca 6—10 mm in diameter, internodes 3—9 mm, roots occasionally bearing swollen tubers. Cataphylls herbaceous, narrowly ovate, apex mucronulate, green, minutely appressed puberulent (14×). Leaf blade herbaceous, surface shallowly undulate, elliptic, apex of larger leaves rounded with an acumen, acuminate in smaller leaves, base rounded, shortly and abruptly acuminate at the junction with the pulvinus, 5—30 cm wide and 9—61.5 cm long. Leaf surface above semilustrous grass-green with a jagged-edged light green pattern along the midrib (ca 1/6 the width of the leaf), glabrous, occasionally minutely puberulent along major veins (14×), not visible to naked eye, midrib minutely tomentose, more densely so near apex. The lower surface dull grey-green, midrib and veins minutely tomentose, and glabrous between the veins. Pulvinus round in cross section, slightly larger in diameter than petiole, light green, glabrous to subglabrous, minutely tomentose along upper side, 0.35—2 cm long. Petiole bearing a shallow groove along the upper side, grass-green, minutely tomentose, 0.6—24 cm long, occasionally absent altogether. Leaf sheath herbaceous, grass-green, minutely puberulent (14×) to subglabrous in upper portion, the basalmost portion (1—2 cm) pink, dense appressed tomentose, 4—45 cm long. Stem grass-green, minutely puberulent (14×). The first inflorescence is terminal on the shoot, additional inflorescences with their concomitant bicarinate prophylls are borne in the axil of the leaf subtending the first inflorescence. In addition, a leafy branch shoot may also be formed in the axil of the subtending leaf and likewise bear 1 or more inflorescences. Bicarinate prophylls subtending axillary inflorescences or shoots green, minutely puberulent, 1.8—7.8 cm long. Peduncle green, subglabrous to minutely tomentose basally, (3) 5.5—28 cm long, the basal 1 cm pale green to whitish, swollen, with age the peduncle bends in

this area reflexing the inflorescence downward. Inflorescences usually several. 1—4 (7) per leafy shoot, cylindric to fusiform, (2) 3—7.5 cm long and 0.8—2.3 cm wide. Bracts (3) 6—15(18) imbricate, spirally arranged, herbaceous, apex erect or occasionally slightly spreading, broadly elliptic to obtrullate in upper bracts, apex acuminate to subacute, lowermost bract occasionally broadly transverse ovate, 1.6—2.2 cm high and 0.8—2 cm wide; each subtending up to 8 flower pairs. Outer bract surface wholly light green or pale whitish-tan with margins tinged purplish, minutely tomentose; within, light green above, paler toward base or white, glabrous. Bicarinate prophyll membranaceous, elliptic to ovate-elliptic, rounded to obtuse, translucent pale green or pale tan, minutely puberulent at apex, 1.3—1.8 cm high and 0.8—1.2 cm wide. Mesophyll membranaceous, narrowly ovate to ovate, obtuse to rounded, translucent pale green or pale tannish, minutely puberulent (14×) at apex, 1.45—1.8 cm high and 0.7—0.8 cm wide. Bracteoles subtending individual flowers, 2 per flower pair, membranaceous, translucent chartreuse or faint tan, glabrous, 1.25—1.9 cm long, 0.3—0.45 cm wide. Each flower pair is provided with an indurate claviculate bracteole, 1.7—2.1 cm long, the lower half translucent white, the upper half stiff, cream-yellow. The flower opens spontaneously. Sepals thin, herbaceous, narrowly obovate-elliptic, acute, white, glabrous, 1.5—1.9 (2.1) cm long and 0.25—0.4 cm wide. Corolla tube white, glabrous, 2.2—2.6 cm long, additionally a staminal tube 3—4 mm long is usually present. Corolla lobes ovate to elliptic, obtuse, white or light purple, 0.8—1.1 cm long and (3.5) 4—6 (7) mm wide. Outer staminode broadly transverse elliptical, circular or broadly elliptical, apex rounded or shallowly retuse, very shortly clawed at the base, white or purple, 0.9—1.2 cm long and 0.7—1 cm wide. Callose staminode spatulate, apical portion petaloid, broadly transverse elliptic, emarginate, lower portion callose, white or marked with purple, 1—1.2 cm long and 0.7—1 cm wide. Cucullate staminode white or purple, 0.45—0.5 cm long and 0.35—0.5 cm wide, provided with a subterminal filiform appendage. Filament white or purple, bearing a lateral petaloid appendage to 2.5 mm wide; anther 2 mm long. Ovary white, glabrous, 1—1.5 mm long. Style and stigma white. Capsule obovoid, trigonous, semitranslucent light green, glabrous with fleshy slightly raised apical rim, 8—9 mm high and 5.5—7 mm wide, crowned by a live expanded persistent calyx, 6.5—7 mm wide. Seeds usually 3, trigonous, rugose on the outer surface, red-brown, 3—4 mm high and 3—4 mm in diameter with a basal white aril 2.5—3 mm high.

TYPE. Panamá: Prov. Colón, Río Guanche, ca 1.5 mi. upstream from the bridge, lowland wet forest, ca 10 m, 23 Aug. 1972, H. KENNEDY and R.L. DRESSLER 1500 (holotype US, isotypes BM, COL, DAV, DUKE, F, GH, K, MO, NY, PMA, U, W).

OTHER COLLECTIONS. Panamá: Prov. Colón, semi-swampy flood plain near bridge over Río Buenaventura, near Portobelo, 4 April 1970, R.B. FOSTER 1689; near Portobelo at the bridge over the Río Buenaventura, 14 Aug. 1970, H. KENNEDY & R. B. FOSTER 445 (B, DUKE, LE, MEXU, MO, P, VEN); semi-inundated forest and tierra firma, 27 Aug. 1970, H. KENNEDY 467 (DAV, MICH, S, UC, US); Río Guanche, 2 mi. upstream from the bridge, mature forest, 17 July 1971, H. KENNEDY, R. B. FOSTER & R. L. DRESSLER 1095 (MO); ca 1.5 mi. upstream from the bridge, 10—20 m, wet lowland evergreen forest, 4 Sept. 1974, H. KENNEDY, R. L. DRESSLER, P. J. M. MAAS & C. TOFT 3383 (BM, BR, GOET, H, M, U); along Río Guanche, 6 km S of Portobelo 1—3.5 km E of Portobelo-Puerto Pilon road bridge, 0—10 m, tropical wet forest, 10 Dec. 1973, M. NEE & A.

Fig. 1. *Calathea portobelensis*. A: Habit. — B: Inflorescence with untripped flowers. — C: Flowers on upper leaf surface, callose and outer staminodes of middle flower purple, white in the others. — D: Capsules with persistent sepals and arillate seeds on upper leaf surface. — Scale in cm.


25
20
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A
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C
D

GENTRY 8689; Río Boqueron ca 6 km upstream from Peluca Hydrographic station, 7 April 1974, R. L. DRESSLER 4651 (US); 6—8 km from Peluca Hydrographic station on the road to Nombre de Dios, 29 Aug. 1974, H. KENNEDY & R. L. DRESSLER 3333 (US). Province unknown, 1911, H. PITTIER 4214 (F).

Flowering mainly during the rainy season, May through December. However, in the Portobelo area a few individuals may be found in flower at almost any time during the year. Occurring along stream banks, in run-off channels and in the sandy soil of old stream beds, or on slopes above the stream. This species differs from other Panamanian and Costa Rican Calatheas by the claviculate bracteoles, pale green irregular pattern along the midrib, the several (rarely 1) small inflorescences of light green or tannish white bracts, and the characteristic tendency toward branching. It is distinguished from the South American *Calathea lietzei* MORREN and *C. lousiae* GAGNAPAIN by its less defined color pattern on the leaf and possession of claviculate bracteoles. The claviculate bracteoles bear an extra-floral nectary subterminally which accounts for the common occurrence of ants on the inflorescences of this species.

The specific epithet refers to its discovery and prevalence in the forested region near Portobelo, Panamá.

Calathea robin-fosteri KENNEDY sp. nov. — Fig. 2

Planta ultra metralis. Folia solitaria longissime petiolata; petioli atrovirides glabri, parte superiore ad 3.2 cm valde conspicue callosa glabra; lamina anguste elliptica apice acuminato vel obtuso base acuta, supra ad medium minutissime puberula, subtus dilute viridis glabra ad medium rubra raro flavo-virens, vagina haud conspicua. Spica e rhizomate ellipsoidea, pedunculo ad 8.6 cm longo subglabro; bracteae spiraliter dispositae minute puberulae; omnis par florum bracteolis indurato-claviculatis comitata; sepala ultra 2.3 cm longa glabra; corollae glabrae; ovarium glabrum.

Herb 1.1—1.65 (1.8) m high, aerial adult shoots bearing a single leaf, rarely two, the several leaves (shoots) connected by a common rhizome. Juvenile shoots bearing several leaves. Rhizome to 1.5 cm in diameter, internodes 0.2—1.2 cm in length. Cataphylls 5—6 per shoot, fleshy toward base, above subcoriaceous, ovate to narrowly ovate-triangular, acute to obtuse in lower ones, purple or green tinged with purple, subglabrous to minutely puberulent, innermost one up to 71 cm long. Leaf blade semi-coriaceous, slightly oblique, narrowly elliptic, apex broadly acute to obtuse, base acute, 36.3—85.5 cm long and 10.1—20.7 cm wide. Leaf surface above green, opaque, glabrous, proximal half of midrib subglabrous, distal half puberulent especially at apex; leaf below light green (in juvenile plants dark purple) dull, midrib red, occasionally yellow-green. Pulvinus glabrous, dark green with red-purple tinge, or reddish-brown, 1.3—3.2 cm long, articulate with petiole, junction on upper side, acuminate. Petiole dark green tinged slightly with purple-brown, glabrous, 32—80 cm long, most commonly 40—55 cm long. Leaf sheath inconspicuous, margins fleshy, highly reduced, to 7.8 (11.7) cm, the basal portion conspicuously swollen, bright pink in young leaves turning pale green to tan with age, 2—3.5 cm long, the outer cells becoming corky. Inflorescence arising directly from the rhizome, shoot bearing the inflorescence is provided with up to 7 bladeless sheaths. Sheaths ovate to narrowly ovate, obtuse to acute, purple, minutely pubescent, the base and the internode of the rhizome below sericeous. Scape dark purple to

Fig. 2. *Calathea robin-fosteri*. A: Habit. Note inflorescence at base of plant. — B: Inflorescence on separate shoot from the rhizome. Note pale needle-like claviculate bracteoles protruding from the bracts. — C: Untripped flower showing shape of callose and outer staminodes. — D: Flower on lower leaf surface. — E: Capsules with persistent sepals and arillate seeds on upper leaf surface. — Scale in cm.

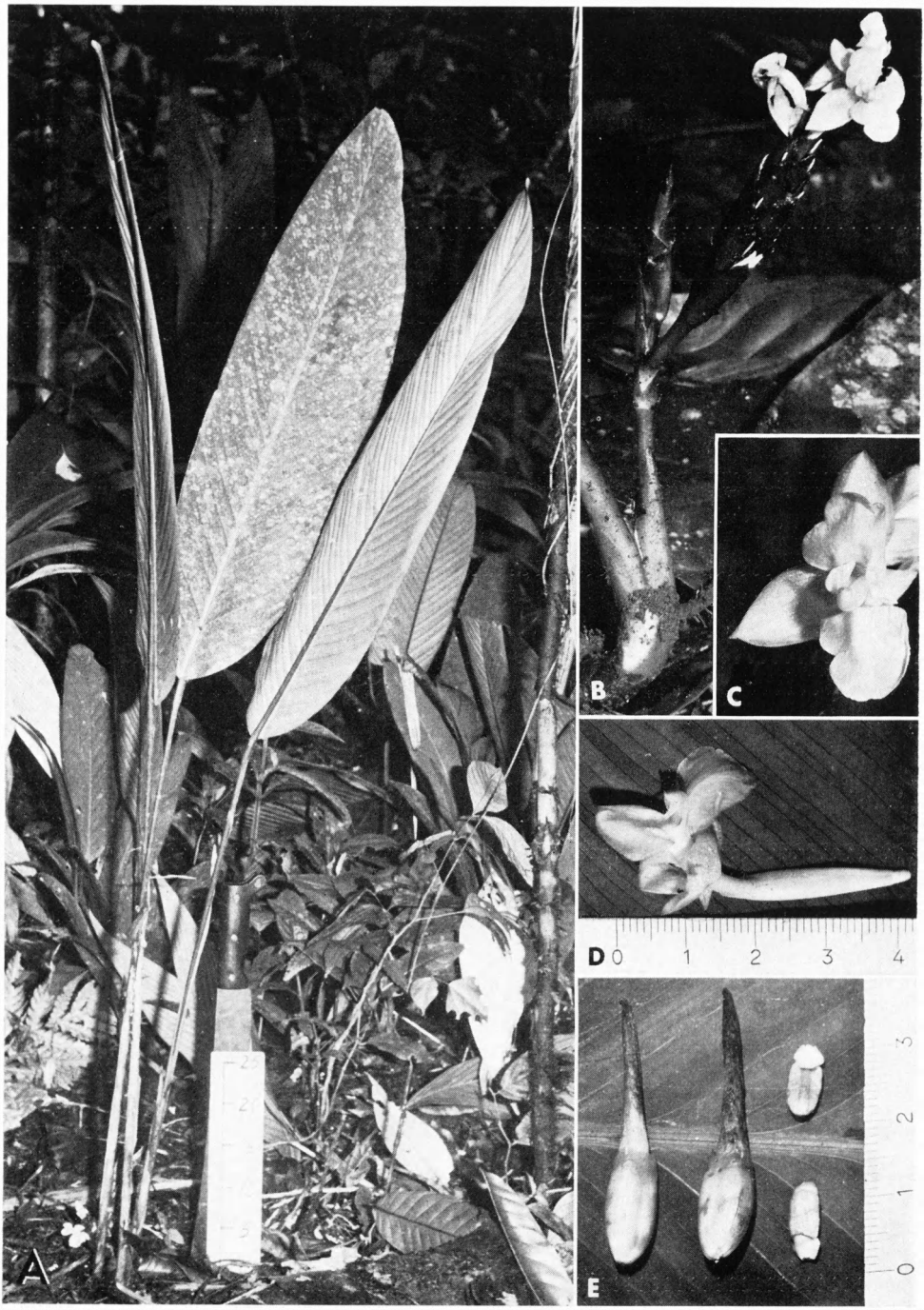

Fig. 2.

purple-brown, subglabrous, 2.2—8.6 cm long, bearing a narrowly ovate, acute sterile purple bract which subtends 2 inflorescences, one borne terminally, the second arising in the axil of this bract separated from the first by a bicarinate prophyll and subtended by a reduced leafless sheath, these last two structures always shorter than the sterile bract. Occasionally only the terminal inflorescence subtended by the sterile bract is developed. Inflorescence spiciform, narrowly ellipsoid-fusiform to subcylindrical, 4.5—7 cm long, 1.3—2.2 cm wide. Peduncle subglabrous, dark purple, 1.1—7 cm long, the terminal one longer. Bracts 9—13, spirally arranged, imbricate, herbaceous to subcoriaceous, dark red-purple to brownish-purple, minutely tomentose, hairs less than 0.3 mm, not visible to the naked eye, mitre shaped, acute, rarely obtuse, 2.3—2.8 cm high and 1.2—1.8 cm wide, each subtending 2 or more flower pairs. Bicarinate prophyll membranaceous, narrowly ovate, acute, margins and apex puberulent, 2—2.5 cm high and ca 0.8—0.9 cm wide. Mesophyll membranaceous, narrowly ovate, acute, apical 1/3 puberulent (14×), 2.4—2.6 cm high and 0.9—1.1 cm wide. Bracteoles subtending individual flowers two per flower pair, membranaceous, narrowly ovate, puberulent at apex, 2.3—2.5 cm long and 5—6.5 mm wide. Each flower pair is accompanied by an indurate claviculate bracteole 2.5—3.1 cm long, yellow-tan apically, tinged purple below. Sepals oblong to narrowly subobovate, acute, glabrous, entirely white or with apical half faintly tinged pink, 2.3—2.6 cm long and 0.4—0.55 cm wide. Corolla tube glabrous, white, (2.3) 2.5—3.0 cm long; lobes subequal, shallowly concave, elliptical acute to obtuse, apical margins incurved, glabrous, entirely white or with the distal half tinged pale pink, 1.5—1.6 cm long and 0.8—1 cm wide. Outer staminode broadly elliptic to suborbicular, apex rounded, irregular, shallowly emarginate, white, 1.25—1.4 cm long and 1.1—1.2 cm wide. Callose staminode petaloid apically, upper half depressed elliptical, apex emarginate, white, 1.5—1.6 cm long and 1.35—1.45 cm wide. Cucullate staminode white, 0.5—0.6 cm long and ca 0.55 cm wide, bearing a subterminal filiform appendage 2—2.5 mm long. Stamen with lateral petaloid appendage to 1.5 mm wide narrowing above, anther ca 2 mm long, apical 1/3 free. Style and stigma white. Ovary white, glabrous, ca 3 mm long and ca 2 mm in diameter. Capsule smooth, fleshy, ellipsoidal, with slight constriction subterminally, with a thickened, raised, apical rim, the apical margin of each valve tridentate, crowned by a persistent calyx. Seeds usually three per capsule, trigonous, rugose on outer surface, brown, 6—7.5 mm long and 3.5—4.5 mm in diameter, provided with a basal white aril ca 3 mm high.

TYPE. Panamá: Prov. Colón, Río Guanche ca 1.5 mi. upstream from bridge, mature forest, 10 m elev., 1 Nov. 1971, H. KENNEDY 1235 (holotype US, isotypes F, MO).

OTHER COLLECTIONS. Panamá: Prov. Colón, Río Guanche, 2 mi. upstream from the bridge, mature forest, 17 July 1971, H. KENNEDY, R. B. FOSTER & R. L. DRESSLER 1083 (GH, K, NY); ca 1.5 mi. upstream from the bridge, mature forest, 10 Aug. 1971, H. KENNEDY, R. L. DRESSLER & H. WIEHLER 1106 (US); lowland wet forest, ca 10 m, 23 Aug. 1972, H. KENNEDY & R. L. DRESSLER 1499 (DUKE, PMA, U); Río Iguanita, ca 1 mi. upstream, lowland wet forest, elev. ca 10 m, 27 Mar. 1975, H. KENNEDY & R. L. DRESSLER 3474 (F). This species was also found in the Río Boqueron drainage, 6—8 km beyond the Peluca Hydrographic station on the road to Nombre de Dios, Colón Province, Panamá.

Flowering mainly during the rainy season, April to November. However, along the Río Iguanita plants were in flower in March. It occurs in moderate to deep shade on well drained sites not subject to flooding.

It is easily distinguished from other Central American Calatheas by possessing a single leaf per shoot and the inflorescence borne on a separate shoot, imbricate bracts, claviculate bracteoles, and a corolla tube shorter than 3.2 cm. Vegetatively it closely resembles the often cultivated

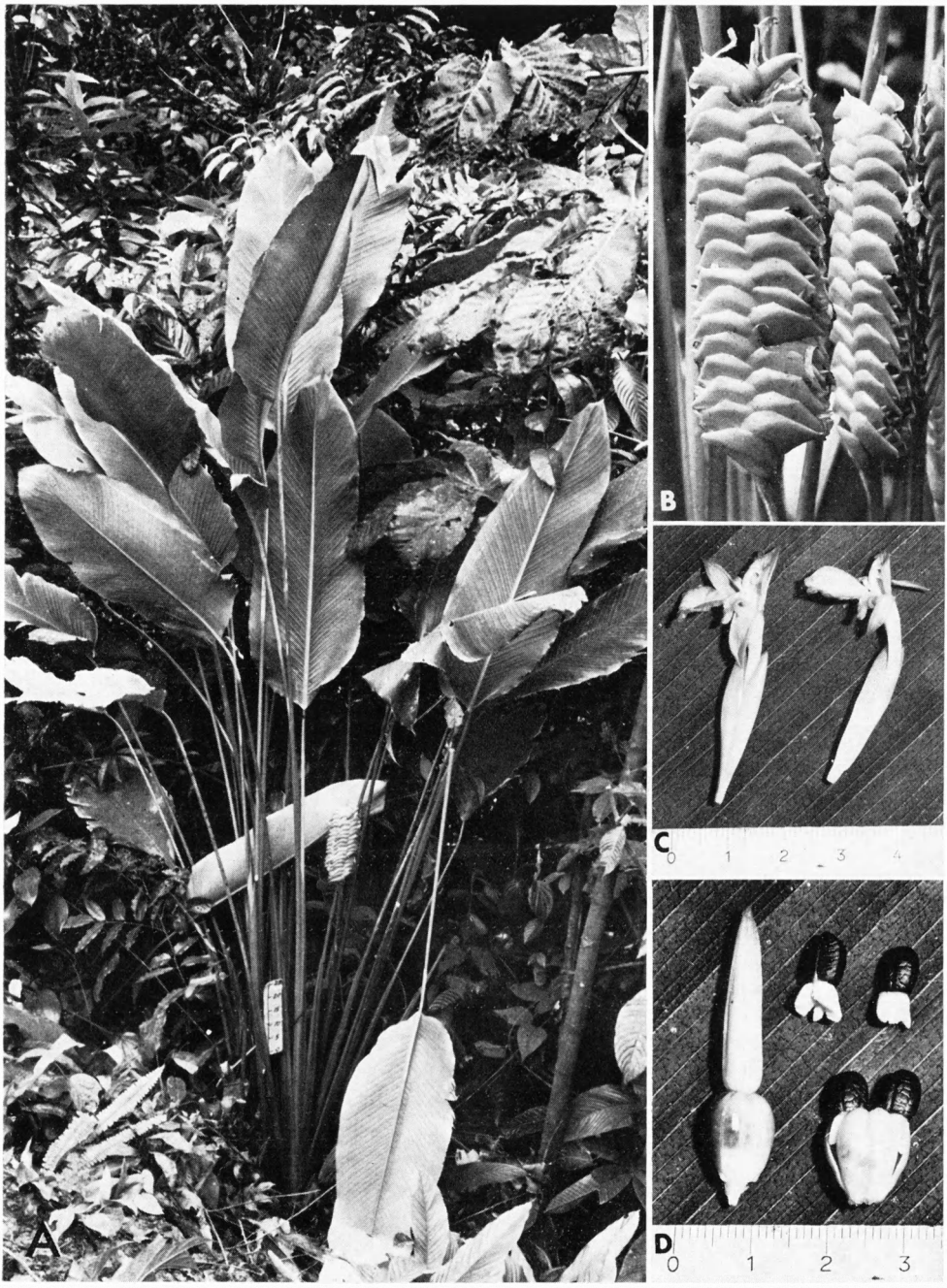

Fig. 3. *Calathea similis*. A: Habit. — B: Inflorescences. — C: Tripped flowers on upper surface of leaf. — D: Capsules with persistent calyx, dehisced capsule with emerging seeds and arillate seeds on upper leaf surface. — Scale in cm.

C. variens KOERNICKE and is distinguished from that species by the glabrous, solid-colored petiole. It differs from other species having separate floral and single-leaved vegetative shoots (*Calathea* Series *Rhizanthe,* SCHUMANN 1902 p. 70) by the imbricate bracts, indurate claviculate bracteoles, acute leaf base and leaf width greater than 10 cm.

This species is named in honor of Dr ROBIN FOSTER whose help and logistic support has greatly aided this study and whose fascination with tropical forests led to his investigation of the Río Guanche area and hence the discovery of this, as well as other new species.

Calathea similis H. KENNEDY sp. nov. — Fig. 3

Planta 1.7—3.2 m alta. Petioli villosi vel glabri, folia ovata acuminata vel subuncinata base obtusa vel rotundata supra dense villosa subtus pars marginalis sparsim villosa ceterum glabra. Spicae ad 24 cm longae folio comitata pedunculis ad 70 cm longis villosis vel glabris; bracteae distichae apice emarginato aureae unctuosae ad marginem villosae valde suaveolentes; paria florum ad 6; sepala ad 2.5 cm longa; corollae aureae tubo ad 3 cm longo.

Caulescent herb 1.7—3.2 m high, shoots bearing 5—8 leaves, 4—7 arising basally, the uppermost leaf which subtends the inflorescences is borne above an elongated stem internode up to 1.3 m long. Rhizome fibrous, semi-woody. Cataphylls usually dead, partially rotted on mature flowering shoots, narrowly ovate, obtuse, mucronulate, abaxially grass-green, villose, especially basally and centrally, innermost cataphyll 40—115 cm long. Leaf blade semi-leathery, pliable, apex acuminate to uncinate, base obtuse to rounded, 80—91 cm long and 32—39 cm wide in subtending leaves, others 75—105 cm long and 25—38 cm wide. Leaf blade above grass-green to dark green, densely villose (hairs ca 2 mm long), midrib yellow-green, villose; leaf surface below light green to glaucous, glabrous, occasionally sparsely villose. Pulvinus round in cross section, olive-green, glabrous, articulate with petiole, the junction light yellow-green, 10.3—12.5 (14) cm long in the subtending leaf, 7.5—16 cm in others. Petiole grass-green to deep green, glabrous to villose, 51—74 cm long in subtending leaf, 45—120 cm in others. Leaf sheath not auriculate, grass-green to deep green, villose throughout or the margins densely villose with the central abaxial portion partially or entirely glabrous; pale green glabrous within, 33—56 cm long in subtending leaves, 60—120 cm in others. Stem grass-green to deep green, subglabrous to villose; puberulent to subglabrous where covered by the leaf sheaths. Inflorescences 2—4 per shoot depending on age, commonly 2, the first one terminal, the second arising in the axil of the subtending leaf with accompanying bicarinate prophylls and bladeless sheaths, rectangular, compressed, 20—24 cm high and (6.5) 7—8 cm across. The subtending bicarinate prophylls yellow-green, villose along the carina. Peduncle grass-green to deep green, villose (21) 40—72 cm long, the peduncle of the first inflorescence longer than the rest. Bracts 26—34 in number, leathery, distichously arranged, reniform, conduplicately folded, apex emarginate, 3.8— 4.1 cm high and 6.8—7.8 cm wide, unfolded, with a strong sweet, fruity fragrance, each subtending 6 or more flower pairs. Abaxial surface of bract shiny, oily in appearance, deep golden yellow to yellow-orange, lower bracts villose with scattered hairs, upper ones more sparsely so; adaxial surface yellow-orange, very shiny with a marked oily appearance, glabrous. Bicarinate prophyll membranaceous, broadly ovate, apex obtuse to slightly rounded, translucent to subopaque orange, abaxial surface of carina villose, the rest glabrous; within glabrous, 2.4—2.8 cm high, 1.1—1.5 cm wide carina to carina, and 1.8—2.4 cm total width. Mesophyll membranaceous, broadly ovate, apex rounded, translucent to subopaque orange, glabrous, occasionally bearing a few hairs at the apex, 2.5—2.7 cm high and 2.1—2.8 cm wide. Bracteoles subtending individual flowers 1 per

flower pair, membranaceous below, apically thickened, stiff, obovate-elliptic, orange, glabrous, 2.4—2.6 cm long and 0.3—0.5 cm wide. Sepals channeled, narrowly obovate, apex acute, translucent cream below, apical 1/3 yellow-orange, occasionally tinged with green, glabrous, 2.2—2.55 cm long and 0.5—0.6 cm wide. Corolla tube light yellow-orange, glabrous, 2.8—3 cm long; staminal tube 2—3 mm long; corolla lobes subequal, narrowly obovate-elliptic, apex obtuse, margins infolded, appearing acute, bright yellow, apical portion yellow-orange, glabrous, 1.3—1.5 cm long and 0.35—0.5 cm wide. Outer staminode broadly elliptic very shortly clawed at the base, apex rounded, bright yellow-orange, 1.1—1.2 cm long and 0.7—0.9 cm wide. Callose staminode rectangular, apical portion petaloid, deeply bifid into two unequal appendages, yellow-orange to dark gold, 1.2—1.4 cm long. Cucullate staminode yellow-orange, 0.55—0.7 cm long and 3.5—4 mm wide provided with a subterminal filiform appendage. Stamen with lateral yellow-orange petaloid appendage to 1.5 mm wide, extending halfway up the anther; anther 3 mm long. Style and stigma golden orange. Ovary cream-colored with faint greenish tinge, glabrous, 2.5—3 mm high. Capsule thin, smooth, obovoid, apex rounded, straw-colored to orange-yellow, 1.1—1.3 cm high and 0.8—0.9 cm wide, crowned by a persistent live, expanded, bright orange calyx. Seeds usually 3 per capsule, trigonous, dark blue, 6—7 mm high and ca 5 mm in diameter bearing a basal white aril 4—5 mm high.

TYPE. Panamá: Prov. Colón. Santa Rita Ridge below the rain gauge, 13 Aug. 1971, H. KENNEDY, R. L. DRESSLER & H. WIEHLER 1127 (holotype US, isotypes F, MO).

OTHER COLLECTIONS. Panamá: Prov. Colón, Santa Rita Ridge road past Santa Rita, 10 July 1969, H. KENNEDY, R. L. DRESSLER & N. H. WILLIAMS 298 (PMA). Prov. Panamá, km 10—12 on the road to Carti, 18 Sept. 1974, H. KENNEDY, P. J. MAAS, R. L. DRESSLER & C. TOFT 3400 (F). Prov. Veraguas, Río Primero Braso, 2.5 km beyond Agriculture School Alto Piedra, near Santa Fe, 700—750 m, 24 July 1974, T. CROAT 25498 (MO). Prov. Bocas del Toro, Punta Peña, vicinity of Chiriquicito, ca 1000 ft, rain forest, 7 June 1967, W. LEWIS et al. (SCZ, UC). — Costa Rica: Prov. Heredia, small hills of cleared agricultural land and areas of remnant original forest now being logged at 150—250 m, near Tirimbina E of the Río Sarapiqui, 10° 24′ N, 84° 7′ W, 12—15 Aug. 1971, W. C. BURGER & M. BURGER 8141 (F); La Selva OTS field station on Río Puerto Viejo, near Pto. Viejo, 27 May 1969, H. KENNEDY 263 (MO); 15 July 1970, H. KENNEDY 405A (CR).

Flowering May to November during the rainy season. Occurring in evergreen wet forests usually at the forest edge and frequently in disturbed areas with full sun in association with second growth species. It appears to be rather shade intolerant. It is most closely related to *Calathea insignis* PETERSEN (with which it has been confused) and *C. trinitensis* BRITTON. It is easily distinguished from other distichously bracted species by the villose upper surface of the leaf, its relatively large size (usually over 2 m), the sparsely, not densely villose bright yellow-orange, unctuose bracts and the absence of claviculate bracteoles. The distinct fragrance of the bracts is sufficient to distinguish it from all other species in the field and might act as a signal to pollinators as it is strongest in young inflorescences. The degree of pubescence varies between populations. The peduncle, petiole and leaf sheath are densely villose throughout in the Panamanian specimens while the petiole, upper portion of the peduncles and the central abaxial portion of the leaf sheath are glabrous in the Costa Rica material.

The specific epithet is from the Latin adjective *similis*, referring to the similarity of its laterally compressed inflorescence with that of *C. insignis* PETERSEN.

Calathea guzmanioides SMITH & IDROBO

SMITH & IDROBO in Caldasia 5: 47 (1948).

This species, previously known only from Colombia in the Departments of Chocó and El Valle, has recently been found in the Atlantic lowlands of Panamá.

Specimens from Panamá (DRESSLER 4214) were compared with the type (KILLIP & CUATRECASAS 38748, US) and clearly represent this species.

Panamá: Prov. Colón, along tributary between Caño Rey and San Lucas, S of Coclé del Norte, 19 Aug. 1972, R. L. DRESSLER 4214 (F, US).

This species is most closely related to an as yet undescribed species from Panamá and Costa Rica and slightly less so to *Calathea allenii* WOODSON, all having a similar inflorescence structure. It is easily distinguished from *C. allenii* by its larger size (up to 2.5 m versus 1.4 m), the nonplicate leaf (*C. allenii* is strongly plicate) and the bract margin entire rather than deeply emarginate. *Calathea guzmanioides* differs from the undescribed species by the entire, instead of emarginate, lower bracts and the seeds oblong-elliptic rather than circular in outline.

ACKNOWLEDGEMENTS

The author acknowledges the invaluable assistance of Dr ROBERT L. DRESSLER during her field studies in Panamá and wishes to thank Dr ROBIN FOSTER for introducing her to the Río Guanche area and Dr WILLIAM C. BURGER for reading the manuscript.

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Lamprocephalus B. Nord., a New Senecioid Genus from South Africa

Bertil Nordenstam

NORDENSTAM, B. 1976 02 09. Lamprocephalus B. Nord., a new senecioid genus from South Africa. — Bot. Notiser 128: 323—326. Lund. ISSN 0006-8195.

Lamprocephalus montanus B. NORD. is described as a new monotypic genus of the Compositae-Senecioneae. It is a shrublet with solitary, discoid capitula and a curiously appendaged style, which is unique in the tribe. The distribution is confined to some mountains of the western Cape Province.

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Lamprocephalus montanus B. NORD., gen. et sp. nov. (Compositae—Senecioneae)

Orig. coll.: SCHLECHTER 10119, Cape Province, Ceres Div., Koude Bokkeveld, in montibus pone Tweefontein, 5500 ft., 24.III.1897 (S holotype; BM, BOL, K isotypes).

Fruticulus erectus vel adscendens, glaber praeter axillas et dorsa foliorum araneosotomentosa. *Folia* alterna sessilia simplicia integerrima imbricata linearia subtriquetra apice mucronata basi semiamplexicaulia. *Pedunculi* terminales solitarii elongati scaposi monocephali. *Involucrum* campanulatum basi truncatum, *bracteis* 11—13 uniseriatis liberis lineari-lanceolatis. *Receptaculum* planum nudum. *Capitulum* homogamum discoideum. *Corolla* tubulosa glabra; lobi triangulares canali resinifero mediano instructi. *Styli* rami dilatati glabri intra area stigmatica continua vestiti, apice appendice oblongo-triangulari minute papillosa et protuberationibus tribus dorsalibus ornati. *Antherae* basi breviter sagittatae apice appendice plana anguste triangulari acuta coronatae. *Achaenia* oblonga truncata demum nigra obscure quinquangulata albopapillata. *Pappi* setae copiosae albae persistentes corolla breviores.

Erect or ascending shrublet, 0.2—0.5 m high, branching basally, glabrous except for a loose cobwebby tomentum in leaf-axils and on adaxial sides of young leaves. Branches becoming nude with age and lepidote with persistent leaf-bases.

Leaves alternate, sessile, simple, imbricated, linear from a broader half-clasping base, (0.5—)1—2(—3) cm long, 1—1.5 (—2) mm wide, suberect—erecto-patent and somewhat curved, more spreading with age, subtriquetrous with flattish or slightly concave adaxial side, abaxially obscurely keeled especially basally, subcarnose or coriaceous, mucronate.

Peduncles terminal, solitary, simple, scapose, 3—25 cm long, ca 1.5 mm thick, with 3—7 scattered filiform-subulate reduced leaves up to 1 cm long.

Involucre cupuliform—narrowly campanulate with a truncate base, 1.5—2 cm high, 1—1.5 cm wide, basally only 3—5 mm wide. Involucral bracts uniseriate, 11—13, equal, free from the base, linear-lanceolate, 1.2—1.8 cm long, 1—2 mm wide, 2—3-veined, coriaceous in the centre and with thinner margins, apically acuminate.

Receptacle flat, nude.

Capitula homogamous, discoid, ca 15—30-flowered. Corolla tubular, 10—14 mm long, probably red with yellowish base, glabrous; lobes narrowly triangular, 1—1.3 mm long, with a distinct resiniferous midvein, thickish, with involute margins and subcucullate tips. Style terete, basally swollen; style branches distinctly broader than

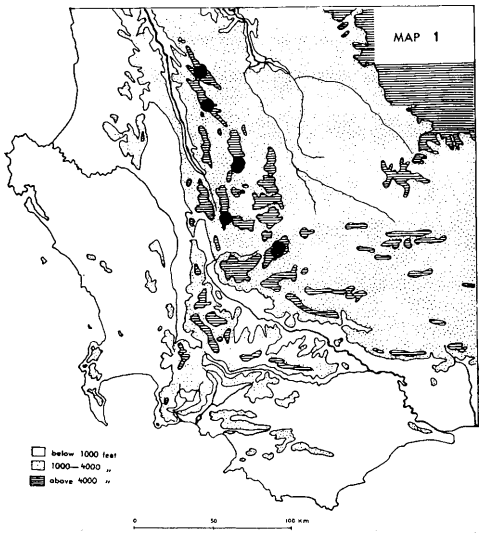

Fig. 1. Distribution of *Lamprocephalus montanus* B. NORD.

the shaft, 4—5 mm long, glabrous, inside with continuous stigmatic areas, outside faintly 3—4-ribbed, apically with a 1—1.5 mm long oblong-triangular obtuse—subacute minutely papillate dorsally 3(—4)-hunched appendage. Anthers 4—4.5 mm long incl. the flat and acute narrowly triangular appendage, basally minutely sagittate; endothecial cells with laxly set thickenings on longitudinal and transverse walls; filament collar ca 1 mm long, basally dilated with somewhat larger cells, broader than the filament.

Achenes narrowly oblong, 6—9 mm long, 1.5—2 mm broad, with rather truncate ends, obscurely 5-angular, brown, eventually black, covered with small whitish mucilaginous papilliform duplex hairs arranged in five longitudinal fields. Pappus bristles copious, pluriseriate, 9—11 mm long, persistent, laxly and minutely serrulate, glossy white.

Flowering period: Dec.—April.

CAPE PROVINCE. Clanwilliam Div.: Cedarberg Mts, Pk S of Sneeuwkop, SW slopes, shale band, 5000 ft, I. 1942, ESTERHUYSEN 7591 (BOL) — S Cedarberg, Apollo Pk, slopes, 4000—5000 ft, III. 1956, ESTERHUYSEN 25526 (BOL). — Ceres Div.: In clivis saxosis montium Skurfdebergen prope Gydouw, 5400 ft, XII. 1891, H. BOLUS 7551 leg. A. BODKIN (BOL, K) — Koude Bokkeveld, in montibus pone Tweefontein, 5500 ft, III. 1897, SCHLECHTER 10119 (BM, BOL, K, S) — Schurweberg Pk, betw. Bokkeveld Sneeukop and Bokkeveld Tafelberg, stony slopes, S aspect, 4500 ft, I. 1962, ESTERHUYSEN 29435 (BOL, S). — Worcester Div.: Plateau betw. Matroosberg and Sonklip, 6000 ft, IV. 1958, ESTERHUYSEN 27679 (BOL) — Matroosberg, shale band, 6500—7000 ft, I. 1959, ESTERHUYSEN s.n. (BOL).

This remarkable new taxon was first collected in 1891 by BODKIN and six years later by SCHLECHTER, who distributed it as "*Senecio lamprocephalus* SCHLTR n. sp." This name was never validly published, although it has been used in herbaria as well as in literature (MUSCHLER 1909 p. 56). It therefore seems appropriate to adopt SCHLECHTER's epithet as a generic name.

In gross morphology the new taxon resembles some *Senecio* species (e.g. those of sect. *Pinifolii*). The peculiar style is very different from anything known in *Senecio*, however. The style branches are unusually stout and crowned by a large sterile appendage. Sweeping-hairs are completely lacking, but the appendage has a papillate surface and a few dorsal hunches near the base. The stigmatic areas are continuous, covering the whole of the inside of the style branches except for the tip of the apical appendage (Fig. 2 C, D). This type of style is quite unique in the tribe Senecioneae. The sterile tips of the style branches in e.g. *Gynura* are very differently shaped. The typical *Senecio* style has discrete stigmatic areas and a terminal brush of sweeping-hairs.

Other characteristics of the new genus are the scapose peduncles with (probably) red-flowered discoid capitula, the uniseriate involucre without a calyculus, and the acute anther appendages. The achenial wall is very firm, and the five veins are best seen after dissection.

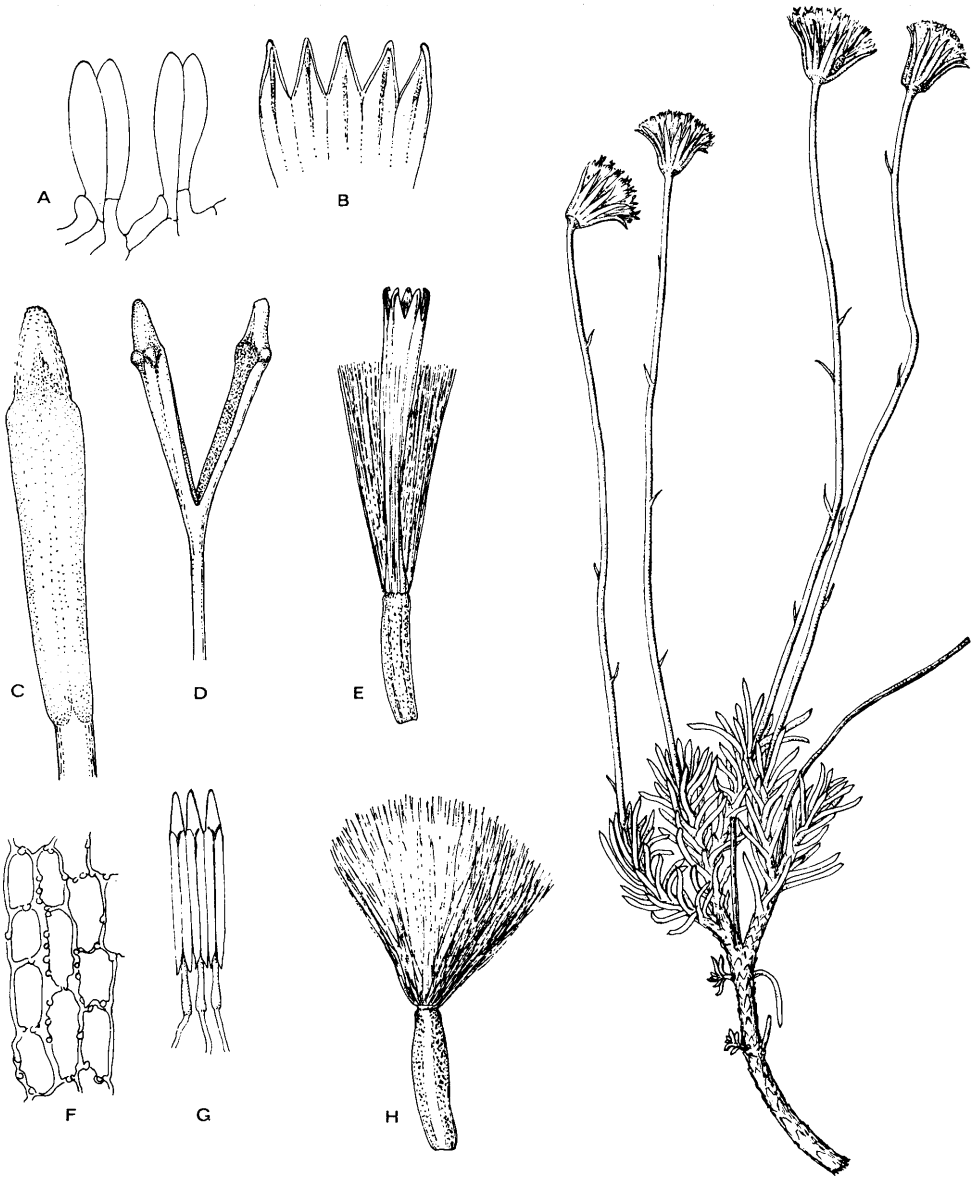

Fig. 2. *Lamprocephalus montanus* B. NORD. (SCHLECHTER 10119, typus). — A: Achenial hair, ×150. — B: Corolla lobes, laid out, ×6. — C: Style branch, inside, ×12. — D: Style branches, ×6. — E: Floret, ×3. — F: Endothecial cells, ×75. — G: Anthers, ×6. — H: Achene, ×3. — Right: Habit, ×1/2. — Del. auct.

The distribution of the monotypic genus is limited to some western Cape mountains, from the Cedarbergen in the north to the Matroosberg in the south (Fig. 1). In the phytogeographical groupings of the Cape floristic element (WEIMARCK 1941, NORDENSTAM 1969) the taxon belongs to the Northwestern Endemics. The apparently rare species seems to favour stony slopes with a southerly or south-westerly aspect at altitudes of between 1200 and 2100 metres.

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A Comparative Study on the Cambial Structure of Some Arid Zone Species of Acacia and Prosopis

A. K. M. Ghouse and Muhammad Iqbal

GHOUSE, A. K. M. & IQBAL, M. 1976 02 09. A comparative study on the cambial structure of some arid zone species of Acacia and Prosopis. — Bot. Notiser 128: 327—331. Lund. ISSN 0006-8195.

The cambial constituents in the different species of *Acacia* and *Prosopis* differ in size, relative number, and extent of area occupied in the cambial zone. The cambium is stratified in *A. catechu* and non-stratified in others. Among the latter, Indian species are characterized by tall, broad, multi-seriate ray initial units with a relatively high proportion of ray initials, while the exotics possess short and narrow ray initial units with a relatively low proportion of ray initials.

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The present report, dealing primarily with the cambial structure of some *Acacia* and *Prosopis* species, forms part of the programme of this laboratory investigating the structure and behaviour of the vascular cambium in tropical trees. It is hoped that the information thus obtained will make it possible to recognize the trends of specialization, if any, in cambia of tropical trees.

MATERIAL AND METHODS

Cambial samples (20—24 for each species) along with some sapwood and inner phloem were collected in September 1973 (2 cm square blocks) from the main trunks of adult trees of *Acacia* and *Prosopis* species, viz. *Acacia catechu* WILLD., *A. farnesiana* WILLD., *A. melanoxylon* R. BR., *A. nilotica* (L.) WILLD. var. *cupressiformis* STEWART (Ramkanta or Ramkati babul), *A. nilotica* var. *telia* TROUP (Godi babul), *A. nilotica* var. *vediana* COOKE (Kauria babul), and *Prosopis spicigera* L., growing in or around Aligarh within a radius of 16 km, and fixed on the spot in FAA. The samples were aspirated for the free access of the fixative into the deeply situated cambial tissue and after five days were preserved in 70 % ethanol. Two- to three-year-old twigs were also collected, fixed, and preserved as above. Transverse and tangential sections through the cambial zone were made from all collections on a sliding microtome at a thickness of 10—12 µ, and stained with tannic acid-ferric chloride (FOSTER 1949) and Heidenhain's haematoxylin. They were mounted in Canada balsam after dehydration in the ethanol series (SASS 1958).

To calculate the area occupied by different types of initials camera lucida drawings were made on tracing paper. Portions of the drawings containing the ray initials were carefully removed and weighed on an electrically operated microbalance. The pieces of paper bearing only fusiform initials (after the removal of the drawings of ray initials) were also weighed separately. The proportion of one type of element to the other in the cambial strip was then calculated per unit area on the basis of the weights thus obtained. To confirm the accuracy the results were compared with those obtained by direct calculation based on the measurements of the size of initials as described by GHOUSE and YUNUS (1974 a).

OBSERVATIONS

The vascular cambium in aerial axes of all the species investigated in the present study appears as a cylinder between the xylem and phloem, and consists

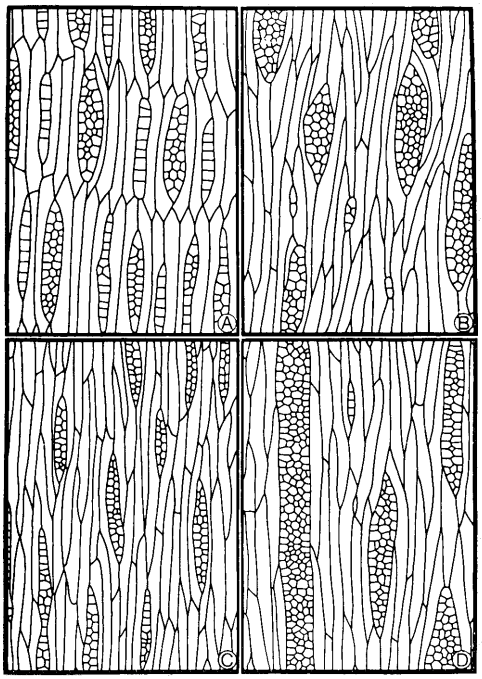

Fig. 1. Camera lucida drawings of the cambial strips of *Acacia* and *Prosopis* as seen in tangential sections. — A: *A. catechu*. — B: *A. farnesiana*. — C: *A. melanoxylon*. — D: *P. spicigera* (all ×30).

of elongated fusiform cells as well as the ray initials. Fusiform cells, in all species except *A. catechu*, are roughly hexangular with long parallel sides and narrow pointed ends which overlap and elongate apically (Figs. 1 B—D, 2). In *A. catechu* on the other hand, fusiform cells, which show no overlapping and apical elongation, remain comparatively short (Fig. 1 A), the cambium stratified.

The length of fusiform cells varies in the different species, ranging from 190—360 μ in *Acacia* species, and 200—320 μ in *Prosopis*. End walls of these cells measure from 10—170 μ in *Acacia* and 45—120 μ in *Prosopis* (Table 1). In all the species studied, the fusiform cells were found to be shorter in younger axes than in the older ones.

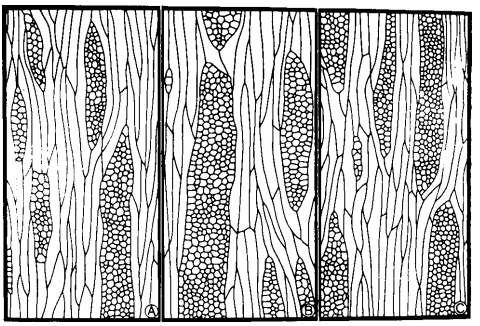

Fig. 2. Camera lucida drawings of the cambial strips of three varieties of *Acacia nilotica* as seen in tangential sections. — A: var. *vediana*. — B: var. *telia*. — C: var. *cupressiformis* (all ×20).

Ray initials aggregate frequently to form fusiform units of varying magnitude in all the species. Often two or more such units unite to form complex bodies running to a greater depth, covering the length of two or more fusiform cells (Figs. 1 D, 2). They form very tall structures in *A. nilotica* and *P. spicigera*, comprising over 70 cells. In *A. catechu*, 98 % of the ray initial units are short (1—15 cells) while in *A. farnesiana* and *A. melanoxylon*, up to 68 % and 80 % respectively are short. In the remaining species about 50 % of the ray units are short, except in the variety *cupressiformis* of *A. nilotica* in which only 27 % of the ray initials units fall within this category (Fig. 3).

Like the depth, the width of ray initial units also differs markedly in the different species studied. In *A. nilotica*, 60—78 % of the ray units are multiseriate (4—9 cells), while in others such broad units are either absent (*A. melanoxylon*) or considerably less in number. *A. catechu*, *A. melanoxylon*, and *P. spicigera* show the maximum of uni-, bi- and triseriate ray initial units respectively (Fig. 4).

Fig. 5 indicates the relative proportions of fusiform and ray initials in the species investigated. Fusiform initials constitute about 82 % of the cambial zone

Table 1. Anatomical data on the variation of cambial cell size and structure in *Acacia* and *Prosopis*. The mean is based on three thousand independent measurements taken at random. Range within parentheses.

Species	Fusiform initials			Ray initials		Ray initials units	
	Mean length (μ)	Mean width (μ)	Mean length of gabled or tapering end (μ)	Tangential diameter (μ)	Radial diameter (μ)	Height (no. of cells)	Width (no. of cells)
Acacia catechu	237 (190—271)	16 (13—17)	30 (10—50)	15 (10—20)	15 (9—18)	12 (3—19)	2 (1—4)
A. farnesiana	290 (230—320)	18 (15—25)	95 (60—170)	18 (10—30)	13 (5—20)	11 (1—32)	4 (1—8)
A. melanoxylon	288 (200—360)	15 (10—20)	63 (30—130)	14 (10—20)	10 (9—15)	11 (1—32)	2 (1—3)
A. nilotica var. *cupressiformis*	280 (220—350)	18 (15—20)	66 (30—100)	15 (7—20)	12 (7—18)	25 (6—62)	4 (2—7)
A. nilotica var. *telia*	274 (200—350)	16 (10—20)	70 (30—100)	15 (10—20)	15 (10—20)	20 (5—70)	5 (1—9)
A. nilotica var. *vediana*	237 (230—360)	16 (10—20)	81 (30—170)	18 (12—23)	15 (7—23)	17 (2—70)	4 (1—8)
Prosopis spicigera	263 (200—320)	20 (15—25)	77 (45—120)	18 (15—20)	17 (10—20)	17 (2—65)	3 (1—4)

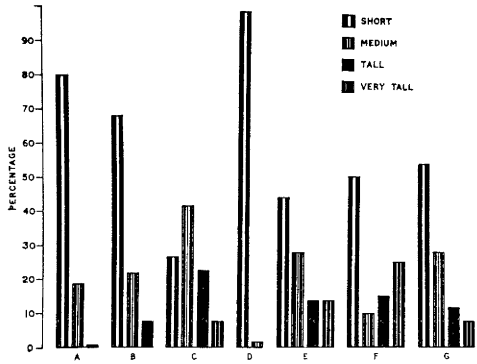

Fig. 3. Histograms showing the frequency of ray initial units of varying height in the cambial zone of *Acacia* and *Prosopis*. — A: *A. melanoxylon*. — B: *A. farnesiana*. — C: *A. nilotica* var. *cupressiformis*. — D: *A. catechu*. — E: *P. spicigera*. — F: *A. nilotica* var. *telia*. — G: *A. nilotica* var. *vediana*. — Short: 1—15 cells. Medium: 16—30 cells. Tall: 31—45 cells. Very tall: 46—70 cells.

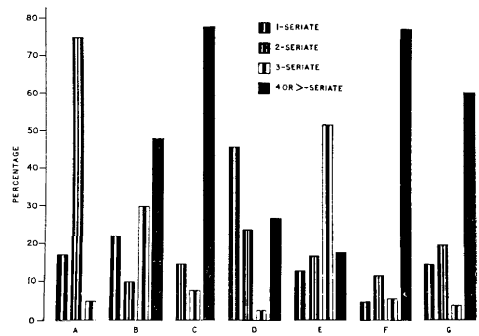

Fig. 4. Histograms showing the frequency of ray initial units of varying width in the cambial zone of *Acacia* and *Prosopis*. — A: *A. melanoxylon*. — B: *A. farnesiana*. — C: *A. nilotica* var. *cupressiformis*. — D: *A. catechu*. — E: *P. spicigera*. — F: *A. nilotica* var. *telia*. — G: *A. nilotica* var. *vediana*.

in *A. melanoxylon*, 78 % in *A. farnesiana*, 70 % in *A. catechu*, 63 % in *P. spicigera* and 57—75 % in *A. nilotica*.

DISCUSSION

Although the cambial components are the same in all species investigated, their composition appears to be species specific. The mode of aggregation and the extent of multiplication of ray initials differ in the different species. Ray initials, for instance, invariably form short and uniseriate structures in *A. catechu*, and mostly tall and broad bodies in *A. nilotica* and *P. spicigera*. It is also worth noting that in *A. farnesiana* and *A. melanoxylon* (both exotics) ray initials from short narrow units, while in rest of the species (all indigenous) tall to very tall and broad multiseriate ray units characterize the cambium (except in *A. catechu*). *A. catechu* having stratified cambium (GHOUSE & YUNUS 1974 b) enjoys a phylogenetically advanced position among other species of the genus *Acacia* in the opinion of BAILEY (1923) and METCALFE and CHALK (1950).

The present findings on the proportions of fusiform cells and ray initials are in opposition to the widely accepted view that fusiform cells constitute about 90 %

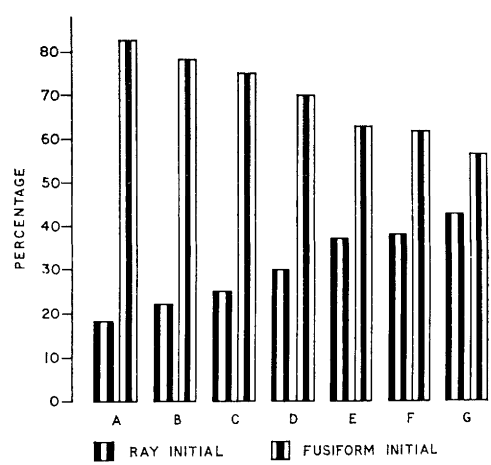

Fig. 5. Histograms showing the proportion of fusiform and ray initials in the cambial zone of *Acacia* and *Prosopis*. — A: *A. melanoxylon*. — B: *A. farnesiana*. — C: *A. nilotica* var. *cupressiformis*. — D: *A. catechu*. — E: *P. spicigera*. — F: *A. nilotica* var. *telia*. — G: *A. nilotica* var. *vediana*.

or more of the cambial zone in different plants or plant groups (BAILEY 1923, WILSON 1963, 1964, KOZLOWSKI 1971, BUTTERFIELD 1972), at the same time confirming the earlier findings made in this laboratory on various tropical trees (GHOUSE & YUNUS 1974 a, c).

The length of fusiform initials varies in different positions within the tree. It gradually increases with the increasing age of the axis till the fusiform cells attain the adult state. Thus the present observations run parallel to those of BAILEY (1923), BANNAN (1962), CARLQUIST (1962), EVERT (1961) and GHOUSE and YUNUS (1973) on some conifers and dicotyledons.

ACKNOWLEDGEMENTS

The authors are grateful to Professor R. KHAN, Head of the Department of Botany, Aligarh Muslim University, Aligarh for providing laboratory facilities. The second author (M. I.) is grateful to the C.S.I.R., New Delhi, for the award of a fellowship. The help rendered by Mr M. YUNUS in preparing the text figures is also gratefully acknowledged.

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Embryo Sac of Hydrobryopsis sessilis (Podostemaceae) – Origin, Organization and Significance

Govindappa D. Arekal and C. R. Nagendran

AREKAL, G. D. & NAGENDRAN, C. R. 1976 02 09. Embryo sac of Hydrobryopsis sessilis (Podostemaceae) — origin, organization and significance. — Bot. Notiser 128: 332—338. Lund. ISSN 0006-8195.

Both Podostemum and Dicraea embryo sac types have been recorded in a single taxon, *Hydrobryopsis sessilis* (Podostemaceae), for the first time. The Dicraea type is reinterpreted. The presence of antipodal cells in the family is refuted. Interrelationships between the Podostemum and Dicraea types are discussed.

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BATTAGLIA (1971) reviewed the existing literature on the embryo sac development in members of Podostemaceae and recognized three major types, viz. (A) the Apinagia type found in the majority of taxa investigated, (B) the Dicraea type confined to the genus *Dicraea* (now *Polypleurum* (TAYL. ex TUL.) WARMING; see HALL 1971) and (C) the Podostemum type the occurrence of which was considered doubtful.

Attempts have been made in this laboratory to understand the development of the female gametophyte in all the Indian genera of Podostemaceae (NAGENDRAN 1974, AREKAL & NAGENDRAN 1975, NAGENDRAN et al. 1976). Since there is no embryological report on *Hydrobryopsis sessilis* (WILLIS) ENGLER — a monotypic genus endemic to South India — the development of the embryo sac has been investigated and its significance presented.

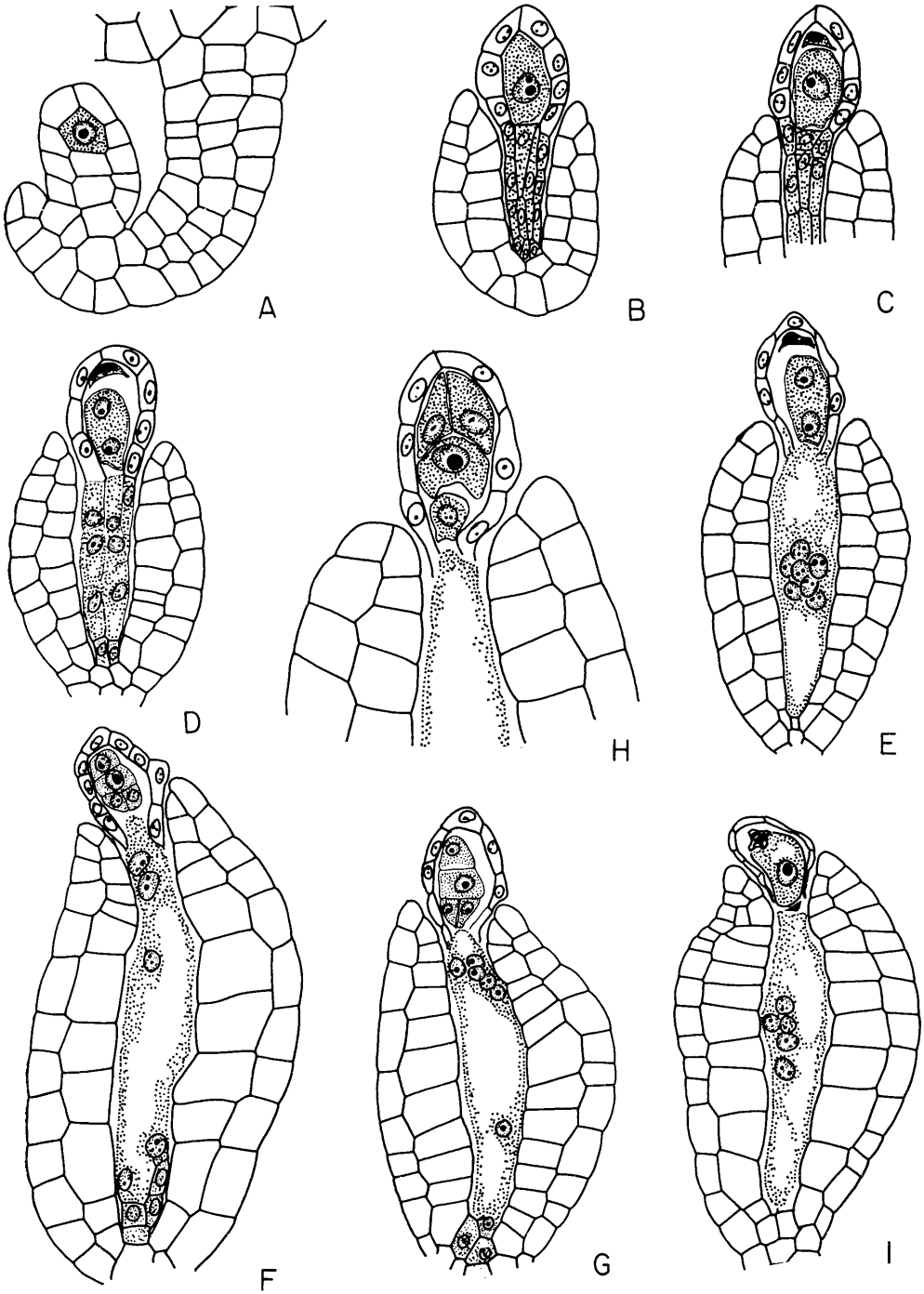
MATERIAL AND METHODS

Material of *Hydrobryopsis sessilis* was collected in formalin/acetic acid/alcohol (FAA) from streams in the South Canara and Chikmagalur districts of Karanataka during January, 1973. Customary methods of dehydration and embedding were employed. Sections were cut on a microtome at 6—10 microns and stained with Heidenhain's Iron alum-Haematoxylin, using erythrosin in clove oil as counter stain.

OBSERVATIONS

The thalloid plant body is pinnately branched and closely appressed to rocks. The flowers are enclosed in 5—7 sessile bracts, only the stamens and stigmas projecting. Each flower has 2 long stamens and 2 staminodes. The pollen is shed as dyads. The ovary is superior, bicarpellary, syncarpous and bilocular with a number of ovules on a massive

Fig. 1. Development of embryo sac in *Hydrobryopsis sessilis*. — A: Ovular primordium with archesporial cell. — B: Megaspore mother cell: outer integument not shown. — C: Functional dyad cell; note degenerated micropylar dyad cell. — D: Two-nucleate embryo sac, just prior to the organization of nucellar plasmodium. — E: Two-nucleate embryo sac; after formation of nucellar plasmodium. — F—G: Organized embryo sacs each with two juxtaposed chalazal synergids, an egg and a micropylar polar cell. — H: Organized embryo sac with two synergids at the micropylar end, an egg below and a chalazal polar cell. — I: Zygote in contact with nucellar plasmodium. — A—B, D—G, I ×640; C ×700; H ×1180.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axile placenta. The fruit is a smooth, subsessile, loculicidal capsule.

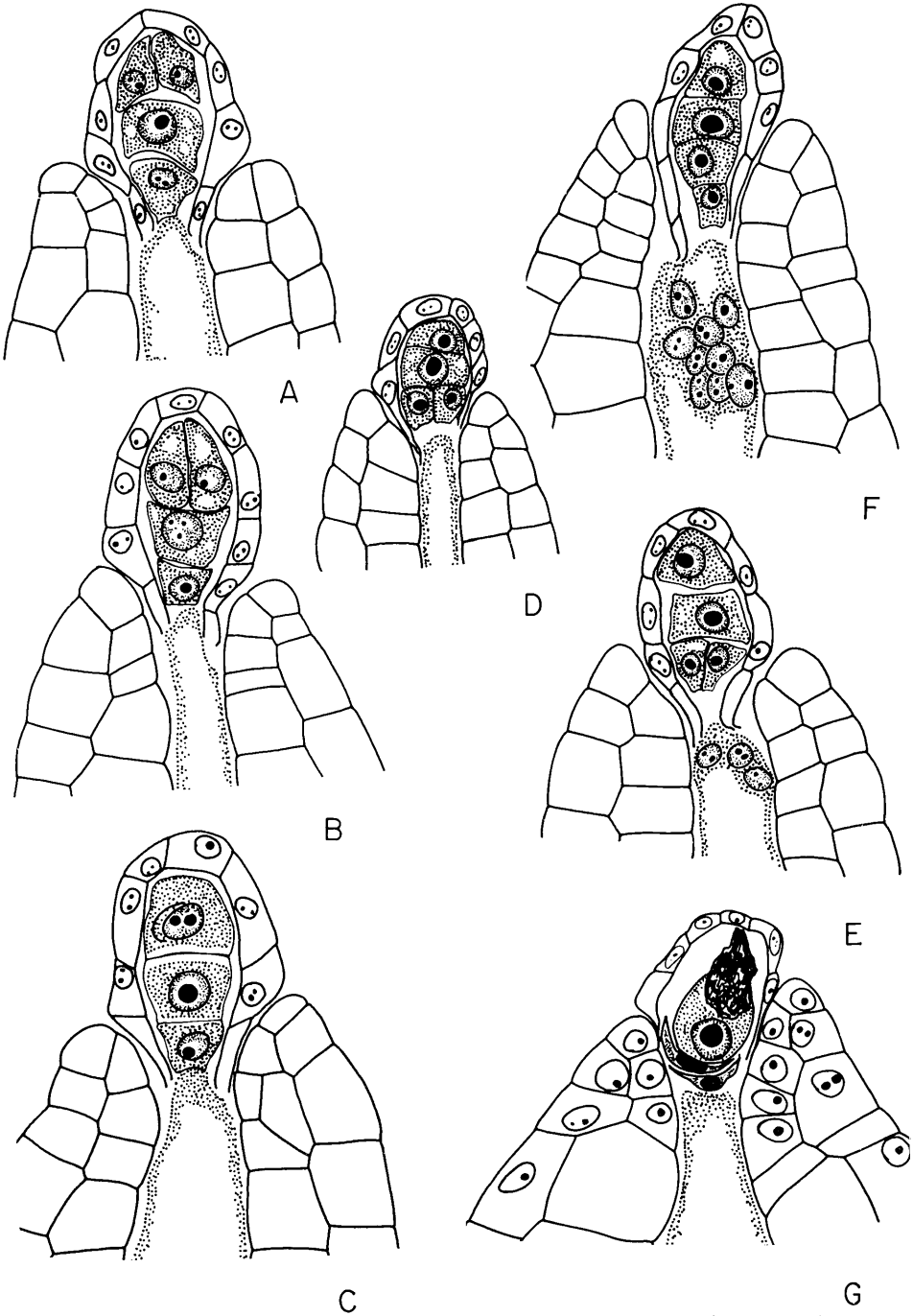
The ovules are anatropous, tenuinucellate and bitegmic. The inner integument is short, the outer alone forming the micropyle. A hypodermal archesporial cell organizes very early in the ovular primordium (Fig. 1 A) and directly functions as megaspore mother cell (Fig. 1 B). It has dense cytoplasm and a large nucleus. The first meiotic division in the megaspore mother cell results in two unequal dyad cells. The smaller micropylar dyad cell soon degenerates and is recognized as a crescent-shaped cap (Fig. 1 C). The nucleus of the lower dyad cell completes the second meiotic division and a two-nucleate embryo sac results (Fig. 1 D—E). The two nuclei move apart and after a simultaneous mitotic division produce four daughter nuclei which contribute to the organization of the embryo sac. In almost 30 % of the ovules the spindles of the two dividing nuclei are disposed in a T-shaped manner. In these ovules, the organized embryo sac has two juxtaposed, pear-shaped synergids at the micropylar end, an egg below them and a polar cell beneath the egg — conforming to the Podostemum type (Figs. 1 H, 2 A—C). On the other hand in 70 % of the ovules the spindles of the two dividing nuclei are oriented in an inverted T-shaped manner. The organized embryo sac consists of two small juxtaposed cells at the narrow chalazal end of the embryo sac, a conspicuous egg above them and a large cell at the broad micropylar end — an embryo sac conforming to the so-called Dicraea type (Figs. 1 F—G, 2 D—E). Occasionally in these embryo sacs, the two smaller chalazal cells may be obliquely disposed or placed one above the other (Fig. 2 F) depending upon available space and the orientation of the spindles of the dividing chalazal nucleus of the two-nucleate embryo sac.

Meanwhile, the nucellar cells situated below the developing megaspore mother cell elongate and become densely protoplasmic (Fig. 1 B). When the embryo sac attains the two-nucleate stage, these cells lose their walls and organize a multinucleate protoplast in which the nuclei are usually situated at one end (Fig. 1 D—I). This is the nucellar plasmodium (AREKAL & NAGENDRAN 1975) that nourishes the future embryo (Fig. 2 G).

DISCUSSION AND CONCLUSIONS

The occurrence of a bisporic tetranucleate embryo sac of the Podostemum type such as noted in the present study was reported by MAGNUS (1913) in *Podostemum subulatus* GARDN., *Farmeria metzgerioides* (TRIMEN) WILLIS and *Zeylanidium olivaceum* (GARDN.) ENGL. Subsequently CHIARUGI (1933) reported a similar type of embryo sac in *Weddellina squamulosa* TUL. However, HAMMOND (1937) who examined *Podostemum ceratophyllum* MICHAUX reported a bisporic five-nucleate embryo sac in which the chalazal nucleus degenerates at the two-nucleate stage (=Apinagia type of BATTAGLIA 1971). A reinvestigation of *Zeylanidium olivaceum* by RAZI (1955) revealed that the embryo sac development conformed to Apinagia type and not to the Podostemum type as stated by MAGNUS (1913). Further, the very existence of the Podostemum type in the family itself has been doubted time and again (P. MAHESHWARI 1937, 1941, 1947, S. C. MAHESHWARI 1955, BATTAGLIA 1971, AREKAL & NAGENDRAN 1975). Nevertheless, the present study has revealed beyond all doubt the existence of the Podostemum type in nearly 30 % of the ovules. The

Fig. 2. Development of embryo sac in *Hydrobryopsis sessilis*. — A—C: Organized embryo sacs with two micropylar synergids, an egg below and a chalazal polar cell. — D—E: Organized embryo sacs with two juxtaposed chalazal synergids, an egg above and a micropylar polar cell. — F: Organized embryo sac with two synergids placed one above the other at chalazal end. — G: Zygote; note degenerated chalazal synergids. — All ×1180.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Podostemum type of embryo sac is simpler than the Apinagia type and closely related to it. Here, the nucleus which would later degenerate and which represents the remnants of the disappearing chalazal quartet of nuclei of an Allium type of embryo sac is not produced at all. The embryo sac is therefore bisporic and tetranucleate, all the four nuclei belonging to the micropylar quartet. Although this type of embryo sac is designated the Podostemum type, its validity could be admitted only when it is consistently found in the genus *Podostemum* MICHAUX. A careful investigation of all species of *Podostemum* would clarify the position.

The occurrence of a bisporic tetranucleate embryo sac of the Dicraea type with two small chalazal cells designated antipodal cells, egg and a single micropylar synergid, both considered as sisters, and without a polar cell, has been reported in *Dicraea elongata* TUL. (MAGNUS 1913), *D. stylosa* WIGHT (MUKKADA 1962, 1964) and *D. agharkarii* NANDI (RAZI 1966). This type has hitherto been regarded as exclusive to the genus *Dicraea*. Its occurrence along with the Podostemum type in ovules of the same ovary in the present study makes it revealing. Actually the Dicraea type presents an inverted image of the Podostemum type and this disposition has neither altered the location nor the size of the egg. The large pear-shaped synergids noted at the micropylar end of the Podostemum type have become much smaller in size with sparse contents and are confined to the narrow region of the embryo sac. There is no doubt that the narrow lower end of the embryo sac is responsible for the smaller size of the cells and their occasional oblique or superposed disposition is due to the orientation of spindles of the dividing nucleus of the lower chalazal zone. Further, these cells can never be regarded as antipodal cells, on the grounds that in the family Podostemaceae itself there is an unmistakable trend towards the elimination of the antipodal complements through the "Strike" phenomenon exhibited by the chalazal nucleus of the two-nucleate embryo sac leading towards simplification in both size and structure. In *Indotristicha ramosissima* (WIGHT) VAN ROYEN (CHOPRA & MUKKADA 1966, and our own observations), the disappearance of the primary chalazal nucleus occurs about the time of the organization of the embryo sac, while in *Farmeria indica* WILLIS emend. AREKAL & NAGENDRAN (AREKAL & NAGENDRAN 1974, 1975) it occurs much earlier. In the Podostemum type, the "Strike" phenomenon is complete and the nucleus which would later degenerate is not produced at all. Thus the Dicraea type of embryo sac is nothing but an inverted Podostemum type and need not be considered unique as in the following description: ". . . the peculiar egg apparatus with a single synergid and egg, the absence of polar nuclei and the presence of two (occasionally only one) antipodal cells are a rare combination of characters not found in any other angiosperm — not even in any other member of the Podostemaceae" (MUKKADA 1964 p. 291). According to our interpretation the organization of the embryo sac in the genera *Dicraea* and *Hydrobryopsis* falls into line with other angiosperms in not having the synergid and egg as sister cells.

As there is only syngamy and no endosperm in the family (BATTAGLIA 1971, NAGENDRAN et al. 1976), the haploid polar cell in members so far investigated appears to have lost its functional significance. While in the Apinagia and Podostemum types of embryo sacs the position of the polar cell is chalazal, in the Dicraea type it is located at the micropylar end. The so-called single synergid reported as sister to the egg (MUKKADA 1964) is therefore nothing but the polar cell hitherto regarded as being absent. This shift in position does not alter the location of the egg which has remained in the middle of the embryo sac whether it is of the Podostemum or the Dicraea type. Further, the nucellar plasmodium that nourishes

the developing embryo has factors for influencing the fertilized egg to extend towards it, irrespective of the disposition of other complements of the embryo sac.

WILLIS (1902) in his taxonomic monograph on the Podostemaceae of India and Ceylon described a new species in the genus *Hydrobryum* ENDL., under the name *H. sessile* WILLIS, from the collections of C. A. BARBER for the South Indian Flora made at Beltangadi, South Canara district in Karnataka State (No. 2520). ENGLER (1930) referred this taxon to a new monotypic genus under the name of *Hydrobryopsis sessilis* (WILLIS) ENGLER, based on fruit characters. The mode of embryo sac development noted in the present study lends support to ENGLER, since it is of the Apinagia type in *Hydrobryum* (NAGENDRAN et al. 1976) and is of both Dicraea and Podostemum types in *Hydrobryopsis*.

SUBRAMANYAM (1962) in his account on aquatic angiosperms inadvertently cited the present taxon as *Hydrobryopsis sessile* (WILLIS) ENGL. But the correct name remains *Hydrobryopsis sessilis* (WILLIS) ENGL. Further, SUBRAMANYAM & SREEMADHAVAN (1969) while providing a key to the Indian genera of Podostemaceae state that the pollen in the present taxon is shed as monads. But in the present study it has been consistently observed that the pollen, as in all other genera of Indian Podostemoideae, is shed as dyads.

Hydrobryopsis sessilis is an interesting taxon which unites several Indian genera of Podostemaceae. It resembles *Zeylanidium* TUL. in vegetative characters, *Dicraea* TUL. and *Podostemum* MICH. in embryo sac types and *Griffithella* WARM. in the smooth, spherical capsule.

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Der Arillus der Gattung Musa

Walter L. Friedrich und Friedrich Strauch

FRIEDRICH, W. L. & STRAUCH, F. 1976 02 09. Der Arillus der Gattung Musa. — Bot. Notiser 128: 339—349. Lund. ISSN 0006-8195.

Arils are found in wild seeded bananas and cultivated edible forms which develop some ovules. The aril consists of simple trichomes embedded in mucilage, arising from the funiculi and surrounding the ovules and younger seeds. The aril and the mucilage begin to disappear in edible and wild bananas when the growth of the pulp starts. In mature fruits of seeded bananas only vestiges of the aril can be recognized in the neighbourhood of the funiculi. In mature edible fruits the mucilage together with the trichomes of the aril are visible as a yellowish mass in which the degenerated ovules are embedded.

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Die Erhaltung von Arillus bei Pflanzenfossilien konnte erstmalig an der fossilen *Spirematospermum wetzleri* (HEER) CHANDLER (Monocotyledones) aus dem Tertiär nachgewiesen werden (FRIEDRICH & KOCH 1972). Dieses Pflanzenfossil ließ sich u. A. auf Grund des trilokularen Aufbaus der Frucht und der arillaten Samen mit Sicherheit zu den Zingiberaceen stellen. *Spirematospermum*, aus 130 Fundstellen aus Eurasien bekannt, ist fast identisch mit dem heute in Indochina vorkommenden *Cenolophon oxymitrum* (SCHUMANN) HOLTTUM (FRIEDRICH & KOCH 1970, KOCH & FRIEDRICH 1971).

Spirematospermum zeigt auch erstaunliche Ähnlichkeiten zu den samenbildenden Musaceen und auch zu der fossilen *Musa cardiosperma* JAIN aus dem Tertiär von Indien. In der Morphologie der trilokularen Früchte und im Bauplan der Samen ist auch die Beziehung zu den samenbildenden Bananen besonders augenfällig.

Die rezenten Zingiberales (=Scitamineae) sind (bis auf wenige allerdings noch ungeklärten Ausnahmen) arillat (Tabelle 1); sie wurden deshalb früher bereits als „Arillatae" bezeichnet (PFEIFFER 1891, ENGLER & GILG 1924 S. 163).

Eine nahe Beziehung zwischen rezenten Zingiberaceen und Musaceen hatte MAURITZON (1935 S. 30) bereits festgestellt; auch MCGAHAN (1961 S. 237) beobachtete ähnliche Bildungen im Bau der Samen bei den beiden Familien.

Der Nachweis des Arillus bei einer fossilen Zingiberacee aus dem Tertiär bestätigt die Theorie von CORNER (1953 S. 469), „The Durian Theory", zumindest in dem Punkt, daß der Prototyp der Zingiberales (=Scitamineae) arillat sei; und zeigt zudem, daß die Reduktion des Arillus bei einigen rezenten Formen als Progression zu deuten ist (FRIEDRICH & KOCH 1972 S. 58). Nach HUMPHREY (1896 S. 34) sind arillare Strukturen besonders häufig bei dehiszenten Früchten, während sie bei indehiszenten nicht anzutreffen sind.

Der Vergleich von *Spirematospermum* mit den rezenten Vertretern der Zingiberales zeigt, daß sich die karpologischen Merkmale in dieser Gruppe, von einigen Progressionen abgesehen, kaum geändert haben. Auffällig ist indessen, daß bei

Musa und *Heliconia* kein Arillus vorhanden sein soll, wie man aus der betreffenden Literatur schließen könnte. WINKLER (1930 S. 526) schreibt: „Niemals besitzen die Samen in der Gattung *Musa* einen Arillus", und auch in A. ENGLER's „Syllabus der Pflanzenfamilien" (POTZTAL 1964) heißt es bei der Unterfamilie Musoideae „Samen ohne Arillus".

MATERIAL UND METHODE

Bei der vorliegenden Untersuchung wurden hauptsächlich Früchte und Samen aus der Sammlung des Botanischen Museums in Kopenhagen verwandt, die unter den Thai-Dänischen Expeditionen der letzten Jahrzehnte eingesammelt worden waren. Außerdem wurde auch Material aus den Botanischen Gärten Köln, Tübingen, Århus, Kew Gardens und Kopenhagen untersucht. Die Früchte und Samen aus dem Botanischen Museum in Kopenhagen waren nur in wenigen Fällen artlich bestimmt; es kann daher bei dem hier besprochenen Material nur eine grobe Einteilung in die beiden Fruchttypen *Musa balbisiana* COLLA (4 Samenreihen pro Kammer) und *Musa acuminata* COLLA (2 Samenreihen pro Kammer) gegeben werden.

Außer samenbildenden, wilden Bananen-Früchten wurden auch Kulturformen in die Untersuchung einbezogen: Pisang aus Java, *paradisiaca*-Typen und gewöhnliche Eßbananen.

Die Früchte wurden in der üblichen Weise über die Alkohol-Reihe entwässert, in Paraffin eingebettet und auf einem Schlittenmikrotom geschnitten. Zur Färbung wurde Toluidin und in einigen Fällen auch Hämatoxylin-Eosin benutzt. Zur Herstellung von Ultradünnschnitten wurde Durcupan als Einbettungsmittel verwandt. Die Präparate wurden mit Glasmessern auf einem Ultramikrotom der Firma Reichert geschnitten. Besonders kontrastarme Strukturen in den Präparaten wurden mit einer Interferenz-Kontrast-Einrichtung nach Nomarski der Firma Zeiss fotografiert.

Das in der vorliegenden Arbeit beschriebene Material wird im Botanischen Museum in Kopenhagen (C) und im Herbarium Jutlandicum Aarhus (AAU) aufbewahrt. Nachstehend einige Angaben zu den abgebildeten Stücken:

MUSA SP. AUS THAILAND: K. LARSEN, S. S. LARSEN, I. NIELSEN & T. SANTISUK 31040, peninsula between Takupah and Surat Thani, limestone area, 6 m high, leaves glaucous underneath, 8° 59 N, 98° 48 E, 200 m, 16.7. 1972 (AAU). TH. SØRENSEN, K. LARSEN & B. HANSEN 4772 (Copenhagen spir. coll: 6627), Wang Tao, common by a small stream, 6.9. 1958 (C). FLOTO 7650, (Copenh. spir. coll. 6628), 12 km from Ban Mussoe, 400 m, 22.7. 1959 (C). TH. SØRENSEN, K. LARSEN & B. HANSEN 4773 (Copenhagen spir. coll. 6630), Wang Tao, common by a small stream, 6.9. 1959 (C).

MUSA SP. AUS JAVA: H. JENSEN s.n. (Copenh. spir. coll. 4243-I), Java, Buitenzorg, 1905 (C).

ENSETE AUS THAILAND: *Ensete* sp. (Syn. *Musa glauca*) K. LARSEN 10000 (Copenhagen spir. coll. 6629) Soi Dao, old clearing near village, 200 m, 11.6. 1963 (C).

HISTOLOGISCHE BEFUNDE

Das Untersuchungsmaterial wurde so ausgewählt, daß die verschiedenen samenbildenden Grundtypen *Musa balbisiana* COLLA (mit 4 Samenreihen pro Kammer) und *Musa acuminata* COLLA (mit 2 Samenreihen pro Kammer), sowie eßbare nicht samenbildende Bananen gleichmäßig repräsentiert sind.

Die Definition des Arillus, die besonders in der älteren Literatur unterschiedlich gehandhabt wird (PLANCHON 1845, WETTSTEIN 1935), ist zumindest in Bezug auf die Zingiberales (Scitamineae) eindeutig; hier faßt man die vom Funikulus ausgehenden und den Samen mehr oder weniger einhüllenden Bildungen als Arillus auf (HUMPHREY 1896, MAURITZON 1935 S. 22). VAN DER PIJL (1955 S. 307) gibt folgende allgemeine Definition: „A postfloral outgrowth from the top of the funicle (the hilum region) covering the seed more or less".

Der Musa acuminata Fruchttyp

Der *Musa acuminata* „Fruchttyp" mit 2 Samenreihen pro Lokulus wurde in verschiedenen Wachstumsstadien untersucht. Im juvenilen Stadium (Fig. 1 A, B) erkennt man deutlich bereits makroskopisch die drei Kammern, in denen die Samen als dunkle Flecke von einer gelblichen, gallertartigen Masse umgeben sind. Diese Masse entspringt von den Funikuli

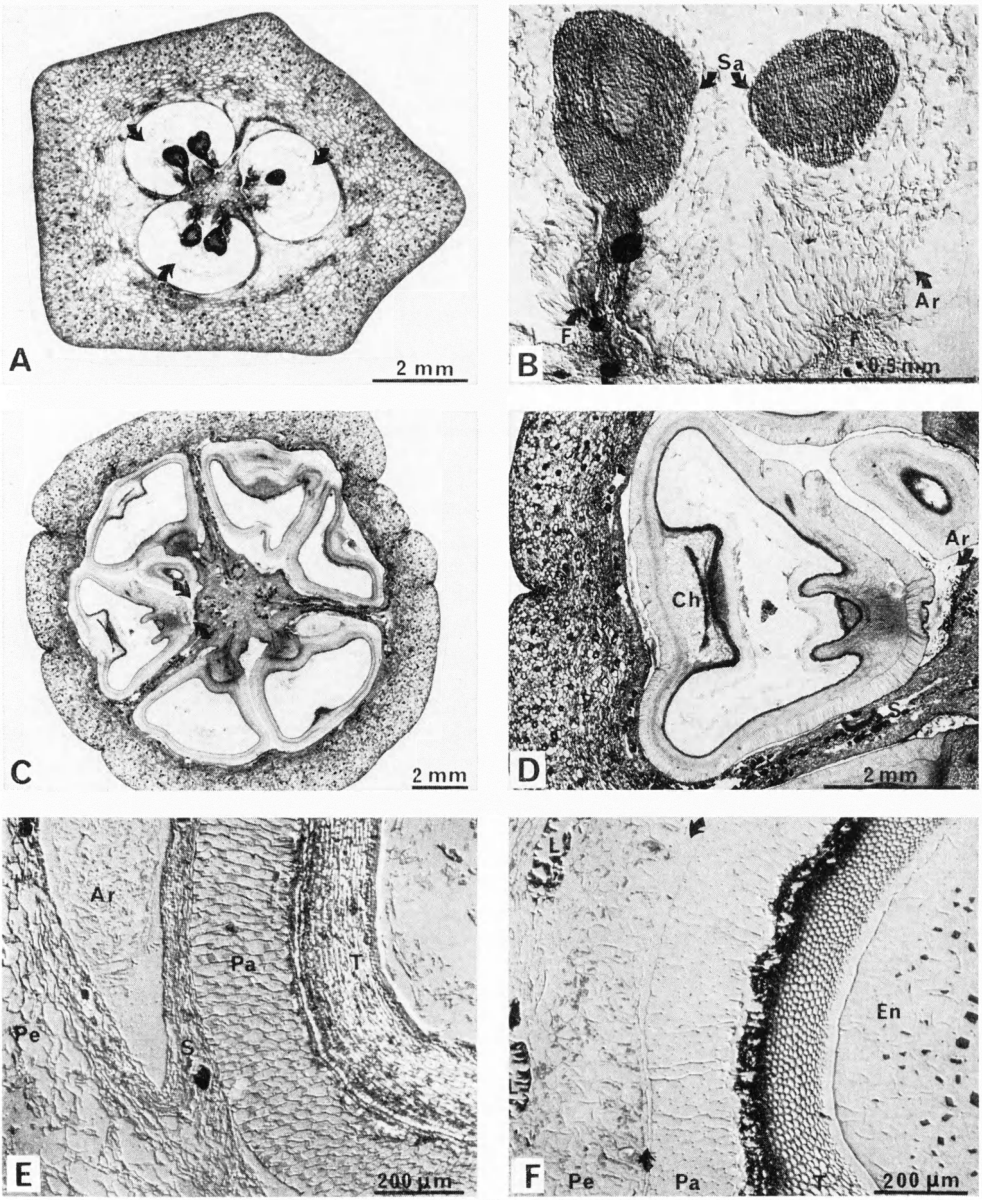

Fig. 1. *Musa* sp. aus Thailand. *M. acuminata* „Fruchttyp" mit zwei Samenreihen pro Lokulus. — A: Nr. 6627, Querschnitt, juveniles Exemplar, Arillus die Samenanlagen umgebend (Pfeile). — B: Gleiches Stück wie A. Arillushaare von den Funikuli ausgehend, die Samenanlagen umgebend. — C: Nr. 6630, Querschnitt, fast ausgereifte Samen, Arillusrelikte nur an den Funikuli (Pfeile). — D: Vergrößerter Ausschnitt aus C. — E: Nr. 31040, Querschnitt durch Teil einer Frucht; fehlgeschlagene Kammer mit Arillus gefüllt. — F: Gleiche Frucht wie E. Kein Arillus zwischen Perikarp und Palisadenzellen des Samens. — B, E, F: Differential-Interferenzkontrast. — Abkürzungen: Ar Arillus. F Funikulus. Ch Chalaza. En Endosperm. Pa Palisadenzellen. Pe Perikarp. Sa Samenanlagen. T Testa. L Latexgefässe. S Septum.

der Samenlagen und füllt die Kammern fast vollständig aus. Bei stärkerer Vergrößerung (Fig. 1 B) lassen sich in dieser Masse offenbar einzellige Trichome erkennen, die aus den Funikuli auswachsen. Nach der Definition handelt es sich um den Arillus. In der Nähe des Funikulus sind sie noch straff geordnet; im distalen Bereich liegen sie unregelmäßig und befinden sich bereits unter Auflösung. Eine Pulpabildung ist in diesem Stadium noch nicht feststellbar, die ja später besonders von der Innenseite des Perikarps einsetzt.

Im fortgeschrittenen Wachstumsstadium (Fig. 1 C, D) füllen die noch unreifen Samen bereits die drei Kammern vollständig aus. Die gallertartige Arillusmasse ist bis auf einige Trichomfragmente in der Nähe der Funikuli und am Hilum, zurückgedrängt. In einer abortierten Kammer ist der fehlgeschlagene Bereich noch von Arillus gefüllt, während in der normal entwickelten Kammer Arillusbildungen nicht mehr feststellbar sind (Fig. 1 E).

Ausgereifte Samen, an der Verfestigung der Testa erkennbar, haben keine Arillusbildungen mehr. Die äußerste Schicht der Testa wird hier von langgestreckten Palisadenzellen gebildet, die direkt an die Innenseite des Perikarpes anliegen. In diesem Wachstumsstadium beobachtet man kleine Stärkekörner in den Parenchymzellen des Perikarps, die die beginnende Pulpabildung anzeigen.

Der Musa balbisiana Fruchttyp

Bei diesem Fruchttyp sind 4 unregelmäßige Samenreihen pro Lokulus entwickelt. Bei juvenilen Früchten sind die Kammern von der gallertartigen Arillusmasse ausgefüllt, in der die Samenanlagen eingebettet sind (Fig. 2). Die Trichome wachsen strahlenförmig aus den Funikuli aus und sind nur in direkter Nähe der Austrittsstellen als Haare zu erkennen. Mit zunehmender Entfernung von den Funikuli gehen sie mehr und mehr in eine formlose Substanz über. Bei diesem Fruchttyp sind Arillusbildungen solange feststellbar, bis die Samen die Kammern vollständig ausgefüllt haben, erst dann setzt die Pulpabildung von der Innenseite des Perikarpes ein und drängt sich zwischen die einzelnen Samen, wie bei einer ausgereiften Frucht von *Musa* sp. (Nr. 31040) aus Thailand beobachtet werden konnte.

Musa sp., Pisang gabu, aus Buitenzorg, Java

Die Früchte dieser Hybride vereinigen Merkmale des *balbisiana* und des *acuminata* „Fruchttypes" (Fig. 3). Unter dem uns vorliegenden Material befindet sich eine Frucht mit drei regelmäßig ausgebildeten Kammern, die jeweils 2 Samenreihen enthalten (Fig. 3 B) und ein Exemplar mit 4 Kammern mit wenigen abortierten Samenlagen (Fig. 3 A, C). In allen Fällen sind die nicht entwickelten Samenanlagen von Arillus umgeben. Makroskopisch erkennt man an Querschnitten durch diesen Fruchttyp drei (seltener 4) halbmondförmige Bereiche, die von einer gelblichen gallertartigen Masse ausgefüllt sind, die sich bei stärkerer Vergrößerung in den Dünnschnitten als Arillusbildung erweist. Bei diesen Früchten ist eine starke Anhäufung der Latexgefäße feststellbar, besonders an der Innenseite des Perikarpes und an den Septen. Im zentralen Bereich der Frucht umgeben sie die Leitungsstränge, so daß sie im Querschnitt ein kreisförmiges Punktmuster ergeben. Von der Innenseite des Perikarpes und der Septen wachsen weitmaschige Parenchymzellen in die Kammern hinein. Sie enthalten Stärkekörner, während die Trichome des Arillus keine Stärkekörner enthalten (Fig. 3 D).

Musa sp.

Die gewöhnliche Eßbanane leitet sich von den beiden Wildformen *Musa balbisiana* und *Musa acuminata* her (SIMMONDS 1962 S. 130). Im Querschnitt durch eine Eßbanane lassen sich makroskopisch nur

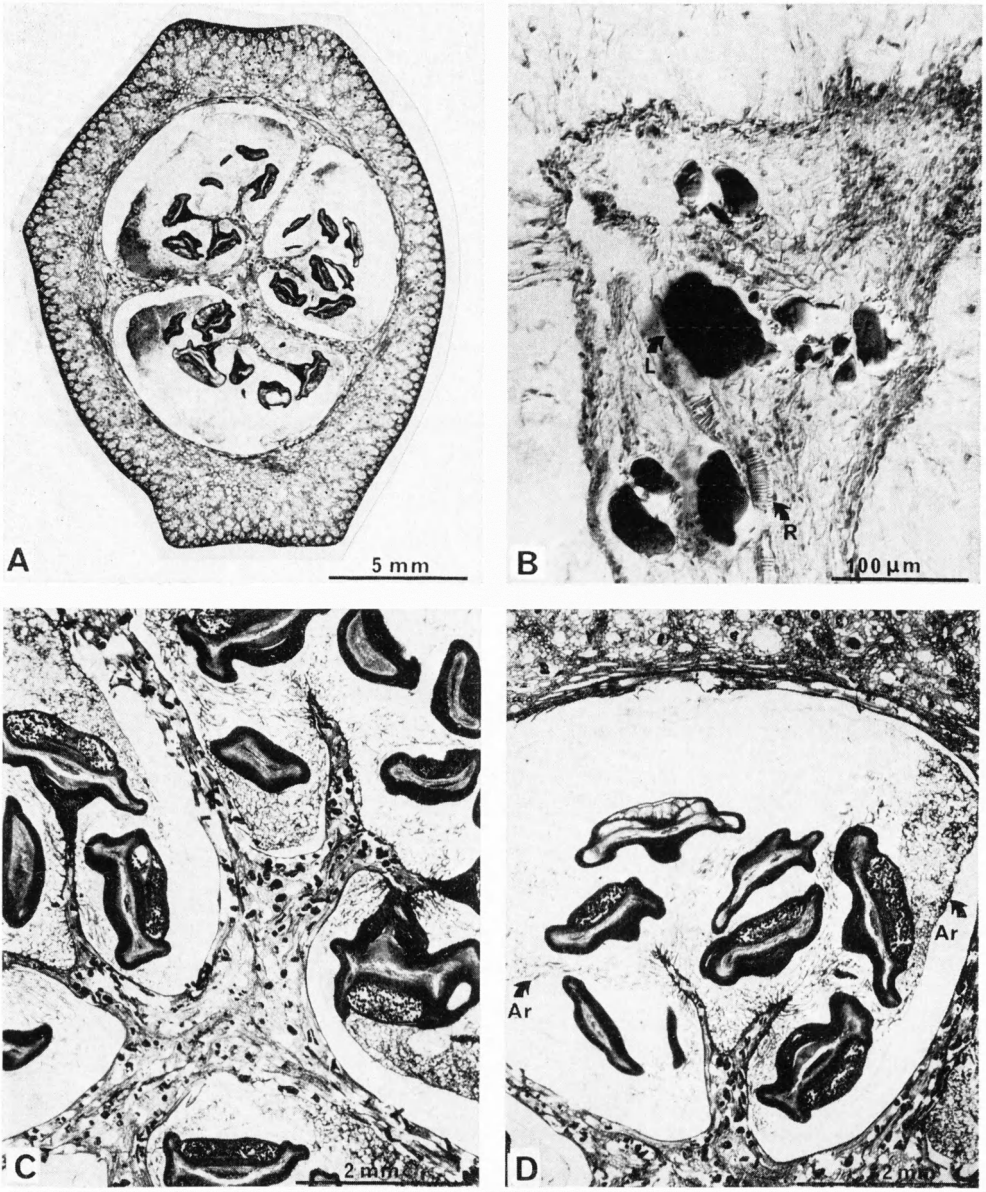

Fig. 2. *Musa* sp., Nr. 6628 aus Thailand. *M. balbisiana* „Fruchttyp" mit vier unregelmäßigen Samenreihen. — A: Juvenile Frucht, Querschnitt. Die Samenanlagen sind von Arillusbildungen umgeben, die von den Funikuli ausgehen und die Kammern fast ausfüllen. — B: Gleiches Präparat wie A. Funikulus mit Raphe und Latexgefäßen aus dem Arillus-Trichome auswachsen. — C, D: Vergrößerte Ausschnitte aus A. — Differential-Interferenzkontrast. — Abkürzungen: Ar Arillus. L Latexgefässe. R Raphe.

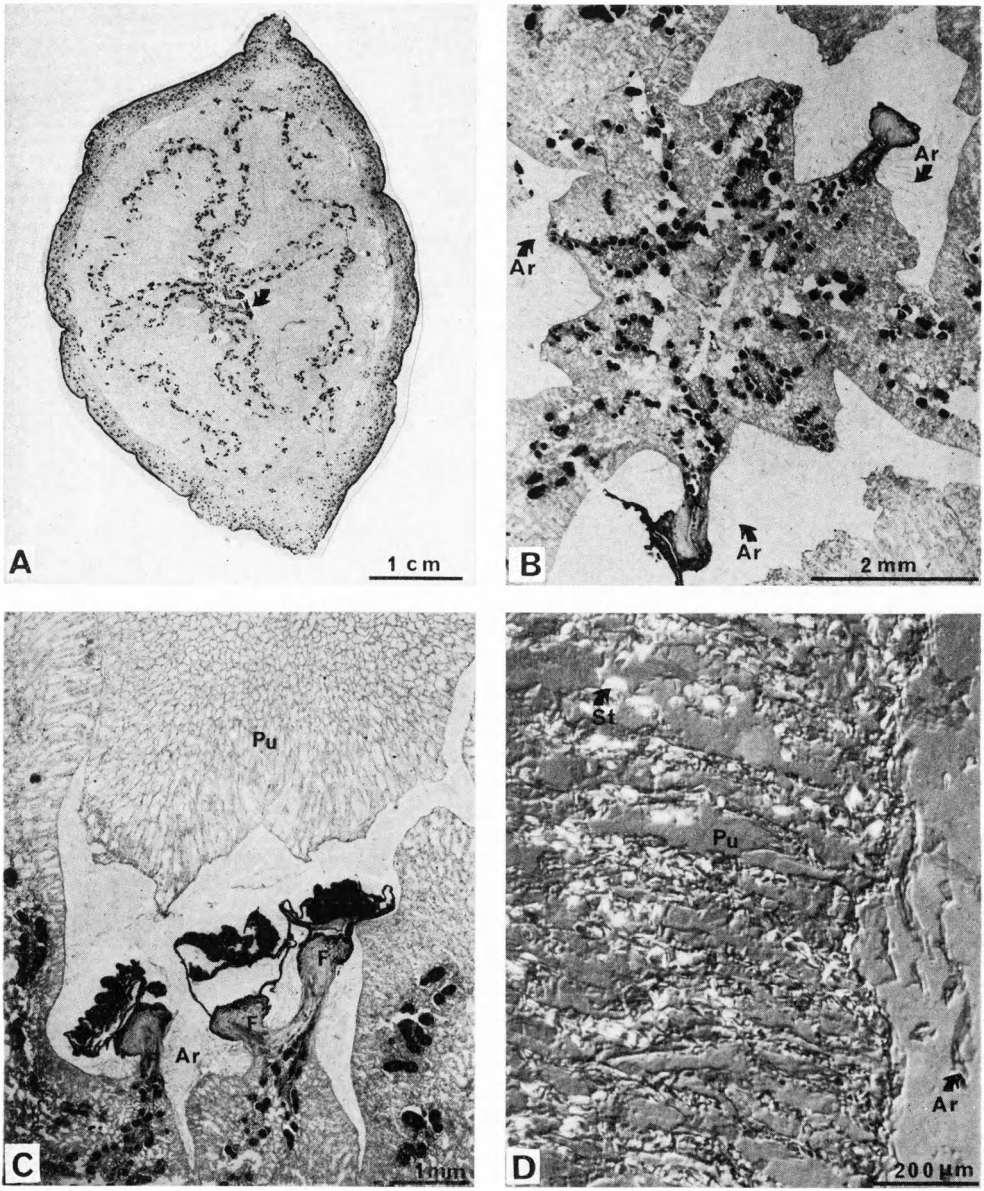

Fig. 3. *Musa* sp. „Pisang gabu". Nr. 4243-I aus Buitenzorg, Java. — A: Frucht mit vier Kammern, Querschnitt. Pfeil zeigt auf den in C vergrößerten Ausschnitt. — B: Zentraler Teil einer trilokularen Frucht mit je zwei Samenreihen pro Lokulus, Querschnitt. Arillusbildungen an den Funikuli (Pfeile). — C: Vergrößerter Ausschnitt aus A. Drei rudimentäre Samenanlagen sind von Arillusbildungen umgeben. Von den Septen und von der Innenseite des Perikarpes wächst Pulpagewebe in die Kammer und verdrängt den Arillus. — D: Ausschnitt aus B. Pulpagewebe mit Stärkekörnern (helle Punkte) angrenzend an Arillus-Trichomen (ohne Stärkekörner). Differential-Interferenzkontrast. — Abkürzungen: Ar Arillus. F Funikulus. Pu Pulpa. St Stärkekörner.

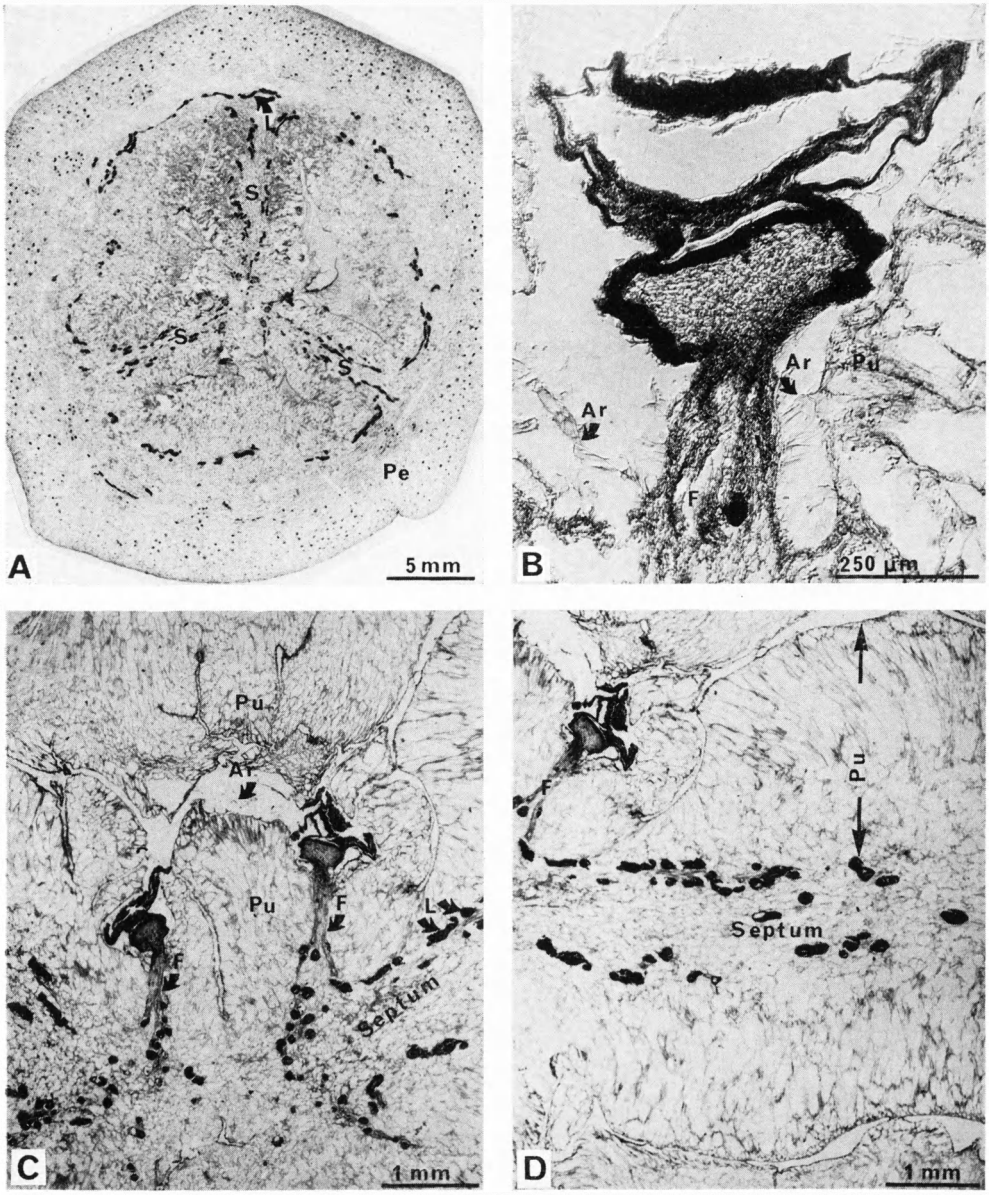

Fig. 4. *Musa* sp. — A: Querschnitt, Eßbanane mit drei Septen. — B: Ausschnitt aus A. Abortierte Samenanlage, umgeben von Arillus-Trichomen, die am Funikulus auswachsen. Differential-Interferenzkontrast. — C: Gleiches Präparat wie A. Zentraler Teil einer Frucht, Querschnitt. Zwei abortierte Samenanlagen in einer Kammer. Pulpabildungen an den Septen, den Funikuli und der Innenseite des Perikarpes verdrängen die Relikte des Arillus. — D: Gleiches Präparat wie A. Querschnitt durch ein Septum mit Latexgefäßen (schwarze Flecke) und abortierte Samenanlage. Starke Pulpabildung am Septum. — Abkürzungen: Ar Arillus. F Funikulus. L Latexgefässe. Pe Perikarp. Pu Pulpa. S Septum.

noch wenige Relikte dieser beiden Stammformen erkennen (Fig. 4 B—D). Die Latexgefäße markieren den Grenzbereich Perikarp zu den mit Pulpa gefüllten Kammern und zeigen die Lage der drei Septen an. Verkümmerte Samenanlagen sind nur selten zwischen den Pulpawucherungen zu finden. Untersucht man die abortierten Samenanlagen, so findet man im Bereich der Plazenten Arillusbildungen in Form von 0,025 mm dicken Trichomen, die aus den Funikuli auswachsen. Mit zunehmender Reife der Frucht werden sie von der Pulpa verdrängt und gehen mehr und mehr in Auflösung.

DISKUSSION DER ERGEBNISSE

Bereits in der älteren Literatur stellte man Haarbildungen im Bereich der Plazenten bei *Musa* fest. WITTMACK (1868 Tafel III, Fig. 25), der eine Beschreibung von *M. ensete* gibt (heute wird *Ensete* als eigene Gattung aufgefaßt), bildet einen Querschnitt von *M. rosea* ab und bezeichnet die Haare an den Samenanlagen als Plazentahaare. HUMPHREY (1896 S. 28), der ebenfalls Samenanlagen und junge Samen von *M. rosea* untersuchte, konstatiert: „The ovule presents nothing noteworthy, except a dense felt of long simple trichomes arising from the sides of the funiculus. No trace of these remains in the seed. As compared with the ovule, the seed shows great lateral extension, so the embryonal cavity is much shorter than broad. The trace of the micropylar opening can still be recognized, and, as might be expected from the indehiscent fruit, no aril is developed."

Sowohl WITTMACK's (1868) als auch HUMPHREY's (1896) Ergebnisse werden von späteren Bearbeitern erwähnt. So benutzt JÄHKEL (1909 S. 23) den Begriff „Plazentahaare" von WITTMACK (1868) und D'ANGREMOND (1915 S. 74) beobachtet: „Die Samenknospen der Bananen sind in einer durchscheinenden Gallerte eingebettet und von vielen Zellfäden umgeben, die aus dem Fuß des Funikulus ihren Ursprung nehmen". Was die Gallerte angeht, so bezieht er sich in einer Fußnote auf JÄHKEL (1909). MAURITZON (1935), der eine umfassende Übersicht über „Samenbau und Embryologie einiger Scitamineen" gibt, erwähnt unter Musaceae nur die Gattungen *Heliconia* und *Strelitzia* und verweist bezüglich der Gattung *Musa* auf frühere Untersuchungen (1935 S. 3). Es ist daher nicht erstaunlich, daß WINKLER (1930 S. 526) in ENGLER-PRANTL behauptet: „Niemals besitzen die Samen in der Gattung *Musa* einen Arillus". Auch in neueren Arbeiten liest man (SIMMONDS 1953 S. 89): „Each loculus bears two rows of ovules embedded (or nearly so) in a strip of mucilage which is pervaded at its axial face by numerous hair-like cells emergent from the axis especially in the neighbourhood of the ovules". Im gleichen Zusammenhang erwähnt er: „The number of hair-like cells in the mucilage seems to increase for the first week or two, but later all traces of them disappears as the mucilage goes". In ähnlicher Weise gibt SIMMONDS diesen Sachverhalt in späteren Arbeiten wieder (SIMMONDS 1959 S. 29 und 1962 S. 78). Es ist daher auch nicht verwunderlich, daß in Übersichtwerken wie A. ENGLER's „Syllabus der Pflanzenfamilien" (POTZTAL 1964 S. 609) unter der Unterfamilie Musoideae erwähnt wird: „Samen ohne Arillus".

Unter Berücksichtigung der bereits oben zitierten Beobachtungen früherer Bearbeiter und unserer eigenen Feststellungen kann zusammenfassend folgendes über den Arillus bei der Gattung *Musa* L. gesagt werden: Bei allen von uns untersuchten *Musa*-Früchten ist in juvenilen Stadien ein Arillus entwickelt. Er besteht aus einfachen Trichomen, die von den Funikuli ausgehen und die Samenanlagen umgeben.

Bei fortschreitender Maturität der Samen wird der Arillus zurückgebildet. Die Auflösung des Arillus erfolgt zu dem Zeitpunkt, wo die Bildung der Pulpa beginnt. Bei reifen Samen ist der Arillus nur noch in Relikten an den Funikuli vorhanden.

Tabelle 1. Karpologische Merkmale der Zingiberales (Scitamineae). Verändert und ergänzt nach KOCH & FRIEDRICH 1971.

Familie	Zingiberaceae				Costaceae	Marantaceae	Cannaceae	Musaceae		Heliconiaceae	Strelitziaceae			Lowiaceae
Genus	Spirematospermum	Cenolophon	Hedychium	Globba	Costus	Maranta	Canna	Musa	Musa	Heliconia	Phenakospermum	Ravenala	Strelitzia	Lowia
fossil/rezent	fossil	rezent	rezent	rezent	rezent	rezent	rezent	fossil	rezent	rezent	rezent	rezent	rezent	rezent
Frucht	Kapsel	Kapsel	Kapsel	Kapsel	Kapsel	Kapsel	Kapsel	Kapsel	Kapsel beerenartig	Kapsel	Kapsel	Kapsel	Kapsel	Kapsel
Zahl d. Lokuli	3	3	3	1	3	1	3	3	3	3	3	3	3	3
Dehiszenz	indehiszent?	indehiszent?	lokulizid	unregelmässig	dehiszent	indehiszent	zuweilen indehisz.	unbekannt	meist indehiszent	septizid	lokulizid	lokulizid	lokulizid	
Plazenten	zentralwinkelständig	zentralwinkelständig	zentralwinkelständig	parietal	zentralwinkelständig		zentralwinkelständig	zentralwinkelständig	zentralwinkelständig	basal	zentralwinkelständig	zentralwinkelständig	zentralwinkelständig	zentralwinkelständig
Samenreihen pro Lokulus	2	2	4		2	nur ein Same	2	1	2 und mehr	1 Same pro Fach	4 und mehr	2	2	2
Deckel	+	+	+		+	+		+	+	+		—		
Arillus	+	+	+	+	+	+ basal	+	vermutlich	+	homolog. Gewebe	+	+	+	+
Mikropylarkragen	+	+			+	+	+	+	+				+	

An Querschnitten von *Ensete* sp. aus Thailand (LARSEN 10 000) waren an den Funikuli der fast reifen Samen keine Arillusbildungen feststellbar; ein abortierter Same in der selben Frucht war jedoch von Arillustrichomen umgeben. Offenbar gilt bei der Gattung *Ensete* in Bezug auf den Arillus derselbe Sachverhalt wie bei *Musa,* nämlich daß der Arillus in juvenilen Früchten entwickelt ist und mit zunehmender Reifung zurückgebildet wird.

Über die biologische Funktion des Arillus bei den Zingiberales haben sich zahlreiche Autoren geäußert. Allgemein nimmt man an, daß er eine Rolle bei der Dehiszenz der Früchte (PFEIFFER 1891) und bei der Verbreitung der Samen durch Tiere spielt. Bei *Musa* sind die Früchte beerenartig und meist indehiszent. Der Arillus hat hier seine Funktion in Folge der Progression verloren. Die Rolle als Lockmittel für Tiere, die die Samen verbreiten, wird von der Pulpa übernommen, die offenbar als Ersatz für den funktionslosen Arillus entwickelt wurde. Pulpabildung tritt ja bekanntlich nicht nur bei Kulturformen sondern auch bei wilden Bananen auf.

Die Entdeckung des Arillus bei der fossilen *Spirematospermum wetzleri* (Zingiberaceae), die sehr nahe verwandt ist mit der rezenten *Cenolophon oxymitrum* und auch in vielen morphologischen und anatomischen Einzelheiten den wilden rezenten Bananen nahe steht, zeigt, daß der Arillus ein sehr altes Element der Zingiberales ist (Tabelle 1). Die gut erhaltenen fossilen Bananenfrüchte aus dem Paleogen von Indien waren unserer Meinung nach wahrscheinlich ebenfalls arillat, da JAIN (1964 S. 46) beobachtet: „The seeds, though filling each locule, show no sign of compression and the space left between the seeds is filled with a non-cellular matrix". Auch die Verdickung der Testa im Bereich des Hilum bei den fossilen *Musa*-Samen spricht für die Existenz eines Arillus, wie JAIN (1964 S. 53) übrigens selbst feststellt, später aber wieder verwirft.

DANK

Für wichtige Hinweise und die freundliche Überlassung des Untersuchungsmateriales möchten wir Dr. B. HANSEN (Kopenhagen) und Professor K. LARSEN (Aarhus) danken. Zahlreiche Anregungen und Diskussionsbemerkungen verdanken wir Lektor B. E. KOCH (Aarhus) und Dr. H. KOCH (Köln). Zu Dank verpflichtet sind wir auch L. THAMDRUP und D. HUNDTOFTE für die Herstellung der Präparate, J. SOMMER für die Fotoarbeiten und A. M. KRISTENSEN für die Reinschrift des Manuskriptes. Finanzielle Unterstützung erhielten wir von Statens naturvidenskabelige Forskningsråd.

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Campanula keniensis Thulin sp. nov., and Notes on Allied Species

Mats Thulin

THULIN, M. 1976 02 09. Campanula keniensis Thulin sp. nov., and notes on allied species. — Bot. Notiser 128: 350—356. Lund. ISSN 0006-8195.

Campanula keniensis THULIN sp. nov., is described from Kenya. Although an annual its nearest ally is believed to be the perennial *C. edulis* FORSK. Crossing experiments between *C. keniensis* and *C. edulis* gave highly sterile offspring. The synonymy of *C. edulis* is given and all names are typified. Crossings between a large-flowered and a small-flowered strain of *C. edulis* yielded an intermediate offspring with no reduction of fertility. Chromosome numbers are reported for *C. afra* (2n=24), *C. dichotoma* (2n=24), *C. edulis* (2n=56), *C. kremeri* (2n=24) and *C. keniensis* (2n=54). *Wahlenbergia tenuiloba* THULIN nom. nov., is proposed for the illegitimate *W. congesta* THULIN.

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Campanula keniensis THULIN sp. nov.
(Figs. 1 A, 2 A, D)

ORIG. COLL.: MOBERG 1415, Kenya, Kaijado Distr., Ngong Hills, south of highest part, along the path to the top, 3.I. 1971 (UPS holotype).

Species nova ab affini *C. edulis* FORSK. habitu erecto annuo, corolla cylindrica 6—8 mm longa lobis erectis 1—1.6 mm longis extus dense puberula, stylo tubo corollae breviore, floribus breviter pedicellatis vix nutantibus et chromosomatum numero 2n=54 diversa.

Annual ± stiffly erect herb, up to 35 cm tall. Stem branched mainly in the upper part, strongly ribbed, hirsute with mixed hairs of very variable length. Leaves sessile, narrowly ovate to ovate above, elliptic to oblanceolate or narrowly ovate towards the base, up to 10—25 mm long, 5—10 mm wide, acute or subacute with truncate, or, at least in the upper leaves, cordate base, hirsute with hairs often bulbous at the base; margin cartilaginous, ± undulate-crenate; midvein and lateral veins prominent beneath. Inflorescence lax with marked overtopping of the terminal flower giving a dichotomous appearance; pedicels short, elongating up to 10 mm in fruit. Hypanthium broadly obconical, with 5 distinct nerves and up to 5 additional ± weak nerves in between them, shortly and densely pubescent but with long hairs on the nerves. Calyx-lobes narrowly triangular, 4—7 mm long, acute, with long hairs at margins and on midvein outside, otherwise shortly and densely pubescent on both sides; calyx-appendages ovate, 1.5—2.5 mm long, reflexed, ± obtuse. Corolla blue or mauve with whitish base, cylindrical, 6—8 mm long, with erect apiculate lobes 1—1.6 mm long; midveins of petals distinct with ± long hairs, corolla otherwise densely puberulous outside, glabrous inside. Stamens with ovate, shortly ciliate filament-bases; anthers 1.3—2.0 mm long. Ovary 3-locular, inferior; style much shorter than the corolla-tube, 3-lobed, with pollen-collecting hairs along most of its length, but with normal hairs at the base. Capsule 3-locular, dehiscing by basal valves. Seeds numerous, elliptic-oblong in outline, compressed, ± 0.6 mm long, almost smooth, yellowish-brown. 2n=54.

Table 1. Chromosome numbers of some species of *Campanula*. Voucher specimens in UPS. *C. afra* and *C. kremeri* are regarded as distinct species for the sake of convenience (see text).

Taxon	Voucher	Origin of material	2n
C. afra	RYMAN 1340	Canary Is., Tenerife	24
C. dichotoma	THULIN 2410	Algeria, El Milia	24
	THULIN 2414 b	Algeria, El Milia	24
	BARKOUDAH s.n.	Algeria, Tizi Ouzou	24
C. edulis	THULIN 1367	Ethiopia, Asella	56
	BJÖRNSTAD 1575	Tanzania, Ngorongoro	56
C. keniensis ..	MOBERG 1415	Kenya, Ngong Hills	54
C. kremeri ...	THULIN 2302	Algeria, Oran	24

C. keniensis is only known from the Ngong Hills, just south of Nairobi in Kenya, where it has been collected in grassland on the summit ridge and along the western slopes at altitudes of between 2150 and 2430 m.

COLLECTIONS. Kenya: Kaijado Distr., Ngong Hills, XII. 1954 BALLY 9889 (K), XI. 1966 ARCHER 528 (EA), XI. 1967 AGNEW 9681 (NAI), I. 1971 MOBERG 1415 (UPS).

DISCUSSION

AGNEW (1974 p. 509) was the first to pay attention to *C. keniensis*. He called it *Campanula* sp. A and pointed to its annual habit and densely pubescent corolla as characters distinguishing it from *C. rigidipila* (=*C. edulis*, see below).

The species shows a striking similarity to, among annual species, the mainly Mediterranean *C. dichotoma* group (*C. dichotoma* L., *C. afra* CAV., *C. kremeri* BOISS. & REUT., *C. semisecta* MURB., etc.) and *C. balfourii* WAGN. & VIERH. on Socotra, which perhaps belongs to the same group. The taxonomic treatment of these species varies considerably (see e.g. MURBECK 1897 p. 115—119, QUÉZEL 1953) and most of them have at times been regarded as subspecies or forms of *C. dichotoma*. The perennial *C. edulis* in eastern tropical Africa and Yemen is also very close to *C. keniensis*. All these species mentioned have calyx-appendages, capsules dehiscing by basal valves or pores, 3-merous gynoecia and are placed in *Campanula* sect. *Medium* A. DC. The only previously known chromosome number among them is 2n=24, reported from Italian *C. dichotoma* by GADELLA (1964 p. 14). 2n=34 in *C. sarmentosa* (a synonym of *C. edulis*, see below) was reported by SUGIURA (1942 p. 431). It is presumably erroneous like many other of his counts (see GADELLA 1964 p. 43). Chromosome numbers obtained by the present author are summarized in Table 1 (see also Fig. 2 A—C).

The subdivisions of the genus *Campanula* by DE CANDOLLE (1830), BOISSIER (1875) and FEDOROV (1957) were reviewed by GADELLA (1964), who considered them all more or less unnatural and proposed a provisional subdivision into seven groups where much importance was ascribed to cytological data. *C. dichotoma* was placed on its own in Group V, but it was presumed that many other annual appendiculate species belonged there although chromosome data were lacking. *C. kremeri*, as could be expected, fits into the same group. The chromosome number 2n=54 in *C. keniensis*, however, cannot easily be derived from 2n=24. Furthermore, the chromosomes of *C. keniensis* are smaller (c. 1—1.5 μm) than in *C. dichotoma* and *C. kremeri* (c. 1.5—2 μm). A close affinity between *C. keniensis* and the *C. dichotoma* group is therefore im-

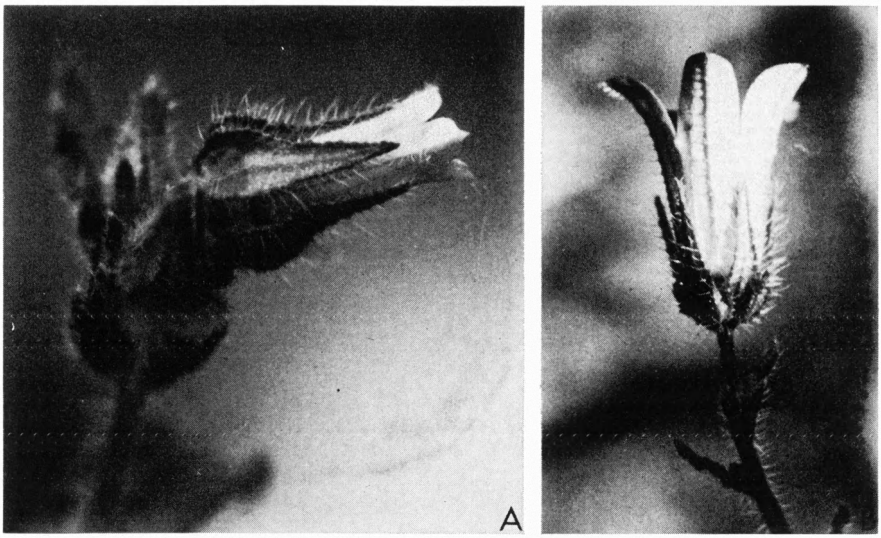

Fig. 1. Flowers of cultivated specimens. — A: *Campanula keniensis,* progeny of MOBERG 1415, ×4.5. — B: *C. edulis,* progeny of a cross between the small-flowered strain THULIN 1367 and the large-flowered strain BJÖRNSTAD 1575, ×2.5.

probable. *C. keniensis* is morphologically distinguishable from this group mainly by its cylindrical corolla with very short and erect lobes (Fig. 1 A). In the *C. dichotoma* group the corolla is ± funnel-shaped with longer lobes, which are spreading to almost perpendicular to the tube (however, in herbarium material this may be difficult to see). The hairiness of the corolla varies within the *C. dichotoma* group, and plants with the outer surface of the corolla densely puberulous as in *C. keniensis* also occur.

The plant described as *C. balfourii* by WAGNER & VIERHAPPER (in VIERHAPPER 1906 p. 301, see also VIERHAPPER 1907 p. 474—476) was previously thought by BALFOUR (1888 p. 148) to be a form of *C. dichotoma.* As distinguishing features VIERHAPPER (1907 p. 475) mainly mentioned the smaller corolla and shorter calyx-lobes and appendages. Compared with *C. balfourii, C. keniensis* seems to be a somewhat more robust plant. Longer hairs such as are present on the midveins of the petals in *C. keniensis* can hardly be seen in *C. balfourii.* The midveins themselves are also more inconspicuous in this species. The corolla is of a more campanulate shape in *C. balfourii* (otherwise the corolla is of a similar size and is also densely puberulous outside in both these species). Further, the hypanthium usually has more than 5, often c. 10 nerves in *C. keniensis* (5 in *C. balfourii*), the additional nerves being ± weak. The best distinguishing character for *C. keniensis* is its short comparatively stout style, usually much shorter than the corolla-tube, versus the slender style, as long as or longer than the corolla-tube in *C. balfourii.* Calyx-lobes and appendices, seeds and pollen grains (3-porate, 30—35 µm in equatorial diameter, and with densely and finely spinular exine) are similar in all essentials in the two species. Until the chromosome number of *C. balfourii* is known it can hardly be determined with certainty whether its nearest affinity is with *C. dichotoma* or with *C. keniensis,* although the former alternative seems most probable.

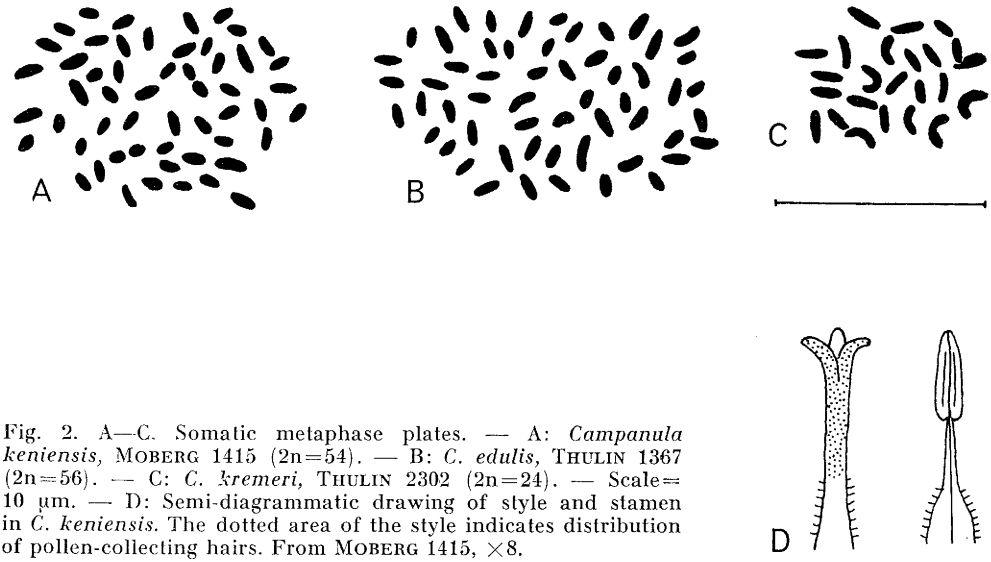

Fig. 2. A—C. Somatic metaphase plates. — A: *Campanula keniensis,* MOBERG 1415 (2n=54). — B: *C. edulis,* THULIN 1367 (2n=56). — C: *C. kremeri,* THULIN 2302 (2n=24). — Scale= 10 µm. — D: Semi-diagrammatic drawing of style and stamen in *C. keniensis.* The dotted area of the style indicates distribution of pollen-collecting hairs. From MOBERG 1415, ×8.

Apart from *C. keniensis, C. edulis* is the only native *Campanula* in Kenya and these two virtually are the only representatives of the genus south of the equator. It is distributed from Yemen, Sudan and Ethiopia in the north to eastern Zaïre and northern Tanzania in the south. In Kenya it seems to be rare and is not known from the Ngong Hills. The nearest localities are in the Aberdares and the Chyulu Hills.

As opposed to the stiffly erect, annual *C. keniensis, C. edulis* is usually a decumbent or ascending perennial with a thick, soon lignified tap-root (however, in cultivation it flowers even during the first year while the tap-root is still very thin). The corolla is usually larger in *C. edulis* and campanulate (Fig. 1 B), but forms with a corolla comparable in size and shape to that in *C. keniensis* also occur. However, the corolla is glabrous or has long hairs on the midveins of the petals only, and is devoid of the dense short pubescence of *C. keniensis.* The style is rather short and stout in *C. edulis* and much shorter than the corolla as in *C. keniensis,* but as this is usually ± deeply lobed the style is often as long as the corolla-tube. The hypanthium is usually more than 5-nerved in both species. The pedicels are up to 5 cm long in *C. edulis* and usually much longer than in *C. keniensis.* The marked nodding of the capsules in *C. edulis* is much less pronounced, if occurring at all, in *C. keniensis.* The basal part of the style below the pollen collecting hairs is glabrous in *C. edulis* but hairy in *C. keniensis* (Fig. 2 D). The leaf shape is very variable in *C. edulis,* and although often having narrower, ± oblanceolate or almost spathulate leaves no clear distinction can be made using this character.

The chromosome number of *C. keniensis,* 2n=54, is most easily explained as a result of a reduction from 2n=56, and probably the species is closely related to and possibly derived from *C. edulis.* The chromosomes are also of a similar size in these two species (1—1.5 µm, Fig. 2 A, B).

Crossing experiments performed between offspring of the holotype of *C. keniensis* and a strain of *C. edulis* (offspring of THULIN 1367, Asella, Ethiopia)

resulted in seed formation in 10 out of 16 pollinated flowers. Vigorous hybrids, intermediate in all respects and with 2n=55, were obtained from all successful crossings. They behaved as annuals, although more long-lived than the parental *C. keniensis*. The pollen fertility of the parents, obtained by counting the percentage of lactic blue staining pollen in a sample of 200 grains, was found to be 95—100 %. In 18 hybrid specimens studied the pollen fertility varied between 10 and 40 % (mean value 30 %). In the parental plants seeds were formed abundantly by autogamy. In the hybrids, however, not a single seed was formed, not even after artificial self-pollination. Thus a strong genetic barrier exists between these species, probably mainly owing to the difference in chromosome number.

C. keniensis and *C. edulis* are not easily placed in any of the groups proposed for the genus by GADELLA. 2n=56 has previously been reported only from *C. vidalii* (sometimes placed in the monotypic genus *Azorina* FEER) on the Azores, which is totally unrelated to *C. edulis* and 2n=54 is a new number for the genus. Group VI includes species with 2n=28, but these are all devoid of calyx-appendages. Obviously the chromosomal diversity and the relationships within the genus are still more complicated than is revealed by GADELLA's work.

The wide variation present in *C. edulis* has given rise to a rather extensive synonymy which is summarized below. All lectotypes have been chosen by the present author.

Campanula edulis FORSKÅL

FORSKÅL 1775 p. 44. — Orig. coll.: FORSKÅL s.n., Yemen, Kurma (C lectotype).

There are three sheets in FORSKÅL's herbarium in C, two of which are without locality. The third specimen, the lectotype, consists of two individuals and apart from the specific name has the locality "ad Kurma" written in FORSKÅL's handwriting. There is also a specimen in Stockholm (S) collected by FORSKÅL and with the locality "ad Hadje". This was originally sent to MONTIN by VAHL in 1780. Hadje is the second locality cited by FORSKÅL (1775 p. 44) for *C. edulis*. Also a specimen without collector and locality in Herb. Thunberg (UPS) was probably distributed by VAHL.

C. esculenta RICHARD 1851 p. 4. — *C. rigidipila* STEUD. & HOCHST. ex A. RICH. var. *esculenta* (A. RICH.) DI CAPUA 1904 p. 236. — Orig. coll.: QUARTIN DILLON & PETIT s.n., Ethiopia, Tigre, Ouodgerate (P lectotype).

C. quartiniana RICHARD 1851 p. 5. — *C. schimperi* VATKE var. *quartiniana* (A. RICH.) VATKE 1876 p. 201, nom. illegit. — *C. rigidipila* STEUD. & HOCHST. ex A. RICH. var. *quartiniana* (A. RICH.) ENGLER 1892 p. 410. — Orig. coll.: QUARTIN DILLON & PETIT s.n., Ethiopia, Tigre, Memsah 8.IX. 1839 (P holotype).

RICHARD cites a QUARTIN DILLON specimen collected in Memsah in September as the type of *C. quartiniana*. The only specimen in Herb. RICHARD with this data has no specific name written on it, but as the specimen agrees very well with the original description there is no reason for doubting that it is the specimen used by RICHARD.

C. rigidipila STEUD. & HOCHST. ex RICHARD 1851 p. 3. — *C. schimperi* VATKE 1874 p. 712, nom. nov. superfl. pro *C. sarmentosa* et *C. rigidipila* (type as for *C. rigidipila*, see ENGLER 1892 p. 410). — *C. schimperi* VATKE var. *rigidipila* (STEUD. & HOCHST. ex A. RICH.) VATKE 1876 p. 201, nom. illegit. — Orig. coll.: QUARTIN DILLON & PETIT s.n., Ethiopia, Tigre, Ouodgerate (P lectotype).

C. sarmentosa HOCHST. ex RICHARD 1851 p. 4. — *C. schimperi* VATKE var. *sarmentosa* (A. RICH.) VATKE 1876 p. 201, nom. illegit. — *C. rigidipila* STEUD. & HOCHST. ex A. RICH. var. *sarmentosa* (HOCHST. ex A. RICH.) ENGLER 1892 p. 410. — Orig. coll.: QUARTIN DILLON & PETIT s.n., Ethiopia, Choa (P lectotype).

Campanula bordesiana MAIRE (1929 p. 188) described from Ahaggar and also reported from Tibesti, is probably also conspecific with *C. edulis*. However, I have seen too little material yet to formally reduce it to a synonym. The area of distribution of *C. edulis* may thus be extended to southern Algeria in the west.

DISCUSSION

C. esculenta was said by RICHARD to differ from *C. edulis* in having a glabrous corolla (however, a few hairs are present near the apex of the corolla-lobes in the syntypes) and obovate-oblong, subspathulate, not lanceolate leaves. It was distinguished from *C. rigidipila* by its leaf-shape and shorter calyx-lobes and appendages.

C. quartiniana was characterized by long, upright, striate and hispid stems with scattered leaves, and by having hairy midveins on the petals.

C. sarmentosa was said to differ from *C. rigidipila* in having thinner and decumbent stems and larger, obovate and obtuse leaves.

The name *C. edulis* in the literature was apparently first used for African material by SCHWARTZ (1939 p. 270). He cited *C. rigidipila* as a synonym. *C. rigidipila* in its turn had long been in use for *C. edulis* in Yemen. CUFODONTIS (1965 p. 1052) cited *C. esculenta, C. sarmentosa* and *C. rigidipila* as synonyms of *C. edulis,* but regarded *C. quartiniana* as distinct, though with hesitation. I agree that this is a rather characteristic form because of the long upright stems (± decumbent at the base, however) and branches, but there are numerous intermediates and I prefer to regard them all as a single polymorphic species.

The most conspicuous variation in *C. edulis* is to be found in the size of the flowers. The corolla ranges from 7 to 25 or occasionally 30 mm in length. However, the variation is continuous, even though large-flowered forms predominate on certain mountains, for instance Mount Moroto in Uganda, Mount Hanang and Ngorongoro Crater in Tanzania, and some others in Ethiopia.

Crossing experiments were performed between the two strains of *C. edulis* cited in Table 1. THULIN 1367 from Ethiopia is a typical "*quartiniana*" form with an 8—9 mm long corolla while BJÖRNSTAD 1575 from Tanzania is closest to a "*sarmentosa*" form with corollas 15 to 20 mm long. Seeds were formed in five out of eight crosses attempted. From all successful crossings hybrids intermediate in corolla length were obtained (Fig. 1 B). Pollen fertility was investigated in 23 specimens of the F1 generation and was found to range from 96 to 100 %. Numerous seeds were formed by autogamy in all of them and an F2 generation was raised without difficulty. No genetic barriers thus exist between these two rather dissimilar strains from quite different parts of the area of distribution of the species. These results strongly support the wide circumscription of the species given here.

ADDENDUM

Wahlenbergia tenuiloba THULIN nom. nov.

Syn. *W. congesta* THULIN 1975 p. 209, nom. illegit. [non *W. congesta* (CHEESM.) N. E. BROWN 1913 p. 336].

Unfortunately N. E. BROWN's combination, which refers to a species in New Zealand, was overlooked in my recent study of tropical African *Wahlenbergia*. *W. tenuiloba* is endemic in Zaïre and only known from the type collection. The new specific epithet refers to the very narrow calyx-lobes of the species.

ACKNOWLEDGEMENTS

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The Total Range of Euphrasia

Eric Hultén

HULTÉN, E. 1976 02 09. The total range of Euphrasia. — Bot. Notiser 128: 357—364. Lund. ISSN 0006-8195.

A new map of the total range of the genus *Euphrasia* L. (Scrophulariaceae) is presented, as well as a more detailed one of its distribution in the Northern Hemisphere. A third map shows the ranges of *E. tatarica, E. frigida* and *E. mollis*. The connection between the ranges in the Old and New Worlds is over the Aleutian Islands.

A few comments on the complicated taxonomy within the genus and on the occurrences in the Southern Hemisphere are made. No attempt is made to outline the history of the genus.

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In connection with the study of the total ranges of Scandinavian plants I became interested in the total area of distribution of the genus *Euphrasia,* and tried to improve earlier maps of the genus. The result of this study is presented here (Figs. 1, 2).

The following maps, at least, of the genus *Euphrasia* have been published: WETTSTEIN (1896 Karte 1); IRMSCHER (1922 Figs. 2, 3); DU RIETZ (1940 p. 224); CROISAT (1952 Figs. 7, 11); BURBIDGE (1960 p. 180); VAN STEENIS (1962 p. 260, 1964 Fig. 7, 1971 Map 2, 1972 p. 285); VAN STEENIS & BALGOOY (1966 p. 97); SCHMITHÜSEN (1968 p. 113); SCHNELL (1970 Fig. 58); HARTL in HEGI (1972 p. 338); THORNE (1972 p. 379).

At least as far as the range in the Northern Hemisphere is concerned they are all based on WETTSTEIN's very schematical map, but since 1896 our knowledge of the distribution of plants has increased very considerably, and none of the above-enumerated maps are sufficiently detailed to give a reasonable idea of the actual conditions. Since WETTSTEIN's map was completed a number of works including the following have appeared, allowing a far more detailed map to be made of the range of the genus in the Northern Hemisphere: FERNALD & WIEGAND (1915); HULTÉN (1930 pp. 107, 290; 1937 pp. 294, 376; 1950 Maps 1568—1580; 1958 Map 32; 1968 p. 814); JØRGENSEN (1919); KARAMYSCHEVA & RACHKOVSKAYA (1973 p. 111); KRYLOV (1939 pp. 2474—87); LI (1953); POPOV (1959 p. 664); PAVLOV (1965 pp. 102—109); SELL & YEO (1970); YAMAZAKI (1963).

The maps presented here are based on information found in these works as well as on that in the about 1,400 taxonomic works enumerated in my work on the circumpolar plants (HULTÉN 1971 pp. 405—446). The herbarium and collection of distributional maps at the Natural History Museum of Stockholm (Riksmuseum) has also been used.

In Ann. Jard. Bot. Madrid 1(17), 1959 pp. 452—458, six species of *Euphrasia* are reported from Peru. Acc. to EDWIN 1971 p. 671 only two of them possibly belong to that genus — and only *E. pubescens* R. & P. is supposed to occur in Peru. The report is based on an old collection kept in the Paris herbarium. No special locality is given and the report most probably is erroneous. Peru is therefore not marked on the map presented here.

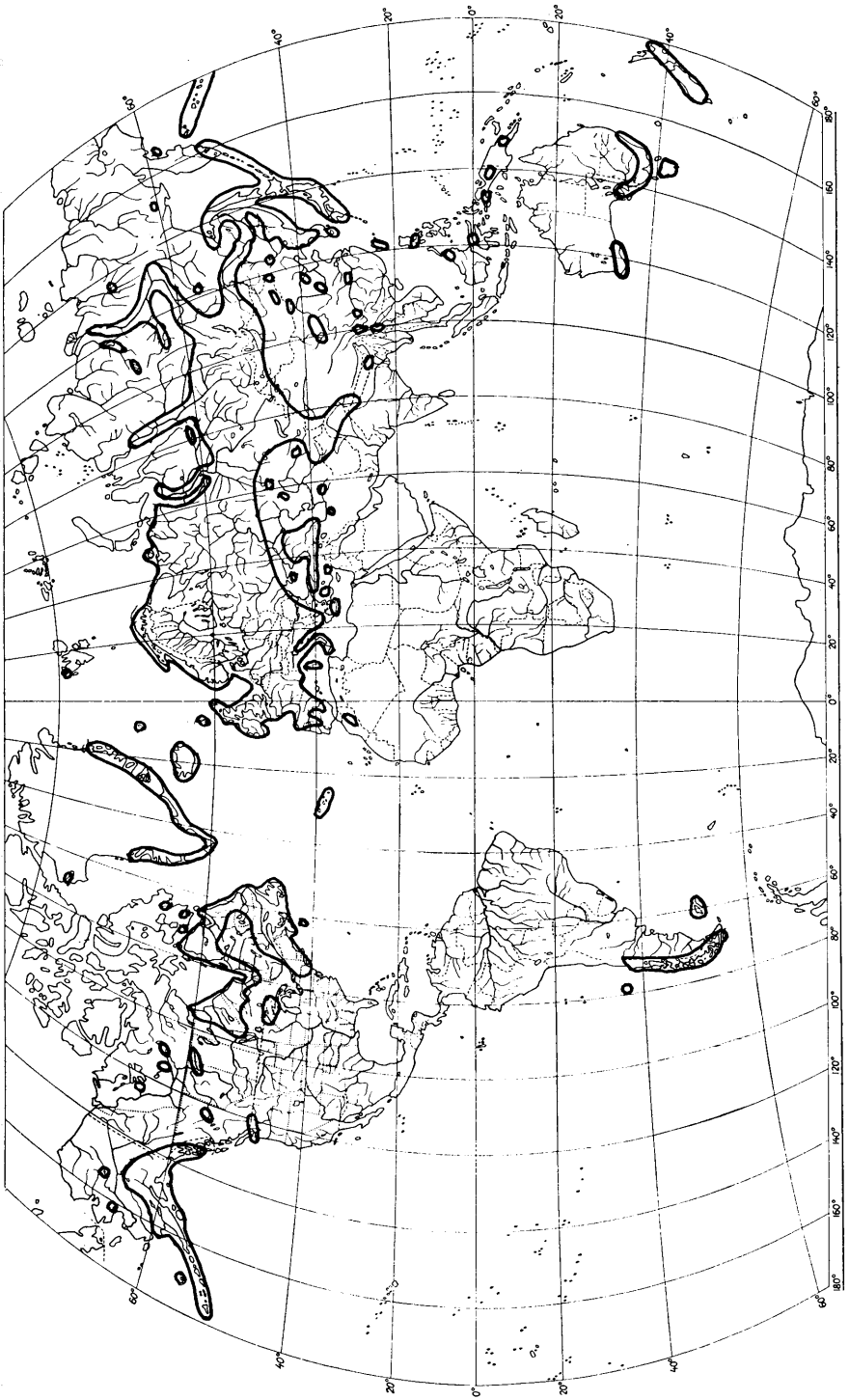

Fig. 1. Total range of the genus *Euphrasia*.

Fig. 2. Total range of the genus *Euphrasia* in the Northern Hemisphere.

COMMENTS ON THE RANGE

The genus *Euphrasia* occupies a circumpolar area in the Northern Hemisphere, but reappears in western South America and on the Falkland Islands and also in New Zealand and Australia with a few intermediate stations, for example on Formosa, Borneo, Celebes and New Guinea. In Africa it only occurs in Morocco.

In the Himalayas *Euphrasia* specimens have been collected above 4000 m, in China up to 4450 m (LI 1953). It is very remarkable that practically all localities in North America are situated on land that was glaciated during the Pleistocene. The genus does not occur in the unglaciated inner parts of Alaska and Yukon. It is especially common in the once inundated areas around southern Hudson Bay, but apparently avoids inner Labrador.

Euphrasia taxa are easily spread, for instance together with hay, and it is therefore not always possible to state their natural range. The isolated occurrences at Thule in N Greenland and on Spitzbergen (at a hot spring) could be taken as being anthropochorous, but the occurrence on the rarely visited Jan Mayen may cast doubt on this.

The genus is lacking in northeastern Siberia, and in northern Siberia it seems only to occur washed down along the large rivers. The connection between Asia and America is formed by a single, fairly characteristic microspecies, *E. mollis* LEDEB., with an almost linear area from southern Alaska over the Aleutian Islands and southern Kamchatka to northern Japan, but lacking in the Bering Strait area (Fig. 3). It is not out of the question that a connection over Bering Sound has existed in earlier warmer periods.

EUPHRASIA IN THE NORTHERN HEMISPHERE

WETTSTEIN (1896) divided the genus into 87 taxa which he gave the status of species, while 22 are regarded as hybrids. He admits that he uses the term species merely for convenience. It must be remembered that WETTSTEIN's admirable study was made before MENDEL's hereditary laws had been rediscovered. His concept of hybridization and its consequences must therefore have been very unclear. However, even later authors, for instance KARLSSON (1974), admit that hybridization seems to play a great part in the variation within the genus.

Since WETTSTEIN's monograph appeared a great number of new taxa ("species") have been described, and WETTSTEIN's concepts and the limitations of many of his species have been changed. Thus, for instance, in the Soviet Union 62 "species" are now recognized in the Flora URSS (JUZEPCHUK 1955 a), and new ones with smaller and smaller ranges are still being described by practically everyone dealing with the genus in restricted areas. Thus, for instance, JUZEPCHUK (1955 b) described 22 new species from the Soviet Union, most of them with very limited areas of distribution. Altogether about 500 taxa given the status of species have been described. In other words, in this respect the genus *Euphrasia* behaves in the same way as a number of other complexes, the members of which are sometimes taken as single collective species, though usually as a conglomerate of "microspecies", e.g. *Betula, Thymus serpyllum* s. lat., *Trapa natans* s. lat., *Polygonum aviculare,* the *Poa pratensis* group and still others. The seasonal dimorphism as well as the fact that *Euphrasia* taxa are hemiparasites contribute to complicate the picture.

In the Northern Hemisphere the genus *Euphrasia* behaves as a complex species, *E. officinalis* s. lat., with the exception of the Azorean and some of the Japanese taxa which are essentially different. It consists of a highly variable circumpolar lowland population, and superimposed on this and poorly differentiated from it a group of arctic-montane taxa (*E. fri-*

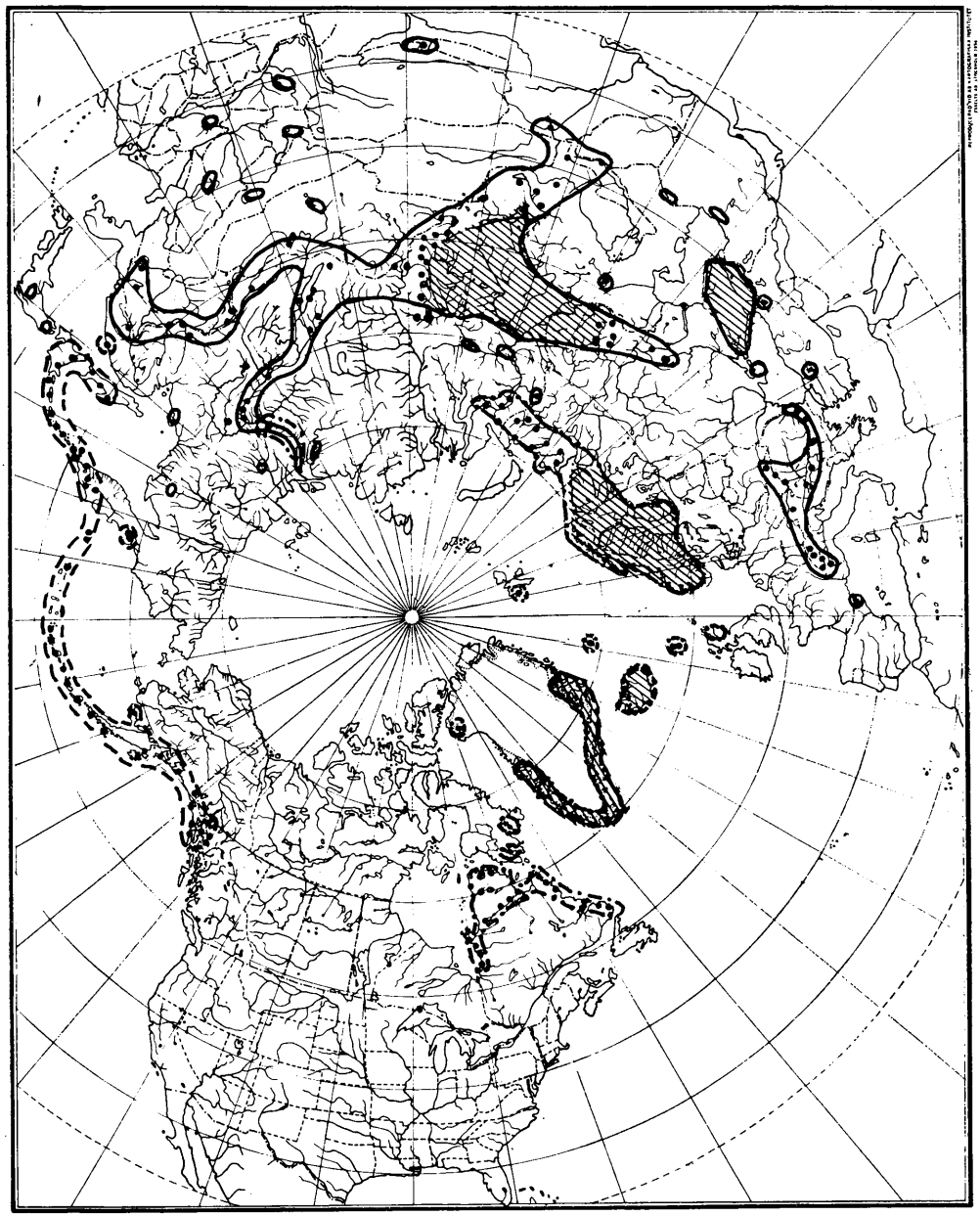

Fig. 3. Range of three remarkable *Euphrasia* taxa. — Unbroken outline: *E. tatarica*. — Outline with dashes and dots: *E. frigida* (including *E. subarctica* Juz. along the Lena River. *E. frigida* occurs according to Yeo 1972 doubtfully in C Europe.) — Broken outline: *E. mollis* (including *E. pseudomollis* Juz.).

gida—minima, E. salisburgensis—lapponica). Many of the lowland taxa are sympatric, often even occurring together in the same population, and they are often connected by dubious forms.

Northern and boreal plants, chiefly occurring in areas that were glaciated during the Pleistocene, are replaced south of their ranges by closely related preglacial counterparts. When the ice retreated biotypes or fragments of this southern population, well adapted to the new climatic and ecological conditions, spread northwards into the new land laid bare by the melting ice. They formed the basis of the present boreal species.

In the case of *Euphrasia* one of these southern taxa is what passes for *E. tatarica* FISCHER ex SPRENG. It occurs in Europe and Asia (Fig. 3), and by FERNALD & WIEGAND (1915 p. 198) was even accepted as occurring in eastern America under the name of *E. stricta* var. *tatarica*. *E. tatarica* is, however, not sharply differentiated from the northern population, especially not from *E. stricta*. Outside the area marked in Fig. 3 it may occur on Sakhalin and in Japan. In Flora Europaea (YEO 1972) part of *E. tatarica* is included in *E. stricta*, the rest in *E. pectinata* TEN. In other respects also *E. officinalis* s. lat. shows great similarity to other complex species. For instance, a number of related but more highly differentiated, isolated taxa occur along the southernmost rim of the whole complex. These taxa are so distinct that they could be regarded as species even using the normal species concept. One such taxon is, for instance, *E. pectinata* which, however, also presents forms that are intermediate between this and the more northern populations.

EUPHRASIA IN THE SOUTHERN HEMISPHERE

Very few plant taxa have a range similar to that of *Euphrasia*, and it can therefore be of interest to discuss this point in greater detail.

Quite a number of taxa with their main range in the Northern Hemisphere reappear in a more or less identical form in southern S America. Some of these have been discussed by ROIVAINEN (1954), others by CONSTANCE et al. (1963). Examples are *Carex pyrenaica* and *C. magellanica*, the genera *Ribes, Empetrum, Sanicula* and *Saxifraga*, as well as a number of western American taxa belonging to the genera *Phacelia, Nama, Agoseris, Microseris, Osmorrhiza* and *Bowlesia*. Some, for instance *Carex macloviana*, the *Phacelia magellanica* complex and the genus *Saxifraga* occur in intermediate stations along the Andes indicating the route of migration.

One species, *Trisetum spicatum* L. s. lat., has a range similar to that of the genus *Euphrasia* with intermediate stations both in eastern Asia and Central and South America. This has been discussed in detail by the author (HULTÉN 1959). In this case the migrational routes seem to have been very well established.

Another plant, *Fimbristylis annua* (DEL.) ROEM. & SCHULT. s. lat., distributed from the hot springs of Kamchatka over Japan, Korea, China and Polynesia to Australia and also occurring in Mexico and S America, may in this connection be worth closer study, as it probably occupies a chain of localities in both hemispheres.

As regards the taxa of the Southern Hemisphere, WETTSTEIN referred those from S America to a separate section, *Trifidae*, on their three-cleft leaves, while those of southeastern Asia, New Zealand and Australia were regarded as a subsection of the section *Euphrasia*, and thus more closely related to the *Euphrasias* of the Northern Hemisphere.

It is therefore extremely remarkable that SKOTTSBERG (1922) described a new perennial species of *Euphrasia* with entire leaves and large flowers from Masafuera off the Chilean coast not belonging to the section *Trifidae*, but showing close

affinities to the New Zealand—Australian group of *Euphrasia* taxa. It is very rarely that taxa which in South America only occur on Juan Fernandez reappear on the other side of the Pacific. Such cases are, according to information received from BENKT SPARRE, for example the following: *Arthopteris altescandens* (COLLA) J. SM. reappearing in Polynesia, Australia and Africa; *Histiopteris incisa* (THUNB.) J. SM. reappearing in Australia, Tasmania and S Africa (introduced in the province of Magellanes); *Santalum fernandezianum* T. PHIL. now extinct, the genus reappearing in Hawaii and E Asia; *Halorrhagis,* four endemic species on Juan Fernandez, the genus reappearing in Polynesia and Australia; *Coprosma,* two endemic species on Juan Fernandez, numerous species in Polynesia and Australia.

Very few phytogeographers today would agree with the conclusion with which DU RIETZ (1940 p. 272) sums up his discussion of the bipolar problem: "To explain the facts of bipolar plant distribution is seems necessary to look for epeirogenetic transtropical highland bridges older than the mountain chains of the Alpine Orogen. Such highland bridges may have existed not only in Africa, but also bordering Alpine geosynclines (i.e. the Andean and Malaysian geosynclines), partly passing over present deep sea bottom."

The old concept of land bridges between continents must be revised in the light of the theory of plate tectonics that is becoming more and more accepted. To what extent this theory can be applied to the history of the genus *Euphrasia* depends on judgements concerning the age of the genus and the time scale of the presumed plate movements.

It seems premature to attempt a sketch of the development of the genus from its presumably Asiatic origin to the present peculiar worldwide range. Knowledge of the present conditions is, however, essential as a base for furthermore discussion.

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Studies on the Flora of Jordan

1. Diplotaxis villosa sp. nov. (Cruciferae)

Loutfy Boulos and Walid Jallad

BOULOS, L. & JALLAD, W. 1976 02 09. Studies on the flora of Jordan. 1. Diplotaxis villosa sp. nov. (Cruciferae). — Bot. Notiser 128: 365—367. Lund. ISSN 0006-8195.

Diplotaxis villosa BOULOS & JALLAD sp. nov. is described from the southern desert of Jordan. The new species seems to represent a unique group within the genus *Diplotaxis* DC. and does not fit into any of the four sections of the genus. A key is given to separate *Diplotaxis villosa* from the four previously known species of *Diplotaxis* in Jordan. A drawing of the plant and a map are presented.

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The genus *Diplotaxis* DC. in Jordan is represented by four species, viz. *Diplotaxis harra* (FORSSK.) BOISS., *D. acris* (FORSSK.) BOISS., *D. erucoides* (L.) DC. and *D. viminea* (L.) DC. (POST & DINSMORE 1932 pp. 118—120, ZOHARY 1966 pp. 305—308, pl. 453—456, JALLAD 1975). The present paper reports the discovery of a new species in the southern desert of Jordan.

Our new species is collected from an area which seems to have been very rarely visited by botanists or has never even been explored botanically. The occurrence of this remarkable new species within a vast area stretching over a few square kilometres, with thousands of individuals almost in pure stands, may draw attention to the need to carry on further floristic studies, as the area may include some other interesting elements which still await discovery. The site where our new species was collected is about 40 kilometres north-east of El-Jafr in the upper course of Wadi Shaumari, a fairly long wadi stretching northwards from El-Jafr for about 60 kilometres.

Diplotaxis villosa sp. nov. seems to constitute a distinct group within the genus *Diplotaxis*. It does not fit into any of the four sections given by SCHULZ (1919) viz. *Hesperidium* O. E. SCHULZ, *Catocarpum*

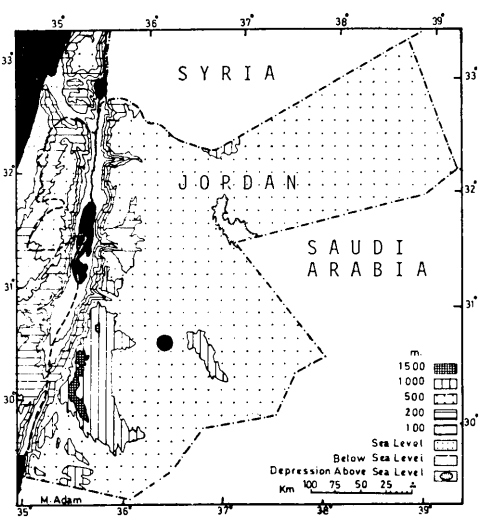

Fig. 1. Distribution of *Diplotaxis villosa*.

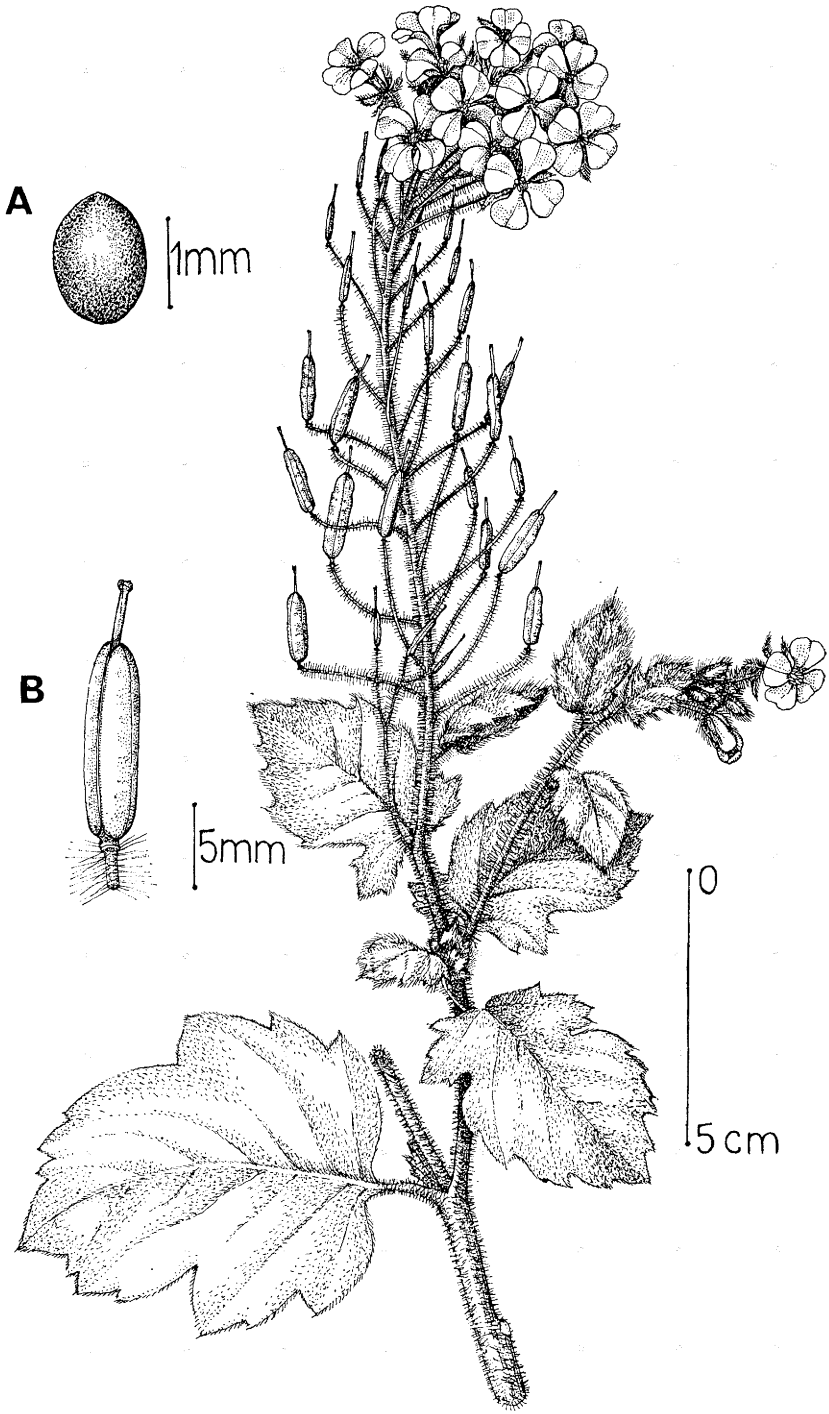

Fig. 2. *Diplotaxis villosa*. — A: Seed. — B: Fruit.

DC., *Rhynchocarpum* PRANTL and *Anocarpum* DC.

We propose to name this species *Diplotaxis villosa* due to the most characteristic white villous hairs which densely cover most of the plant parts. It may be described as follows:

Diplotaxis villosa BOULOS & JALLAD, sp. nov. — Fig. 2

Annua, albo-villosa, 5—60 cm alta, plerumque valde ramosa. Folia petiolata, sinuato-dentata usque lyrata, inferiora sparse pilosa, superiora dense villosa. Inflorescentia racemosa, multiflora, usque 30 cm longa. Flores laete flavi, 1.2—1.5 cm diametro, pedicellis 1—1.5 cm longis adscendentibus usque patentibus. Sepala 5—7 mm longa, villosa, sub anthesi patentia. Petala (unguiculo incluso) 1—1.2 cm longa. Stamina longiora exserta, filamentis anguste alatis. Pedicelli sub fructu 1.5—2.5 cm, adscendentes, villosi. Fructus 13—17 mm, erectus, cylindricus, glabrescens; valvae uninerves, sutura prominenter carinata. Stylus 2—3 mm longus, glaber. Semina 1×1.2 mm, numerosa, in quoque loculo biseriata, brunnea, late elliptica, glabra, rugulosa.

HOLOTYPE: Wadi Shaumari, upstream, c. 40 kms northeast of El-Jafr. 9 April 1975. BOULOS & JALLAD 7994. University of Jordan Herbarium, Amman. Isotypes: BM! CAI! G! K! LD! RNG! S!

Annual, white-villous, 5—60 cm high. Stem erect or ascending, usually richly branched. Cauline leaves petiolate, petiole 1—2.5 cm long, blade 4—7×3.5—7 cm, sinuate-dentate to lyrate, sparsely hairy on both surfaces; upper leaves short-petioled, blade 1.5—3×1—2.5 cm, densely villous. Inflorescence a many-flowered raceme, up to 30 cm long. Flowers bright yellow, becoming orange-yellow when dry, 1.2—1.5 cm in diameter; flowering pedicels 1—1.5 cm long, ascending to spreading, narrowly cylindrical, villous. Sepals 5—7 mm long, villous, yellowish-green in bud, green and spreading during anthesis, lanceolate to ovate-lanceolate. Petals 1—1.2 cm long including the claw, limb obovate, veined. Long stamens exserted; filaments narrowly winged. Fruiting pedicels 1.5—2.5 cm long, ascending, villous. Fruit 13—17×3—5 mm, erect, cylindrical, glabrescent; beak seedless, valves uninerved, with a prominent ridge along the suture; replum membranous. Style 2—3 mm long, glabrous; stigma bilobed; gynophore very short. Seeds 1×1.2 mm, numerous, in two rows in each cell, brown, broadly elliptic, glabrous, rugulose.

KEY TO THE DIPLOTAXIS SPECIES KNOWN FROM JORDAN

1. Flowers yellow
   2. Biennials or perennials, fruit deflexed ..... *D. harra*
   2. Annuals, fruit erect to ascending
      3. Plants densely white-villous, fruit cylindrical ..... *D. villosa*
      3. Plants glabrous or glabrescent, fruit compressed ..... *D. viminea*
1. Flowers white, pink or violet
   4. Flowers pink or violet, over 16 mm long ..... *D. acris*
   4. Flowers white, up to 16 mm long ..... *D. crucoides*

ACKNOWLEDGEMENTS

We wish to thank Mr H. K. AIRY SHAW, The Herbarium, Royal Botanic Gardens, Kew, for his kind help with the Latin diagnosis. Thanks are also due to UNESCO and to the Jordan Research Council, Amman, for providing facilities and financial support.

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Studies on the Flora of Jordan

2. Seven Species New to the Flora of Jordan

Loutfy Boulos, Walid Jallad and Jamil Lahham

BOULOS, L., JALLAD, W. & LAHHAM, J. 1976 02 09. Studies on the flora of Jordan. 2. Seven species new to the flora of Jordan. — Bot. Notiser 128: 368—370. Lund. ISSN 0006-8195.

Seven species are recorded as new to Jordan: *Papaver glaucum* BOISS. & HAUSSKN. (Papaveraceae), *Hypericum olivieri* (SPACH) BOISS. (Guttiferae), *Linum corymbulosum* Reichb. (Linaceae), *Allium sindjarense* BOISS. & HAUSSKN. (Alliaceae), *Colchicum crocifolium* BOISS. (Liliaceae), *Consolida tomentosa* (AUCHER) SCHRÖD. subsp. *oligantha* (BOISS.) DAVIS (Ranunculaceae) and *Thalictrum isopyroides* C. A. MEY. (Ranunculaceae). The genus *Thalictrum* L. has not previously been known from Jordan.

Loutfy Boulos, Walid Jallad and Jamil Lahham, Faculty of Science, University of Jordan, Amman, Jordan.

The present paper reports seven species new to the flora of Jordan. Specimens of these species are deposited at the University of Jordan Herbarium, Amman.

Papaver glaucum BOISS. & HAUSSKN. in BOISS.

This species is not among the six species enumerated by ZOHARY (1966) from Jordan. CULLEN (1965) gives the following distribution for *P. glaucum*: Turkey (eastern Anatolia), the Syrian desert, northern Iraq and western Iran; Irano-Turanian element. According to MOUTERDE (1970) the geographical distribution is: Turkey, Syria, Iraq and Iran.

Specimens collected from Jordan: c. 30 km northeast of H-4, 9 April 1974 (fl., fr.) BOULOS, JALLAD & LAHHAM 6861. — Wadi Ruweishid, 12 km east of H-4, 11 April 1974 (fl.) BOULOS, JALLAD & LAHHAM 6918. — 9 km north of Aqaba, 5 April 1974 (fl., fr.) BOULOS, JALLAD & LAHHAM 6671. — Wadi Yutum, upper stream, 15 km north of Aqaba, 21 March 1975 (fr.) BOULOS, JALLAD, LAHHAM & ABU-HMAIDAN 7476. — 4 km south of Rum Rest House, along the road to Rum Police Station, 23 March 1975 (fr.) BOULOS, JALLAD, LAHHAM & ABU-HMAIDAN 7674.

Hypericum olivieri (SPACH) BOISS.

The specimens were determined by N. K. B. ROBSON. Dr ROBSON (verbal comm.) did not see any material of this species from Jordan during his many years of research on the genus *Hypericum* L. ROBSON (1967) refers to this species as being from Turkey, the Syrian desert and western Iran. MOUTERDE (1970) gives the following geographical distribution for *H. olivieri*: "Turquie, Syrie, presque sûrement Iraq et Transjordanie, W. de l'Iran." This shows that he suspected its presence in Jordan; however, he did not give enough evidence of its occurrence. There is no mention of this species in ZOHARY 1966.

Specimens collected from Jordan: Hussein Housing District, Amman, 10 June 1974 (fl.) S. ORAN s.n. — University Campus, Al-Jubaiha, near Amman, 22 July 1974 (fr.) BOULOS 7286. — Duplicates of both specimens in BM!

Linum corymbulosum REICHB.

POST and DINSMORE (1932) as well as ZOHARY (1972) recorded this species

from Palestine but not from Jordan. DAVIS (1967) gives the general distribution of *L. corymbulosum* as follows: South Europe, Crimea, Southwest Asia, East Africa; Mediterranean element. He gives no details about any particular countries in Southwest Asia.

Specimen collected from Jordan: 12 km north of Irbid (3 km north of Sal), 26 April 1975 (fl., fr.) BOULOS, JALLAD & LAHHAM 8173.

Allium sindjarense BOISS. & HAUSSKN.

According to MOUTERDE (1966) this species is known from southern Turkey, Iraq and Syria. POST & DINSMORE (1932) report its occurrence in Syria. Our find from Jordan comes from a locality very close to the Syrian border.

Specimen collected from Jordan: 80 km northeast of H-4, near the Syrian border, 10 April 1974 (fl.) BOULOS, JALLAD & LAHHAM 6881.

Colchicum crocifolium BOISS.

POST & DINSMORE (1933) do not mention this species in their treatment of the genus *Colchicum* L. However, MOUTERDE (1966) gives the following geographical distribution for *C. crocifolium*: Syria, Turkey, Iraq and Iran.

Specimen collected from Jordan: 35 km northeast of H-4, 11 April 1974 (fr.) BOULOS, JALLAD & LAHHAM 6952.

Consolida tomentosa (AUCHER) SCHRÖDGR. subsp. **oligantha** (BOISS.) DAVIS

ZOHARY (1966) enumerates three species of *Consolida* (DC.) S. F. GRAY from Jordan. Our species is not among these three. DAVIS (1965) reports on the geographical distribution of our species as follows: Turkey, North Iraq and the Syrian Desert? Irano-Turanian element. He adds: "Some Syrian specimens are intermediate between subsp. *oligantha* and subsp. *tomentosa* (Syrian Desert and N. Iraq) . . . its presence in Turkey remains in doubt."

Our find represents an extreme southern extension in the geographical range of the species (Fig. 2).

Specimen collected from Jordan: 5 km south of Shaubak, 29 June (fl., fr.) JALLAD, LAHHAM & HANANIA 616.

Thalictrum isopyroides C. A. MEY.

According to DAVIS et al. (1965) the geographical distribution of *Thalictrum isopyroides* is as follows: Soviet Armenia, Northern Iraq, Turkey (scattered mainly in eastern Anatolia), the Syrian Desert, Iran, Afghanistan and Altai; mainly in the Irano-Turanian region. MOUTERDE (1970) gives a more or less similar distribution for the same species. LECOYER (1885) already gave an almost identical distribution for *T. isopyroides* in his monographic treatment of the genus *Thalictrum*. The plant grows in mountainous regions (LECOYER 1885) among volcanic rocks (POST & DINSMORE 1932).

Thalictrum isopyroides was collected in southern Jordan, 1—3 km south of Ras en Naqb, 30°01′N and 35°28′E. This locality represents the extreme southwestern limit of the geographical range of the species. Djebel Druz, southern Syria, was the southwestern limit before the discovery at Ras en Naqb, Jordan. The genus *Thalictrum* L. is entirely new to the flora of Jordan.

The presence of *Thalictrum isopyroides* as far south as Ras en Naqb, about 90 kilometres northeast of the Gulf of Aqaba, the Red Sea, is probably due to the high altitude of this area (c. 1400 m). Moreover, the plants were collected on the western slopes of the Ras en Naqb escarpment, which may provide a milder microclimate within that area.

Among the rare and interesting species collected by the authors at Ras en Naqb are: *Biebersteinia multifida* DC., *Tulipa polychroma* STAPF, *Iris palaestina* BOISS.

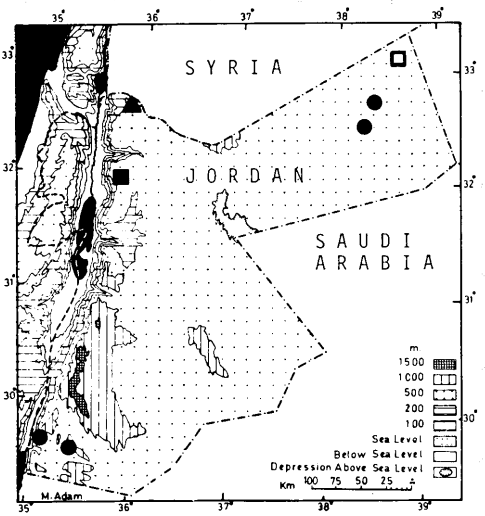

Fig. 1. The distribution within Jordan of *Papaver glaucum* (dots), *Hypericum olivieri* (filled square), *Linum corymbulosum* (triangle), and *Allium sindjarense* (unfilled square).

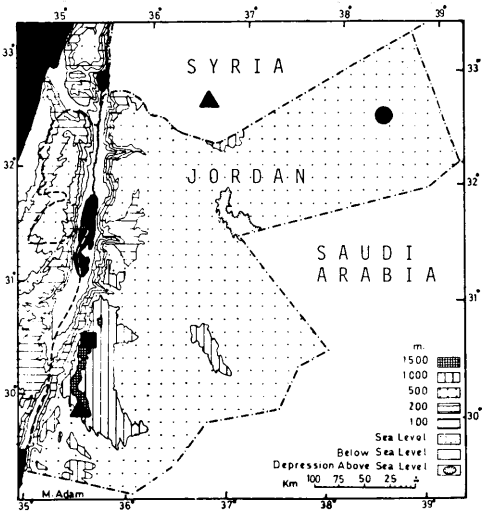

Fig. 2. The distribution within Jordan of *Colchicum crocifolium* (dot), *Consolida tomentosa* subsp. *oligantha* (square), and *Thalictrum isopyroides* (triangles). For *T. isopyroides* the southwesternmost Syrian locality (Djebel Druz) is also shown.

and *Pyrethrum santolinoides* DC. In Jordan these species and probably others are almost restricted to Ras en Naqb and hardly exist outside this area.

Specimens collected from Jordan: 1—3 km south of Ras en Naqb, 12 March 1974 (fl. buds) BOULOS, AL-EISAWI & JALLAD 5997. — 1—4 km south of Ras en Naqb, 19 March 1975 (fl.) BOULOS & JALLAD 7353. — 1—2 km south of Ras en Naqb, 4 April 1975 (fr.) BOULOS & JALLAD 7803.

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The authors are indebted to the Director, Deputy Director and Staff of the Herbarium and Library, Royal Botanic Gardens, Kew for the facilities and help they were afforded during the preparation of this work. Thanks are also due to the Salén Foundation, Sweden and the Jordan Research Council for their financial support. The facilities offered by UNESCO and the University of Jordan during the field trips are much appreciated.

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Botanical Literature

MIÈGE, J. & STORK, ADÉLAÏDE L. (eds): Origines des flores africaines et malgaches. Nature-speciation. Comptes rendus de la VIIIe réunion de l'AETFAT, Vol. 1. — Boissiera 24 a. Genève 1975. 422 pp.

Since its first meeting in Brussels in 1951 the "Association pour l'Etude Taxonomique de la Flore d'Afrique Tropicale" (AETFAT) has organized eight conferences at various institutions involved in the study of African flora and vegetation. The latest conference took place at the Conservatoire et Jardin Botanique de la Ville de Genève in September 1974 and was attended by more than a hundred botanists from a wide range of European and African countries.

It has been the general practice at the AETFAT meetings to devote the main part of the conference to papers relating to a selected topic of general interest. At the 1974 meeting the topic was "The Origin of the Floras of Africa and Madagascar and the Nature of Speciation". Papers on a number of other subjects within AETFAT's sphere of research were also read, including progress reports on expedition activities, and progress in the publication of distribution and vegetation maps, recurrent subjects at AETFAT meetings. A total of more than 70 papers was read at the Geneva meeting. The present Volume 1 of the "Comptes-rendus" comprises 47 papers, mainly those with themes relating to the main topic of the meeting. The remaining papers, including the progress reports and a number of papers on nature conservation, will appear in a forthcoming volume.

The 47 papers in Volume 1 are grouped around a number of themes: Records of fossil pollen; changes in floras and vegetation during the Pleistocene; micro-evolution in mountain habitats; distribution maps of Sahelian plants; phytogeographical papers on local endemism and on the relation between the floras of Madagascar and of tropical East Africa; taxonomic, morphological and phylogenetic papers on various African genera and families; phytochemistry, mainly of the genera *Acacia* and *Adansonia*; numerical taxonomy and biometry of the grass genera *Aristida* and *Panicum*; computerization of herbaria with important collections of African plants. It is very difficult to select any of the papers for reviewing in detail.

The general impression one receives from the papers as a whole is that of a very rich and many-faceted research activity. The present volume, and indeed all the volumes from the AETFAT meetings, is indispensable to students of the flora of Africa as the proceedings represent up-to-date cross-sections of the many themes of African botany at present under study in European and African herbaria and universities. But the disjointed nature of the contents of the papers also clearly indicates how far there is still to go before reaching the goal suggested by the main topic of the meeting: an exhaustive description and explanation of the origin of the floras of Africa and Madagascar.

IB FRIIS

BONEY, A. D.: Phytoplankton. Studies in Biology 52. Edited by the Institute of Biology. — Edward Arnold Ltd. London 1975. 116 pp. Price £ 3.80 (boards); 1.90 (paperback).

The phytoplankton, the most important vegetation in about 73 % of the earth's surface area, is the subject of this book.

Both marine and freshwater phytoplankton are dealt with in the 116 pages. It, however, concentrates mostly on the marine organisms. The title "Phytoplankton" indicates that no attempt has been made to restrict this enormous subject and the impression remains after reading the book. It must, however, be stated that the author has succeeded in giving information on much of the subject "phytoplankton".

The three major chapters deal with the organisms, factors affecting their growth and their succession. Briefer accounts treat buoyancy, interactions with other organisms, biomass, production, pollution and other effects made by man.

In my opinion the chapter on the organisms gives too short an introduction to each of the taxonomic groups of the phytoplankton. It would have been to advantage if the classes had been subdivided into orders as well. The chapter "Factors Affecting Phytoplankton Growth" treats light, temperature and nutrients in a way easy to survey for a beginner in the study of phytoplankton. Part of the chapter takes up the important tool of phytoplankton studies — culture techniques.

The succession of phytoplankton is a subject which has interested many scientists and a great deal of work has been done. General conclusions are very difficult to draw, but those which exist are dealt with in an interesting way.

In the chapter on the buoyancy of phytoplankton aspects of outgrowths on the cell, physiological regulations and the importance of water movement are summarized. Recent authors seem to consider that water movement is the determining factor, which is stated by the author. More stress could have been laid on this.

The book ends up with a short chapter on man-made effects, giving very brief accounts of a number of effects. This part can be looked upon as a stimulus to further reading.

My only objection is the lack of references in the text or at least after each chapter. This I consider necessary in a small book like this covering such an extensive subject.

LARS EDLER

SCHUSTER, RUDOLF M.: The Hepaticae and Anthocerotae of North America East of the Hundredth Meridian. Vol. III. XIV+880 pp. 475 figures. "1974" (in fact published on April 24, 1975). — Columbia University Press, New York and London. Price £ 12.50 (cloth).

The third volume of this work maintains the same high standard of print and illustrations found in the previous two issues (Vols. I, 1966, and II, 1970). These were reviewed in Bot. Notiser 124 (1971) pp. 176—178. The appreciative summary "This work is much more than a flora of North American liverworts, it is a treasure of information in all fields of this topic" may just as aptly be attributed to the present volume.

Vol. III treats a major portion of the order Jungermanniales, i.e., the four families Gymnomitriaceae (primarily, also in Vol. I p. 386, known as Marsupellaceae; the change has been necessary under the Code of Nomenclature), Scapaniaceae, Antheliaceae and Cephaloziaceae and ends with the genus *Odontoschisma*. Particularly the first two have undergone extensive and complex speciation in the Arctic. Dr SCHUSTER has spent four full summers in Ellesmere Island and Greenland; this has given him the unique opportunity to study several critical taxa under very extreme conditions. His discussions on the differentiation within a species are based largely on study of living specimens rather than of herbarium material.

The infraspecific variation and its response to environmental conditions is treated in great detail. In some cases, "phenotypes which are so far out of the normal range exhibited that I assume they represent genetic variants" have been

described as forms. The modificative variation has often been recorded with terms like "mod. *colorata, parvifolia, integrifolia*" which have no status under the Code of Nomenclature.

The author has restricted himself to conditions seen in nature. He has not tried to make a "biosystematic" analysis of the variation. Hence it must remain as an open question how the taxonomic characters can be modified under varied climatic conditions (under cultivation) such as light and humidity. Recent research of this kind has shown an unexpectedly high variability within otherwise well-known "species" or "varieties" of bryophytes. Cf., e.g., KAI WIGH, "Studies on the Moss Family Brachytheciaceae with Special Reference to the Genus *Brachythecium*". (Thesis, Department of Plant Taxonomy, University of Gothenburg, 1975).

In his preface Dr SCHUSTER declares that he takes a "conservative" attitude to nomenclature. "Consideration of whether *Scapania nemorosa* should be called *S. nemorea* is a waste of valuable intellectual energy." The critical reader can easily find several cases to discuss. *Gymnomitrion* "Sect. 4. *Corallodes* SCHUST., sect. n." is recorded (p. 147) without a description. In the Index it is met with as "*corralloides.*" *Gymnomitrion* Sect. "*Apiculatae*" should be *Apiculata*, and *Odontoschisma* Sect. "*Denudatae*" should be "*Denudata*" (both neuter plural; cf. Code of Nomenclature, Art. 21). *Odontoschisma* "Sect. *Macouniae*" founded on *O. macounii* is inadmissible under the Code.

In Vol. I (1966) this work was projected to comprise 3 volumes. It is evident that its scope has been changed to some extent during the past ten years. The sequence of families has sometimes been altered when one compares with the classification proposed in Vol. I. As several large groups remain to be treated we may expect one, perhaps two, further volumes in order to complete this monumental treatise.

OVE ALMBORN

Drawings of Scandinavian Plants 109–110

Epilobium L. Sect. Epilobium

Alf Oredsson and Sven Snogerup

OREDSSON, A. & SNOGERUP, S. 1976 05 06. Drawings of Scandinavian plants 109—110. Epilobium L. sect. Epilobium. — Bot. Notiser 128: 375—379. Lund ISSN 0006-8195.

Drawings and descriptions are given for *E. collinum* C. C. GMEL. and *E. montanum* L.

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The two species nos. 109 and 110 are closely related. Intermediates are few, but some of them, e.g. from southernmost Sweden, are apparently wholly fertile. Thus the genetic relationship of these species probably merits further investigation. They may be isolated by ecological differences and predominant autogamy rather than by barriers of intersterility.

109. **Epilobium collinum** C. C. GMELIN 1826

Perennial herb, (5—)15—35(—60) cm high. Stem often unbranched, but more or less stunted branches usually present in most leaf axils, sometimes prolonged and giving the plant a densely branched habit. Stem usually with 6—15 pairs of leaves below the inflorescence, leaves usually longer than the internodes, producing one or several (1—)3—6(—12)-flowered inflorescences. Stolons subterranean or occurring at the surface, very short and inconspicuous or up to 10 mm, reddish, with dense, scale-like leaves. Turions epigean, formed late in the autumn as dense rosettes of 10—20 fleshy, broadly obovate leaves 3—6 mm long, or rarely prolonged up to 20 mm with small and very thick leaves, reddish with green on the upper sides of the leaves.

Stem 0.5—2(—3) mm thick, quite terete, usually rather densely hairy, especially in the upper part and below the midribs of the leaves, hairs 0—0.25 mm, recurved to adpressed or some very short glands patent, mostly eglandular, only some of the shorter ones glandular.

Most leaves opposite, usually only the bracts alternate, all petiolate, petioles in middle and upper leaves 1—5 mm, in basal ones up to 10 mm, leaf bases usually not united, never decurrent. Basal leaves smaller, spathulate to obovate or elliptical. Middle cauline leaves 10—30 (—40) mm long, 5—12(—22) mm broad, ovate to narrowly ovate, obtuse to acute, regularly serrate with usually 6—12 up to 1 mm long, forwards-pointing teeth on each side. Upper leaves smaller, short-petiolate, usually narrowly to very narrowly ovate, sharply tapering to the acute or obtuse apex. Leaves sparsely hairy, denser on margins and both sides of the midrib, hairs like those of the stem.

Pedicels erect in all stages. Buds ellipsoidal to obovoidal, with a broad conical tip, not mucronate. Sepals (3—)3.5—6 mm, connate to 0.8—1.5 mm at base,

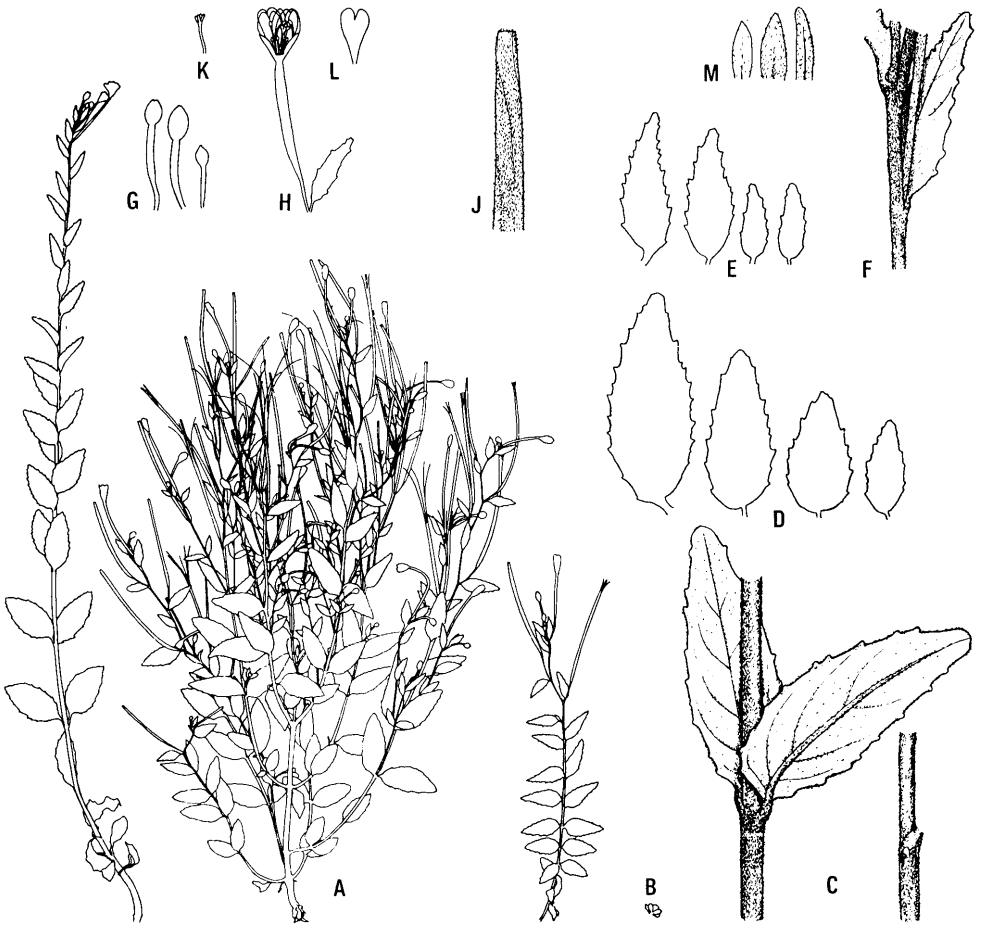
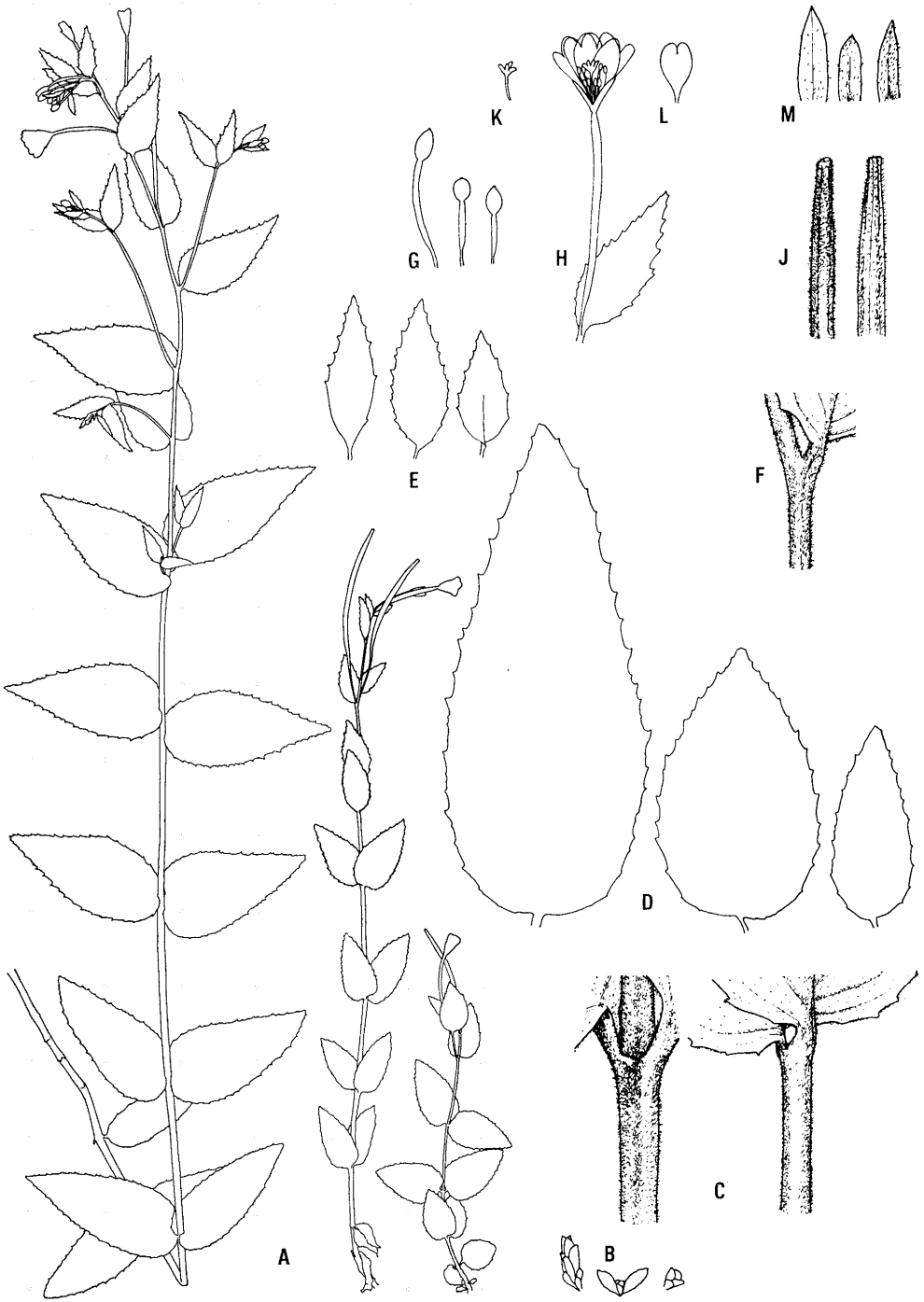


Fig. 109. *Epilobium collinum* C. C. Gmel. — A: Habit, ×1/3. — B: Winter bud, ×1/2. — C: Stem nodes, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem part with leaves, ×2.5. — G: Buds, ×1. — H: Flower, ×1. — J: Apical part of capsule, ×2.5. — K: Style, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.

narrowly ovate to lanceolate, reddish or pure green, moderately to densely hairy at base, sparsely above. Petals (5—)6—7.5(—9) mm, notched to 1—1.5 mm, reddish to purplish-pink, very rarely light pink or white. Anthers (0.5—)0.65—0.8 mm, long filaments 3.5—5(—6) mm, short filaments 3—3.5(—4) mm. Style usually shorter than the long stamens, stigma 4-lobed, lobes 1—2 mm.

Capsule stalk (3—)6—10(—20) mm. Capsule (30—)40—50(—60) mm, densely

Fig. 110. *Epilobium montanum* L. — A: Habit, ×1/3. — B: Winter buds, ×1/2. — C: Stem nodes, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem part with leaf, ×2.5. — G: Buds, ×1. — H: Flower, ×1. — J: Apical part of capsules, ×2.5. — K: Style, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.


A
B
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hairy, hairs like those of the stem, mostly eglandular, incurved to adpressed. Seeds 1—1.1(—1.2) mm long, 0.4—0.5 mm broad, narrowly obovoidal, obtuse at apex, tapering to an acute base, without a neck, flattened side with a marked obtuse ridge and two furrows, surface with many ± irregular rows of small but distinct papillae, chalazal hairs usually 40—45, 5.5—7.5 mm long. Flower homogamous.

E. collinum occurs mostly in rather dry habitats such as hillsides and rocks. It is rather common in Norway except for the arctic parts, in Sweden from Halland, Västergötland and Östergötland north to Medelpad and Jämtland, and in the southern coastal areas of Finland. In southernmost Sweden and in the more northeastern parts of Sweden and Finland it occurs only in more or less scattered localities. In the southern part of the mountain chain it grows up to at least 1250 m.

E. collinum is a European endemic, occurring in most parts of the continent but stated to be absent from the British Isles, the Netherlands and Denmark.

Known hybrids: with *E. lamyi, montanum, obscurum, palustre* and *roseum.*

110. **Epilobium montanum** L. 1753

Perennial herb, 20—60(—90) cm high. Stem usually simple or branched in the upper part only, but more or less stunted branches present in most leaf axils, rarely prolonged and some specimens thus branched from the base. Stem producing one or several 4—10(—15)-flowered inflorescences, usually with 3—8 pairs of leaves below the inflorescence, leaves usually shorter than the internodes. Stolons formed at the surface or subterranean, very short and inconspicuous or up to 10 mm, reddish, with dense scale-like leaves. Turions epigean, formed late in the autumn as dense rosettes of 10—15 fleshy, broadly obovate leaves 4—10 mm long, reddish with green on the upper side of the leaves.

Stem (1—)2—3(—4) mm thick, quite terete, usually sparsely hairy below, moderately to densely above, hairs 0—0.3 mm, patent to incurved, mostly glandular, the eglandular ones long and incurved.

Most leaves opposite, only the bracts alternate, all petiolate, petioles in middle and upper ones 1—6 mm, in basal ones up to 10 mm, leaf bases usually not united, never decurrent. Basal leaves smaller, spathulate to lanceolate or elliptic. Middle cauline leaves (20—)35—60(—90) mm long, (10—) 20—30(—45) mm broad, ovate or rarely narrowly ovate, acute, serrate with usually 20—40, ± irregular teeth up to 1 mm long on each side. Upper leaves smaller, short-petiolate, ovate to narrowly ovate, acute. Basal leaves subglabrous, middle and upper ones gradually becoming more hairy especially on the margin and both sides of the veins, hairs like those of the stem.

Pedicels erect in all stages. Buds ellipsoidal, blunt with a small but usually distinct mucro. Sepals (5—)6—7.5 mm, connate to 1.5—2.5 mm at base, lanceolate, acute, pure green or more or less reddish, sparsely to moderately hairy. Petals (7—)9—12(—15) mm, notched to 1.5—2 mm, reddish to purplish pink, very rarely light pink or white. Anthers (0.7—)0.8—1.0 mm, long filaments 5.5—7.5(—8.5) mm, short filaments 3.5—5 mm. Style about equalling the long stamens, stigma 4-lobed, lobes c. 2 mm.

Capsule stalk (5—)10—15(—20) mm. Capsule (40—)60—70(—80) mm, densely or rarely sparsely hairy, hairs like those of the stem, mostly glandular, erect, eglandular ones only on the ridges. Seeds (1.15—)1.2—1.3 mm long, 0.4—0.5 mm broad, narrowly obovoidal, obtuse at apex, tapering to an acute base, without a neck, flattened side with a rather inconspicuous ridge and two shallow furrows, surface with many ± irregular rows of small but distinct papillae, chalazal hairs usually 45—55, 7.5—10 mm long. Flower homogamous.

E. montanum occurs in moist woods and similar shady habitats, sometimes also

in open, moist places, but also along small roads and in other disturbed habitats. It is common in the southern lowlands of Scandinavia up to c. 62°N and along the Norwegian west coast, with scattered occurrences further north and up to c. 600 m in the mountains. It is lacking in the northern part of Finland.

E. montanum occurs throughout Europe except in the southernmost parts, and through western and northern Asia to Japan.

Known hybrids: with *E. collinum, glandulosum, hirsutum, lactiflorum, obscurum, palustre, parviflorum, roseum* and *tetragonum.*

The Iris Subgenus Susiana in Lebanon and Syria

Shaukat A. Chaudhary, Grace Kirkwood, and Carolyne Weymouth

CHAUDHARY, S. A., KIRKWOOD, G. & WEYMOUTH, C. 1976 05 06. The Iris subgenus Susiana in Lebanon and Syria. — Bot. Notiser 128: 380—407. Lund. ISSN 0006-8195.

Twenty-three taxa belonging to *Iris* subgenus *Susiana* SPACH (Oncocyclus irises) from Lebanon and Syria have been described, their limits established, and their inter-relationships discussed. Five of the taxa are new, two represent new combinations.

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The irises belonging to the subgenus *Susiana* SPACH are commonly treated as subgenus or section *Oncocyclus,* or simply referred to as oncocyclus irises, or sometimes as oncos only. *Iris susiana,* the type species for this subgenus was described by LINNAEUS in 1753 from material cultivated in Europe. During the latter part of the 19th century BOISSIER, BERBEY, BAKER and FOSTER described some *Oncocyclus* species from the region. The largest number of species, however, was described by DINSMORE from the region described as Syria, Palestine and Sinai (1933, 1934). DAVIS (1954) considered DINSMORE's species to be microspecies. The authors, on the other hand, have found DINSMORE's observations to be much more reliable in most cases compared with those of some of the later workers. WEST (1953) and later others following WEST have observed that *I. susiana* L. does not differ greatly from *I. basaltica* DINSM. and that *I. susiana* had therefore probably been introduced into Europe from the *I. basaltica* populations in Syria. Unfortunately the present authors are not very familiar with *I. susiana* but would like to point out that *I. kirkwoodi* (including its infraspecific taxa), *I. sofarana, I. sofarana* subsp. *kasruwana* and *I. westii* have often been confused even by professional taxonomists as have other taxa, too. One need only look in almost any herbarium to see the confusion in identification of the oncocyclus species from this region when pigmentation has been the major criterion used. We feel that it would require more intensive study to say with any degree of confidence whether *I. susiana* is the same as *I. basaltica.*

In the present work the authors have tried to make use of criteria such as the rhizome, the number of leaves, the number of nodes, the kind of beard, the kind of beard hair, the morphology of style branches, the kind of pollinator tunnels, to some extent the kind of pigments (Table 1), and the cytological evidence so far available. At the same time the undesirability of exaggerated lumping together or splitting up has been kept in mind.

MATERIAL

The oncocyclus irises are notoriously unsatisfactory for studying from herbarium material. As far as was possible, therefore, natural colonies of the different taxa were surveyed. This was generally re-located live material that was collected and directly studied, or planted at the farm of the American University of Beirut in the Beqa'a Valley of Lebanon for comparison and investigation during subsequent springs. Where colonies could not be relocated or reached

Table 1. Presence/absence of absorption peaks in different nM ranges in ethanol extracts from one fall + one standard of some *Iris* subgen. *Susiana* taxa. (+) denotes that peaks are present in some of the biotypes investigated. — Peak patterns could be used as an indicator of relationships. *Iris sofarana* f. *franjieh* is a mutant and has some peaks that differ from normal populations. All colour variations in normal *I. sofarana* subsp. *sofarana* were analysed to discount minor peak variations. — A Beckman DB-G self-recording spectrophotometer was used.

Taxon	nM ranges																
	750—740	670—660	655—645	620—615	572—567	560—550	537—527	525—465	450—445	400	395—337	325—322	320—315	300—290	285—275	272—257	230—210
kirkwoodii subsp. *calcarea*	+	+	−	+	+	+	−	+	+	+	−	−	+	−	−	−	+
kirkwoodii var. *kirkwoodii*	+	+	−	+	+	+	+	+	+	+	−	−	+	+	−	−	?
kirkwoodii var. *macrotepala*	+	+	−	+	+	+	+	+	+	−	−	−	+	+	−	−	?
basaltica	+	+	−	+	+	+	+	−	+	+	−	−	+	+	−	−	+
sofarana subsp. *kasruwana*	+	+	−	+	+	+	+	−	+	+	−	−	+	−	+	−	+
sofarana subsp. *sofarana*	+	+	−	+	+	+	+	+	+	+	−	−	+	−	+	−	+
yebrudii subsp. *yebrudii*	+	+	−	+	+	+	−	+	+	+	−	−	+	+	−	−	+
hermona	+	−	+	+	+	+	−	+	+	+	−	−	+	+	−	−	+
jordana	+	+	−	+	+	+	+	−	+	+	+	−	+	+	+	+	+
bostrensis	+	+	+	+	+	+	−	−	+	+	+	−	+	+	−	−	+
auranitica f. *auranitica*	+	+	−	+	+	+	−	−	+	+	+	−	+	+	−	+	+
auranitica f. *wilkiana*	+	+	−	+	+	+	−	−	+	+	+	−	+	−	−	+	+
swensoniana	+	+	−	+	+	+	−	−	+	+	−	−	+	−	−	−	+
assadiana	+	+	−	+	+	+	?	+	+	+	−	−	+	−	+	−	+
sofarana f. *franjieh*	+	−	+	−	(+)	(+)	−	−	+	+	−	+	−	−	(+)	+	+

live material was obtained, generally through the courtesy of the Aril Society International and its members — such material included taxa from localities which, because of the political situation, are inaccessable from Lebanon. The present studies are based upon observations on live material from natural populations, except for eight taxa in which case studies are based upon imported authentic material (from natural colonies) grown together with the other taxa under the same conditions, or only on herbarium material or literature as indicated under the respective taxa in the text. The herbarium material studied is from the collections in the Post Herbarium (BEI) at the American University of Beirut, the Royal Botanic Gardens, Kew (K), and the P. MOUTERDE Herbarium, part of which is at Geneva (G) part constituting the Herbarium of the Lebanese National Council for Scientific Research (LNRC).

MORPHOLOGY

The plants belonging to this subgenus are rhizomatous; the rhizomes, though sometimes stoloniferous, are generally short and compact, the plants forming clumps. The leaves are usually arcuately upright, sometimes very strongly recurved and even circinate, the degree of curvature often changing during cultivation. The number of leaves varies from 5 to 13 in the species in the region. The stem varies in length from about one decimeter to one metre. The general appearance of the plants is such that they can easily be identified as belonging to this subgenus on their vegetative parts alone, provided one is somewhat familiar with the group. The plants are uniflorous. The peduncle varies in length and may be completely covered by the leaves or exposed — the number of nodes visible above the basal leaves is very often a reliable character in the identification of some of the taxa. The flower has the characteristic iris morphology. It is enclosed by a pair of spathes or "valves" which may be inflated or not and then

tightly clasping the ovary. The outer perianth leaves are known as "falls" which in this subgenus are usually recurved and even folded back. The basal half of the fall has a patch of dense or sparse hairs on the dorsal face, the hairs constituting the beard. The beard hairs may be long (up to about 1 cm) or more often short (not exceeding 0.5 cm). When the beard is dense, the hairs may be longest in the middle gradually decreasing in length towards the sides, or the hairs may form a brush along the median region and the lateral piles may then be of very short hairs. Along the median region at the end of the beard a signal spot usually of a darker colour is present. In paler biotypes the signal spot can be paler or even indistinct. The inner perianth leaves, the standards, are erect and often laterally recurved. The petaloid style is trifurcate, the three branches superposed above the falls, each having a stamen tucked beneath it. At the tip each branch is divided into two lobes (the lobes have also been referred to as crests). These are upright, often recurved, and are usually the same colour as the falls.

The style branches are usually arched or keeled and laterally incurved. These branches, that by the degrees of their arching and lateral incurving form tubular, straight or oblique—horizontal or arched tunnels, are referred to here as pollinator tunnels, the floors of which are contributed by the respective fall. There are variations in the form and structure of the pollinator tunnels — in some the style branches and the falls contribute equally to the lateral walls of the tunnel, or the falls may contribute the floor only while the lateral walls are made by the proportionately wider style branches; or the style branches may be raised horizontally or obliquely upwards above the falls forming a sort of laterally open tunnel. Below the tip of each style branch is a pouch-like structure, the stigmatic pouch, facing outwards. The anthers lie almost parallel with and covered by the style branch, the tip of the anther hardly ever reaching beyond the base of the stigmatic pouch. Presumably, the floral pigmentation (together with the smell in certain cases) attracts the particular kind/s of pollinator/s to the flower. The wider the range of the pigments present the greater the number of different kinds of insects attracted may be. The size and the shape of the pollinator tunnel could possibly restrict the number of kinds of pollinators. The beard hairs are directed outwards and the pollinator, therefore, presumably riding the hairs reaches up first the stigmatic pouch (where any pollen that the pollinator may be carrying on its dorsal side would get deposited) and then the anthers.

The fruit is a 3-chambered capsule which is usually inflated, often appearing 6-lobed because of the two rows of seeds present in each chamber; in one species at least the pod is cylindrical and not lobed except when it begins to shrink during the process of drying up. The dehiscence of the capsule is longitudinal loculicidal. The seeds on drying up are usually dark, almost black in colour with a prominent white, circular, "sucker-mouth" aril. The term oncocyclus was probably derived from this "circular-callosity" by SIEMSSEN (1846) who first used it.

It could be of significance that in species inhabiting areas that are relatively more arid the style branches and their lobes are of a paler colour, contrasting with the falls. Moreover, the yellow pigment in these species is to some extent discernable, while the flower size and shape also differ to some extent from those of the species found growing in the western Lebanese ranges and the Anti-lebanon.

DELIMITATION, PHYLOGENY AND SUBDIVISION

Contrary to a number of treatments (e. g. LAWRENCE 1953, RODIONENKO 1961),

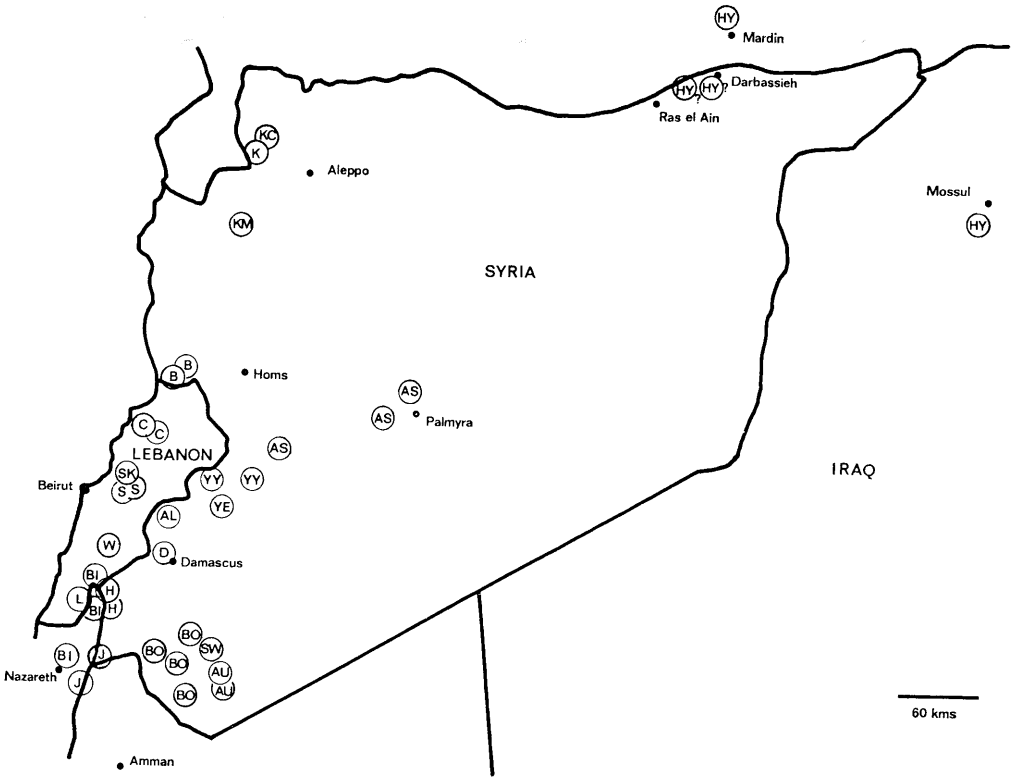


Fig. 1. Map of the region showing the distribution of the following *Iris* taxa: AL *antilibanotica*. — AS *assadiana*. — AU *auranitica*. — B *basaltica*. — BI *bismarckiana*. — BO *bostrensis*. — C *cedreti*. — D *damascena*. — H *hermona*. — HY, HY? *heylandiana*. — J *jordana*. — KC *kirkwoodii* subsp. *calcarea*. — K *kirkwoodii* subsp. *kirkwoodii* var. *kirkwoodii*. — KM *kirkwoodii* subsp. *kirkwoodii* var. *macrotepala*. — L *lortetii*. — SK *sofarana* subsp. *kasruwana*. — S *sofarana* subsp. *sofarana*. — SW *swensoniana*. — W *westii*. — YE *yebrudii* subsp. *edgecombii*. — YY *yebrudii* subsp. *yebrudii*.

the authors consider that the oncocyclus irises constitute a group sufficiently distinct both morphologically and cytologically to merit consideration at subgenus level — *Iris* subgenus *Susiana* SPACH. Morphologically, this group can be identified even on vegetative characters. Cytologically it is characterized by the basic chromosome number x=10, and in having probably the most asymmetrical karyotype in the genus *Iris*. The synonymy given below is reproduced chiefly from LAWRENCE (1953) and WERCKMEISTER (1967).

Iris L. subgenus **Susiana** SPACH

SPACH 1846 in Ann. Sc. Nat. Ser. 3, 5: 110; 1846 in Hist. Nat. Veg. 12: 70—71.

Genus *Oncocyclus* SIEMSS. 1846 in Bot. Zeit. 4: 706—707.

Subgenus *Oncocyclus* (SIEMSS.) ALEF. 1863 in Bot. Zeit. 21: 296; BAKER 1877 in J. Linn. Soc. Lond. (Bot). 16: 142.

Section *Oncocyclus* (SIEMSS.) BAK. 1876 in Gard. Chron. Ser. 3, 5: 788.

Subgenus *Pogoniris* RANDOLPH 1948 in Bull. Amer. Iris Soc. 109: 4; non SPACH 1846, nec BAK. 1876.

Subsection *Oncocyclus* (SIEMSS.) BENTH. as in LAWRENCE 1953 in Gentes Herb. 7, Fasc. 4: 346; as in RODIONENKO 1961, Genus Iris, Akad. Nauk. USSR.

On the basis of the present studies, the authors propose four definite groups of oncocyclus irises in the region (Fig. 1): (1) the species growing in the Lebanese western ranges and extending northwards into Syria; (2) the Antilebanon group of species; (3) the southern Syrian, Jordanian and partly Palestinian group of species; and (4) the eastern Syrian desert and northeastern Syrian group of species. The western Lebanese range and adjacent southwestern Syrian group includes *I. sofarana, I. cedreti, I. basaltica,* and *I. kirkwoodii.* The Antilebanon group includes species growing on this range and on the adjoining plateaux, viz. *I. bismarckiana, I. hermona, I. lortetii, I. antilibanotica, I. damascena,* and *I. yebrudii. I. westii* occupies a position midway between the above two groups. The Jabl-Druze, Hauran, northern Jordan and northeastern Palestine regions have species with clavate non-echinate beard hairs, and dense beards (except *I. jordana*). In most of these species the yellow pigment is discernable through the dense purple spotting, or the style branches are shades of yellow-orange. The eastern Syrian desert and its northeastern region have two reported species: *I. heylandiana,* and *I. assadiana.* Both of these have clavate-cylindrical, non-echinate beard hairs. *I. assadiana* is stoloniferous and, probably, so too is *I. heylandiana.* The latter has a linear beard of uniform-sized, relatively sparse hairs which spread out laterally near the base of the falls. *I. assadiana* has a linear median brush of long, dense hairs surrounded laterally by very short, dense, purple hairs. This beard character is intermediate between the northern Syrian—southern Turkish group of irises in the north and the Hauran—northern Palestine—Jordanian group in the south. Obviously, the northern Syrian—southern Turkish group of oncos needs to be studied in detail to establish the species limits in the complex. *I. jordana* is a taxon which shows similarities to the Hauran group of oncos though the beard and foliage characters are strikingly different and point to the possibility of another complex (or only a relict?) in the Palestinian region.

It has often been suggested (e.g. DAVIS 1954) that the oncocyclus group in the Levant has evolved from a southwestern expansion of the Irano-Turanian groups from the mountains south—west of the Caspian. Cytological evidence (WEYMOUTH & CHAUDHARY 1974) indicates that the species partly comprising the group *Sofaranae* of WEYMOUTH & CHAUDHARY and endemic to the western Lebanese ranges and to the adjoining Syria in the North are the most primitive of the species studied. The species endemic to Jabal-Druze, the Hauran, northern Jordan and the adjoining region are apparently the most advanced of the species investigated. Considering this evidence it could be suggested that the species endemic to the western Lebanese ranges and the adjoining Syrian territory in the north at least, have originated from a southerly expansion of the group from southern Turkey. Such a view would be supported by the karyotype of *I. kirkwoodii* subsp. *calcarea,* which could be regarded as the most primitive, a possibility suggested by WEYMOUTH and CHAUDHARY (1974).

In the present work we have followed WEYMOUTH and CHAUDHARY in dividing the subgenus *Susiana* into two groups — their "*Sofaranae*" and "*Purpuro-aurantae*". However, we feel that these groups should be treated as sections of the subgenus, and therefore, propose the sections as below. The species within a section have been arranged according to the sequence that we feel is the most natural in view of the information at present available. However, *I. jordana, I. heylandiana* and *I. assadiana* (*I.* sp. affin. *barnumae* in WEYMOUTH & CHAUDHARY 1974) have been placed under the section *Bostria* (group "*Purpuro-aurantae*" of WEYMOUTH & CHAUDHARY) only for the sake of convenience. They probably belong to other

complexes which may need to be separated as more information becomes available.

We do recognize section *Oncocyclus* (SIEMSS.) BAK. (with *I. paradoxa* STEVEN as the type species) as a section under the subgenus *Susiana,* which name has priority at the rank of section. This section is, apparently, quite distinct from those proposed below and is not represented in the region.

Section Sofaria

Group *Sofaranae* of WEYMOUTH & CHAUDHARY 1974.

Tepala externa fere numquam longiora quam 1 1/2 lata. Barba sparsa, capillis papillato-echinatis. In taxis a nos cognitis chromosomata quod longitudinem in series bene distinctas divisa.

Falls usually not more than 1.5 times as long as wide. Beard of sparse, papillate—echinate hairs. In the taxa for which the information is available (WEYMOUTH & CHAUDHARY 1974), the chromosomes fall into distinct length groups and do not intergrade from the longest to the shortest.

Type species: *I. sofarana* FOST.

Species included: *I. antilibanotica* DINSM., *I. basaltica* DINSM., *I. bismarckiana* DAMM. & SPRENG., *I. cedreti* DINSM. ex CHAUDHR., *I. damascena* MOUTRD., *I. hermona* DINSM., *I. kirkwoodii* CHAUDHR., *I. lortetii* BARB., *I. sofarana* FOST., *I. westii* DINSM., and *I. yebrudii* DINSM. ex CHAUDHR.

Section Bostria

Group *Purpuro-aurantae* of WEYMOUTH & CHAUDHARY 1974.

Tepala externa plerumque sescuplo longiora latiora. Barba densa, pulvino similis vel linearis (sparsa ut in *I. jordana*) vel capillis clavato-cylindratis, non echinatis. In taxis a nos cognitis longitudo chromosomatum variat sine limite distincto.

Falls usually more than 1 1/2 times as long as wide (except *I. jordana*). Beard hairs clavate—cylindrical, not echinate; beard dense and cushion-like or linear or both, or sparse (as in *I. jordana*). In the taxa for which information is available the chromosomes intergrade in length from the longest to the shortest without a sharp break into length groups.

Type species: *I. bostrensis* MOUTRD.

Species included: *I. assadiana* CHAUDHARY et al., sp. nov., *I. auranitica* DINSM., *I. bostrensis* MOUTRD., *I. heylandiana* BOISS. & REUT., *I. jordana* DINSM., *I. swensoniana* CHAUDHARY et al., sp. nov.

KEY TO THE TAXA IN LEBANON AND SYRIA

1. Falls usually not more than 1.5 times as long as wide; beard of sparse and/or papillate—echinate hairs 2
1. Falls usually more than 1.5 times as long as wide and/or the beard hairs clavate—cylindrical, not echinate 16
2. Rhizome stoloniferous ..... 10. *bismarckiana*
2. Rhizome not stoloniferous 3
3. Falls uniformly red-purple to dark purple or almost so, without any veins or spots ..... 16. *antilibanotica*
3. Falls obviously veined, dotted or spotted, not uniformly coloured 4
4. Width of a style branch equal to or greater than the combined width of its two lobes 5
4. Width of a style branch less than the combined width of its two lobes 8
5. Flower shades of pink—red; standards white with pink—violet veins; bases of standards tending to converge below style branches ..... 12. *lortetii*
5. Flowers not shades of pink—red, but shades of purple—dark purple 6
6. Venation of falls typically felty-thick, embossed on both surfaces; stem leaves 3—4 ..... 4. *basaltica*
6. Venation of falls not felty-thick, if embossed then only on upper surface; stem leaves less than 3 7
7. Venation of falls very dense (10—13 per cm); style branches less than 3 cm wide ..... 8. *cedreti*

7. Venation of falls less dense; style branches 3 cm wide or more ..... 7. *sofarana* subsp. *kasruwana*
8. Peduncle length usually more than 15 cm from the last node; stem leaves 2 or more 9
8. Peduncle length usually 15 cm or less from the last node; stem leaf 0—1 10
9. Leaves 5—7, about 1.5 cm wide; falls ovate—orbiculate, 8 cm long or less; signal spot nearer the distal end ..... 1. *kirkwoodii* var. *kirkwoodii*
9. Leaves 8—9, about 1 cm wide; falls ovate—oval, about 10 cm long; spot almost equidistant from the two ends ..... 2. *kirkwoodii* var. *macrotepala*
9. Leaves 7—9, about 1.5 cm wide; falls obovate—orbiculate, about 8 cm long or less; signal spot nearer the distal end ..... 3. *kirkwoodii* subsp. *calcarea*
10. Leaves more than 1 cm wide 11
10. Leaves 1 cm wide or less 13
11. Falls white or yellow, the yellowness due to dense spots of varying shades of yellow ..... 6. *sofarana* f. *franjieh*
11. Falls not white—yellow but shades of purple, maroon-purple or violet purple 12
12. Standards in striking contrast to the falls clear white with widely spaced very fine veins; leaves not widely divergent ..... 11. *hermona*
12. Standards without the clear white or dirty white colour dominating; the veins and dots thick and/or dense; leaves divergent, not closely appressed ..... 5. *sofarana* f. *sofarana*
13. Style branches more than 3 cm wide ..... 15. *yebrudii* subsp. *edgecombii*
13. Style branches 3 cm wide or less 14
14. Length of style branches including the lobes not more than 5 cm .... 13. *damascena*
14. Length of style branches including the lobes more than 5 cm 15
15. Style branches oblique—horizontal; plants rather tall (up to about 30 cm); leaves not strongly arched, usually exceeding 15 cm ..... 9. *westii*
15. Style branches arched downwards; plants usually not exceeding 20 cm; leaves strongly arched, hardly exceeding 15 cm ..... 14. *yebrudii* subsp. *yebrudii*
16. Beard linear or brush-like in the median region 17
16. Beard dense or cushion-like or of sparse hairs but not linear or brush-like 18
17. Plants small, hardly ever exceeding 20 cm; rhizome very small, stoloniferous; beard a median brush of yellow hairs more than 5 mm long and surrounded by lateral bands of very small, purple hairs ..... 18. *assadiana*
17. Plants taller; rhizome medium (stoloniferous?); beard linear, of white, uniform-sized, relatively sparse hairs spreading laterally in the basal region of the fall .... 17. *heylandiana*
18. Flowers yellow or bronze; flowering May—June 19
18. Flowers not yellow—bronze; flowering March—April 20
19. Falls and standards with fine, red—purple veins and very fine, dense dots ..... 21. *auranitica* f. *auranitica*
19. Falls and standards without fine, red—purple veins or dots .. 22. *auranitica* f. *wilkiana*
20. Leaves about 2 cm wide; beard of sparse hairs, not cushion-like ..... 19. *jordana*
20. Leaves usually 1 cm wide or less; beard of dense hairs, cushion-like 21
21. Falls and standards with the ground golden yellow, with dense spotting of purple (when apparently purple, the yellow ground still showing through it as dots or spots); beard hairs all yellow, minutely tipped with purple; style branches golden yellow with very minute dark brown—purple spots which become streaks towards the sides and the lobes ..... 20. *bostrensis*
21. Falls and standards uniformly purple; style branches orange, strongly streaked with purple; beard hairs in a golden yellow median band and purple lateral bands ..... 23. *swensoniana*

1. **Iris kirkwoodii** CHAUDHARY subsp. **kirkwoodii** var. **kirkwoodii** — Fig. 2

CHAUDHARY 1972 in Bot. Notiser 125: 499. — Orig. coll.: Syria, Bishmishly, April 1972, KIRKWOOD & CHAUDHARY 787 (holotype, BEI).

Plants up to 75 cm. Rhizome large, compact, yellowish-brown. Leaves 5—7 in number, rather grassy—droopy, up to 1.5 cm wide, 30 cm long, pale green. Stem leaves one or two with one or two internodes showing through or above the basal leaves; peduncle length usually 25 cm or more. Flowers about 15 cm tall, 8—10 cm wide; valves tightly clasping, not inflated, about 11 cm; ovary 3—3.5 cm, almost

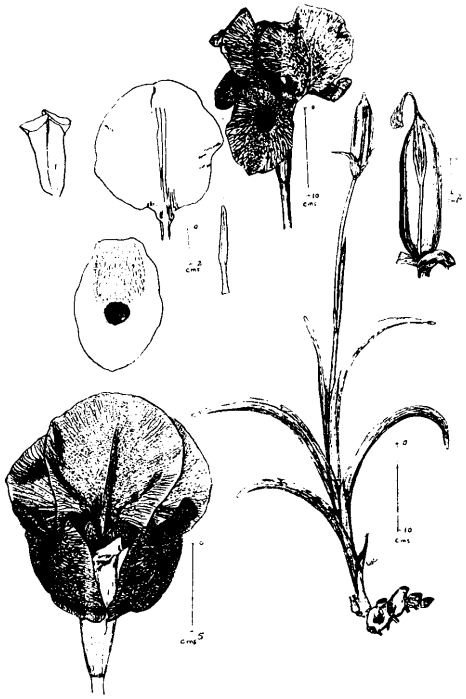


Fig. 2. *Iris kirkwoodii* subsp. *kirkwoodii* var. *kirkwoodii*.

terete or slightly trigonal with a stalk about 0.5 cm; perianth tube 2.5—3 cm. Falls 6—8 cm long, 4—5 cm wide, ovate—orbiculate, often strongly recurved, embossed with dark purple veins and fine dots densely scattered on a pale greenish or white, clear ground, the spots larger and denser below and to the sides of the signal spot; the signal spot orbicular, sometimes ovate, 1.5—2 cm long, about 1.5 cm wide; beard of long, maroon-purple or rusty-brown hairs. Standards about 8.5 cm long, 6—7.5 cm wide, orbicular—ovate, abruptly clawed with the claw channelled and about 1 cm; the standards with fine blue-purple veins and dots on a clear pale blue ground, the dots and veins embossed only near the base and along the midrib. Anthers 2—3.5 cm, purple-backed; filaments 1.2—2 cm, purple-dotted. Style branches about 7 cm long including the lobes, 3—4 cm wide, dark maroon in the middle, dark purple to the sides, ridge keeled, the ridge prominent; the lobes minutely serrate, turned upwards; the width of the two lobes greater than the width of the style branches; lobes with fine embossed veins and very fine dots like the falls; pollinator tunnel similar to that in *I. sofarana* subsp. *sofarana* (Fig. 4 C a). Pods about 9 cm long, cylindrical, not lobed, the veins thick, prominent, raised above the surface or level with it.

DISTRIBUTION: Endemic to the Bishmishly area in northern Syria.

MATERIAL: The natural population at the type locality and transplants from that locality.

2. **Iris kirkwoodii** CHAUDHARY subsp. **kirkwoodii** var. **macrotepala** CHAUDHARY et al., var. nov. — Fig. 3

Orig. coll.: Northern Syria, El-Bara, April 1974, KIRKWOOD 1403 (holotype, BEI).

Planta c. 1 m alta. Folia 8—10. Flores c.

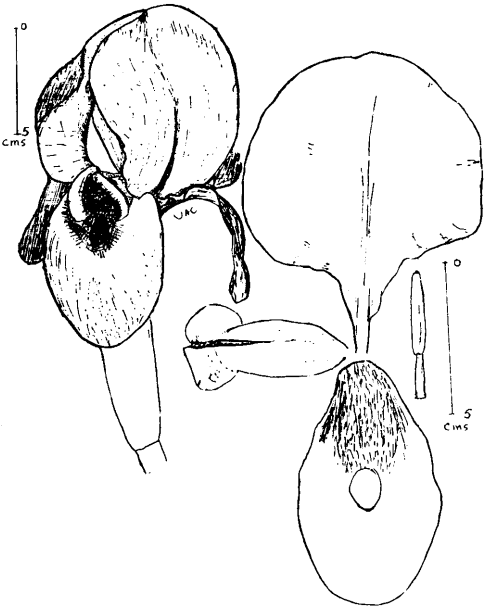


Fig. 3. *Iris kirkwoodii* subsp. *kirkwoodii* var. *macrotepala*.

17 cm longi a basi spatharum, 10—12 cm lati. Tepala externa ovato-elliptica, c. 10 cm longa, c. 6 cm lata, maculae et venae parum caelatae, maronino-purpureae ad violaceo-purpureae. Tepala interna orbiculata, abrupte unguiculata, c. 11.5 cm longa, c. 9.5 cm lata.

Plants about one metre. Rhizome large, compact, yellowish-brown. Leaves 8—10, about 1 cm wide, up to 50 cm long, grassy—droopy, pale green; stem leaves usually 3, with 2 or 3 nodes showing through or above the basal leaves. Peduncle about 20 cm. Flowers 15—17 cm tall from the base of the valves, 9—11 cm wide; valves 8—10 cm, purple-tinged, tightly clasping; ovary 3—3.5 cm; perianth tube about 2.5 cm. Falls about 10 cm long, 6 cm wide, ovate, ground creamy-white, the dots and veins slightly embossed, maroon-purple to violet-purple; signal spot oval or orbicular, enclosed in a dense band of strongly embossed maroon-purple dots; about 2 cm long and 1—1.5 cm wide; beard of violet-purple or golden hairs. Standards about 11.5 cm long, 9.5 cm wide, orbiculate, rather abruptly clawed, the claw about 1.5 cm, channelled; the ground pale blue with fine, violet-purple veins and dots, the latter denser and bigger towards the central and basal areas. Anthers about 3 cm, purple-backed; filaments about 2 cm. Style branches about 7 cm long including the lobes, 3.5 cm wide, ridge-keeled, the ridge very prominent; the width of the two lobes greater than the width of the style branch; pollinator tunnel similar to that in *I. sofarana* subsp. *sofarana*. Pod?

DISTRIBUTION: Endemic to the El-Bara area in northern Syria.

3. **Iris kirkwoodii** CHAUDHARY subsp. **calcarea** CHAUDHARY et al., subsp. nov. — Fig. 4 A

I. calcarea DINSMORE in sched. — Orig. coll.: Syria, Deir Semaan, April 1971, CHAUDHARY 785 (holotype, BEI).

Planta 30—80 cm alta. Rhizoma magnum, compactum. Folia 7—9, c. 25 cm longa, 1—1.5 cm lata, plus minusve firmiter recurva; folia caulina 2 vel 3. Flores 15—25 cm longi a basi spatharum, c. 8 cm lati; pedunculi 15—25 cm longi a nodo ultimo. Tepala externa obovato-orbiculata, c. 8 cm longa, 5—6 cm lata, maculis caelatis vel venis purpureis-atromaroninis; fundus leviter viridis: macula media 2—2.2 cm lata, 1.5—2 cm longa, atromaronina; barba capillis longis, non densis, atromaroninis. Tepala interna 8—11.5 cm longa, 5.5—8 cm lata, orbiculata, unguibus parvis; venis purpureis vel atropurpureis; maculae caelatae; fundus caeruleus, clarus. Antherae 2—2.2 cm longae; fila c. 1.5 cm, robusta. Rami styli c. 7 cm longi (lobis inclusis), 2.5—3 cm lati, cristati et carinati; maculae et venae loborum ut in tepalis externis; uterque lobus rami styli latior; canaliculus pollinicus fere ut in *I. sofarana* subsp. *sofarana*.

Plants 30—80 cm. Rhizome large, compact, light yellow to brownish-yellow. Leaves 7—9, 1—1.5 cm wide, up to 30 cm long, rather strongly recurved or droopy, pale green; stem leaves 2—3, the 2—3 nodes visible through or above the basal leaves. Peduncle 15—25 cm. Flowers about 15 cm tall from base of the valves, about 8 cm wide; valves rather leathery, tightly clasping, purple-tinged. Ovary 3—3.5 cm, almost terete; perianth tube about 4 cm. Falls about 8 cm long, 5—6 cm wide, obovate—orbiculate, embossed dotted and/or veined with dark purplish-red on a pale green ground: signal spot 2—2.2 cm wide, 1.5—2 cm long, velvety dark maroon; beard of long, dark maroon, rather sparse hairs; the signal spot and the peripheral part of the beard often surrounded by or heavily outlined with dark, dense, larger spots, the signal spot then appearing very large. Standards 8—11.5 cm long, 8 cm wide, the limb orbiculate, tapering to a thick claw about 1.5 cm; veined with purple or dark purple, the dots embossed, the veins not so, the ground light blue, clear, covered almost uniformly on and between the veins in the central area with blue-purple dots which become sparse towards the margin and denser and maroon towards the base. Anthers 2—2.2 cm; filaments about 1.5 cm, rather stout. Style branches about 7 cm long including the lobes, 2.5—3 cm wide, ridge-keeled,

the ridge more prominent near the lobes; the lobes upturned, slightly fringed at the margins, dotted and veined like the falls; the width of the two lobes greater than the width of the style branch; pollinator tunnel more or less like that in *I. sofarana* subsp. *sofarana* only flatter. Pod about 9 cm, cylindrical, not inflated, the veins thick, prominent, raised above the surface or level with it.

DISTRIBUTION: Endemic to the Deir Semaan area, Syria.

MATERIAL: Live culture. — Collections: April 1972, KIRKWOOD 790 (BEI); April 1938, DINSMORE 20393 (BEI).

NOTES: MOUTERDE (1969) considered this taxon was no different from *I. sofarana* subsp. *sofarana*. One of us (CHAUDHARY 1971) had also proposed the name *I. sofarana* var. *calcarea* (published only as an abstract of a paper read). However, a more careful study has shown that this taxon has its closest affinities with *I. kirkwoodii*, the affinities even with *I. basaltica* being closer than with *I. sofarana*.

4. **Iris basaltica** DINSMORE — Fig. 4 B

DINSMORE 1933, Pl. Post. Dinsm. 2: 9; 1934 in POST & DINSMORE, Fl. Syr. Pal. & Sin. 2: 597; MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 317. — Orig. coll.: Syria, Kalaat-ul Husn (Krak de Chevaliers) area, March—April 19--, WEST (DINSMORE Herbarium? not seen).

Plants up to 70 cm. Rhizome large, compact, dark brown. Leaves 9—12, thickish, slightly arched, 1.5—2 cm wide, about 24 cm long; stem leaves usually 3 or 4, the nodes bearing these visible through or above the basal leaves. Peduncle 15—25 cm. Flowers about 15 cm tall from the base of the valves, about 9 cm wide; valves about 11 cm, tightly clasping, distinctly keeled, purple-tinged in the top 1/4; ovary about 2.5 cm, trigonal; perianth tube about 2.8 cm. Falls about 9 cm long, about 5 cm broad, rather tightly clasping at the base, ovate or somewhat lanceolate, embossed with thick, almost felty, dark purple to almost black veins both on the upper and the lower faces, the dots restricted mostly to the middle region below the signal patch and laterally above the signal patch; the ground pale greenish, clear; signal patch usually truncate-triangular or orbiculate, about 1.5 cm long and 1.5 cm at its widest; beard of rather sparse, long, maroon-purple hairs tipped with rusty yellow. Standards 8.5—10.5 cm long, 7—7.5 cm wide, the limb almost orbicular, abruptly narrowed into a claw about 2 cm long and about 1 cm wide, with embossed (felty-thick) finer, dark purple veins and embossed dots on both surfaces, the dots restricted to the central area, the ground pale greenish, clear; more than 1/4 of the basal part with scattered long purple hairs, the hairs denser in the channel of the claw. Anthers creamy white, about 3 cm; filaments about 1.5 cm, stout. Style branches about 8 cm long including the lobes, about 3.5 cm wide, densely maroon-purple-spotted, the dots increasing in size towards the lobes; keel very prominently ridged; lobes with embossed dark spots and veins like the falls, irregularly serrate; the width of the lobes not more than the width of the style branch; pollinator tunnel rather flat and long, both the fall base and the style branch contributing to the walls of the tunnel. Pod inflated, 6-lobed, 6—11 cm, the veins lying in the furrows.

DISTRIBUTION: Endemic to the Tell Kalakh-Hadidia region, Syria. In danger of extinction.

MATERIAL: Tell Kalakh, Hadidia, and Kalaat-ul-Husn (type locality) populations, and cultivated material from the above areas. — Collections: Krak de Chevaliers, April 1943, DINSMORE 15956 (BEI, not in good condition); Hadidia, April 1972, CHAUDHARY 791 (lectotype, BEI).


A
B
C
D
a
a

5. **Iris sofarana** FOSTER subsp. **sofarana** f. **sofarana** — Fig. 4 C

FOSTER 1889 in Gard. Chron., iii. 26: 389; POST & DINSMORE 1933, Fl. Syr. Pal. & Sin. 2: 598; MOUTERDE 1966, Nouv. Fl. Lib. Syr. 2: 319. — Orig. coll.: Lebanon, Sofar (Ayen Sofar), April 18--, FOSTER (not seen).

Plants up to 40 cm. Rhizome rather large, compact, yellowish-brown. Leaves 8—9, 1.2—2.5 cm wide, up to 25 cm long, somewhat divergent, if falcate then not strongly so; the node bearing the single stem leaf only rarely visible above the basal leaves. Peduncle usually 11—14 cm (often longer under culture). Flowers 15—18 cm tall from base of valves, 10—12 cm wide: valves up to 11 cm, inflated, green; ovary about 3.5 cm, trigonal; perianth tube about 2.5 cm. Falls 8—8.5×5—6.5 cm, obovate, the limb orbiculate, rarely ovate, the base tightly clasping the style branches laterally; the ground creamy white, thickly covered with brown-purple to bluish-purple veins and spots, the colour range varying from bluish-purple to red-purple; beard hairs dark purple, rather scattered; signal spot orbiculate, wider than long, 1.2—1.5 cm long, 1.5—2 cm wide, dark purple, located more than halfway towards the apex. Standards about 9.5—10.5×7—8 cm, orbiculate, the limb abruptly narrowed into a short claw; the ground clear white to inky blue with the veins fine, blue-purple to dark purple or maroon-purple; the dots similar in colour to veins, very fine, rather dense in the central area making it look blue-purple or dark maroon-purple; the veins not dense (6—11 per cm). Stamens about 4 cm; anthers 2.5—3 cm, creamy yellow: filaments 1—1.5 cm, purplish. Style branches about 7 cm long including the lobes, 3 cm wide, the ridge of the keel very prominent; lobes of style branch upturned, crenate, veined and spotted like the falls; the total width of the two lobes more than the width of the style branch; pollinator tunnel formed by the fall and the style branch, the base of the fall tightly clasping the style branch (Fig. 4 C a). Pods about 10.5 cm long, 3 cm wide, inflated and 6-lobed, narrowed towards both ends.

DISTRIBUTION: Endemic to Lebanon in two known localities.

MATERIAL: The Falougha area (probably the type locality) and the Zehleh Pass population were investigated. — Collections: Falougha area: May 1963, EDGECOMBE A-1333, A-1189 (BEI); May 1964, EDGECOMBE B-295 (BEI); May 1972, CHAUDHARY 1215 (lectotype, BEI). Zahleh Pass area: May 1963, EDGECOMBE B-298 (BEI); May 1964, SLOANE (BEI). Between Beirut and Damascus (probably Falougha colony) May 1955, TROTT 3002 (K).

6. **Iris sofarana** FOSTER subsp. **sofarana** f. **franjieh** CHAUDHARY et al., f. nov.

Orig. coll.: Lebanon, Falougha area, April 1974, CHAUDHARY 1405 (holotype, BEI).

Haec forma differt a f. *sofarana* floribus flavis vel candidis pigmento purpureo carentibus.

This form differs from f. *sofarana* only in lacking blue-purple pigmentation in floral parts which may be pure silky white with yellow showing near the bases of floral parts, or the falls only are yellow on the basal half, or the falls look completely yellow and the standards lighter yellow or white. The yellowness of the floral parts is due to yellow, dense spots, the shades of yellow only varying.

DISTRIBUTION: So far these apparently mutant forms have been observed growing in the type locality only near Falougha in Lebanon.

NOTE: This form is named after Mrs IRIS FRANJIEH, patroness of the Horticultural Society of Lebanon.

Fig. 4. A: *Iris kirkwoodii* subsp. *calcarea*. — B: *Iris basaltica*. — C: *Iris sofarana* subsp. *sofarana* var. *sofarana*. — D: *Iris sofarana* subsp. *kasruwana*. — a: pollinator tunnel.

7. **Iris sofarana** FOSTER subsp. **kasruwana** (DINSMORE) CHAUDHARY et al., comb. nov. — Fig. 4 D

I. kasruwana DINSMORE 1933, Pl. Post. Dinsm. 2: 9; 1934 in POST & DINSMORE, Fl. Syr. Pal. & Sin. 2: 597. — *I. sofarana* f. *kasruwana* (DINSMORE) MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 319. — Orig. coll.: Lebanon, Naba-al-Asal, May 19--, WEST (DINSMORE Herbarium? not seen).

Plants about 50 cm. Rhizome rather large, compact, brown. Leaves up to 10, 1.2—1.7 cm wide, up to 20 cm long, not wide-spreading; stem leaves usually 2, often ending at about the same level. Peduncle about 22 cm, often the two nodes bearing the stem leaves visible above or through the basal leaves. Flowers about 18 cm tall from the base of the valves, about 10 cm wide; valves to about 9 cm, ventricose, pinkish-purple in the upper half; ovary 3—4.5 cm, broadly triangular; perianth tube 3.5—4 cm. Falls 8—10 cm long, 6—7.5 cm wide, ovate, the base rather flat, not tightly clasping; densely streaked and dotted with dark purple, the dots more prominent, smaller, and dense near the signal patch; the signal patch more or less tearshaped, longer than wide, 1.5—2.5×0.6—1.5 cm; the lower end of the signal spot more than halfway up the length of the fall towards the base; beard hairs sparse, purple, tipped with yellow or rusty brown. Standards 8—11 cm long, 6—8 cm wide, obovate, gradually tapering to a claw, the claw about 1 cm, channelled; the ground clear white to purplish-white to inky blue with dark purple veins and dots, the dots finer, elongating and anastomosing in the middle basal parts. Stamens up to 4 cm; anthers about 2.5 cm, creamy yellow or purple-backed; filaments about 1.5 cm, purple all over or towards the base only. Style branches 5.5—7.5 cm long including the lobes, 3—4 cm wide, maroon-purple in the middle, dark purple to the sides, ridge keeled, the ridge very prominent; the lobes of the style branches irregularly spotted and streaked like the falls; the width of the two lobes hardly if at all exceeding the width of the style branch; pollinator tunnel formed mainly by the style branch with the base of the fall contributing the floor of tunnel (Fig. 4 D a). Pods up to 10 cm long, up to about 4 cm wide, 6-lobed, narrowed towards both ends.

DISTRIBUTION: Endemic to Lebanon; in two known populations.

MATERIAL: The Naba-al-Asal (type locality) and the Laqlouq populations were investigated. — Collections: Naba-al-Asal April 1971, CHAUDHARY 790 (lectotype, BEI); May 1952, MOONEY 4383 (K).

8. **Iris cedreti** DINSMORE ex CHAUDHARY — Fig. 5 A

CHAUDHARY 1972 in Bot. Notiser 125: 497—499. — Orig. coll.: Lebanon, vicinity of Cedars of Lebanon, May 1972, CHAUDHARY, CHAUDHARY & WEYMOUTH 789 (holotype, BEI).

Plants rarely exceeding 40 cm. Rhizome medium, compact, light yellow. Leaves 8 or 9, 1—2 cm wide, up to 23 cm long, narrowed to the tip; stem leaf none or one. Peduncle 9—12 cm. Flowers about 18 cm tall from the base of the valves, up to 9 cm wide; valves about 10 cm, reaching to the level of the falls, inflated, green; ovary about 3.3 cm, triangular, 6-lobed, the ovary stalk 0.5 to 1 cm; perianth tube 2.5—3 cm. Falls 6.5—9.5 cm long, 4.5—5.5 cm wide, ovate, narrowed to the tip, finely crenate—irregularly serrate, the ground clear, white to lead-white; veins very fine, embossed, densely arranged (10—13 per cm), dark-maroon to maroon-purple; dots very fine, more embossed around the signal spot and the area above this level; in the darker biotypes the dots on the falls are larger, anastomosing so closely that the dots form the ground and the ground appears as irregular white spots; signal spot orbiculate, 1.7—2 cm long and about 1.5 cm wide, located almost in the middle of the fall, dark maroon-

purple; beard of sparse hairs, the hairs rusty brown, pink, purple or mottled on a pale green ground. Standards 8.5—11 cm long, 6—7.5 cm wide, obovate, clawed, the claw about 1.5 cm long, channelled; the ground characteristically white to lead-white; veins very fine purplish—dark maroon, rather embossed, parallelly densely arranged (13—20 per cm); dots very fine, very sparse near the margin, larger and sparse in the central area, finer and denser in the lateral zones; the inner and outer faces of the standard with distinctly different shades (a character very rarely to be seen in *I. sofarana* subsp. *sofarana* and often in *I. jordana*); on the inner face the white to lead-white ground dominates while on the outer face the purplish—dark maroon dominates. Stamens 3.5—4 cm, the anthers usually more than twice as long as the filaments, the anthers creamy white, sometimes purple-backed. Style branches 5.5—6 cm long including the lobes, about 2 cm wide, strongly arched along the arch of the fall (the latter contributing only the floor of the pollinator tunnel), strongly narrowly keeled, the keel with a small ridge, maroon-purple; the lobes about 1 cm long and wide, the total width of the two lobes not exceeding the width of the style branch; the lobes upturned, veined and spotted like the falls. Pod about 8 cm, inflated, lobed, narrowed towards both ends.

DISTRIBUTION: Endemic to the Cedars of Lebanon area. Also reported from Ehden and Hasrun areas of Lebanon but not seen recently.

MATERIAL: Vicinity of Cedars of Lebanon, 1940, DINSMORE 20513 (BEI); May 1880, BLANCHE 11095 (?); May 1966, ALBURY, CHEESE & WATSON 925 (K).

9. **Iris westii** DINSMORE — Fig. 5 B

DINSMORE 1933, Pl. Post. Dinsm. 2: 8; 1934 in POST & DINSMORE, Fl. Syr. Pal. & Sin. 2: 596. — *I. sofarana* FOSTER f. *westii* (DINSMORE) MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 319. — Orig. coll.: Lebanon, Tawmat-un-Niha, May 1930, WEST 1896 (holotype, DINSMORE Herbarium), not seen.

Plants up to about 30 cm. Rhizome medium, compact. Leaves 6—8, 1 cm wide or less, about 20 cm long, slightly falcate; stem leaf one or two. Peduncle 8—16 cm. Flowers 12.5—15 cm in diameter; valves about 11 cm, slightly inflated; ovary 3—4.5 cm, with a stalk about 1 cm; perianth tube 3—4 cm. Falls 5—8 cm long, 5—5.5 cm wide, elliptical—obovate, veins and spots prominently embossed, brown-purple to purple, the spots dense; signal spot about 1.5 cm long and wide, located in the middle of the fall; beard of long, rather sparse purple hairs, rather wide, extending almost to the edges of the fall and to almost the lower edge of the signal spot. Standards 6—9 cm long, 5—6 cm wide, obovate—cuneate, gradually narrowed into a claw about 1 cm long; the limb orbiculate; lilac-blue veins and minute dots on a pale lilac ground, the dots becoming bigger and embossed towards the base. Anthers about 2 cm; filaments about 1.7 cm. Style branches horizontal-oblique (apparently not arched downwards as seen in the herbarium material), 6—6.5 cm long, about 3 cm wide, thickly dotted-streaked with brown-purple on a "wine-coloured" ground; lobes upturned, dotted and veined like the falls; the width of the two lobes more than that of the style branch; pollinator tunnel is apparently mostly open, the fall and the style branch meeting only towards the basal area. Pod?

DISTRIBUTION: Endemic to heights in the Mashghara—Jezzine area, Lebanon.

MATERIAL: Heights between Jezzine and Mashghara, May 1965, EDGECOMBE B-571 (BEI).

NOTE: MOUTERDE (1966) included this taxon under *I. sofarana* as f. *westii*: indeed he included also *I. kirkwoodii* subsp. *calcarea* under f. *westii* (MOUTERDE 1969

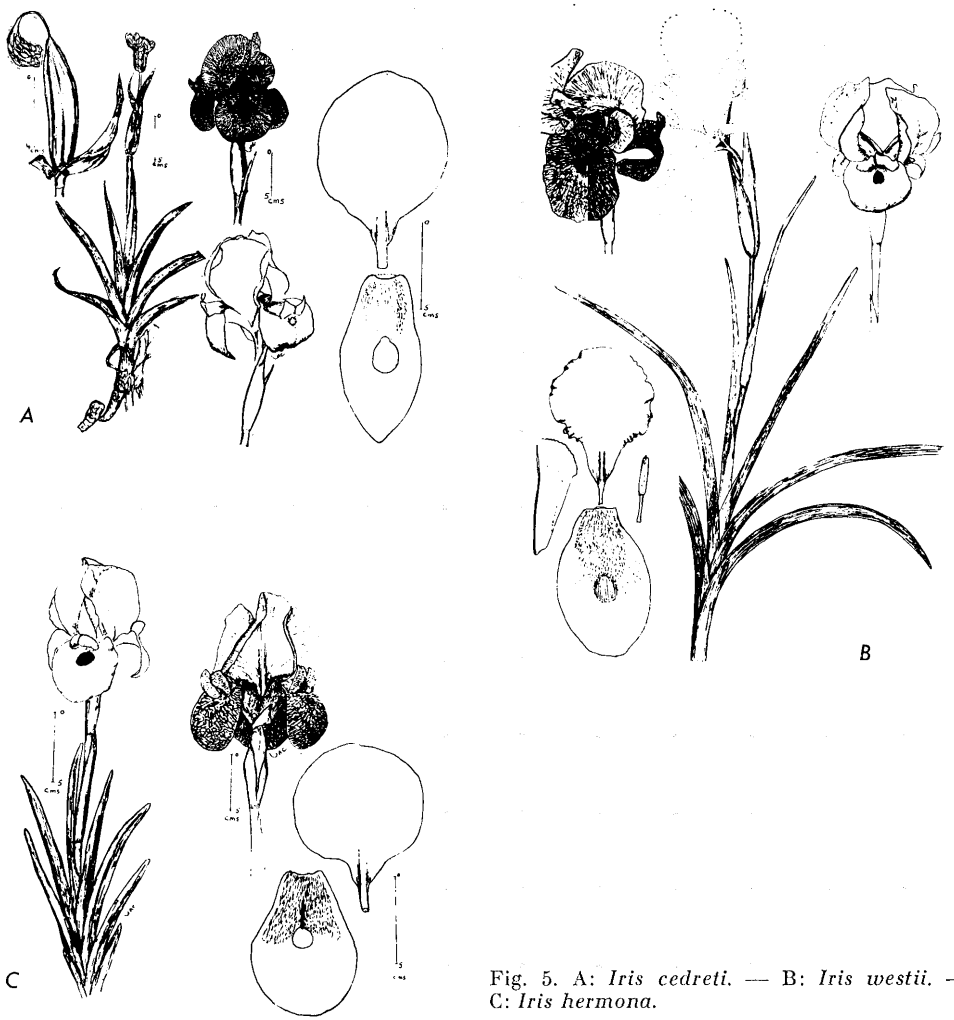


Fig. 5. A: *Iris cedreti.* — B: *Iris westii.* — C: *Iris hermona.*

p. 674). The authors consider that this taxon has the closest affinities with *I. hermona* and not with *I. sofarana;* the affinities with *I. kirkwoodii* subsp. *calcarea* being still remoter. In spite of all efforts the authors have not been able to rediscover any of the *I. westii* colonies during the past four years. It was possible to improve the original description by DINSMORE by studying the material collected by Mrs EDGECOMBE in 1965. From the characters of leaves, the flower and in particular the style branches combined with the general appearance of the plant, the authors feel that the taxon *I. westii* differs strikingly from any other taxon in the region and unless more evidence turns up from any future study of live material this taxon should retain is separate identity.

The sketches of flowers in Fig. 5 B are based upon photographs kindly supplied by Dr PETER WERCKMEISTER.

10. **Iris bismarckiana** E. DAMMAN & C. SPRENGER

E. DAMMAN & C. SPRENGER, May 1890 in Damman & Co. Catal. 51: 4, fig. 4; WEINER, Aug. 1890 in Illustr. Gartenzeitung 15: 352—353, fig. 72; BAKER 1892, Irid. 18. — Orig. coll.: Northern Palestine c. 1890, G. EGGERS (no record).

I. saarii SCHOTT var. *nazerena* (FOST. ex HERB), Herb and Wulle Catal. primo 1893, "sari"; HOGG (?) May 1893 in J. Hort. Ser. 3, 26: 373, "nazarensis". — *I. nazarena* (FOST. ex HERB) DINSM. 1934 in POST & DINSMORE Fl. Syr. Pal. & Sin. 2: 596.

Plants 30—50 cm. Rhizome medium—large, stoloniferous with long stolons. Leaves usually 8, spreading fan-like, rather obtuse, 2—3 cm wide, 25—40 cm long, oblique, closely sheathing. Flowers often 15 cm wide; perianth tube 7 cm. Falls 6—7 cm long, round—ovate; the ground creamy, thickly covered with oblong, embossed, red-brown spots, veined with maroon or purple, often with a few small crimson or red-brown spots; beard hairs dark purple; signal spot large, more or less orbicular, blackish red-purple. Standards 7—8 cm long, orbicular, with a white ground except at the yellowish base; veins blue, dots dense, prominent, purple. Style branches relatively long, marked with reddish-brown spots on a creamy ground. Pollinator tunnel apparently as in *I. sofarana* subsp. *sofarana,* only markedly longer.

DISTRIBUTION: Endemic to southern slopes of Mt Hermon and the areas to the south.

NOTE: MOUTERDE followed C. SPRENGER (Gard. Chron. 1904) and considered *I. saarii* SCHOTT var. *nazarena* FOST. ex HERB (*I. nazarena* (FOST. ex HERB) DINSM.) and *I. bismarckiana* "REGEL ex SPRENGER" to be one and the same taxon, as the collections on which the two taxa were based were made by the same person, G. EGGERS of Jaffa. Unfortunately, the authors are not very familiar with either of the above two taxa. Comparing the descriptions of rhizomes and leaves of *I. bismarckiana* (WEINER 1890, and in Gartenflora, 1893, both reproduced partly in WERCKMEISTER's Catal. Irid. p. 94) with those of *I. nazarena* (FOST. ex HERB) DINSM. we find that both have stoloniferous rhizomes ("like *I. iberica*", which is stoloniferous, in *I. bismarckiana*) and both have relatively very wide leaves. These characters were not mentioned by DINSMORE (1933, 1934) who, apparently, copied the description from BAKER (1892). The taxon *I. nazarena* (FOST. ex HERB) DINSM. is apparently the same as *I. bismarckiana* DAMMAN & SPRENGER (often quoted as *I. bismarckiana* REGEL ex SPRENGER). However, the inclusion of *I. hermona* under *I. bismarckiana* (as treated by MOUTERDE) is not justified. *I. hermona* has non-stoloniferous, compact rhizomes, narrower and almost erect leaves, and more orbiculate perianth leaves as compared with *I. bismarckiana.* Indeed, AWISHAI (1971) mentions seeing populations of *I. hermona* and "*I. nazarena*" as almost overlapping on the southern slopes of Mount Hermon. The synonymy of this taxon has very kindly been provided by Dr DAN NICOLSON.

11. **Iris hermona** DINSMORE — Fig. 5 C

DINSMORE 1933, Pl. Post. Dinsm. 2: 8; 1934, in POST & DINSMORE, Fl. Syr. Pal. & Sin. 2: 596; under *I. bismarckiana* REGEL in MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 320. — Orig. coll.: Syria, S of Qunaitra April—May 19--, DINSMORE 1895 (holotype, DINSMORE Herbarium? not seen).

Plants up to about 50 cm. Rhizome rather large, compact, yellowish-brown. Leaves usually 9, more or less erect, up to 1.8 cm wide and up to 30 cm long, very gradually narrowed to the apex; stem leaf usually one, the node bearing the stem leaf showing above or through the basal leaves. Peduncle up to 12 cm. Flowers about 18 cm tall from the base of the valves, about 10 cm wide; valves 8—10 cm, inflated; ovary 3.5—4 cm; perianth tube 2.5—3 cm. Falls about 8.5

cm long, 6 cm wide, obovate, gradually narrowed to the base, the limb appearing orbiculate, embossed dotted and embossed veined with brown-purple on a creamy yellow to creamy white ground, the ground showing prominently; the signal spot almost orbicular, about 1.2 cm long and 1.5 cm wide, darker brown-purple; beard of sparse, brown-purple hairs with the greenish-yellow ground showing through them. Standards about 9.5 cm long, about 8 cm wide, orbiculate, abruptly narrowed into a triangular basal area and then into a strongly channelled claw about 1 cm long; the limb wider than long, creamy white (dirty white in some biotypes), with widely spaced, very fine, purple and light purple veins, and very finely dotted with violet-purple, the dots and veins near the claw brown-purple, rather embossed. Anthers about 2.5 cm, yellowish white; the filaments about 1.7 cm, purple. Style branches about 6.5 cm long, about 4 cm wide, ridge-keeled with the ridge double and prominent, rather flattened out at the sides and then curving down to form a flattened pollinator tunnel with the base of the fall, red-purple and spotted in the middle, dark-purple to the sides; the lobes of the style branches creamy white, spotted with embossed, dark purple, irregularly crenate, overlapping. Pod?

DISTRIBUTION: Lebanon, Sarada area; Syria, near Qunaitra and southern slopes of Mt Hermon.

MATERIAL: Qunaitra, April 1943, DINSMORE 3895 (lectotype, BEI); live material from a population from the area of distribution (probably Qunaitra) April 1974 from culture, CHAUDHARY 1325 (BEI).

NOTE: The live material studied was obtained through the courtesy of Mr HERBERT MCKUSICK. It is presumed that the material was originally collected from near Qunaitra, Syria when the area was under Israeli control.

MOUTERDE treated this taxon under *I. bismarckiana* REGEL ex SPRENGER which does not appear justified. The rhizome and the leaf characters definitely show the two taxa to be different. Also see the note under *I. bismarckiana*.

12. **Iris lortetii** BARBEY — Fig. 6 A

BARBEY 1882, Herborization au Levant Pl. VII; in BOISSIER 1884, Fl. Orient. 5: 131; POST & DINSMORE 1934, Fl. Syr. Pal. & Sin. 2: 597; MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 319. — Orig. coll.: "Palestine", Mays to Hunin, May 1880, LORTET (holotype, G, not seen).

Plants about 40 cm. Rhizome short, compact, pinkish. Leaves usually about 8, 1—1.5 cm wide, characteristically obtuse and then abruptly narrowed into a tip; stem leaf usually one, erect. Peduncle about 8 cm. The flowers in general of pink-maroon shades, up to 13 cm long from base of valves, up to 8.5 cm wide. Falls about 5.5—6 cm long, 3—4 cm wide, obovate—oblong, densely spotted with maroon on a clear, lead-white ground; beard of small, yellowish-red, rather sparse hairs; signal spot dark maroon. Standards erect, about 7 cm long, 5 cm wide, limb orbicular, gradually narrowed into a claw, the claw about 0.5 cm; white with deep pink veins. Style branches about 5 cm long including the lobes, about 2.5 cm wide, horizontal—oblique, maroon, keeled; the lobes spotted with maroon like the falls, reflexed; the combined width of the two lobes less than the width of the style branch; pollinator tunnel mainly constituted by the style branch, the fall constituting the floor of the tunnel nearer the base. Like in *I. samariae* DINSM. the standards characteristically tend to converge below the style branches. Pod?

DISTRIBUTION: Southern Lebanon and "North Palestine". Endemic.

MATERIAL: Mays to Hunin May 1943, DINSMORE 15388 (BEI).

NOTE: The authors have not been able to study any live material because of the extreme hazard involved in collecting it from near the southern border of Lebanon with Israel. The sketch of the flower (Fig. 6 A) is based upon a photograph by Mr HERBERT MCKUSICK.

13. **Iris damascena** MOUTERDE — Fig. 6 F

MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 318—319. — Orig. coll.: Syria, Jabl Qasyoun 1951, PABOT P—5 (holotype, MOUTERDE Herbarium, now at G).

I. sofarana FOST. f. *quassiomensis* WERCKMEISTER 1957 in (Brit.) Iris Soc. Yearbook, nomen nudum.

Plants rarely more than 30 cm. Rhizome short, compact. Leaves 5—8, usually 7, arched—strongly recurved, 1 cm wide or less, up to 27 cm long; stem leaf one. Peduncle up to 15 cm. Flowers up to 15 cm long from base of the valves, about 9 cm wide; the base of the valves often partly enclosed by the upper one or two leaves; valves up to 10 cm, inflated, a little coloured with pale violet-purple. Falls obovate—elliptical, up to 8 cm long, about 5 cm wide, rather flat in the basal area, droopy from immediately beyond the beard area; ground creamy white, densely dotted and veined with dark brown-purple like *I. sofarana* subsp. *sofarana*; the dots and veins slightly embossed; signal spot small, elliptical, about 1.5 cm long, about 1 cm wide, dark purple; beard of sparse, purple hairs. Standards oval, about 9 cm long, about 6 cm wide, ground creamy white, densely fine-dotted and fine-veined with purple, the veins denser and embossed in the basal area; narrowed into a triangular area and then abruptly clawed, the claw about 1 cm long and with long, purple hairs; the veins denser and embossed in the basal area. Anthers about 2.5 cm; filaments about 1.5 cm. Style branches short, 4—5 cm long including the lobes, narrowly ridge-keeled, strongly arched, hardly produced beyond the spread of the standards; the lobes rather short, the combined width of the two lobes not more than the width of a style branch; pollinator tunnel rather short as compared with other taxa, like that in *I. sofarana* subsp. *kasruwana*. Pods?

DISTRIBUTION: Endemic to Jabl Qassoun near Damascus, Syria. In danger of extinction.

MATERIAL: Jabl Qasyoun, Syria, March 1952, HIGHWOOD (K); March 1975, KHATEEB (BEI).

NOTE: Figure 6 F is a pen and ink resketch of a plate of this taxon in the Kew Herbarium of the Royal Botanic Gardens, permitted to be published in the present form by courtesy of the Director of the Herbarium. The sketches of the flower parts are from fresh material collected from the type locality.

14. **Iris yebrudii** CHAUDHARY subsp. **yebrudii** — Fig. 6 C

CHAUDHARY 1972 in Bot. Notiser 125: 259—60. — Orig. coll.: Syria, Yebrud, May 1971, CHAUDHARY 786 (holotype, BEI).

Plants usually 15—18 cm, up to 30 cm under cultivation. Rhizome small, compact, pale yellow. Leaves 5—8, covering the whole of the stem or the stem leaf reaching beyond middle of the valves, usually less than 1 cm wide, up to 21 cm long, dark green to bluish-green with a white bloom, strongly recurved to slightly so; stem leaf one. Peduncle up to 11 cm. Flowers about 13 cm long from base of the valves, 8—9.5 cm wide; valves 7—9 cm, reaching above the level of the falls, keeled, purplish-pink in the upper half, inflated; ovary about 3 cm, broadly trigonal; perianth tube about 2.0 cm. Falls about 7 cm long, 5 cm wide, oval to obovate, the ground pale yellow with dark brown-purple, embossed veins prominent all around except in the area below the signal patch to the margin which has only fine spots, the spots

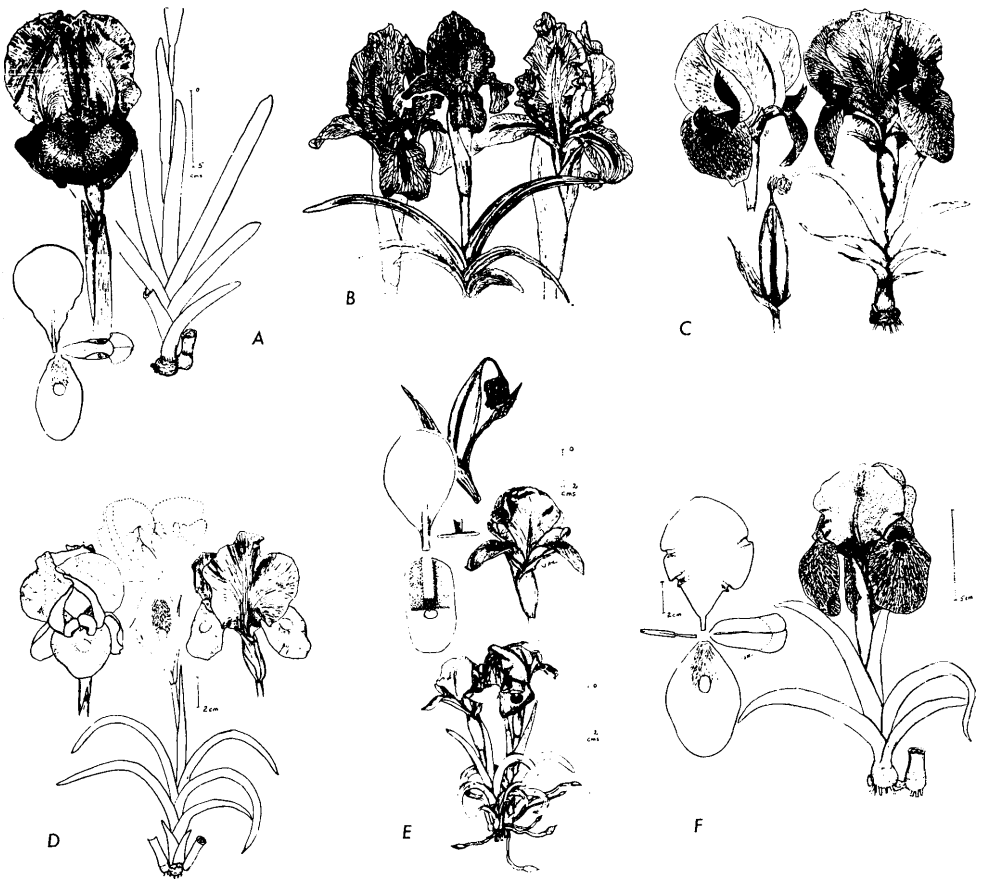


Fig. 6. A: *Iris lortetii*. — B: *Iris ? heylandiana*. — C: *Iris yebrudii* subsp. *yebrudii*. — D: *Iris antilibanotica*. — E: *Iris assadiana*. — F: *Iris damascena*.

denser and anastomosing immediately below the signal spot; signal spot dark purple, about 1×1 cm, rhomboid to transversely ovate; beard of long, purple hairs, the hairs reaching below the signal spot on either side. Standards about 7.5 cm long, about 6.5 cm wide, with the claw about 1 cm, orbicular, reflexed at sides, pale yellow with prominent but fine, purple veins and dots; the dots very fine, sparse in the middle region, denser towards the margin; the major veins and those in the central top end usually distinctly yellow; a few long hairs usually present on the inner basal area. Anthers about 3 cm, tapering, yellow on the back; filaments about 1.5 cm. Style branches 5.5—6.5 cm long, 2—3 cm wide, rather narrowly (transversely) curved, dark-purple to maroon-purple towards the base, speckled with dark purple in the outer half, the keel with a double prominent crest is also speckled; the width of the two lobes more than the width of the style branch; pollinator tunnel as in *I. sofarana* subsp. *sofarana*. Pods about 7 cm long, about 2 cm wide, usually with the 3 major lobes more prominent.

Variant biotypes with purplish slaty-grey ground both in the falls and the standards with only fine, darker dots, densely and uniformly distributed.

DISTRIBUTION: Endemic to the Yebrud area in Syria.

MATERIAL: Yebrud, Syria, May 1935, DINSMORE 25515 (BEI); May 1974, CHAUDHARY & RASHID SHAD 1310 (BEI); Deir Atiyeh, May 1879, POST (K).

15. **Iris yebrudii** DINSMORE ex CHAUDHARY subsp. **edgecombii** CHAUDHARY

CHAUDHARY 1972 in Bot. Notiser 125: 499—500. — Orig. coll.: Syria, Kastel, April 1972, KIRKWOOD 788 (holotype, BEI).

Plants 25—40 cm. Rhizome small, compact, light yellow-brown. Leaves 6—7, greyish-green, about 8 mm wide, about 11 cm long, strongly recurved; stem leaf one, erect, reaching or surpassing the valves. Peduncle c. 11 cm. Flowers about 15 cm (often more) tall from base of the valves, c. 12 cm wide; valves 7—9 cm, inflated keeled, pink-tinged; ovary about 5 cm, broadly trigonal; perianth tube about 3.5 cm. Falls about 9 cm long, about 7 cm wide, ovate to orbiculate, covered with red-purple embossed dots and fine, dark purple veins, the latter perceptible only at or above the level of the signal spot (in pale biotypes the red-purple dots much smaller and the red-purple veins visible all along the margin); the ground pale yellow or pale greenish, clear; signal spot ovate, about 1.5 cm long, 1 cm wide, maroon-purple with darker veins perceptible through it; beard of dark purple hairs tipped with yellow, the hairs covering part of the signal spot and coming down its side to about 1/4 the length. Standards about 10 cm long, 8.5 cm wide, the limb orbiculate and gradually tapering to a small claw, uniformly covered with maroon-purple veins more distinct near the margin and small densely arranged dots on a white, clear ground; the margin slightly crenulate, the inner basal area with a few long yellow hairs (pale biotypes with the standard uniformly pale yellow, clear with very fine purple veins and sparsely scattered, fine purple dots or the standard with uniformly densely scattered fine purple dots only, or with larger, sparse dots only). Anthers about 3 cm, with minute red-purple dots on the back; filaments about 1.5 cm. Style branches flattish, about 7 cm long including the lobes, 4 cm wide, with minute dark purple dots on the maroon, median and pale greenish lateral bands; lobes upturned, continuing as a prominent double crest over the keel, sometimes the crest folded over near the lobes, the double crest dotted and streaked with red-purple like the lobes; pollinator tunnel more or less as in *I. sofarana* subsp. *sofarana*, only flatter. Pod about 11 cm long, 2.7 cm wide, inflated-lobed, gradually tapering to the top.

DISTRIBUTION: Endemic to Kastel area in Syria. In danger of extinction.

MATERIAL: Transplants from this population.

16. **Iris antilibanotica** DINSMORE — Fig. 6 D

DINSMORE 1933, Pl. Post. Dinsm. 2: 10; 1934 in POST & DINSMORE, Fl. Syr. Pal. & Sin. 2: 599; MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 316. — Orig. coll.: Syria, above Bludan, May 19--. WEST (holotype, DINSMORE Herbarium?).

Plants up to 40 cm. Rhizome small, compact. Leaves 7—8, usually 1 cm wide or less, up to 20 cm long, falcate, sheathing 2/3 or more of the stem; stem leaf one. Peduncle up to 10 cm. Flowers about 13 cm tall from base of valves, about 10 cm wide; valves relatively large, about 7—9 cm, slightly inflated; ovary about 2 cm; perianth tube about 3.5 cm. Falls 6—8 cm long, up to 5 cm wide, oblong, darker than the standards, maroon or

reddish-brown with a purple cast, varying in depth of colour, without veins or dots; signal spot small; beard of usually pure yellow, sometimes purple-tipped or of reddish-purple hairs on a creamy—bright yellow ground; beard hairs only slightly papillate-echinate, especially near the tip. Standards up to 10 cm long, up to 8 cm wide, ground intense purple without any dots and with veins of a darker colour or the veins sometimes not discernable. Anthers about 2.5 cm; filaments about 1.5 cm. Style branches light brown, about 5.5 cm including the lobes, about 2.5 cm wide, strongly keeled; lobes coloured like the falls; pollinator tunnel apparently oblique. Pods?

DISTRIBUTION: Endemic to heights above Bludan, Syria.

MATERIAL: Above Bludan, May 1953, KHATEEB 24 (lectotype, BEI and Damascus Univ. Herbarium).

NOTES: The above description has been adopted from those of DINSMORE (1933), MOUTERDE (1966), WERCKMEISTER (1957), WEST (1935), and modified in places from the study of herbarium material.

Sketches of flowers in Fig. 6 D are based upon photographs by PETER WERCKMEISTER.

17. **Iris ? heylandiana** BOISSIER & REUTER — Fig. 6 B

BOISSIER & REUTER 1877 in BAKER in J. Linn. Soc. 16: 142; BOISSIER 1884, Fl. Orient. 5: 130—131; POST & DINSMORE 1934, Fl. Syr. Pal. & Sin. 2: 596; MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 317. — Orig. coll.: Turkey, between Diarbekir and Mardin, 18--, KOTSCHY 307 (syntype); Iraq, between Mossul and Baghdad, 18--. OLIVER (syntype, not seen).

Plants up to 35 cm. Rhizome medium—small, shortly creeping (apparently stoloniferous). Leaves up to 9, less than 1 cm wide, about 20 cm long, strongly arched; stem leaf 0—1. Peduncle about 9 cm. Flowers about 15 cm tall from base of the valves, about 7 cm wide; valves about 7 cm, more or less inflated, with a brownish-pink tinge. Falls obovate—cuneate, veined and spotted with brown-violet forming an open pattern on a whitish, clear ground, dark brown at the throat (?); signal spot dark, narrow, elongate with the distal edge irregular in outline; beard linear but spreading out laterally near the base; beard hairs white, relatively sparse (like *I. barnumae*), of almost uniform length, less than 5 mm in length. Standards broader than the falls, orbiculate—unguiculate, white with fine purplish-brown veins and sparse dotting. Style branches horizontal—oblique, rahter wide, orange (?); the lobes short, crenate, the width of the two lobes less than the width of the style branch; pollinator tunnel constituted mainly of the style branch, the fall contributing the floor near the base only, otherwise the tunnel open on the lower side and the linear beard laterally visible. Pod?

DISTRIBUTION: Reported from north-eastern Syria, southern Turkey, and from between Mosul and Baghdad in Iraq.

MATERIAL: Syria, Derbassieh, April 1940, DINSMORE 21512 (BEI); between Derbassieh and Ras-el-Ayen, April 1934, GOMBAULT 5769 (LNRC)?

NOTES: The authors have not seen any live material. The above description has been adopted from the original and modified in places based upon study of herbarium material from the Darbassieh area and descriptions and pictures kindly supplied by Mr CLAY H. OSBORNE and Mr HERBERT MCKUSICK. Sketch of this taxon based upon pictures provided by Mr OSBORNE.

I. heylandiana is apparently a component of the complex of species in southern Turkey and north-eastern Syria. GOMBAULT 5769 bears the name *I. gombaultii* DINSMORE but MOUTERDE cited this sheet as *I. heylandiana*. The rhizome in

this plant is long stoloniferous, the leaves arcuate making a complete circle and covering the stem to a little below the valves. Is this a normal variation within the species *I. heylandiana*? Or is it a separate taxon as considered by DINSMORE? The syntypes for *I. heylandiana* are material collected from two relatively widely separated localities. BRIAN MATHEW of Kew Herbarium states (pers. comm.) that *I. heylandiana* material is "large-flowered" while the Derbassieh material is "small-flowered" and presents aspects of *I. meda* STAPF from Iran. Only further studies of live material from the two syntype localities can prove whether the two syntypes truly represents one taxon or two separate taxa or that the Derbassieh material represents an entirely different taxon. The Derbassieh region complex is characterized by the linear beard as too is the *I. barnumae* complex. However, in *I. heylandiana* (photographs seen by the authors) the linear beard appears to spread out transversely near the base. Another taxon which has an apparent linear beard is *I. assadiana*; but in this species the median brush of longer hairs (more than 5 mm) is more densely arranged and is surrounded on either side by a dense band of very short hairs — in other words, this taxon has the median brush of longer hairs as in *I. heylandiana* and *I. barnumae* complexes and a denser beard with the lateral bands of dense (though very short) hairs as in the Hauran group of oncocycli.

The beard and beard-hair characters used in the key and given in the text are from material collected from the Derbassieh area and pictures provided by Mr CLAY OSBORNE.

18. **Iris assadiana** CHAUDHARY et al., sp. nov. — Fig. 6 E

Orig. coll.: Syria, Sadad area, April 1974, KIRKWOOD 1312 (holotype, BEI).

I. barnumae FOSTER & BAKER var. *zenobiae* MOUTERDE (in part) 1966, Nouv. Fl. Lib. Syr. 1: 315—316.

Planta c. 15 cm alta. Rhizoma parvum, stoloniferum. Folia 6—8, firmiter arcuata, 4—12 cm longa, 1 cm vel infra lata. Flores odoriferi, 9.5—13 cm longi a basi spatharum. Tepala externa 5—6.5 cm longa, 2.5—3.5 cm lata, uniformiter purpurea, venis paucis fuscioribus instructa; macula media fuscior, latior quam longior; barba in medio capillis longis (supra 5 mm), flavis, ad margines brevissimis lineis purpurascentibus. Tepala interna 6—8 cm longa, 4—5 cm lata, obovata, unguiculis parvis. Antherae 1.3—1.8 cm longae; fila 1.8—2 cm longa. Rami styli obliqui—aequi arcuati, non-carinati, 4—5.5 cm longi (lobis inclusis), amborum loborum latiores, lutei: canaliculus pollinicus apertus, tepalis externis basi tantum convenientibus. Capsula c. 4 cm longa, 1.25 cm lata.

Plants up to 15 cm. Rhizomes at base of individual shoots very small, the buds at the base only a few and forming small clumps; several long, spindly or stout stolons (of several nodes each) coming from the base of each shoot constitute the main rhizome; stolons up to 12 cm long, becoming conical at the base of the single plantlet that develops from the apical bud on each stolon. Leaves 6—8, usually falcate, strongly reflexed, 1 cm wide or less, 4—12 cm long, usually the single stem leaf or the uppermost leaf longer than the stem. Peduncle about 4 cm. Flowers odorous, about 9.5—13 cm long from base of the valves, 6—7.8 cm wide; valves about 5.5—7 cm, rather inflated, keeled, pale green to yellowish-pink on drying; ovary about 2 cm; perianth tube about 2 cm. Falls 5—6.6 cm long, 2.5—3.5 cm wide, uniformly dark-maroon to dark-purple to almost black with a few darker veins; signal spot velvety, darker, transversely oval, wider than long, notched, less than 1 cm long, about 1 cm wide or slightly more; beard of a median band (about 0.5 cm wide) of long (about 1 cm) hairs; the hairs on either side of the median band very short; the long hairs bright yellow, either without purple tips or some with very small purple tips or the bright yellow masking the purple tips; the short hairs purple; the ground below the long hairs bright yellow, in some biotypes the

beard hairs completely lacking and only a yellow band on the falls present. Standards 6—8 cm long, 4—5 cm wide, obovate, gradually narrowed to the base into the claw; the claw 1—1.5 cm long, channelled, the channel with a few yellow hairs, maroon-purple with darker veins, some biotypes dark purple. Anthers creamy white, 1.3—1.8 cm; filaments 1.8—2 cm. Style branches 4—5.5 cm long including the lobes, strongly arched, not keeled, if keeled then not ridged, pale orange (not purple as described by MOUTERDE 1966), streaked with purple, becoming darker towards the centre, with a purple median streak; width of the two lobes less than the width of the style branch; pollinator tunnel constituted mainly by the style branch, the fall forming only a part of the tunnel floor near the very base; the style branches often raised relatively high above the falls and the long beard hairs then laterally visible. Pods about 4 cm long, about 1.25 cm wide, tapering.

DISTRIBUTION: Apparently endemic to the Syrian desert.

MATERIAL: Ain-al-Baida, Syrian desert, April 1944, MOUTERDE 8159 (now at G); Chalky hills, Palmyra Road, April 1943, DAVIS 5769 (K); Qaryatein, April 1943, DAVIS 5721, 5668 (K); Hafar, April 1935 (?), DINSMORE 24313 (K); loc. ? (probably Syrian desert) April 1913, EGGERS (K).

NOTES: W. R. HIGHWOOD reports having seen white, yellow, and lighter-colored forms, apparently around the Qaryatein area.

MOUTERDE described this taxon as *I. barnumae* var. *zenobiae* and included the Tell Chehan material (*I. swensoniana* sp. nov.) under this taxon. The stoloniferous habit of the desert material was apparently overlooked by him because the type specimens that he used for description are without rhizomes while the Tell Chehan material that he probably used in his description (MOUTERDE 7558) does have the non-stoloniferous rhizomes. Also, the type of beard in the two taxa was confused by him. *I. assadiana* apparently shows close affinities to *I. barnumae*, but is probably even closer to *I. heylandiana* found in the extreme north of the Syrian desert on the southern Turkish border. Also, *I. barnumae* and all of its infra-specific taxa have a distribution in mountainous, non-desert habitats. The stoloniferous habit, the median band of long hairs amidst lateral piles of very short hairs, the non-echinate beard hairs, the presence of darker veins in the perianth and its distribution justifies, we feel, treating the desert material as a separate species, *I. assadiana* sp. nov.

This species is named after Mr H. ASSAD, Patron of the Horticultural Society of Syria.

19. **Iris jordana** DINSMORE — Fig. 7 A

DINSMORE 1933, Pl. Post. Dinsm. 2: 9; 1934 in POST & DINSMORE, Fl. Syr. Pal. & Sin. 2: 598; MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 316. — Orig. coll.: Jordan Valley, near Baysan, April 1921, DINSMORE 1893 (holotype, DINSMORE Herbarium), not seen.

Plants up to 40 cm. Rhizome rather large, compact. Leaves usually 9, slightly falcate, erect, about 2 cm wide, up to 30 cm long, the two uppermost sometimes ending at the same level, sheathing the stem completely. Peduncle about 12 cm. Flowers 13—18 cm long, from base of the valves; valves 10—12 cm, light green, often streaked with purple; ovary about 4 cm; perianth tube about 3 cm. Falls about 9×5 cm, rather leathery, obovate—elliptical, slightly irregularly crenate, densely red-purple spotted and with dark purple veins, the spotting so dense that the ground appears as lead-white spots through the dense spots and veins; signal spot orbicular, about 2 cm in diameter, velvety, very dark purple, almost black, wider and diffusing towards the tip end; beard of relatively sparse hairs, the hairs

creamy white, tipped with very small, purple dots. Standards 10.5—13 cm long, 7.5—9.5 cm wide, orbicular, abruptly narrowed into a triangular area and then into a channelled claw, the claw about 2 cm; densely spotted with fine red-purple dots and dark purple veins, the dots very dense and the veins very thick in the central area on a lead-white ground; the dots sparser on the inner face and the lead-white ground much more prominent. Anthers about 4 cm, creamy white; filaments about 1 cm. Style branches about 6 cm long, about 4 cm wide, greenish-yellow, densely finely spotted with dark purple, with the greenish-yellow colour showing through, ridge-keeled, the ridge prominent; lobes of the style branches turned upwards, darker, the width of the two lobes more than the width of style branches; pollinator tunnel rather similar to that in *I. sofarana* subsp. *kasruwana* (Fig. 4 D a). Pods?

DISTRIBUTION: Endemic to the Jordan River Valley.

MATERIAL: Live material in culture apparently from around the type locality. — Collections: Near Yarmouk river, April 1943, DINSMORE 5893 (BEI); Baysan area (?), from culture, April 1974, CHAUDHARY 1403 (BEI).

NOTE: The live material studied was obtained through the courtesy of the Aril Society International, but is definitely from the Jordan valley under Israeli administration at present. The original supplier identified it as *I. jordana* DINSM. which indicated that it had come from area around Baysan, the type locality for *I. jordana*. The type localities for *I. jordana* and *I. hauranensis* DINSM. lie on opposite banks of the river Jordan about 30 kms apart. However, DINSMORE also labelled his no. 5893 (BEI) *I. jordana,* collected near the Yarmouk river (April 1943), apparently from the East bank of the Jordan river. The two taxa were published by DINSMORE at the same time in the same publication. MOUTERDE (1966) considered the two taxa to be identical. From the study of limited material, while we tend to support MOUTERDE's treatment of the two taxa, we cannot with confidence say that they should be united. A thorough study of material from both localities is needed to clear up this point.

20. **Iris bostrensis** MOUTERDE — Fig. 7 B

MOUTERDE 1954 in Bull. Soc. Bot. France 101: 420—421; based on *I. atropurpurea* BAKER var. *purpurea* DINSMORE 1933 in POST & DINSMORE, Fl. Syr. Pal. & Sin. 2: 600; MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 317. — Orig. coll.: Syria, 10 km N of Draa, March 1952, HIGHWOOD HG 6 (holotype, Herb. MOUTERDE, now at G).

Plants up to 40 cm. Rhizome short, compact, brown. Leaves usually 8, less than 1 cm wide, up to 20 cm long, weakly or strongly recurved or erect; stem leaf one. Peduncle about 12 cm. Flowers about 14—17 cm tall from base of the valves, about 8 cm wide; valves pale green to yellowish-green, slightly inflated, about 9 cm; ovary about 3.5 cm; perianth tube about 3 cm. Falls 6.5—7.5 cm long, 3—4.5 cm wide, reflexed, often folded back; the limb ovate, abruptly narrowed into the haft, the latter rather tightly clasping the style branch; densely spotted and veined with dark brown-purple so that the yellow ground appears spotted through the dark brown-purple; signal spot semi-circular, usually truncate, often notched or with two shallow notches, wider than long, 1.5—2 cm wide, about 1.5—1.6 cm long, velvety dark maroon-purple; beard dense, beard hairs all bright yellow, minutely purple-tipped, about 0.5 cm long in the middle, gradually reduced in length towards the sides; the bright or pale yellow ground visible throughout the beard. Standards about 8—10 cm long, about 5—7 cm wide, limb orbiculate, rather abruptly narrowed into the claw, the claw channelled, about 1.5 cm long with fine yellow hairs, densely finely streaked with dark

brown-purple, the spotting density variable, giving rise to different shades; the ground brownish-yellow to greenish-yellow. Stamens creamy white; anthers about 2 cm; filaments about 1 cm. Style branches 5.5—6.5 cm long including the lobes, about 2.5 cm wide, ridge-keeled, golden yellow with dense, very minute, dark brown-purple spots, the spots becoming bigger or streaks towards the sides and the lobes; the two lobes as wide as or wider than the style branch; pollinator tunnel almost like that in *I. sofarana* subsp. *sofarana,* but the style branches rather obliquely raised above the falls away from the immediate basal areas. Pods about 8 cm long, about 1.25 cm wide, 6-lobed, slightly inflated.

DISTRIBUTION: The Hauran, Syria. The commonest of the "black irises", often a weed in grain-fields.

MATERIAL: Live culture. — Collections: Salkhad to Bosra, April 1964, WEGMANN B-157 (BEI); Shehba Road, April 1972, CHAUDHARY & KIRKWOOD 795 (BEI); Jabl Druze region, April 1973, WEYMOUTH 1298 (BEI); in fields around Damascus-Jordan road, April 1952, HIGHWOOD (K).

21. **Iris auranitica** DINSMORE f. **auranitica** — Fig. 7 C

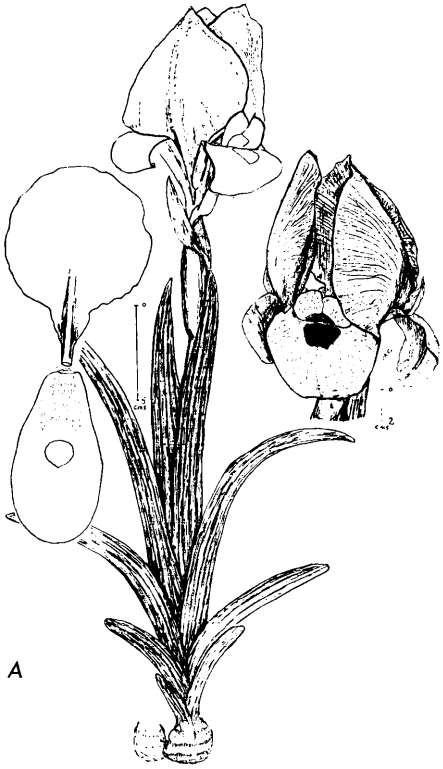
I. auranitica DINSMORE 1933, Pl. Post. Dinsm. 2: 11; 1934 in POST & DINSMORE, Fl. Syr. Pal. & Sin. 2: 601; MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 315. — Orig. coll.: Syria, Jabl Kulayb, May 1933, DINSMORE 13045 (DINSMORE Herbarium), not seen.

Plants up to 50 cm. Rhizome medium, compact, yellow. Leaves up to 9, about 1 cm wide or rarely more, about 25 cm long, erect or slightly arched, sheathing the stem almost to the top; stem leaves one or two. Peduncle up to 15 cm. Flowers odorous, about 15 cm tall from base of the valves, valves rather tightly clasping, 8—9.5 cm long, greenish-yellow; ovary about 4 cm long, 1 cm broad with a stalk about 5 mm; perianth tube about 2 cm. Falls about 7×4 cm, obovate, bronze, with very minute, uniformly and rather densely distributed purplish-red spots and very fine reddish-purple veins or without spots and with only faint venation; signal spot about 1.5×1.5 cm, orbiculate to pendulum-shaped, dark maroon or reddish-yellow; beard dense, the hairs bright yellow with very minute purple-red tips; the hairs longest in the middle (about 0.5 cm) and gradually becoming shorter towards the sides. Standards about 8.5×5.5 cm, obovate, golden-yellow to bronze, with very fine purplish-red veins or without dots and with only faint veins; claw about 1 cm long, channelled, with golden yellow, dull brown-tipped, dense hairs. Anthers about 2.2—3 cm, tailed, creamy white to light yellow; filaments about 1—2 cm, light yellow. Style branches 4.7—5.5 cm long including the lobes, about 3 cm wide, golden yellow with very fine purple to brownish-purple dots, rather oblique and arched, ridge-keeled, the ridge more prominent near the lobes; the lobes not wider than the width of the style branches, upturned, spotted and veined like the falls; the style branches forming a rather short pollinator tunnel with the falls near their bases, the tunnel open away from base. Pods about 8 cm, rather narrow.

DISTRIBUTION: Endemic to the Jabl Druze area in Syria.

MATERIAL: Jabl Kulayb, May 1943, DINSMORE 15095 (damaged, BEI); Mayamas near Tell Jaffna, April 1973, CHAUDHARY & KIRKWOOD 800 (BEI) (collected in bud and brought to Beirut where it flowered and fruited).

Fig. 7. A: *Iris jordana.* — B: *Iris bostrensis.* — C: *Iris auranitica* f. *auranitica.* — D: *Iris swensoniana.*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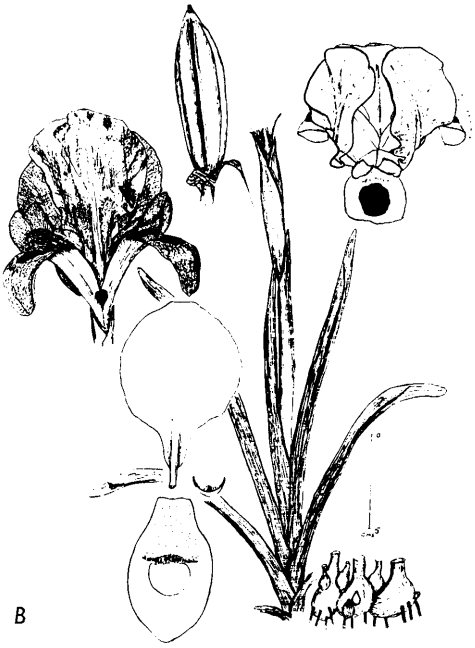
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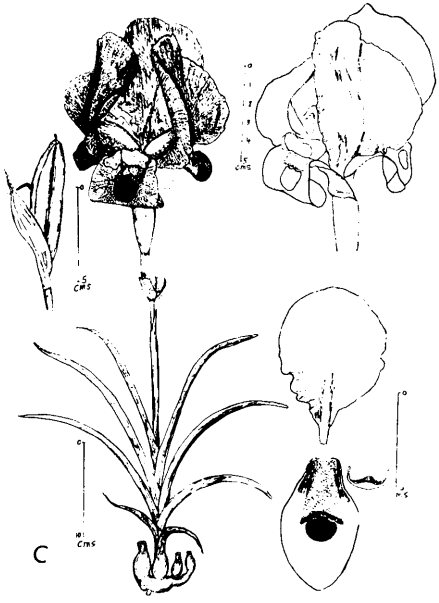
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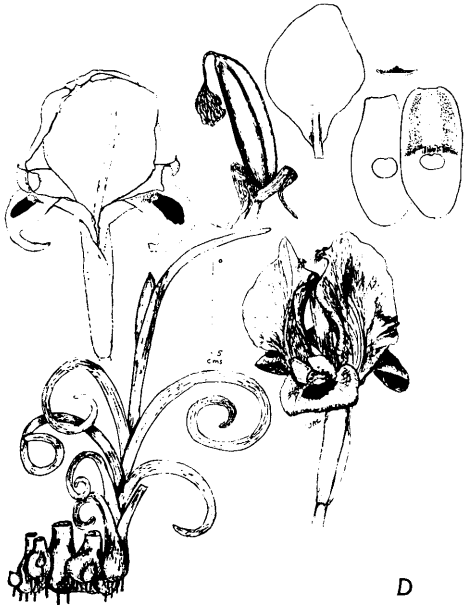
D

22. **Iris auranitica** DINSMORE f. **wilkiana** CHAUDHARY et. al., stat. et nom. nov.

Base: *I. auranitica* DINSMORE var. *unicolor* MOUTERDE 1953, Fl. Djebel Druze, p. 82; 1966, Nouv. Fl. Lib. Syr. 1: 315. — Orig. coll.: Syria, Tell Jaffna (type not indicated); Mayamas near Tell Jaffna, April 1973, CHAUDHARY & KIRKWOOD 800-A (neotype, BEI).

This form differs from f. *auranitica* in having bright yellow flowers without red-purple dots or veins. The falls and standards often tend to be wavy. MOUTERDE considered this to be a variety (*unicolor*) which is inappropriate as both the forms are found growing together — the differences are apparently minor genetic variations and the biotypes best merit recognition as forms. The name "unicolor" could be misleading and be contrued as implying that the biotypes were completely lacking in any other pigment except yellow which is not so, or that the falls and standards were like-coloured (as in f. *auranitica*).

NOTE: This form is named after Mr THOMAS WILKES of the Aril Society International, USA.

23. **Iris swensoniana** CHAUDHARY et al., sp. nov. — Fig. 7 D

Orig. coll.: Syria, Tell Chehan, April 1972, CHAUDHARY & KIRKWOOD 796 (holotype, BEI).

I. barnumae FOSTER & BAKER var. *zenobiae* MOUTERDE (in part) 1966, Nouv. Fl. Lib. Syr. 1: 315—316.

Planta c. 40 cm alta. Rhizoma parvum, compactum. Folia c. 8, infra 1 cm lata, c. 20 cm longa, infirmiter recurva, etiam circinata. Flores odoriferi, c. 15 cm longi a basi spatharum. Tepala externa 6—7 cm longa, 3—3.5 cm lata, ovato-spathulata, saepe retroflexa, uniformiter atropurpurea, venis fuscioribus; macula media orbicularis—reniformis; barba sicut pulvinus, capillis densis, marginem versus gradatim brevioribus, infra 5 mm longis, in medio flavis, ad marginem purpurascentibus. Tepala interna 6—8.5 cm longa, 3.5—5 cm lata, uniformiter purpurea vel maronina, unguiculata. Antherae 2—3.5 cm longae; fila 1—1.5 cm. Rami styli 4—6 cm longi (lobis inclusis), 2.5—3 cm lati, lineis interruptis, cristati et carinati; canaliculus pollinicus praecipue e ramo styli formatus. Capsula 8—10 cm longa, c. 2.5 cm lata.

Plants about 40 cm. Rhizomes small, compact, yellowish-brown. Leaves up to 8, less than 1 cm wide, about 20 cm long, strongly recurved, even circinate; stem leaf one. Peduncle about 15 cm. Flowers odorous, about 12—19 cm long from base of the valves, 7—8 cm wide; valves more or less inflated, keeled, pale green to green, ovary 2.5—4 cm, terete—broadly trigonal; perianth tube 2—4 cm. Falls 6—7 cm long, 3—3.5 cm wide, ovate—spathulate, narrowed or not into a haft, strongly recurved, often folded back; uniformly dark purple, almost black, with darker veins; signal spot orbiculate-reniform, notched, wider than long, 1—1.5 cm long, 1.5—2 cm wide, velvety dark maroon—dark purple (almost black); beard of purple-tipped bright yellow hairs (less than 0.5 cm long) in the median region on yellow ground, the hairs gradually becoming shorter towards the sides where they are purple on a purple ground. Standards 6—8.5 cm long, 3.5—5 cm wide, oblong, gradually or abruptly narrowed into the claw; claw 1—1.5 cm, channelled, the channel with a few purple and yellow hairs; limb uniformly purple or dark maroon, slightly lighter than the falls. Stamens creamy white; anthers about 2—3.5 cm; filaments 1—1.5 cm. Style branches 4—6 cm long including the lobes, 2.5—3 cm wide, orange, strongly streaked with purple, becoming darker towards the tip, ridge-keeled; lobes coloured and veined like the falls, triangular, crenate, recurved; lobes narrower than the style branch; pollinator tunnel formed mainly by the style branch, the fall contributing only part of the tunnel floor. Pod 8—10 cm long, about 2.5 cm wide.

DISTRIBUTION: Endemic to Tell Chehan area, Syria.

MATERIAL: Live culture. — Collections: Tell Chehan, April 1943, MOUTERDE 7558 (LNRC); April 1973, WEYMOUTH 1299 (BEI).

NOTES: PETER WERCKMEISTER (pers. comm.) has made a very interesting comment: "The Chehan (Tell Chehan) iris has close clumps. There is an interesting equilibrium between the luxurient growth of its rhizomes with an astonishing multiplication of its sprout buds and the existence of the larvae of a lepidoptera (a kind of iris-borer): the plants would die out without the borer, as the plants would be unable to get enough nutrition for so many sprouts" (from the poor soil? auths.).

This species is named after the late Dr. S. P. SWENSON, former Dean of the Faculty of Agriculture at the American University of Beirut, Lebanon and at the University of Agriculture, Lyallpur, Pakistan.

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Peroxydase Isozymes in Quercus petraea and Quercus robur

Ulf Olsson

OLSSON, U. 1976 05 06. Peroxydase isozymes in Quercus petraea and Quercus robur. — Bot. Notiser 128: 408—411. Lund. ISSN 0006-8195.

An investigation of the occurrence of multiple molecular forms of peroxydases in the leaf tissues of *Q. petraea* and *Q. robur* has been carried out. In all, eleven different isozymes have been found. These are classified into four groups, one of which is only found in *Q. petraea* and introgressive populations. However, one of the *petraea* populations examined also lacks this group of peroxydases. The possibility of the occurrence of introgressive individuals not revealed by morphological analysis is discussed. The intraspecific variation of the zymograms is great, indicating the genetic heterogeneity of oak populations.

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It has been found that a number of different enzymes exist in multiple molecular forms (isozymes), within a species, or within the tissues of a single plant or animal and even within a single cell. A well-known example of this is lactate dehydrogenase (LDH). This enzyme exists in five different forms, each of which has been found to consist of four polypeptide chains of two different types only. These are coded by two different genes. The discovery of this molecular heterogeneity among enzymes has led to such applications as the analysis of genetic variation in plant populations (SCOGIN 1968, CONKLIN & SMITH 1971, JUO & STOTZKY 1973, RUDIN & RASMUSON 1973).

The aim of this investigation is to evaluate interspecific differences and, in some cases to find out the degree of introgression, or the occurrence of hybrid trees, in sympatric populations of *Q. robur* and *Q. petraea*.

Extractions of proteins from green oak-leaf tissues were separated by anodic disc electrophoresis and the polypeptides stained for the presence of peroxydases.

MATERIAL AND METHODS

Collections and Growth Conditions

The material used was in the main obtained from mature trees of *Q. petraea* (MATTUSCHKA) LIEBL. and *Q. robur* L. and their intermediates growing in natural stands in southern Sweden as in the population investigation (OLSSON 1975), viz. two *petraea,* three *robur,* three intermediate or mixed oak populations and one progeny sample of *Q. robur* (Fig. 1). Twigs taken from the south sides of the trees were brought to the laboratory in plastic buckets filled with tap water. They were exposed to daylight at room temperature (20° C). In addition, leaves were taken from seedlings grown from acorns of a single individual of *Q. robur*. The seedlings were grown under greenhouse conditions with a combination of daylight and artificial fluorescent light, and a minimum temperature of 20° C and transferred to the laboratory. Fresh, well-developed leaves of medium size were removed not more than two days after twigs and seedlings had been moved to the laboratory, and the enzymes immediately extracted.

Extraction and Electrophoresis

To extract peroxydase, oak-leaf tissue with the thickest veins removed was homogenized with a pestle and mortar in a buffer con-

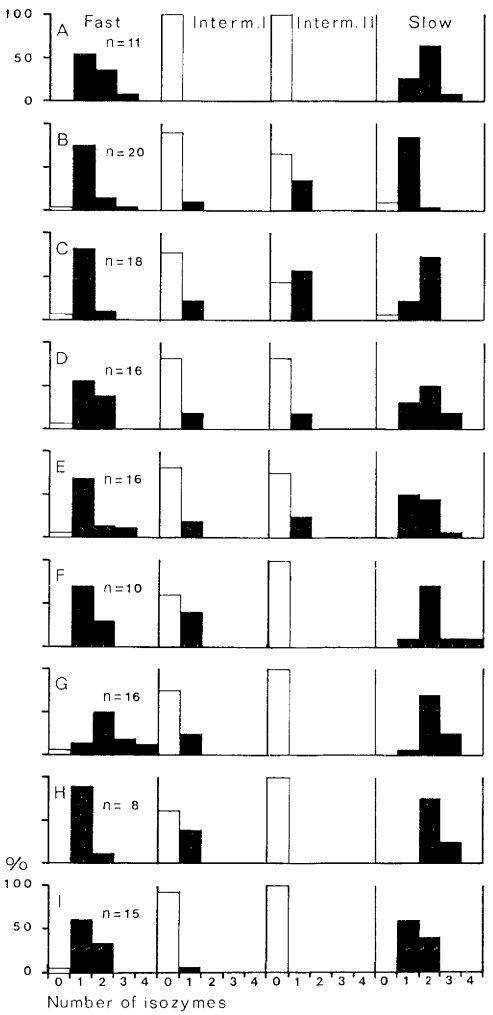

Fig. 1. *Quercus robur* and *Q. petraea*. The results of an analysis of isoperoxydases in leaves from mature trees and from the progeny of a given oak. Histograms show the frequency distribution of individuals with 0 (unfilled colums) or 1, 2, 3, 4 (filled columns) isozymes within each of four groups of peroxydases with different relative mobilities. — A, B: Populations of *Q. petraea*. — C, D, E: Introgressive populations. — F, G, I: Populations of *Q. robur*. — H: Progeny of *Q. robur*.

taining 0.02 M 2-amino-2-hydroxymethyl-1, 3-propanediol (TRIS) and 0.19 M glycine (the same as was used in the electrode

Table 1. A comparison of isoperoxydase activity in fresh and frozen oak leaf material. QA refers to a population of *Q. petraea*, QO to *Q. robur*. The relative degree of activity as seen in the densitometer traces of the bands is indicated by +, ++ and +++. The change in relative mobility is noted for each sample.

Oak no.	RELATIVE MOBILITIES		
	Fresh	Frozen	Absolute difference
QA 06	0.60 ++	0.64 ++	0.04
	0.27 ++	0.26 ++	0.01
	0.23 ++	0.19 +	0.04
QA 07	0.58 ++	—	—
	0.23 +++	0.24 ++	0.01
	0.17 +	—	—
QA 08	0.66 ++	0.66 ++	0.00
	0.59 +	0.59 +	0.00
	0.54 +	—	—
	0.25 +++	0.25 +++	0.00
	0.19 ++	—	—
QA 09	0.64 ++	0.68 ++	0.04
	0.61 ++	0.65 ++	0.04
	0.24 +++	0.26 +++	0.02
	0.18 ++	—	—
	Fresh 26/7 (1973)	Fresh 20/8 (1973)	
QO 04	0.62 +++	0.59 ++	0.03
	0.60 +++	0.56 ++	0.04
	0.22 +++	0.22 ++	0.00
	—	0.12 +	—
QO 05	0.58 +++	0.59 +++	0.01
	0.22 +++	0.23 +++	0.01
	0.17 +	—	—

assembly) supplemented with 12 % sucrose and 1 % unsoluable Polyclar AT. (A similar substance often used is unsoluable polyvinylpyrrolidon, PVP.) The buffer was combined with tissue in the ratio of 10:1. After homogenization the preparations were centrifuged at 3650 g for 5 minutes. 20 µl from each supernatant sample was used for disc electrophoresis with the Shandon kit. Buffers and gels were prepared according to the Canalco system (Canalco Instructions 1965) with the following modifications. First the stacking solution (pH 8.8—9.0) was polymerized by means of UV-light (360 nm) and then the separating solution by means of D-riboflavin. The sample was layered over the stacking gel and anionic enzymes and other proteins were separated out at 2 mA per sample tube for 60 minutes. There was sufficient pigment in the oak leaves to make the

use of a tracking dye unnecessary. After electrophoresis the gels were stained for isoperoxydases with 3,3′-dimethoxybenzidine by means of the H_2O_2-o-dianisidine method (WORTHINGTON 1969). The banding patterns of the gels were scanned for absorbancy by using a densitometer (580—650 nm). The distance from the stacking-separating gel interphase reached by each enzyme was measured and the relative mobility (RM) calculated as percentage of the run of the pigment.

Introductory Trials

To test the presence of isozymes in oak leaves six extracts samples from *Q. robur* L. (3), *Q. robur* L. f. *pendula* (1), *Q. robur* L. f. *pyramidalis* (1) and *Q. hungarica* KIT. (1) were prepared and analysed according to the Canalco system. The material (except for *Q. robur* L.) was taken from the garden of The Svalöf Seed Association, Svalöv, Sweden, and the preliminary analysis carried out at the laboratory there.

Two tests on each oak sample gave identical results as follows: peroxydases (4—5 bands) in all samples; phosphatases and esterases no bands at all. (Note: corresponding analyses of hybrids of *Linaria repens* × *vulgaris* in the same electrophoresis indicated the presence of three isoesterases.)

A comparison of enzyme activity (here only used in the sense of degree of quantity as seen in the zymograms) in fresh and frozen plant material, together with a test to show possible changes in peroxydase activity on two occasions about one month apart, gave some information about the reproducibility of the experiments. Frozen oak leaves seem to lose some isozymes. In one case the remaining bands displayed a lower activity (in Table 1 indicated by +, ++ or +++ according to the value of relative mobility, RM). Repeated analyses of fresh leaves at different times showed a similar decrease of activity later in the growing season. The isozymes present on both occasions showed a difference in RM not exceeding 0.04.

RESULTS

A maximum number of seven different isoperoxydases was found in individual trees of *Q. robur* and in leaves from putative hybrids. A total of eleven different peroxydases have been found. With this method it is not possible to make an analysis of the segregation of genes for the different polypeptide chains that combine to form the isozymes (here seen as narrow bands), owing to the very slight differences in migration rates. Although the same type of pattern is obtained repeatedly for a given individual, a given peak of the zymogram obtained in two succeeding analyses of the same extract may differ. The difference may be equal to the differences in migration rate between the same isozyme and an adjacent one or it may be greater than this. Therefore from the calculations of relative migration rates the enzymes are divided into four groups, viz. fast, intermediate (I), intermediate (II), and slow (Fig. 1). Within each of these four groups of peroxydases the frequency distribution of individuals with 0, 1, 2, 3 or 4 isozymes is noted. All populations of *Q. robur* including the progeny sample lack isozymes belonging to the second intermediate group. However, one of the *Q. petraea* populations (A) also lacks the same isozymes.

A comparison of zymograms discloses the diverse profiles of enzymes of different trees in a natural stand of oaks of either species. The enzyme patterns or phenotypes of the seedlings grown from a single tree of *Q. robur* may also indicate heterozygosity. This is shown in Fig. 2 (A—E, *Q. robur*; F—J, progeny of *Q. robur*). In addition the zymograms show that the peroxydase activity in full-grown seedling leaves is a rule quantitatively somewhat greater than that of full-grown leaves from mature trees picked at the same time of the year.

As pointed out elsewhere (OLSSON 1975) the indigenous oak species in Sweden hybridize spontaneously forming introgressive populations so that it is very difficult to find isolated stands of *Q. petraea*. The biotopes considered to be preferred by *Q. petraea* are relatively small in Sweden. Adjacent sites of both species and sites that are within potential crossing distance may be occupied by *Q. robur* as

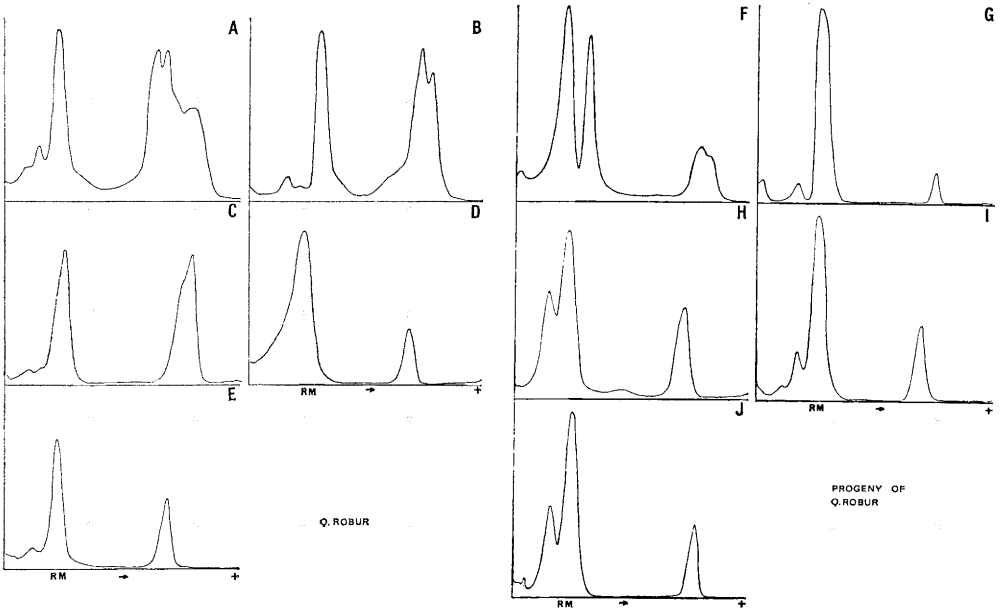

Fig. 2. *Quercus robur*. — Densitometer traces of anionic isoperoxydase banding patterns from adult trees (A—E) and seedlings (F—J) of leaf enzyme extracts. The zymograms show the heterozygosity in the controlled progeny of a mother tree as well as the diverse phenotypes (chemotypes) of mature trees in natural biotopes. Material was taken from five mature trees and five seedlings. — RM: relative mobility. The gels are scanned for absorbancy or optical density in the absorption interval 580—650 nanometers.

a result of spontaneous migration or of having been planted.

The species populations used in this investigation are the most representative judged by the results of analyses of the morphological structure. However, there may be reason to suspect gene flow between the species. Where introgression is concealed or displayed in minor morphological differences only it may be disclosed by the isozyme profile. Thus the unexpected lack of isoperoxydases in the group Intermediate II of the *Q. petraea* population (A) may be due to the presence of introgressive individuals (Fig. 1).

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The Structure of Stellate Trichomes and Their Taxonomic Implication in Some Quercus Species (Fagaceae)

Ulf Olsson

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An indumentum analysis of leaf material from populations of oak in regions of sessile oak (*Quercus petraea* (MATTUSCHKA) LIEBL.) in southern Sweden and from herbarium specimens (LD) from the same area has been performed. The combined results of this study and other morphological observations are reported. About 40 % of the pedunculate oaks have the same kinds of stellate trichomes as *Q. petraea* and may constitute introgressive intermediates of *Q. robur* and *Q. petraea*. In the glabrous individuals of the *Q. robur* material pollen stainability is on the average higher than in the pubescent ones. According to the criteria in the subspecies concept given there is no reason to subdivide *Q. robur* into pubescent and glabrous subspecies. It would be more reasonable to treat *Q. robur* and *Q. petraea* as subspecies.

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SCHWARZ (1964) treats twenty-four oak species in Europe. The indumentum characteristics of the leaves are of great diagnostic value, but there are still many questions about the frequency and the type of hairs in some species. SCHWARZ (1936) has a detailed description of all hair types observed. The present study is limited to *Q. petraea* (MATTUSCHKA) LIEBL. and *Q. robur* L. in southern Sweden with the aim of analysing and discussing the presence of stellate trichomes on the abaxial side of the leaves in relation to other characteristics. These species have in past times probably been mutually influenced in morphological characters including pubescence by spontaneous intercrossing and introgression. The resulting great variation of oak types has led many authors of *Quercus* taxonomy to describe a number of taxa within each species.

An extreme point of view is represented by FRIES (1865) and DE CANDOLLE (1864) who join *Q. robur* and *Q. petraea* in one species, whereas later botanists have shown that the apparently fertile intermediate forms have meiotic disturbances pointing to a hybrid origin (HOEG 1929). This suggests that *Q. petraea* and *Q. robur* are to some extent reproductively isolated species. SALISBURY (1940) and WEIMARCK (1947 c) described the somewhat different ecological claims of the two species. The author (OLSSON 1975) has shown, as did COUSENS (1963), that the species intercross to a rather high extent in natural populations.

SCHWARZ (1937) and WEIMARCK (1947 a) have noted the presence or absence of stellate trichomes on the abaxial side of the leaves of *Q. robur*. SCHWARZ designates the pubescent kind of pedunculate oak *Q. robur* ssp. *pedunculata* var. *puberula* and the glabrous one, ssp. *pedunculata* var. *glabra*. WEIMARCK raises the pubescent variety to the rank of subspecies naming it *Q. robur* L. ssp. *puberula* (LASCH) WEIM. According to WEIMARCK, *Q. robur*

L. ssp. *pedunculata* DC. may have "very thin, simple winding hairs" but lacks stellate trichomes of any kind. The naming of the subspecies (WEIMARCK 1947 b) is not in accordance with the now-existing international code of botanical nomenclature. If the two subspecies are maintained the proper name of the taxon which lacks stellate trichomes would be *Q. robur* L. ssp. *robur*. The name of the subspecies with stellate trichomes would be *Q. robur* L. ssp. *puberula* (SCHWARZ) WEIM. (see Taxonomy below).

In this paper some of the oaks examined are grouped according to WEIMARCK (1947 a, b; 1963). However, the author has not unreservedly accepted the taxa. The evidence of the present material does not support maintaining the two subspecies under *Q. robur*. The taxa are used here as samples or statistical groups which are compared.

MATERIAL AND METHODS

Three categories of oak have been investigated. (A list of localities is given in Appendix 1.)

(1) Herbarium Specimens

In the Scandinavian Herbarium of the Botanical Museum in Lund (LD) specimens of the following taxa were borrowed for a preliminary examination of the morphological variation in the most important kinds of Swedish oaks:

(A) *Q. robur* L. ssp. *puberula* (SCHWARZ) WEIM.
(B) *Q. robur* L. ssp. *robur* (*Q. robur* L. ssp. *pedunculata* DC.)
(C) *Q. petraea* (MATTUSCHA) LIEBL.
(D) *Q. petraea*×*robur*

The classification is confirmed by the author by a comparison with the results of the population investigation (OLSSON 1975). Thus B corresponds to the *robur* phenotype and C to the *petraea* phenotype and A and D to the intermediate or interspecific phenotypes.

(2) Pedunculate Oaks from Skåne

The oak material was taken from throughout the woodlands of Skåne and is considered as being representative. Planted oak forests of uncertain origin or of foreign provenance were avoided. In the area concerned *Q. petraea* is rare or absent.

(3) Populations in Regions of Sessile Oaks

The population structure of oak woods within the distribution range of sessile oak in Sweden has previously been reported on (OLSSON 1975). The results of an indumentum analysis of different phenotypes of that plant material are given in the present study.

A disadvantage of the investigation may be the grouping of the material in three "samples" investigated separately. Owing to differences in sampling technique and in time of collecting, and varying possibilities of obtaining suitable material to demonstrate all characters, new methods of analysis were subsequently adapted and introduced. The combined results are discussed. Indeed the three different oak samples used may better represent the variation in these taxa than one type of sample alone would have done. The first sample of herbarium specimens was used to obtain a general idea of some of the diagnostic characters hitherto applied in *Quercus* taxonomy. My own taxonomic views are grounded primarily on the results of the population studies (3) (cf. OLSSON 1975).

Biometry

Measurements were made chiefly for leaf characters. At least five samples of leaves were examined from each oak collection (A—D). The measurements used are illustrated in Fig. 1. Samples collected by the author are more representative of an oak individual than the corresponding herbarium material owing to the sampling technique used. A minimum of ten leaves was used for each character examined. In addition to the study of various characters of leaves as well as flowers and fruits, the percentage of pollen stainable in cotton blue in my own material has also been calculated. Maximum and minimum values with standard errors are given for some characters (Table 1). In the population analysis (OLSSON 1975) the variation in pubescence and other characters were shown in scatter diagrams.

Some Definitions and Methods Applied to Biometry

Leaf shape: The ratio of the length of the apical part above widest point to the total leaf length is used as a numerical value of the leaf outline. From Fig. 1 it can be

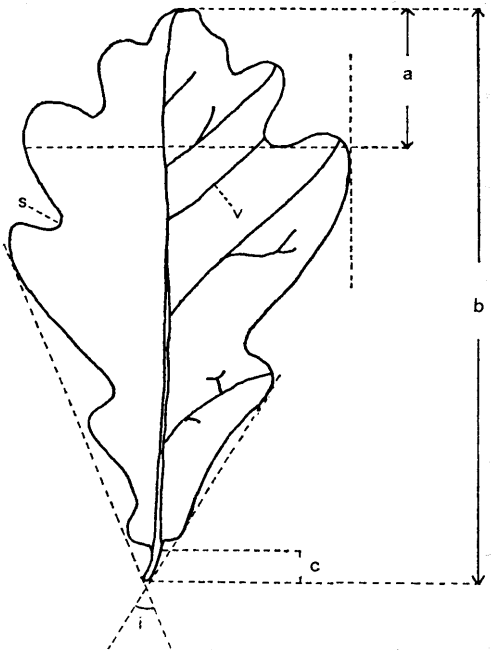

Fig. 1. General view of an oak leaf. Code to the measurements. — a. Length of apical part of leaf above widest point (mm). — b. Total length of leaf (mm). — c. Length of petiole (mm). — i. Angle of leaf base (degrees). — v. Sinus vein. — s. Sinus.

seen that the inequality $1 > a/b > 0.50$ represents an ovate leaf and $0 > a/b > 0.50$, an obovate leaf. The leaf shape value of about 0.50 characterizes the elliptical leaf.

Leaf veins (Coefficient of venation): A numerical value for the absence or presence of sinus veins is the ratio of the number of sinus veins to the number of sinuses of one side of a leaf. This coefficient varies between 0 and 1.

Peduncle "length": The distance between the base and the first flower bract or scar of bract.

RESULTS

Habit

Q. petraea and *Q. robur*: Deciduous trees with a decurrent habit forming wide crowns and with short trunks when growing in open fields. In closed stands the habit is modified with tall trunks and rather narrow crowns.

Q. robur: Angles between stem and branches rather wide; leaves clustered forming an open crown.

Q. petraea: Narrower angles between branches; foliage uniformly distributed, forming a more or less dense crown.

The modification of these gross morphological characters is marked and can lead to difficulties in identification when the trees have dropped their leaves.

Oaks have a certain tendency to form epicormic shoots. This capability is heritable and varies with the provenance.

Table 1. Biometric data of *Quercus*. — A: *Q. robur* ssp. *puberula*. — B: *Q. robur* ssp. *robur*. — C: *Q. petraea*. — D: *Q. petraea*× *robur*. — E: Pedunculate oak (Skåne). — MM: Average mean value. — m: Standard error. — n: Number of mean values (trees). — I: Angle of leaf base (degrees). — II: Leaf shape. — III: Length of petiole (mm). — IV: Coefficient of venation. — V: Peduncle length (mm).

		Min. value	MM ± m	Max. value	n
I	A	45	58.1 ±1.2	77	20
	B	40	60.7 ±1.6	82	20
	C	48	70.1 ±1.4	102	20
	D	20	64.0 ±2.1	110	20
	E	43	59.8 ±1.1	80	57
II	A	0.28	0.40 ± 0.01	0.61	20
	B	0.25	0.40 ± 0.01	0.54	20
	C	0.23	0.41 ± 0.01	0.58	20
	D	0.24	0.41 ± 0.01	0.59	20
III	A	2	5.7 ±0.4	10	20
	B	3	6.0 ±0.4	14	20
	C	5	12.8 ±0.6	23	20
	D	3	9.9 ±0.6	17	20
	E	4	6.3 ±0.2	12	57
IV	A	0	0.66 ± 0.03	1	20
	B	0	0.63 ± 0.05	1	20
	C	0	0.19 ± 0.03	1	20
	D	0	0.37 ± 0.03	1	20
	E	0	0.61 ± 0.02	1	55
V	E	6	31.1 ±1.4	59	53

An increase in light condition initiates the formation of the epicormics. Another type of branch, the so-called Lammas shoots can also affect the form of the crown. This second type of shoot is developed from a new terminal bud of the annual shoot.

Morphology — Herbarium Specimens

The following summary of the results of the analysis of the artificial aggregates of herbarium specimens should first be used as a provisional assessment of the amplitudes of certain characters. The same number of specimens has been used within each taxon, which of course does not correspond to the natural distribution.

Leaf shape (outline): All oak leaves examined are on the average obovate and the shape of the leaf is in practice unreliable as a discriminating character.

Leaf base: Nearly all *Q. robur* leaves have cordate bases with inflexed margins (ears). In *Q. petraea* the leaf base is obtuse or cuneate. Aberrant forms occur, often with an oblique base, sometimes more truncate than obtuse, especially in the putative hybrid material.

Venation: (Figs. 1, 2, Table 1: IV). The average MM-values lie closer to 0 for *Q. petraea* and closer to 1 for the *Q. robur* subspecies. The value for *Q. petraea*× *robur* (D) is intermediate.

The length of the petiole: On the average the length of the petiole of *Q. petraea* is twice that of *Q. robur*, the hybrid material being intermediate. Observe the small differences between the *Q. robur* subspecies (Table 1: III).

Leaf base angle: (Table 1: I). The differences between the oak taxa are rather marked, but there is a certain tendency towards higher values, i.e. wider angle, in *Q. petraea.*

Buds: All buds of *Q. robur* are more or less obtuse. About two thirds of the *Q. petraea* buds examined are more or less acute. Most of the hybrids resemble *Q. robur* in this character.

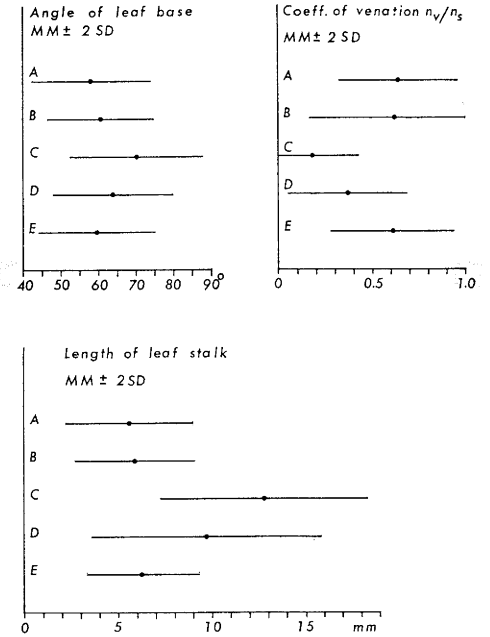

Fig. 2. Average means and doubled standard deviations (MM± 2 SD) of three characters examined.

Observe that *Q. robur* ssp. *puberula* (A) is nearly identical with *Q. robur* ssp. *robur* (B) in all morphological characters except pubescence.

Indumentum

The frequencies of different types of trichomes were determined under the microscope (×125). Five fields distributed over the abaxial surface of the leaf make up to a total area of about 5 mm².

Two kinds of simple hairs are recognized. First, thin multicellular hairs of a glandular nature with bulbous bases are found in all oak taxa in this study. The majority of these small hairs often have a withered appearance (Figs. 7 A, 3). Secondly, one can find a type of simple hair which retains its form when dried as do the bifurcate and stellate trichomes. The "simple hair" in Table 2 belongs to

Table 2. Density of hairs on abaxial surface of leaf in *Quercus*. Mean number of trichomes per mm² and percentage (within brackets) of total number of trichomes observed within each taxon. — A: *Q. robur* ssp. *puberula*. — B: *Q. robur* ssp. *robur*. — C: *Q. petraea*. — D: *Q. petraea*×*robur*.

Type of hair	Taxa							
	A		B		C		D	
Simple	1	(12.4)	0	(—)	1	(4.7)	1	(15.7)
Bifurcate	2	(33.6)	0	(—)	6	(38.1)	3	(43.3)
3-branched	1	(7.5)	0	(—)	2	(11.6)	1	(8.0)
4-branched	3	(45.5)	0	(—)	6	(45.3)	2	(31.7)
5-branched	< 1	(0.8)	0	(—)	< 1	(0.2)	< 1	(0.7)
6-branched	< 1	(0.1)	0	(—)	0	(—)	< 1	(0.1)
7-branched	< 1	(0.1)	0	(—)	< 1	(0.1)	0	(—)
8-branched	0	(—)	0	(—)	0	(—)	< 1	(0.4)
Total	7	(100.0)	0	(—)	c. 15	(100.0)	c. 7	(100.0)

the second type. The first type of trichome will be termed "glandular hairs" and the second type "simple hairs" or "simple trichomes".

Stellate trichomes: Each branch of a stellate trichome is unicellular. Under the SEM the stellate trichomes are often seen to be a combination of simpler units forming multibranched hairs joined at the base (Fig. 3 C, D). The characteristics of the constituent elements (1—4-branched trichomes) are maintained. No attempt is made to describe the distribution of the different combination types of multibranched trichomes.

The author has confirmed that the "glabrous" *Quercus* material is *Q. robur* ssp. *robur*. In addition to the "glandular hairs" found on all oak leaves, if more than five areas/leaf are examined a few isolated trichomes may be revealed. ("Glabrous" is used below in the meaning of "no one simple trichome or branched trichome observed".)

Bifurcate and four-branched stellate trichomes dominate the indumentum of the pubescent specimens (Fig. 7 B). The percentages are 79, 83.4 and 75, respectively, for taxa A, C, and D (Table 2). However, trichomes with up to eight branches have also been found. Note the density of trichomes in *Q. petraea* (C), on an average c. 15 per mm², compared with 6—7 trichomes per square unit in *Q. robur* ssp. *puberula* (A) and the putative hybrid material (D).

Tufts of hairs in the vein axils on the abaxial side of the leaf have been regarded as a rather good character for distinguishing sessile oaks. The tufts consist of especially long simple and stellate trichomes (Fig. 7 C). *Q. robur* ssp. *puberula* usually lacks these tufts of hairs. In this subspecies one can see conspicuously long trichomes along the midribs.

Pedunculate Oaks (Skåne)

The oak material (Table 1 E, Fig. 2) was analysed as one (statistical) sample. No preliminary subdivision into pubescent and glabrous material was made. The oaks may include the subspecies *puberula* and *robur* (A, B resp.) and the putative hybrid intermediates (cf. D) of *Q. robur* and *Q. petraea*. Morphological data (except for pubescence) are presented in brief as follows.

The average mean values (MM) in Table 1 for the *Quercus* group E agree well with the MM values of the subspecies of *Q. robur* (A, B) previously described. The length of the petiole (III) and the venation (IV) are two characters of pro-

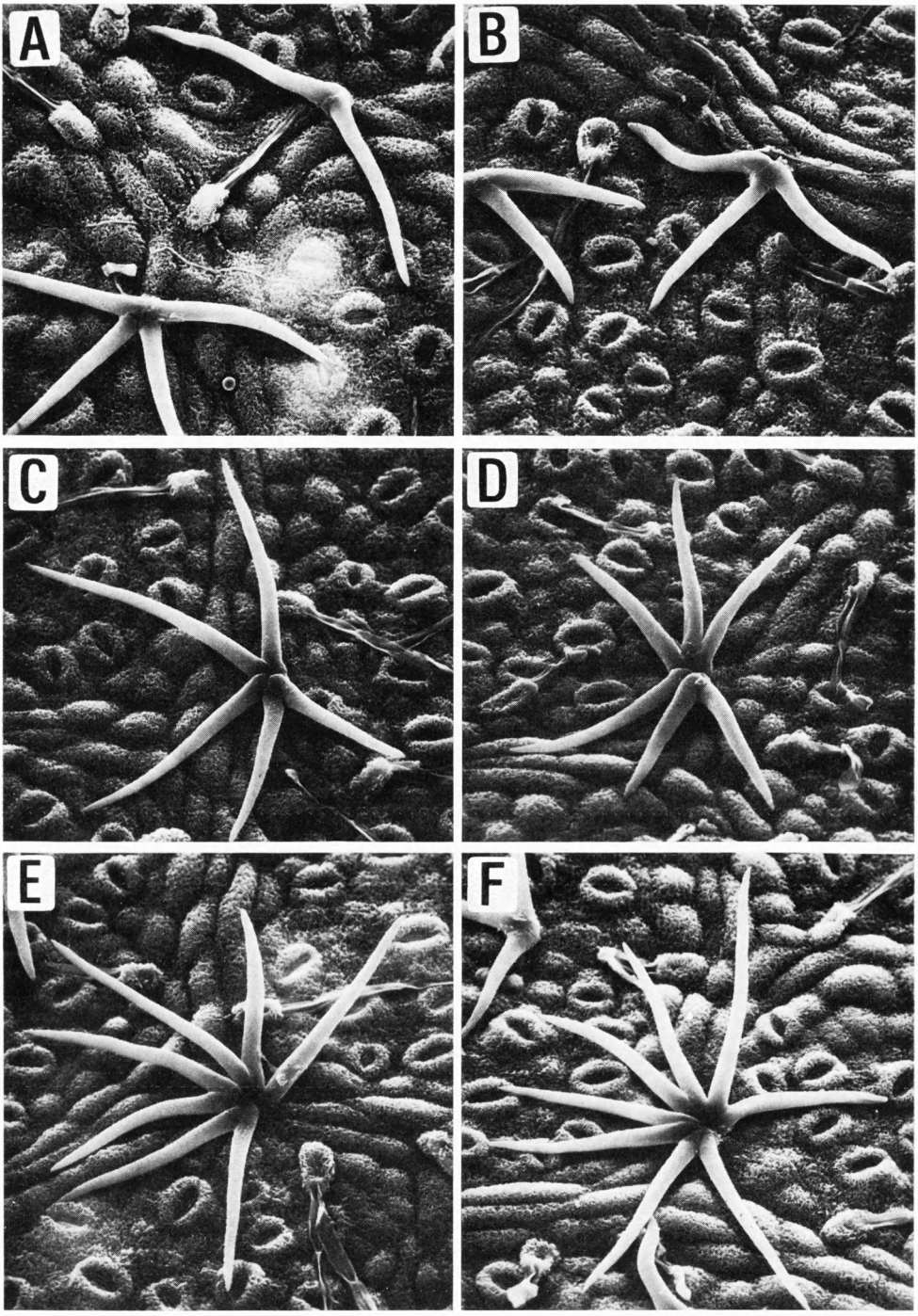

Fig. 3. Types of stellate trichomes (A—F) with 2—8 branches; SE micrographs ×600.

Table 3. Pedunculate oak (Skåne). Correlation between percentage stainable pollen and morphological variation. — a: Leaf base angle (degrees). — b: Petiole length (mm). — c: Peduncle length (mm). — d: Ratio, length/width of acorn. — e: Density of trichomes. "Glabrous" oaks excluded. — f: Coefficient of venation.

Character	t^2	Degrees of freedom	Limits of signif. (P %)	Correlation (r)
a	14.60	1/48	$P < 0.1$	+0.48
b	109.07	1/48	$P < 0.1$	+0.83
c	8.89	1/45	$1 > P > 0.1$	+0.41
d	0.26	1/45	$P > 5$	—0.08
e	132.00	1/18	$P < 0.1$	+0.94
f	456.00	1/47	$P < 0.1$	—0.003

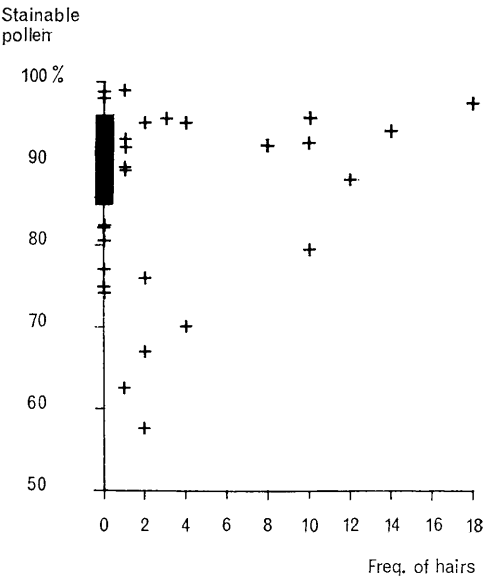

Fig. 4. Pedunculate oak (E). Correlation between pollen stainability and density of trichomes. Each + sign represents one individual. The dark field indicates a sample of twenty-two glabrous oaks.

nounced diagnostic value. Observe the slight displacement of the MM-values of the E oaks towards the hybrid group (D) indicating that some of the material from Skåne (E) is of hybrid origin. Another possible indication of this is revealed in the comparison of morphology and percentage stainable pollen (below).

The average mean for peduncle length as defined above is 31.1 ± 1.4 mm (53 trees).

Two types of female catkins with reduced fruits occur. The commonest fructification has many undeveloped acorns at the top of the peduncle. One can also find catkins with acorn rudiments along the entire axis or on both sides of one or two normal acorns. This second type of catkin discloses reduced female fertility. A corresponding reduction in percentage of stainable pollen in the same individual has in some cases been observed.

The shape of the acorn and its cupule varies. The involucre can be shallowly cupular or relatively deep and funnel-shaped. The commonest type of acorn has a length/width quotient of 1.5.

Indumentum

43.9 per cent of the *robur* oaks collected in Skåne were pubescent. Four types of trichomes are found on the abaxial surfaces of the leaves: simple, bifurcate and 3- and 4-branched. As a rule bifurcate and 4-branched trichomes dominate. The density ranges from 1 to 18 per mm^2. In this oak material (E) no trichomes were found with more than four branches (Table 2).

Pollen Stainability and Morphological Variation

The percentage of pollen grains stainable in cotton blue is often used as a measure of pollen fertility. The correlation between pollen stainability and distribution of morphological characters is shown in Table 3. The length/width of the acorn and the venation coefficient seem to be entirely unrelated to pollen stainability.

The distribution of the individuals with low and high degrees of pollen stainability in relation to different degrees of pubescence is seen in Fig. 4 (cf. Table 3 e).

Fifty oaks were examined, thirty of which are glabrous. Note that the pubescent oaks have a tendency to display higher stainability with increasing density of trichomes ($r = +0.94$; $P < 0.1$). The oaks with a very low degree of pollen stainability (< 70 per cent) have a trichome density of less than five per mm^2.

The histograms in Fig. 5 illustrate the distribution of pollen stainability in glabrous and pubescent oaks of the material from Skåne in a different way, the frequency of trichomes not being taken into consideration.

In glabrous oaks there is a relatively high degree of stainability. In 78.6 per cent of them pollen stainability is more than 85 per cent. The corresponding value for the pubescent oaks is 72.7 per cent. However, one can find a group (18 per cent) with a low stainability, falling below the minimum value for the glabrous oaks. This indicates to some degree that the glabrous oaks are closer to the species state (*robur*).

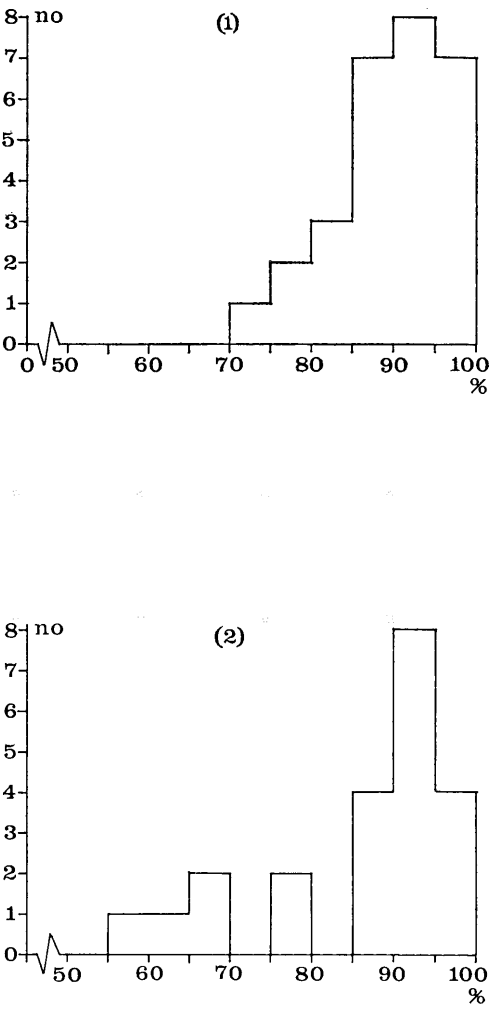

Fig. 5. Pedunculate oak (E). Frequency distribution of glabrous (1) and pubescent (2) individuals in different classes of pollen stainability.

The Distribution of Pubescent Phenotypes within Natural Populations of Oak

In view of the preceding observations it would be of great interest to study the distribution of the indumentum characters, in particular of the representatives of spontaneously introgressive oakwoods. In the following report, where not otherwise stated, the results refer to a previous examination of oak stands (Olsson 1975) where the population structure as regards nine different phenotypes (*a*—*i*) was demonstrated by the use of pictorial scatter diagrams. Six of the nine types of combined characters include pubescence. In the study referred to the pubescent phenotypes were designated *a*, *b*, *c*, *d*, *e*, and *g* respectively (Olsson 1975 Fig. 4). Divided into classes according to distance from either species type, pubescent individuals are to be found in the classes I—IV. Taken in this order the classes of phenotypes (as means of combined coordinates in the scatter diagram) constitute a line introgression with a gene flow from the pubescent species (*Q. petraea*) to the glabrous species (*Q. robur*).

Of especial interest is the distribution of *d* (ssp. *puberula*). It is noteworthy that this phenotype has approximately the same centre of distribution as the *robur* type (*i*), (Olsson 1975 Fig. 3 A, C, E).

This agrees well with the result of the comparison of the *robur* subspecies in the herbarium material (1). In twenty per cent of the "*puberula*-phenotypes" pollen stainability lies below 70 per cent, wich may indicate that they are to some extent hybrids or introgressives.

Multibranched trichomes: Stellate trichomes with more than four branches are unusual. They are found in 7 per cent of the oaks examined, mainly among the sessile oaks (fourteen trees of phenotype *a*.) But two other oak types were also represented, viz. four oaks of phenotype *b* which is rather closely affined to *a*, and finally one individual only of the intermediate type *d*.

There is a remarkable degree of correlation between low pollen stainability and occurrence of multibranched trichomes. Thus the distribution of pollen stainability in the sessile group (*a*) of fourteen oaks with multibranched trichomes is as follows, 2 (21—30 %), 1 (61—70), 5 (71—80), 3 (81—90), 3 (91—100). The stainability in all oaks of type *b* with multistellate trichomes is above 85 per cent.

CONCLUSIONS AND DISCUSSION

Controversial Aspects of Hybridity

In Skåne and many other parts of southern Sweden the climatic, topographic and edaphic conditions are very varied within a relatively small area, so that the different *Quercus* species can grow together in the same area. Thus gene exchange is possible. Ecological conditions for the establishment of new hybrids are also good.

Phenological factors, such as different times of flowering in *Q. robur* and *Q. petraea*, may prevent the formation of hybrids. However, KRAHL-URBAN (1957), who studied leaf-shedding and flowering found that any extreme difference between provenances of a single species far exceeds the difference between the average characteristics of the two species.

A few crossing experiments have been carried out to determine the presence or absence of incompatibility factors. PYATNITSKII (1939) crossed species within the subgenus *Quercus* (syn. *Lepidobalanus* (ENDL.) ÖRSTED) as well as from different subgenera. He records a very low percentage successful crosses. DENGLER (1941) confirms this result and reports two per cent fertile seeds from the cross *Q. robur* (♂) × *Q. petraea* (♀). He also made successful reciprocal crosses, unlike PYATNITSKII who failed to cross *robur* (♀) and *petraea* (♂).

The results of the investigation of artificial and spontaneous hybrids noted above demonstrate that many of the intermediate forms in actual fact constitute hybrid offspring of *Q. robur* and *Q. petraea*.

DENGLER (1941) and JONES (1959) believe that spontaneous hybrids in nature do not exist to the extent often stated. This is grounded on the difficulty in obtaining a high percentage of fertile acorns with artificial cross-pollination. This theory has not been verified and may be wrong. Better methods of pollination may raise the yield of hybrid acorns. DENGLER discloses the fact that a change in the method of pollination increased the crop of acorns from 29 to 61 per cent in intraspecific (*Q. robur*) cross-pollination. Even a frequency of less than one to two per cent in natural intercrossing might be sufficient for the formation of introgressive populations.

Given that the prevailing view regarding species interpretation (SCHWARZ 1964, KOMAROV 1970) holds, the occurrence of introgressive intermediates of *Q. robur* and *Q. petraea* must be very high. In fact, c. 40 per cent of the pedunculate oaks (Skåne) have the same kinds of stellate trichomes as *Q. petraea*. This view is confirmed by the results of the population study (3). 45 per cent of all oaks examined are interspecific. If the two phenotypes

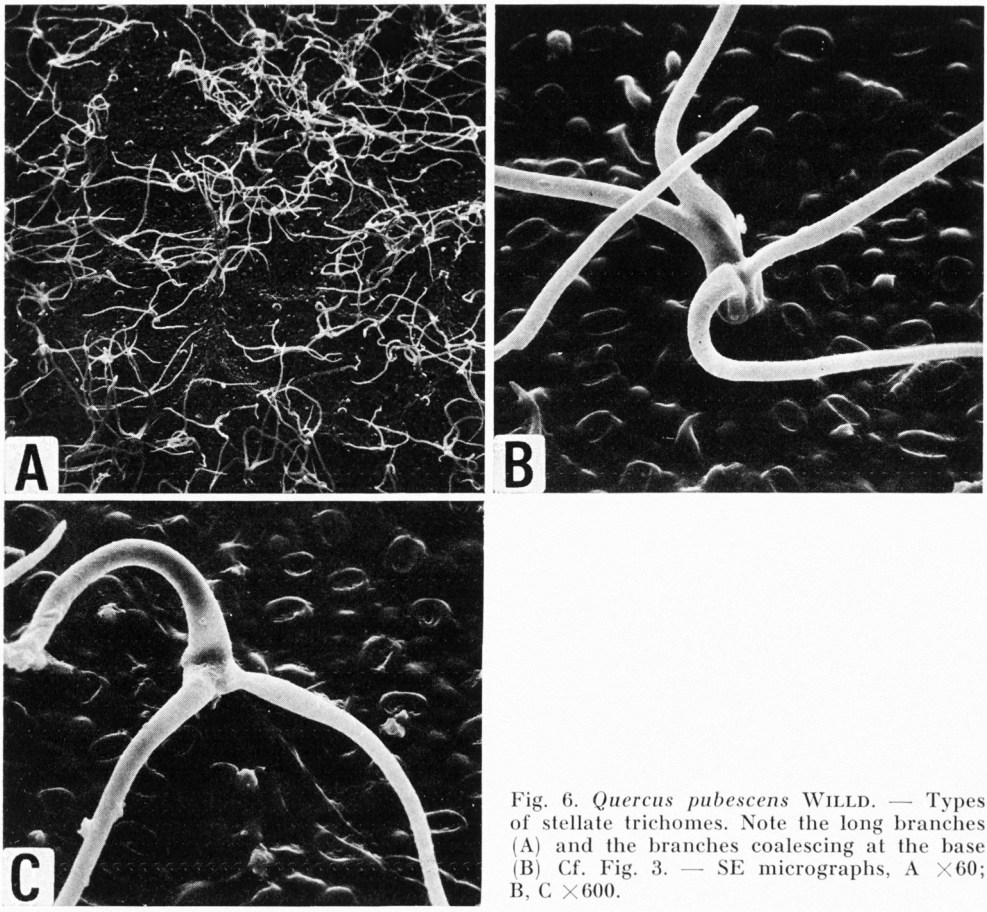

Fig. 6. *Quercus pubescens* WILLD. — Types of stellate trichomes. Note the long branches (A) and the branches coalescing at the base (B) Cf. Fig. 3. — SE micrographs, A ×60; B, C ×600.

b and *h* (OLSSON 1975 Table 2) are excluded, the phenotypes *c*—*g*, which are presumably introgressives, still constitute about 17 per cent of the material.

The morphological observations presented in this investigation also suggest that hybridization occurs between the species. As *Q. robur* is the commonest oak in Sweden a displacement of the gene pool of *Q. petraea* in the direction of *Q. robur* has probably occured. Due to introgressive hybridization the evolution of *Q. robur* from glabrous to pubescent forms has probably taken place. This statement is also supported by the fact that in the glabrous individuals of the *Q. robur* material pollen stainability is on the average higher than in the pubescent ones.

Some authors have expressed the possibility of including a third oak species in the intercrossing system of *Q. petraea* and *Q. robur*. WEIMARCK (1947 a) argues that *Q. pubescens* WILLD. may be a possible parent. A comparison of trichome types and the epidermal structure of the species concerned indicates that no crossing has taken place between *Q. pubescens* and either sessile or pedunculate oak as regards these characteristics (Figs. 3 and 6).

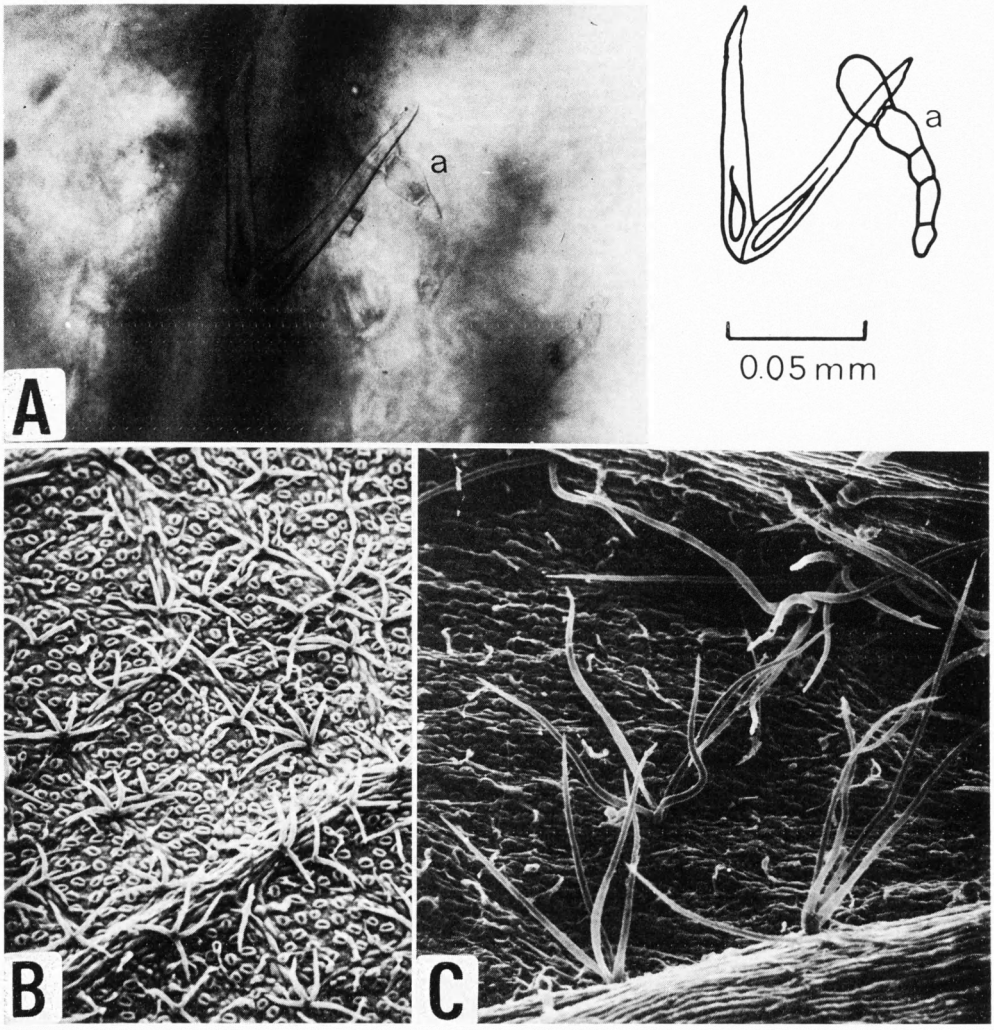

Fig. 7. Light and SE micrographs of hairs on the abaxial side of *Quercus* leaves. — A: Bifurcate trichome with unicellular branches and multicellular glandular hair (a) (see drawing on right). — B: General view of pubescent side of a leaf of sessile oak. — C: Tufts of stellate and simple hairs in the vein axils of sessile oak.

TAXONOMY

Pubescent and glabrous types of *Q. robur* considered above belong to different subspecies according to WEIMARCK (1947 a) and other authors. In my opinion the glabrous state represents the "pure species" state of *Q. robur*. Part of the material of *puberula* probably represents the hybrid *Q. petraea*×*robur* or the derivatives thereof. As regards the remainder of the material evidence of hybridity other than pubescence is lacking. However, it is possible that also this material represents introgressives.

The author follows the subspecies concept given by RUNEMARK (1961), "that two populations are referred to different subspecies if (1) the gene exchanges between them is restricted on genetic grounds or is limited or made impossible by external means and if (2) they are separated by a more or less strong hereditary discontinuity in one or several basic morphological characters or a combination of such characters". According to these criteria there is no reason to subdivide *Q. robur* into pubescent and glabrous subspecies, but it would be more reasonable to treat *Q. robur* and *Q. petraea* as subspecies.

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APPENDIX 1. Localities of Oaks Examined

A. Quercus robur ssp. puberula

SKÅNE. Brönnestad, Harröd, 300 m NW Lillsjödal (H. WEIMARCK): 450201 — Lund (T. HÅKANSSON): 450301 — Löderup (T. HÅKANSSON): 450401 — Riseberga (T. HÅKANSSON): 450501 — Löderup, Sandhammaren, close to the lighthouse (H. WEIMARCK): 450601 — N Mellby, W Furutorp, pine forest (H. WEIMARCK): 450701 — Genarp, Skoggård (H. WEIMARCK): 450801 — Gladsax, sand meadow (H. WEIMARCK): 450901 — Höör, hill NNE Fogdaröd (G. OLSSON): 451001 — Rörum (H. WEIMARCK): 451101 — Torna Hällestad, Boreslund, sand hills (H. WEIMARCK): 451701 — southern lake shore of Vomb (J. LINDERS): 451801 — Torna Hällestad, beech-hill, sand (H. WEIMARCK): 451901 — S Mellby, hill slope ENE Gladelund — SMÅLAND. Färgaryd, Ulfshult (H. WEIMARCK): 450101 — V Torsås, Nybygden (H. WEIMARCK): 451601 — VÄSTERGÖTLAND. Borås, Hultberg (A. HOLMERZ): 451501 — Göteborg, Liseberg (H. C. KINDBERG: 451401 — ÖSTERGÖTLAND. Fjärstad, Boda (H. WEIMARCK): 451301 — UPPLAND. Roslagen, Gregersboda (H. & A. FRIES): 451201.

B. Quercus robur ssp. robur

SKÅNE. Bosjökloster. (T. HÅKANSSON): 453401 — Löderup, Sandhammaren, close to the lighthouse (H. WEIMARCK): 453501 — Visseltofta, 1 km W Boalt (H. WEIMARCK): 453601 — Brösarp, pine forest at the railway station (H. WEIMARCK): 453701 — S Mellby, 1 km NE Svinaberga (Stenshuvud)

(T. HÅKANSSON): 453801 — Riseberga, 400 m SSE Skäralid (T. HÅKANSSON): 453901 — Riseberga, 300 m S Skäralid (T. HÅKANSSON): 454001 — SMÅLAND. Jät, Lindeberg (H. WEIMARCK): 452301 — Väckelsång, Esbjörnamåla (H. WEIMARCK): 452401 — Värnamo, Hjulshammar—Funtabo (H. WEIMARCK): 452501 — Bolmsö, close to the church (H. WEIMARCK): 452601 — Långaryd, Yttersjöholm (H. WEIMARCK): 452701 — Öjaby (G. BJÖRNSTRÖM): 452801 — Bosebo, Bolbynäs (H. WEIMARCK): 452901 — Nydala, Moboda (H. WEIMARCK): 453001 — Villstad, Sännås (H. WEIMARCK): 453101 — V Torsås, Piparelid (H. WEIMARCK): 453201 — Virestad, Högelid (H. WEIMARCK): 453301 — HALLAND. Gunnarp, Strättebo (H. WEIMARCK): 452101 — Gunnarp, Joarsbo (H. WEIMARCK): 452201.

C. Quercus petraea

SKÅNE. Osby, Skansen (H. WEIMARCK): 460101 — V Sönnarslöv, NW Kroken (T. DONNÉR & H. WEIMARCK): 460201 — Konga (T. HÅKANSSON): 460301 — Riseberga (T. HÅKANSSON): 461101 — Röke, 1 km E Slättsjö, rubble gravel (H. WEIMARCK): 461201 — Klöva Hallar, V Sönnarslöv (T. HÅKANSSON): 461301 — Osby, 600 m S. Sibbarp, morain (H. WEIMARCK): 461901 — Riseberga, 1 km WNW Slåaröd, rubble gravel (H. WEIMARCK): 462001 — SMÅLAND. Ryd (O. TEDIN): 460601 — Hovmantorp (T. HÅKANSSON): 460701 — Bolmsö close to the ferry-station (G. OLSSON): 460801 — Möckelsnäs (N. JOHANSSON): 460901 — HALLAND. Askome, Fyllekleva (H. WEIMARCK): 461401 — Ljungby, Gislestad (H. WEIMARCK): 461501 — Askome, Hansabo (H. WEIMARCK): 461601 — Ränneslöv, Perstorp (G. OLSSON): 461701 — Fjärås (H. C. KINDBERG): 461801 — VÄSTERGÖTLAND. Närryda, Rävelås (H. FRIES): 460401 — Göteborg, Slättskogen (J. H. KYLIN): 460501.

D. Quercus petraea × robur

SKÅNE. S Mellby, hill slope ESE Gladelund (H. WEIMARCK): 471301 — Osby, Hönjarum (F. LUNDBERG): 471401 — S Mellby, Stenshuvud (E. ASPLUND): 471501 — Hanaskog (TH. LANGE): 471601 — Örkelljunga, 1 km ENE Havabygget (H. WEIMARCK): 471701 — Ässjö, close to Storegård farm (H. NILSSON): 471801 — N Sandby (A. OREDSSON): 471901 — BLEKINGE. Nättraby, Skärva Korpanabben (B. HOLMGREN): 472001 — Karlshamn, Bellevue (I. LINDERHOLM): 470401 — SMÅLAND. Gullabo, Lönbomåla (H. WEIMARCK): 470501 — Färgaryd, Ekenäs-Skoga (H. WEIMARCK): 470601 — Burseryd, 2 km S church (H. WEIMARCK): 470701 — Villstad, Markås (H. WEIMARCK): 470801 — Gnosjö, Bottningabo (H. WEIMARCK): 470901 — HALLAND: Ysby, Skogaby (T. PERSSON): 471201 — VÄSTERGÖTLAND. Ljushult, Hallaved (O. OLSSON): 471001 — Borås, Ryås (C. SANDBERG): 471101 — ÖSTERGÖTLAND. Oppeby, 1 km ESE Björkfors (H. WEIMARCK): 470101 — VÄRMLAND. Visnumskil, Dyrön (H. WEIMARCK): 470201 — Millesvik, Staglerud (H. WEIMARCK): 470301.

E. Pedunculate Oaks Collected by the Author

SKÅNE. Frueräften, 3 km NW S Sandby: 462101 — Måryd, 100 m N Måryd farm: 462201 — 2 km NNE Torna Hällestad church: 462301 — Tryggaröd (by the road Broby—Hässleholm): 462701 — 2 km N Bosjökloster: 462801 — Långstorp, 5 km NNW Höör: 462901 & 463001 — Höör, 2 km N Sjunnerup: 463101 — Höör, 2.5 km N Sjunnerup: 463201 — Höör, Misseröd (Höör—S Rörum): 463301 — Kvesarum, E the castle: 463401 — S Rörum, 1 km W church (S side of the road): 463501 — S Rörum, 1 km W church (N side of the road): 463601 — S Rörum, Bjävröd: 463701 — Sösdala, Oskarsfarm: 463801 — Silvåkra, NE Skrivaremöllan: 463901 — Silvåkra farm, SW Krankesjön: 464001 — Hasslemöllan, 2 km E Veberöd: 464101, 464201 — 3 km E Anklam: 464301, 464401 — 1.5 km NE Lövestad (Lövestad—Andrarum): 464501 — Ry, at the "county" boundary SSW Andrarum church: 464601 — 5.2 km NE Lövestad: 464701 — SW Molleröd (Sillaröd—Vallarum): 464801 — 3 km E Eslöv, Skoghuset: 464901 — Fairyhill (W lake of V Ringsjön): 465001 — Stehag, Värlinge farm: 465301 — Stockamöllan, Hasslebro 465401 — Stockamöllan, Mickelborg: 465501 — ENE Billinge (close to Rönne river): 465601 — ENE Billinge, Hultseröd: 465701 — NW Hallaröd, N Hultarp: 465801 — Hallaröd—Färingtofta at the "county" boundary: 465901 — Rögnaröd, 3 km S Färingtofta: 466101 — Forestad, SW Färingtofta: 466201 — Perstorp, Hunseröd farm: 466301 — Perstorp, Gustavsberg: 466401 — Perstorp, Bosarp: 466501 — 2 km E Tyringe: 466601 — Finja, 0.5 km N Mölleröd farm: 466701 — N Stoby church: 466801 — Hästveda, Amundtorp: 466901 — Veberöd, Grönland: 467001 — Everlöv, Kumlatofta: 467101 — Sövdeborg: 467301 — NW lake Snogeholm, shore: 467401, 467501 — between the lakes of Ellestad and Snogeholm: 467601 — NE lake Snogeholm, Eriksdal at the cross-roads: 467701 — 0.5 km NW S Åsum church: 467801 — Övedskloster: 467901, 468001 — Gammalstorp, NE Äspinge: 468101 — N Vismosse, E Äspinge: 468201 — Påbro, E Tormestorp: 468301.

Contribution à l'étude du genre Cololejeunea

V. Quelques espèces de la région indo-pacifique

P. Tixier

TIXIER, P. 1976 05 06. Contribution à l'étude du genre Cololejeunea. V. Quelques espèces de la région indo-pacifique. — Bot. Notiser 128: 425—431. Lund. ISSN 0006-8195.

Five new species of the genus *Cololejeunea* (SPRUCE) STEPHANI are described and illustrated, viz. *C. hebridensis, C. mackeeana, C. plagiochiliana, C. sophiana* and *C. stoniana.*

P. Tixier, I.N.A. d'El Harrach, Alger Xème, Algérie.

Nous définirons la région indo-pacifique, sur le plan bryologique, comme un vaste courant allant à l'ouest de l'Afrique Orientale, a l'est de la Nouvelle Zélande et remontant vers le nord jusqu'au Japon et aux îles Hawaii.

Ici nous n'insisterons pas sur la systématique du genre *Cololejeunea.* Ce grand genre, qui représente à peu près 50 % des espèces dans les florules épiphylles d'Hépatiques, peut être, chez les Orchidées, au point de vue complexité, comparé par exemple au genre *Dendrobium.* Cela nous évite des développements même brefs sur ce point.

Rappelons seulement que M. MIZUTANI (1961), PAN CHIEH CHEN et PAN CHENG WU (1964) ont fourni des monographies pour le genre au Japon et en Chine, en ce qui concerne les flores tropicales représentant les franges extérieures des flores indo-malaises.

E. H. BENEDIX (1953) n'a envisagé qu'un certain nombre du sous-genres du genre *Cololejeunea* en Indo-Malaisie. Le travail demeura incomplet. R. M. SCHUSTER (1963) a fourni dans son synopsis des genres appartenant aux Lejeuneacées, une revue des différents sous-genres de *Cololejeunea.* Cela n'est qu'un premier aperçu qui demanderait à être complété. Aussi, donnons-nous ici cinq nouvelles espèces: une originaire de Madagascar, une de Malaisie et trois de Mélanésie.

Cololejeunea hebridensis P. TIXIER sp. nov. — Fig. 1

Planta modica, albo viridis, foliicola, substrato appressa. Caules usque ad 1 cm longi, pauciter ramosi, 0,05 mm crassi, cum foliis 1,4 mm lati. Folia sub angulo 90° inserta, interseque 0,4 mm distantia. Cellulae cum trigonibus incrassionibus intermediis in cellulis basalibus. Margo sine cellulis hyalinis. Cellulae marginales 8×10 μ; cellulae partis mediae 15×15 μ; cellulae basales 30—50× ×15—20 μ. Lobus reniformis cum sinu inter lobum carenamque, caulem tegens 0,9 mm longus, 0,6 mm latus. Lobulus saccatus, leviter inflatus 0,3 mm longus, 0,2 mm latus. Apex lobuli laxe truncatus cum 3 dentibus, dente subapiculi, dente apicali, dente media. Papilla hyalina haud visa. Propagulis discoideis, 70 μ in diametro, cum 28 cellulis. Planta monoica. Flos femineus lateralis. Perianthia sub foliis floralibus. Folia floralia cum lobo 0,9 mm, 0,6 mm lato, lobuloque elongato 0,04 mm longo, 0,15 mm lato. Perianthia cum rostro notato, cum alis parvis sinibuque ventralibus, 0,7 mm alta, 0,6 mm lata. Flos masculus lateralis, sessilis, 0,4 mm altus, cum bracteis 3 jugis.

ECHANTILLON EXAMINÉ. Nouvelles Hébrides: Vaté, en forêt dense, 200—300 m, 1973, M. SCHMID s.n. (holotype PC).

Plante moyenne, blanc verdâtre, épiphylle, appliquée au support. Tiges longues

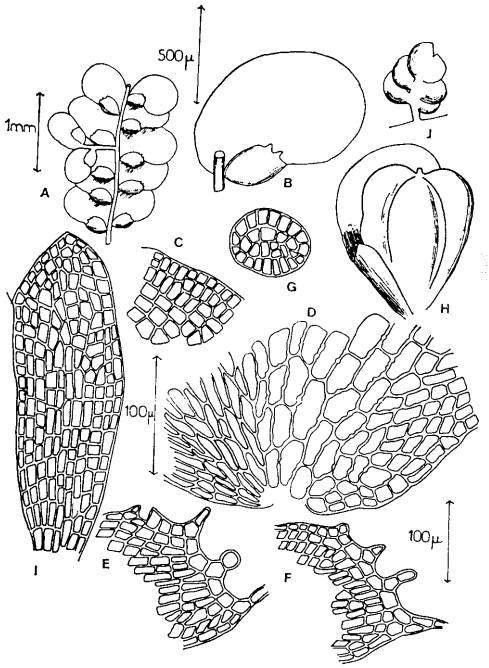

Fig. 1. *Cololejeunea hebridensis*. — A: Tige. — B: Feuille. — C: Apex du lobe. — D: Base du lobe. — E, F: Apex du lobule. — G: Propagule (p=28). — H: Périanthe. — I: Lobule de la bractée périanthaire. — J: Inflorescence mâle.

atteignant jusqu'à 1 cm; peu divisées, épaisses de 0,05 mm, larges avec les feuilles de 1,4 mm. Feuilles insérées sous un angle de 90° et distantes entre elles de 0,04 mm. Cellules présentant des trigones et des épaississements intermédiaires dans les cellules basales. Pas de marge hyaline. Cellules marginales 8×10 µ; cellules de la partie moyenne 15×15 µ; cellules basales 30—50×15—20 µ. Lobe réniforme avec un sinus entre le lobe et la carène recouvrant la tige long de 0,9 mm, large de 0,6 mm. Lobule en sac, moyennement gonflé, long de 0,3 mm, large de 0,2 mm. Sommet largement ouvert, à trois dents avec la présence d'une petite dent surapicale. Papille hyaline non observée. Propagules discoïdes, de 70 µ et avec 28 cellules. Plante monoïque. Inflorescence femelle latérale. Périanthe inclus dans les bractées périanthaires. Bractées périanthaires avec un lobe long de 0,9 mm et large de 0,6 mm, lobule allongé, long de 0,4 mm, large de 0,15 mm. Périanthe à bec bien marqué, à oreillettes et avec deux plis ventraux, haut de 0,7 mm, large de 0,6 mm. Inflorescence mâle latérale courte, implantée directement sur la tige, de 0,4 mm de haut avec 3 étages de bractées fertiles.

Nous classons cette espèce au sous-genre *Pedinolejeunea* (BENEDIX) MIZUTANI dû à son aspect macroscopique (plante très appliquée au support avec un aspect glauque brillant) et à un certain nombre de caractères microscopiques (cellules sans ornements, lobule à trois dents, etc.).

Cololejeunea mackeeana P. TIXIER sp. nov. — Fig. 2

Planta parva, foliicola, substrato appressa. Caulis longus usque ad 5 mm, pauciter ramosus, 40 µ crassus, cum foliis 1 mm latus, in sectione, 5 cellulis visis. Folia sub angulo 40° inserta interseque 0,3 mm distantia. Folia lingulata, lobo 0,4 mm longo, 0,3 mm lato. Margo irregulariter denticulatus. Cellulis cum parietibus plus aut minus tenuibus, incrassionibusque intermediis. Cellulae marginales 30—20×20—15 µ; cellulae basales 40—20× ×20—15 µ. Lobulus usque tertiam partem folii, saccatus, inflatus, cum apice late truncato, duae dentes, apicalis brevis, media plus aut minus hamata. Papilla hyalina ovalis, 20 µ longa, sub angulo. Stylus hyalinus unicellularis, 20 µ altus. Flos femineus lateralis. Folia floralia cum lobo crenulato, 0,5 mm longo, 0,17 mm lato, lobuloque 0,3 mm longo, 0,10 mm lato. Perianthia 4-plicata, denticulata, 0,6 mm alta, 0,3 mm lata. Flos masculus lateralis, 0,6—0,3 mm altus, cum bracteis 3—4 jugis.

ECHANTILLONS EXAMINÉS. Nouvelle Calédonie: Forêt de montagne sur terrain serpentineux, épiphylle sur *Rapanea*, 900 m, 15.V. 1975, MC KEE 30117 (holotype PC). — 24.IV. 1975, MC KEE 30082. — Pic du Rocher, Montagne des Sources, pente ombragée d'un entonnoir, sur feuilles de fougère, 960 m, 8.III. 1951, H. HÜRLIMANN 2394, 2395. — Montée de la "route de Gomen", vers le sommet de l'Ignambi, en forêt de montagne sur Rubiacée, 1200 m, 17.VIII. 1951, H. HÜRLIMANN 2851. — Dumbéa, vallée de la Sunshine, côté du Mont Do, sur Hymenophyllacées, 700 m, 28.VII. 1951, H. HÜRLIMANN 2748.

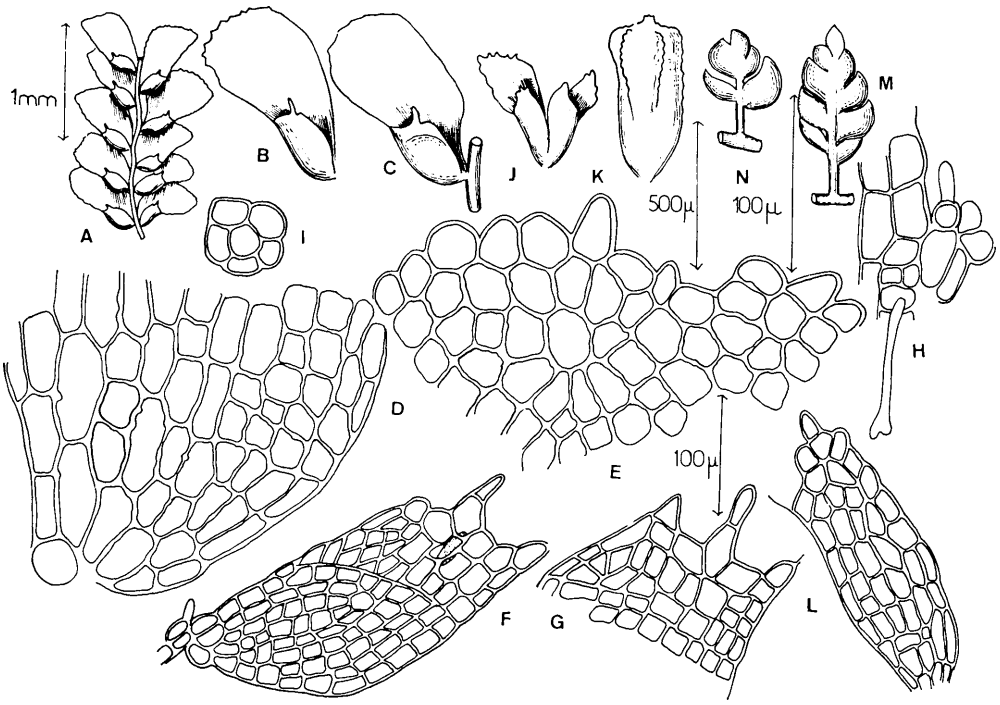

Fig. 2. *Cololejeunea mackeeana*. — A: Tige. — B, C: Feuilles. — D: Base du lobe. — E: Apex du lobe. — F, G: Lobule. — H: Base du lobule. — I: Coupe de la tige. — J: Bractées périanthaires. — K: Périanthe. — L: Lobule de la bractée. — M, N: Inflorescences mâles. — A, B, D—F, H—J, L: MAC KEE 30082. — C, G: MAC KEE 30117. — K, M, N: HÜRLIMANN 2394.

Plante petite, vert pâle, épiphylle, appliquée au support. Tige longue atteignant jusqu'à 0,5 mm, peu ramifiée, épaisse de 40 µ, large avec des feuilles de 1,4 mm, à 5 cellules en section. Feuilles insérées sous un angle de 40° et distantes entre elles de 0,3 mm. Feuille spatulée, à lobe long de 0,5 mm, large de 0,3 mm. Marge irrégulièrement dentelée, rappelant la marge de *Diplasiolejeunea cornuta* STEPHANI. Cellules à parois moyennement minces avec épaississements intermédiaires. Cellules marginales 30—20×20—15 µ; cellules basales 40—20×20—15 µ. Lobule long, dépassant le tiers de la longueur de la feuille, en sac, gonflé, largement ouvert au sommet. Deux dents au sommet, dent apicale courte, dent médiane de deux cellules plus ou moins en crochet. Papille hyaline ovale, allongée, longue de 20 µ, sous le lobule. Style hyalin unicellulaire, haut de 20 µ. Inflorescence femelle latérale. Bractées périanthaires à lobe crénelé, long de 0,5 mm, large de 0,17 mm, lobule long de 0,3 mm, large de 0,10 mm. Périanthe à quatre plis dont deux ventraux, à bords denticulés, haut de 0,6 mm, large de 0,3 mm. Inflorescence mâle latérale de 0,3 à 0,6 mm de haut et avec 3—6 paires de bractées fertiles.

Cette espèce appartient au sous-genre *Lasiolejeunea* BENEDIX, elle diffère de toutes les espèces du sous-genre du Pacifique Sud tropical.

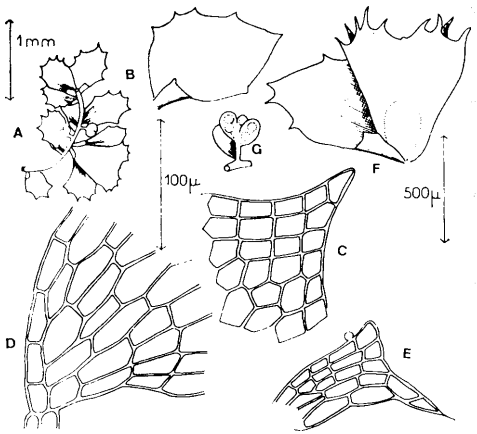

Fig. 3. *Cololejeunea plagiochiliana*. — A: Tige. — B: Feuille. — C: Apex du lobe. — D: Base du lobe. — E: Lobule. — F: Périanthe. — G: Inflorescence mâle.

Cololejeunea plagiochiliana P. TIXIER sp. nov. — Fig. 3

Planta fragilis, viridis, foliicola ad substratum appressa. Caules usque ad 1 cm longi, 0,04 mm crassi, cum foliis 0,6 mm lati, folia sub angulo 90° inserta interseque 0,4 mm distantia. Cellulae magnae, parietibus tenuibus. Cellulae marginales 20×40 µ, basalesque 60—40×20 µ. Folia scutulata, ad marginem denticulata. Lobus 0,7 mm longus, 0,4 mm latus. Lobulus reductus, circum 15 cellulis. Dens media sola visa. Papilla hyalina ad marginem lobuli, sphaerica, 10 µ in diametro. Perianthia lateralia, folia floralia, tam longiora quam perianthia, similia foliis caulis. Perianthia complanata, sine sinibus ventralibus, apice cum alis notatis, ciliatis, 0,6 mm alta, 0,4 mm lata, rostrum parvum. Flos masculus, parvus, lateralis, cum bracteis 2—3 jugis fertilibus cuique cum 2 antheridibus.

ECHANTILLON EXAMINÉ. Madagascar: Périnet, épiphylle en forêt, 3.IX. 1951, R. BENOIST s.n. (holotype PC).

Plante fragile, verte, épiphylle, appliquée au support. Tige atteignant jusqu'à 1 cm de long, épaisse de 0,04 mm, large avec les feuilles de 0,8 mm, feuilles insérées sous un angle de 90° et distantes entre elles de 0,4 mm. Cellules grandes à parois minces, cellules marginales de 20×40 µ, cellules basales 60—40×20 µ. Feuilles rhomboïdales à bords denticulés. Lobe long de 0,7 mm, large de 0,4 mm, lobule réduit à une quinzaine de cellules. Dent médiane seule marquée, papille hyaline sur le bord du lobule de moins de 10 µ de diamètre. Style non-observé. Périanthes latéraux, bractées égales au périanthe, de même forme et de même taille que les feuilles caulinaires. Périanthe aplati, sans plis ventraux, sommet à oreillettes marquées, munies de cils, plus ou moins longs, haut de 0,6 mm, large de 0,4 mm, bec peu visible. Inflorescence mâle, petite, latérale de 2—3 étages de bractées fertiles comportant 2 anthéridies.

Espèce proche de *Cololejeunea apiculata* (E. W. JONES) SCHUSTER, espèce unique, supposons nous, de la section *Apiculatae* de SCHUSTER.

Cololejeunea sophiana P. TIXIER sp. nov. — Fig. 4

Planta parva, foliicola, albo-viridis, substrato appressa. Caules usque 0,9—1 cm longi, 0,1 mm crassi cum foliis 2 mm lati, folia sub angulo 60° inserta interseque 0,4 mm distantia, parietibus cellularum tenuibus cum trigonibus incrassionibusque intermediis, margo semihyalina, cellulis exterioribus lobi hexagonalibus, 30 µ in diametro, cellulis basalibus, elongatis, 40 µ longis, 20 µ latis. Folia rotundata, lobus 0,8 mm longus, 0,5 mm latus. Lobulus rotundatus, adplanatus, saccatus 0,15 mm longus, 0,15 mm latus. Apex laxe truncatus cum duobus dentibus, apicali mediaque parvis. Papilla hyalina ovalis, ad basin proximam dentis mediae, 20 µ longa. Propaguli discoidei ovales 90 µ longi, in statu, 28 cellularis. Species monoica. Perianthia lateralia majora quam folia floralia, flora floralia cum lobo 0,8 mm longo, 0,5 mm lato, lobuloque 0,3 mm longo, 0,1 mm lato. Perianthia cordiformia complanata cum duobus sinibus ventralibus, rostro minus notato. Flos masculus lateralis, 0,5 mm altus, bracteis 4 jugis.

ECHANTILLONS EXAMINÉS. Nouvelle Calédonie: Mont Panié, forêt de pente à palmiers, épiphylle, 800 m, I.XII. 1972, M. SCHMID 248 (holotype PC), 260, 261. — Monts Dzumac, forêt basse sur péridotites, épiphylles sur *Cupaniopsis*, 15.II. 1973, J. VEILLON s.n.

Espèce dédiée à Mme SCHMID.

Plante petite, blanc verdâtre, épiphylle, appliquée au support. Tige d'environ 0,5 à 1 cm de long, épaisse de 0,1 mm, large avec des feuilles de 2 mm, feuilles insérées

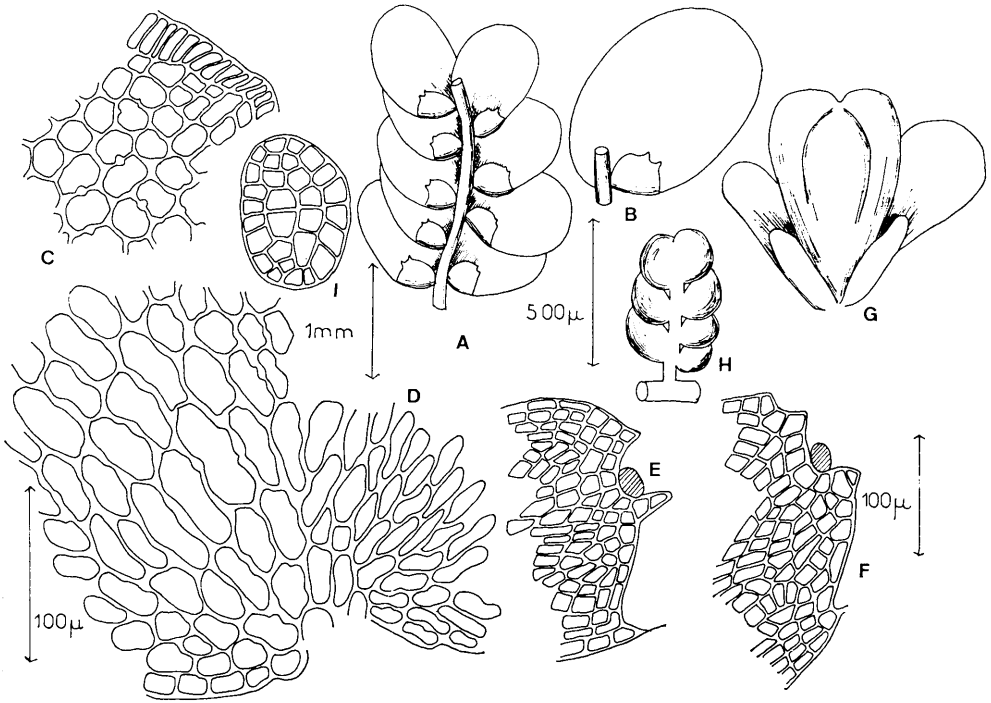

Fig. 4. *Cololejeunea sophiana*. — A: Tige. — B: Feuille. — C: Apex du lobe. — D: Base du lobe. — E, F: Apex du lobule. — G: Périanthe. — H: Inflorescence mâle. — I: Propagule (p=28).

sous un angle de 60° et distantes entre elles de 0,4 mm. Cellules à parois minces, à trigones et épaississements intermédiaires. Marge semi-hyaline constituée de cellules allongées, arrondies de 20 µ de long et de 7—8 µ de large. Cellules périphériques du lobe hexagonales de 30 µ de diamètre, cellules de la base allongées de 40 µ de long et de 20 µ de large. Lobe arrondi, recouvrant largement la tige, long de 0,8 mm, large de 0,5 mm. Apex largement tronqué avec deux dents, apicale et médiane à faible développement. Propagules en forme de disque, ovales, longues de 90 µ et avec 28 cellules. Espèce monoïque. Périanthe latéral dépassant les bractées périanthaires, bractées périanthaires à lobe long de 0,8 mm, large de 0,5 mm, lobule long de 0,3 mm et large de 0,1 mm. Périanthe cordiforme aplati avec deux plis ventraux peu marqués, haut de 0,6 mm, large de 0,4 mm. Inflorescence mâle latérale, haut de 0,5 mm, avec 4 étages de bractées fertiles.

Espèce assez difficile à classer à un des sous-genres classiques, se rapprochant du sous-genre *Pedinolejeunea* (marge et agencement de la feuille). On peut rapprocher cette espèce de *C. caledonica* STEPHANI, de *C. pulchella* (MITT.) SCHUSTER et de *C. virotiana* P. TIXIER nom.sol.

Cololejeunea stoniana P. TIXIER sp. nov. — Fig. 5

Planta parva, viridis, foliicola, substrato appressa. Caules usque ad 1 cm longi, 0,09 mm crassi, cum foliis 1,2 mm lati. Folia sub angulo 60° inserta interseque 0,4 mm distantia. Cellulis cum trigonibus incrassionibusque intermediis praecipue visis in vicinate marginis,

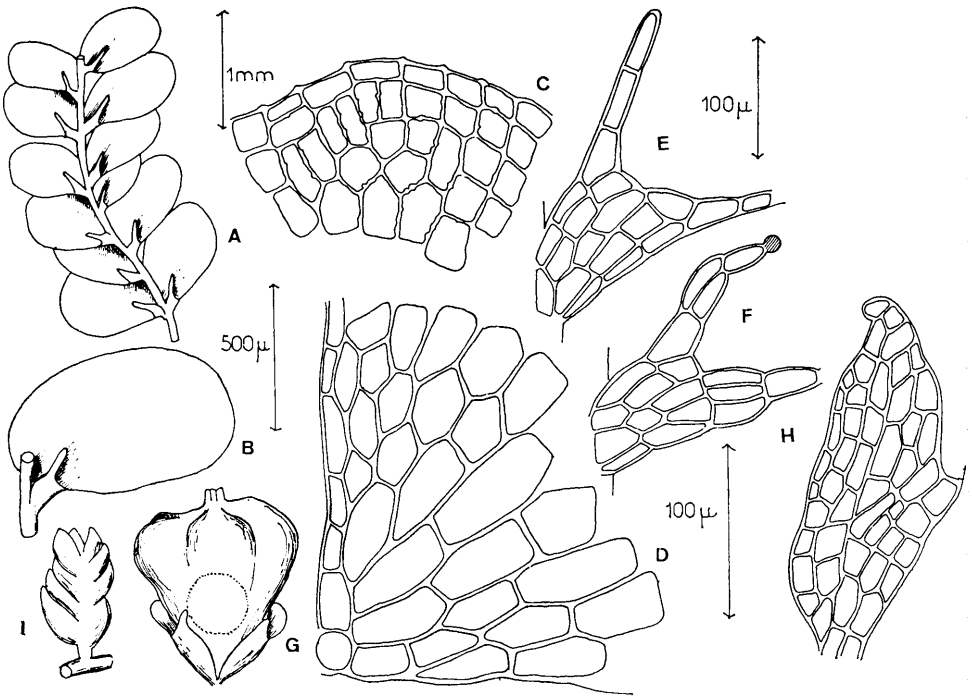

Fig. 5. *Cololejeunea stoniana*. — A: Tige. — B: Feuille. — C: Apex du lobe. — D: Base du lobe. — E, F: Lobule. — G: Périanthe. — H: Lobule de la bractée périanthaire. — I: Inflorescence mâle.

cellulis marginalibus rectangularibus 20×10 µ metientibus, cellulis basalibus majoribus 60—30×20—15 µ. Lobus obovatus fere caulem tegens 0,6 mm longus, 0,4 mm latus. Lobulus minutus, ciliatus, plus aut minus decurrens sub caule, 0,2 mm altus, 0,2 mm latus. Papilla hyalina, sphaerica, 10 µ in diametro. Planta monoica. Flores feminei laterales, foliis floralibus brevibus, cum lobo 0,3 mm longo, 0,15 mm lato, lobuloque 0,2 mm longo, 0,1 mm lato. Perianthia complanata, 4-plicata, duobus sinibus ventralibus fortiter notatis, cordiformia, 0,45 mm alta, 0,45 mm lata. Rostrum magnum. Flores masculi parvi, 0,4 mm alti, laterales, cum 3—5 jugis bractearum fertilium.

ECHANTILLON EXAMINÉ. Malaisie: Johore, Mont Ophir, brousse secondaire auprès du réservoir, 300 m, épiphylle, 20.IV. 1972, P. TIXIER 6248 (holotype PC).

Plante petite, verte, épiphylle, appliquée au support. Tige atteignant jusqu'à 1 cm, épaisse de 0,09 mm, large avec des feuilles de 1,2 mm. Feuilles insérées sous un angle de 60° et distantes entre elles de 0,4 mm. Cellules à trigones et épaississements intermédiaires surtout marqués vers la marge. Cellules marginales rectangulaires de 20×10 µ, cellules sous-adjacentes des 20×20 µ. Cellules à la base de la feuille, plus grandes, de 60—30×20—15 µ. Lobe obovale couvrant à peine la tige, 0,6 mm de long sur 0,4 mm de large. Lobule réduit, cilié plus ou moins décurrent sur la tige; haut de 0,2 mm, large de 0,2 mm. Papille hyaline sphérique de 10 µ diamètre. Inflorescences femelles latérales, bractées périanthaires courtes, lobe long de 0,3 mm, large de 0,15 mm et lobule long de 0,2 mm, large de 0,1 mm. Périanthe aplati avec 4 plis, dont deux ventraux peu marqués, cordiforme de 0,45 mm de large et de 0,45 mm de haut, bec bien visible. Inflorescence

mâle petite, de 0,4 mm de haut, latérale, avec 3—5 paires de bractées fertiles très imbriquées.

Espèce difficile à classer parmi les sous-genres *Pedinolejeunea* (BENEDIX) MIZUTANI et *Lasiolejeunea* BENEDIX. On peut rapprocher cette espèce de *C. plagiochiliana* décrite plus haut, à cause du tissu foliaire, l'agencement du lobule et des petites inflorescences mâles.

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Studies in the Lentibulariaceae

7. The Development of Endosperm and Embryo in Utricularia coerulea var. filicaulis Clarke

Saeed A. Siddiqui

SIDDIQUI, S. A. 1976 05 06. Studies in the Lentibulariaceae. 7. The development of endosperm and embryo in Utricularia coerulea var. filicaulis Clarke. — Bot. Notiser 128: 432—437. Lund. ISSN 0006-8195.

The development of endosperm conforms essentially to the Scutellaria type of SCHNARF (1917). The first division in the primary endosperm cell is transverse. The division in both primary endosperm chambers is longitudinal and the walls laid down are complete. Thus four completely partitioned cells are produced. The micropylar endosperm haustorium differentiates at the 8-celled stage of the endosperm. However, a typical chalazal endosperm haustorium does not differentiate. The mature endosperm is strongly curved. Considerable variations in the plane and in early cell divisions in the development of endosperm have been observed. Free nuclear divisions frequently occur in the cells of the young endosperm. Occasionally the endosperm develops by repeated transverse divisions.

Three types of embryogeny have been observed. Usually the embryo development conforms to the Capsella variation and occasionally to the Ruta variation of the Onagrad Type. Sometimes the proembryonic tetrad may be linear and the embryogeny appears to conform to the Chenopodiad or Solanad Type. The mature embryo does not differentiate into the usual embryonal parts. The only differentiation is the epidermis of the embryo and its meristematic apical region.

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The life history of *Utricularia coerulea* L. has been described by KAUSIK (1935, 1938) and KAUSIK and RAJU (1956). The present investigation was undertaken to compare the embryological features of the main species with that of its variety *Utricularia coerulea* var. *filicaulis* CLARKE.

The material of *U. coerulea* var. *filicaulis* was collected from Manbhum, (Bihar) India. The conventional method of embedding in paraffin wax was adopted. The sections were cut at 8—10 μ. The preparations were stained with safranin and fast green combination.

OBSERVATIONS

Endosperm

The development of the endosperm is cellular and conforms to the Scutellaria type of SCHNARF (1917). The first division in the primary endosperm cell is transverse, dividing the embryo sac into micropylar and chalazal endosperm chambers (Fig. 1 A, B). The division in the micropylar chamber precedes that in chalazal (Fig. 1 C, D). The division in both primary chambers is longitudinal and the walls laid down are complete. Thus four completely partitioned cells are produced (Fig. 1 C—E). The cells of the micropylar chamber divide earlier than the chalazal cells (Fig. 1 F). The second division in both the endosperm chambers is transverse. Thus at the 8-celled stage the endosperm cells are arranged in plate-like form (Fig. 1 G). The four cells of the middle two tiers give rise to the endosperm proper while the two micropylar cells differentiate as a 2-celled micropylar haus-

torium. The two chalazal cells are considerably elongated. However, a typical chalazal endosperm haustorium does not differentiate. The partition walls of these haustoria disappear soon and both of them become 2-nucleate.

Variations in the plane and sequence of cell divisions occur during the early stages of endosperm development. In one case the primary chalazal endosperm chamber is dividing transversely (Fig. 1 H) and after wall formation the arrangement of the four cells would have been T-shaped. In another case the primary micropylar endosperm chamber is dividing transversely, while the chalazal chamber is still undivided (Fig. 1 I). In still another case it appears that the primary micropylar endosperm chamber has divided transversely and the chalazal chamber longitudinally. There are three free nuclei in the upper daughter cell of the micropylar chamber, whereas the lower one is 1-nucleate (Fig. 1 J). Rarely is the second division in the micropylar chamber vertical instead of transverse (Fig. 1 K). In an 8-nucleate endosperm the micropylar endosperm chamber is 2-celled, the middle tier having two cells with two nuclei each. The nuclei of the two cells of the chalazal chamber are dividing (Fig. 1 L). In a 10-nucleate endosperm, one of the two cells of the micropylar tier contains three free nuclei, while the other has only one; the two cells of the middle tier have two free nuclei each and there are two 1-nucleate cells in the chalazal chamber (Fig. 1 M). Still in another case the endosperm cells are disposed in three tiers, the micropylar tier consists of two longitudinally partitioned cells with two nuclei each. In the middle tier one of the two cells has two nuclei. The nuclei in the two cells of the third tier are undergoing division (Fig. 1 N).

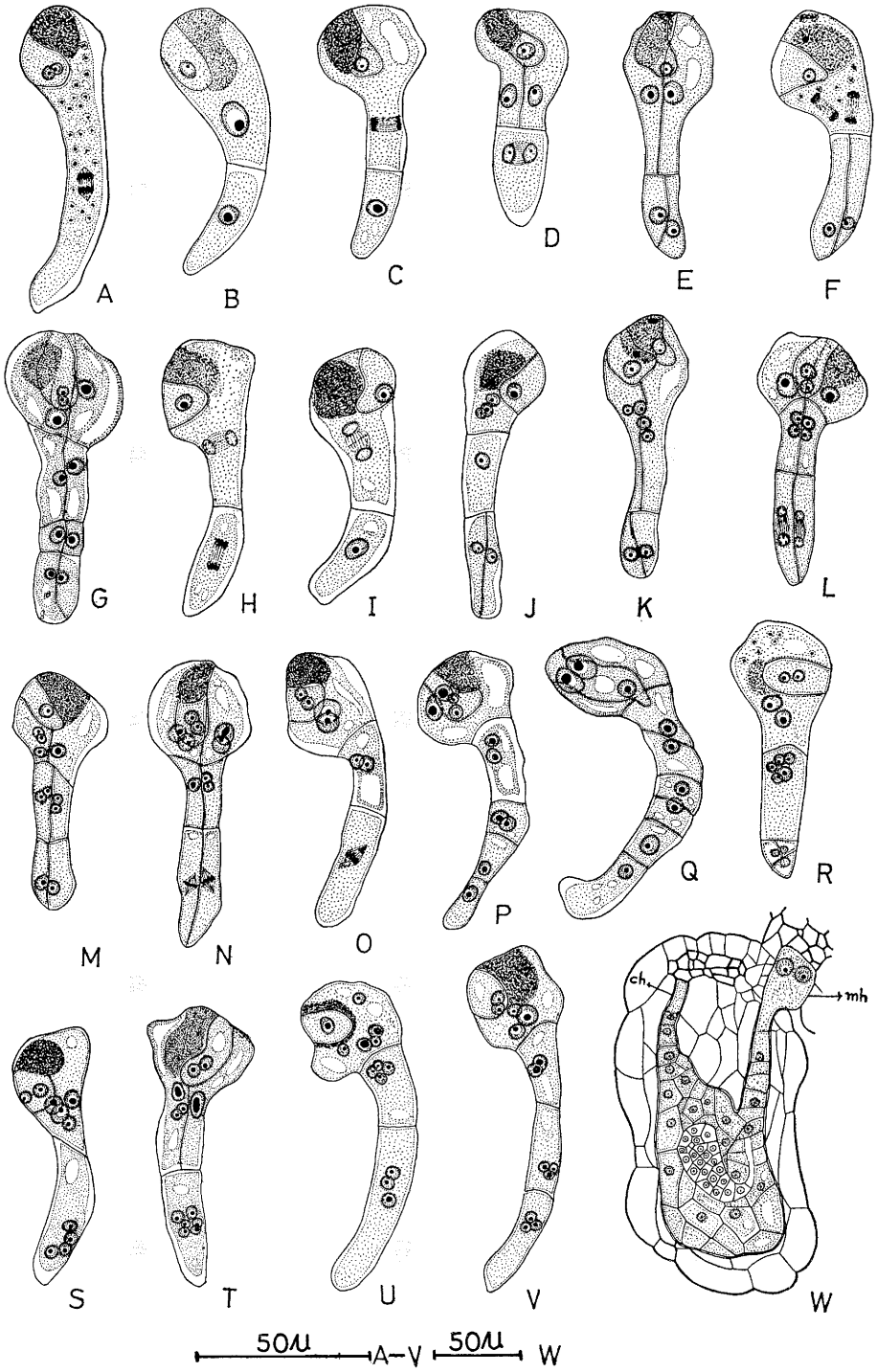
In some cases the divisions are transverse in the early stages of the endosperm development, particularly so in the chalazal chamber (Fig. 1 O—Q). In one case the chalazal endosperm chamber is dividing transversely, while two divisions have already been completed in the micropylar chamber (Fig. 1 O). In an 8-nucleate endosperm, the four cells of the chalazal chamber have a T-shaped arrangement (Fig. 1 P). In another 8-nucleate endosperm the micropylar haustorium is 2-nucleate, below which six endosperm cells are arranged in a linear fashion. The basal cell of the row is elongated and could have differentiated as a 1-nucleate chalazal haustorium (Fig. 1 Q).

An interesting phenomenon of free nuclear division has been observed in the cells of the young endosperm (Fig. 1 R—V). This is a novel feature and cannot be assigned to any principal type of endosperm development.

The micropylar haustorium is very aggressive and all the cells of placental "nutritive tissue" are consumed in the older stages of seed development. The haustorium remains 2-nucleate throughout. The so-called chalazal haustorium consists of two juxtaposed cells. It does not cause any damage to the chalazal "nutritive tissue" at any stage (Fig. 1 W). The chalazal end of the endosperm is directed towards the funicle from the very beginning. The curvature of the ovule, and consequently of the endosperm, becomes more pronounced in the advanced stages. Ultimately the endosperm assumes a U-shape (Fig. 1 W).

Embryogeny

The tubular zygotic tube contains the nucleus in its dilated apex (Fig. 2 A). The nucleus divides transversely producing a small apical cell (ca) and a long basal cell (cb; Fig. 2 B). cb divides transversely to produce the cells m and ci (Fig. 2 C), while ca divides vertically producing two juxtaposed cells, q (Fig. 2 D). Now ci divides transversely giving rise to the cells n and n' (Fig. 2 E) followed by a vertical division in m (Fig. 2 F). Later the cells of the tier q undergo vertical divisions and the quadrant stage is reached (Fig. 2 F, G).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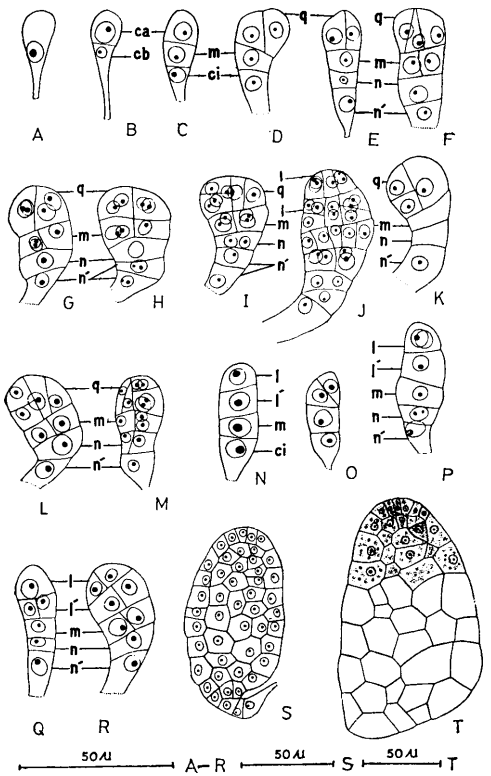

Fig. 2. Embryo development (see text).

n' divides transversely (Fig. 2 H). Meanwhile the quadrant cells segment transversely (Fig. 2 I), consequently at the octant and post octant stages the derivatives of the apical cell are disposed in two tiers, l and l' (Fig. 2 I, J). Vertical divisions in m produce four or more daughter cells (Fig. 2 I) and n undergoes two vertical divisions (Fig. 2 J). The development of the embryo could not be followed closely because further divisions in the proembryo become irregular. Presumably the daughter cells of m and ci take part in the construction of the embryonal body and a part of ci gives rise to the uniseriate suspensor (Fig. 2 J). Thus the embryogeny conforms to the Capsella variation of the Onagrad Type.

Occasionally the T-shaped proembryonic tetrad may develop in conformity to the Ruta variation of the Onagrad Type. Here one of the two juxtaposed cells of q is segmented transversely and the other one longitudinally (Fig. 2 K, L). m divides vertically and ci transversely (Fig. 2 L). In Fig. 2 M the two superposed quadrant cells divide vertically producing four cells, whereas the two cells placed side by side have not entered upon division. One of the daughter cells of m has divided vertically and the division in n has produced two juxtaposed cells (Fig. 2 M). Further stages of this type of embryo development could not be followed. However, the disposition of the proembryonic cells suggests that it had developed according to the Ruta variation of the Onagrad Type.

Sometimes a linear proembryonic tetrad develops by two transverse divisions in the zygote (Fig. 2 N). Rarely the apical cell will divide by producing an oblique wall which results in a condition intermediate between T-shaped and linear proembryonic tetrads (Fig. 2 O). The sequence of division in the tiers l and l' is variable (Fig. 2 P, Q). The tiers l and l' divide vertically giving rise to quadrants (Fig. 2 R). m divides vertically and ci transversely (Fig. 2 R). Further stages of the proembryo could not be observed. The proembryo could have belonged to the Chenopodiad or to the Solanad Type.

The embryo elongates along its axis. In a longitudinal section it appears to be elliptical and the suspensor is clearly seen (Fig. 2 S). The mature embryo rounds off at both ends and the suspensor ultimately disappears (Fig. 2 T). The embryo narrows at its apical end. There is a well-marked apical growing region represented by small

Fig. 1. Endosperm development (see text). — A—G: Normal development. — H—V: Abnormal development. — W: L. S. old ovule showing older endosperm and the embryo. — mh = micropylar haustorium; ch = chalazal haustorium.

Table 1. The present investigation reveals that *U. coerulea* var. *filicaulis* differs from *U. coerulea* in the following embryological features.

U. coerulea var. *coerulea*	*U. coerulea* var. *filicaulis*
The walls laid down in the two primary endosperm chambers are incomplete, thus four incompletely partitioned cells are produced.	The walls laid down are complete and result in four completely partitioned cells.
A 2-nucleate chalazal endosperm haustorium differentiates.	A typical chalazal endosperm haustorium does not differentiate.
The wall of the micropylar haustorium dissolves. The cells of the placental nutritive tissue break down and their contents are incorporated into the cytoplasm of the haustorium.	The haustorium is quite aggressive. The wall of the micropylar haustorium persists. The contents of the cells of the placental nutritive tissue are not incorporated into the haustorium.
Repeated transverse divisions do not occur during endosperm development.	Repeated transverse divisions occur during early stages of the endosperm development.
Free nuclear divisions do not occur.	Free nuclear divisions frequently occur in the cells of the young endosperm.
The embryogeny conforms to the Ruta variation of the Onagrad Type.	The embryogeny conforms to the Capsella variation of the Onagrad Type.

meristematic cells (Fig. 2 T). The remaining part of the embryo consists of large and polygonal cells which are rich in starch grains and some food material of unknown chemical nature. The usual embryonal parts are not differentiated in the mature embryo.

Irregularities during the early developmental stages of the proembryo and the lack of differentiation of the usual embryonal parts in the mature embryo does not allow a precise classification of embryogeny in the species. However, on the basis of early cell divisions in the development of the proembryo it appears that the embryogeny in the species generally conforms to the Capsella, occasionally to the Ruta variation of the Onagrad Type and sometimes to the Chenopodiad Type or Solanad Type.

DISCUSSION

The development of endosperm conforms to the Scutellaria type of SCHNARF (1917) in the investigated species of *Utricularia*. In *U. flexuosa* (KHAN 1954), *U. reticulata* (KAUSIK & RAJU 1955), *U. stellaris* var. *inflexa*, *U. arcuata* and *U. uliginosa* (FAROOQ 1964, 1965 a, 1965 b) and *U. stellaris* (FAROOQ & SIDDIQUI 1967) the partition walls laid down at the time of first division in the primary endosperm chambers are incomplete towards their micropylar and chalazal ends respectively, whereas in *U. coerulea* var. *filicaulis* these walls are complete, thus four completely partitioned cells are produced. In *U. striatula* (FAROOQ 1966) the two cells at the chalazal end of the endosperm are completely partitioned, while those in the micropylar chamber are incompletely partitioned.

The occasional occurrence of repeated transverse divisions during the early stage of endosperm development as described here has been reported in *U. flexuosa* (KHAN 1954) and *U. vulgaris americana* (FAROOQ & SIDDIQUI 1966). From outside the family, *Villarsia reinformis* (STOLT 1921) and *Phacelia congesta* (SVENSSON 1925) may be cited as examples in which this type of endosperm development occurs normally.

Frequent free nuclear divisions at different stages of endosperm development as

described here rarely occur in *U. scandens* (FAROOQ & BILQUIS 1966 b) and *U. arcuata* (FAROOQ 1965 a). This type of endosperm development resembles that of *Hyoscyamus niger* (SVENSSON 1926).

The Capsella variation of the Onagrad Type of embryogeny as described in *U. coerulea* var. *filicaulis* has been reported earlier in *U. uliginosa* and *U. striatula* (FAROOQ 1965 b, 1966), while in *U. coerulea* (KAUSIK & RAJU 1956) and *U. scandens* (FAROOQ & BILQUIS 1966 a) the embryogeny conforms to the Ruta variation of the Onagrad Type. The Chenopodiad Type of embryogeny usually occurs in *U. stellaris* var. *inflexa* (FAROOQ 1958), whereas its occasional occurrence has been reported in *U. coerulea* (KAUSIK & RAJU 1956) and *U. scandens* (FAROOQ & BILQUIS 1966 a) and rarely in *U. coerulea* var. *filicaulis*. Thus it is concluded that the embryogeny in the genus *Utricularia* is variable.

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Contribution To the Embryology of Celsia coromandeliana Vahl. With a Discussion On Its Affinities With Verbascum thapsus L.

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The development of the endosperm, embryo and testa of *Celsia coromandeliana* VAHL. is described. A single hypodermal archesporial initial functions as the megaspore mother cell. The tetrad is linear, and the chalazal megaspore develops into an 8-nucleate embryo sac of the Polygonum type. The endosperm is cellular with 4-celled micropylar and chalazal haustoria. The endosperm is ruminate due to unequal elongation of a few endothelial cells. The embryogeny conforms to the Onagrad type. The testa of the mature seed consists of epidermis, compressed middle layers and an endothelium with thickened inner tangential and radial walls.

The morphology and embryology of *Celsia coromandeliana* indicates that it is distinct from *Verbascum thapsus* L.

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Celsia coromandeliana occurs in India throughout the plains and also in the Himalayan regions upto 1525 metres extending to Afghanistan, Burma and China (DUTHIE 1960). SANTAPAU (1950) considered *Celsia coromandeliana* and *Verbascum thapsus* to be cogeneric and suggested that the former is a synonym for the latter. FERGUSON (1971) also merged *Celsia* with *Verbascum* because according to him the presence of four or five stamens is not always constant and some species of both *Celsia* and *Verbascum* have four stamens with a staminode. The present investigation was undertaken to study the embryology of *C. coromandeliana* and to resolve on comparative exomorphic and embryological features whether this taxon is *pro parte V. thapsus.*

MATERIAL AND METHODS

Buds, flowers and fruits of *Celsia coromandeliana* were collected from Yamuna Banks, Delhi, India and fixed in Formalin-acetic-alcohol or Carnoy's fluid and subsequently stored in 70 per cent ethanol. The material was dehydrated and cleared by conventional methods and embedded in paraffin wax. Seeds were immersed for a week in a mixture of 10 per cent glycerine and 70 per cent ethyl alcohol (1:1 v/v) before dehydration which rendered the seeds quite soft, suitable for sectioning. Serial sections were cut between 5 and 12 microns thick and stained with either Safranin-fast green or Heidenhain's iron alum haematoxylin with a counterstain of fast green.

OBSERVATIONS

External Morphology

Celsia coromandeliana grows in moist shady places. The inflorescence is a panicle bearing numerous small, yellow, bisexual flowers. Calyx and corolla are pentamerous (Fig. 1 A, B). The androecium consists of four epipetalous stamens (Fig. 1 B). Each stamen has a dorsifixed, reniform and bilobed anther (Fig. 1 C),

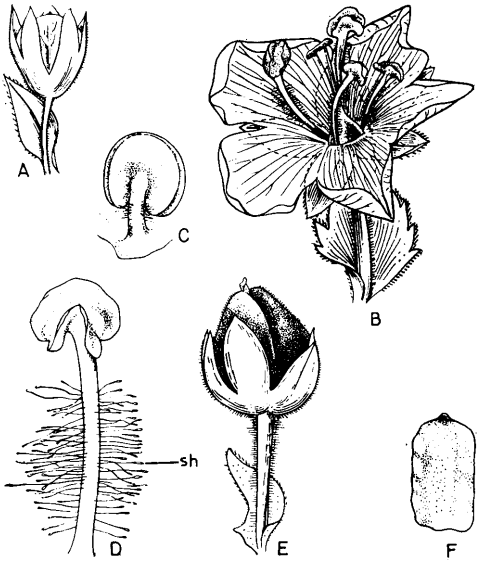


Fig. 1. *Celsia coromandeliana* (sh, staminal hairs). — A: Young bud. — B: Flower. — C: Young stamen. — D: Dehisced stamen. Unicellular hairs are present on the filaments. — E: Fruit with persistent calyx. — F: Mature seed. — A—B, E ×3, C—D ×6, F ×20.

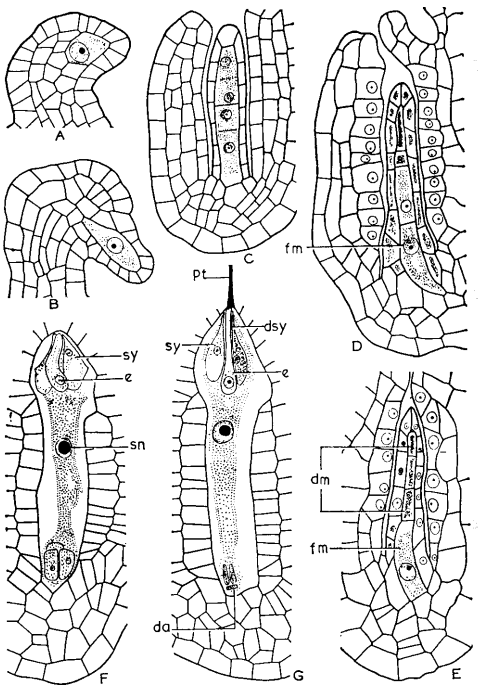


Fig. 2. *Celsia coromandeliana* (dm, degenerating megaspore; fm, functional megaspore; da, degenerating antipodal cells; dsy, degenerating synergids; e, egg; pt, pollen tube; sn, secondary nucleus; sy, synergid). — A: Archesporial initial. — B: Megaspore mother cell. — C: Dyad in division. — D—E: Megaspore tetrads; note degeneration of non-functional megaspores from the micropylar end and curvature of the functional megaspore. — F—G: Embryo sacs at maturity. In G, the pollen tube enters through the micropyle and discharges its contents into the degenerating synergid. A—E ×340, F—G ×550.

the filaments of the mature anthers are densely covered with hairs (Fig. 1 D). The gynoecium is bicarpellary and syncarpous with numerous ovules. The style is long and ends in a simple bilobed stigma (Fig. 1 B). The ovary is bilocular with axile placentation at the base but becomes unilocular with parietal placentation at the apex. The fruit is a septicidal capsule with a persistent, hairy calyx (Fig. 1 E), while the seeds are oblong and contain ruminate endosperm (Fig. 1 F).

Megasporangium and Megasporogenesis

The ovular primordia arise as small protuberances on the massive placentae. Differential rates of growth of each primordium makes the developing ovule curve towards the direction of the placenta. Usually a single hypodermal archesporial cell with prominent nucleus and dense cytoplasm differentiates (Fig. 2 A). It does not cut off a parietal cell but functions directly as the megaspore mother cell (Fig. 2 B). Occasionally two archesporial initials are observed. The megaspore mother cell elongates considerably and then undergoes meiosis resulting in a dyad. Meiosis II in both these cells is simultaneous (Fig. 2 C) forming a linear tetrad of megaspores (Fig. 2 D, E). The non-functional micropylar megaspores degenerate (Fig. 2 D, E) and only the chalazal member functions (Fig. 2 E).

Female Gametophyte

The functional megaspore elongates and becomes slightly curved (Fig. 2 D, E). Many tiny vacuoles appear in the cytoplasm, the megaspore nucleus then undergoes three mitotic divisions and produces the 8-nucleate embryo sac. The mature embryo sac comprises an egg apparatus, a secondary nucleus and three antipodal cells (Fig. 2 F). The egg is pyriform, the synergids have prominent hooks, two polar nuclei fuse to form the secondary nucleus and the antipodal cells are uninucleate. The development of the embryo sac conforms to the Polygonum type. Pollen tubes are frequently seen in the micropyle (Fig. 2 G) and although the actual process of double fertilization has not been observed, the pollen tube entry into the embryo sac destroys one of the synergids. The antipodal cells degenerate.

Endosperm

The primary endosperm nucleus lies in the centre of the embryo sac (Fig. 3 A, B) and divides prior to the division of the zygote. The division is followed by a transverse wall, resulting in micropylar and chalazal chambers (Fig. 3 C). The development of the endosperm is cellular. The first two divisions in the micropylar and chalazal chambers are longitudinal (Fig. 3 D), the four cells of the chalazal chamber form the chalazal haustorium directly, whereas the four elongated micropylar cells divide transversely (Fig. 3 E). The derivatives of the upper tier form the four-celled micropylar haustorium while the lower four cells divide in longitudinal and transverse planes to form the endosperm proper (Fig. 3 F, I).

The four-celled chalazal haustorium is short and non-aggressive. It has one nucleus in each cell (Fig. 3 F, J) and is early to organize and early to degenerate. The four-celled micropylar haustorium is also non-aggressive with uninucleate cells (Fig. 3 F, H). The remnants of the micropylar and chalazal haustoria persist in the mature seed (Fig. 5 G).

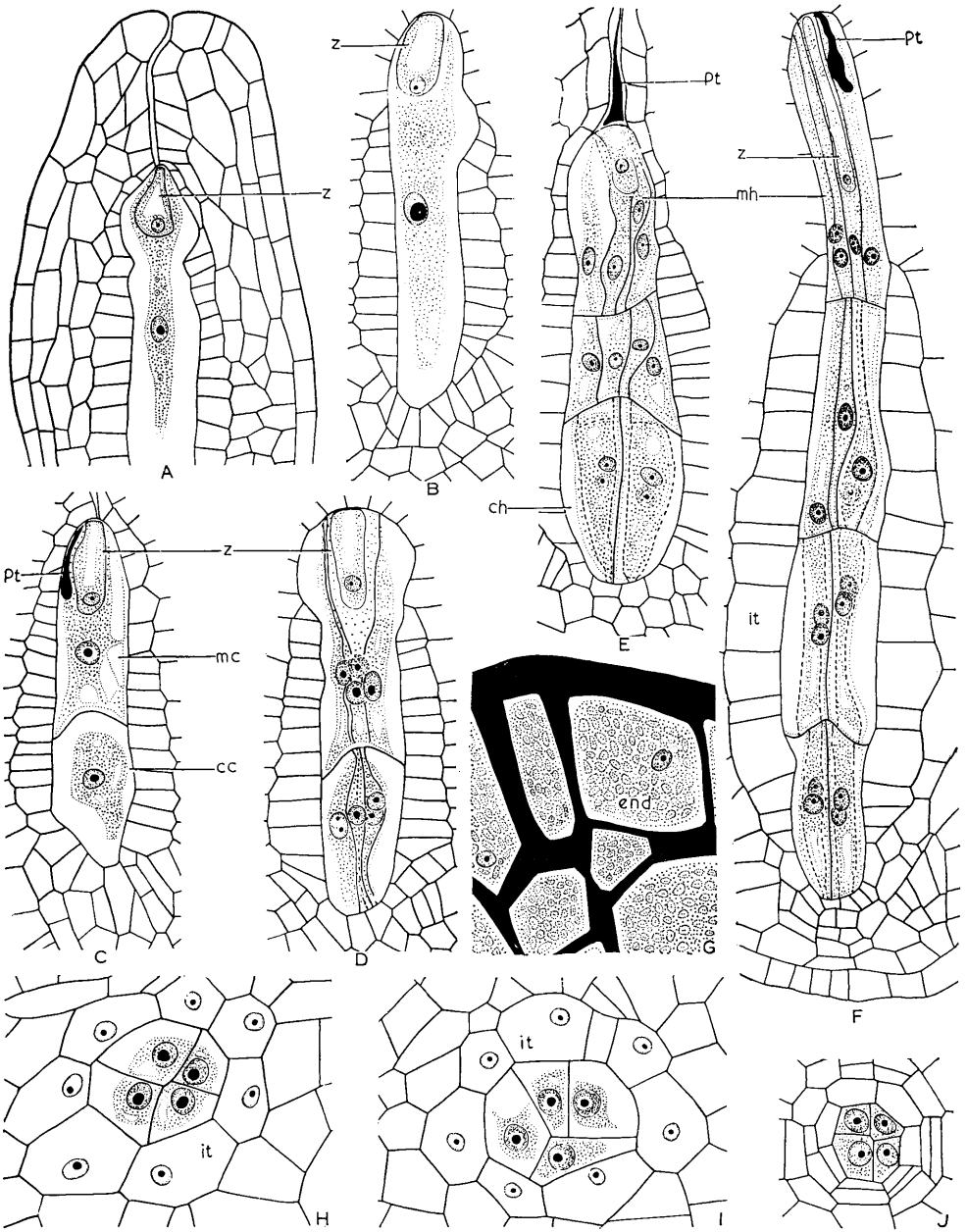
The endothelium is a prominent layer and increases in size after fertilization (Fig. 5 F). Some endothelial cells elongate both in radial and tangential directions causing the surface of the endosperm to become wavy and irregular (Fig. 5 H). The endosperm is thus at maturity, ruminate (unpublished observation) and its cells are full of reserve food materials (Fig. 3 G).

Embryogenesis

The zygote elongates considerably (Fig. 4 A), becomes tubular, enters the central mass of endosperm and remains quiescent for a long time. The nucleus migrates and occupies the distal end of the zygote. A transverse division produces the terminal cell ca and basal cell cb (Fig. 4 B). The next vertical division occurs in the terminal cell resulting in two juxtaposed cells (Fig. 4 C, D). The basal cell cb segments transversely to form two superposed cells m and ci, resulting in a proembryonal tetrad arranged in an ⊥-shaped manner (Fig. 4 D).

Each of the two derivatives of the terminal cell ca, divides vertically at right angles to the previous plane giving rise to the quadrant q (Fig. 4 E, F). The four cells of the quadrant engender the octant by transverse divisions (Fig. 4 G, H). The cells of the octant are thus disposed in two tiers of four cells each, designated as l and l' (Fig. 4 H). Division in the tier l occasionally lags behind that of l' during

Fig. 3. *Celsia coromandeliana* (cc, chalazal chamber; ch, chalazal haustorium; end endosperm; it, integumentary tapetum; mc, micropylar chamber; mh, micropylar haustorium; pt, pollen tube; z, zygote). — A: Longitudinal section of seed showing zygote, primary endosperm nucleus and seed coat. — B—D: Longitudinal sections of seeds to show central cell, two- and eight-celled endosperm respectively. The chalazal chamber forms the



4-celled chalazal haustorium directly in D. — E—F: Same as above. The micropylar chamber segments transversely and the upper tier forms the micropylar haustorium in E. The middle tier forms the endosperm proper by further transverse and longitudinal divisions, in F. — G: A few cells of the mature endosperm enlarged to show thickenings and reserve food materials. — H—J: Transections of endosperm at the levels of micropylar haustorium (H), middle region (I) and chalazal haustorium (J). — A—J ×560.

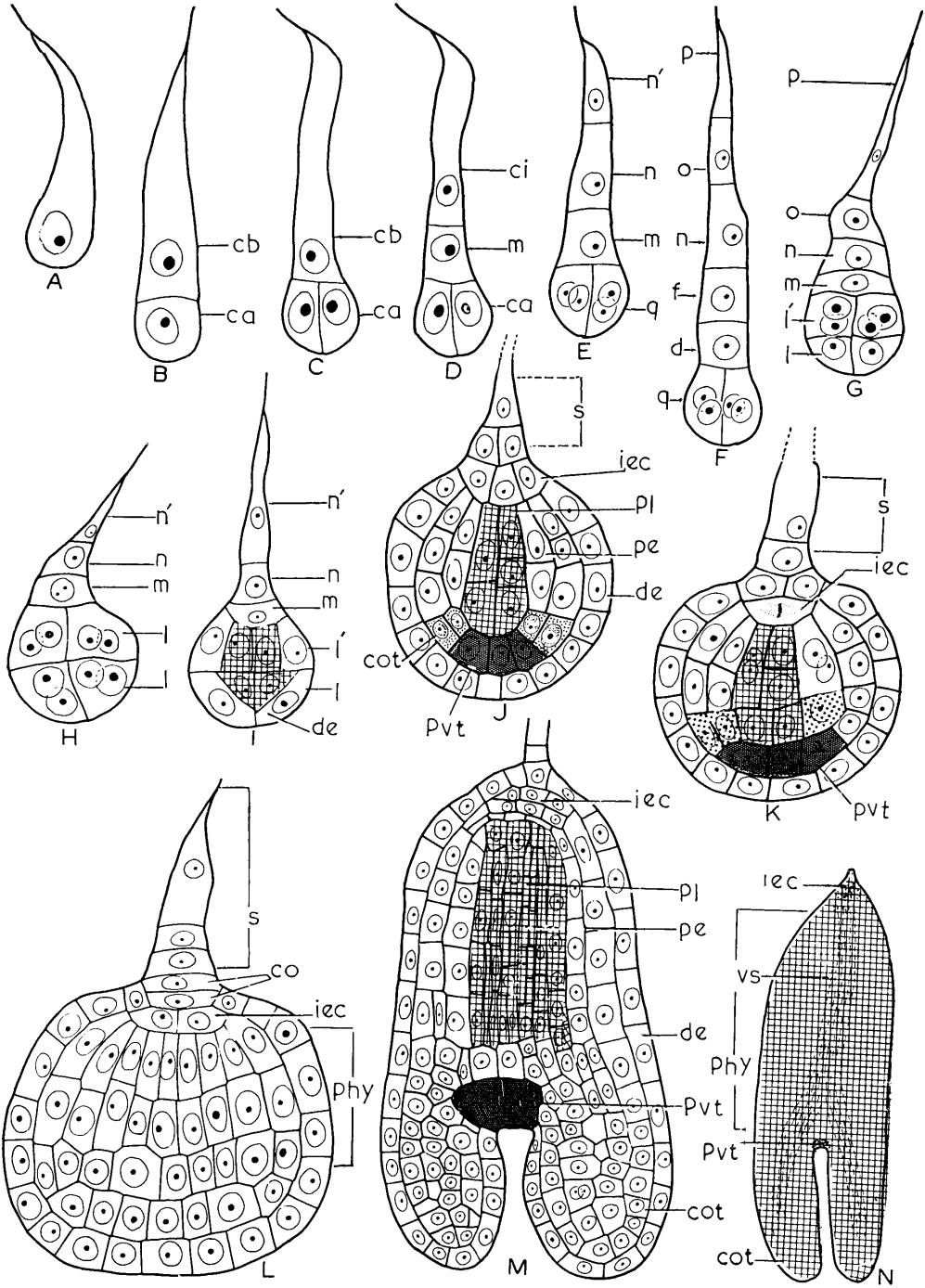
the formation of the octant (Fig. 4 G). Periclinal divisions occur simultaneously in both the tiers 1 and 1' demarcating dermatogen (de) from the inner group of cells (Fig. 4 I, J). The inner group of cells of tier 1' gives rise, by vertical divisions to periblem and plerome (pe, pl Fig. 4 J). Longitudinal and transverse divisions in the inner group of cells of tier 1 yield two cotyledonary initials (cot) and an embryo apex (epicotyl, pvt), while those of 1' form the hypocotyledonary region of the proembryo (phy, Fig. 4 J—L).

Meanwhile the uppermost cell ci of the proembryonal tetrad undergoes a transverse division resulting in cell n and n' (Fig. 4 E). The division in the cell ci is not constant and produces either a long or a short suspensor (Fig. 4 F—I, L). The middle cell m sometimes divides to form d and f (Fig. 4 F) but it usually undergoes a few vertical divisions forming 2 or 3 juxtaposed cells, and contributes to the root cortex and root cap (iec, co) (Fig. 4 J—L). The globular proembryo (Fig. 4 L) differentiates into the heart-shaped and dicotyledonous embryo (Fig. 4 M, N). The mature embryo comprises two prominent cotyledons, epicotyl, hypocotyl and root apex. The embryogeny corresponds to the Onagrad type (MAHESHWARI 1950).

Seed Coat

In the young ovule, initiation of integument occurs at the archesporial cell stage (Fig. 5 A). At megaspore mother cell stage (Fig. 5 B), the integument comprises three layers of parenchymatous cells at the top, and four layers below. The outer epidermis at this stage is well differentiated and divides periclinally. The number of layers comprising the testa remain unchanged at dyad stage. Cells of the inner epidermis however, show pronounced radial elongation, with uniform, dense cytoplasm and prominent nuclei (Fig. 5 C). The seed coat consists of five layers of cells during the functional megaspore stage and the cells of the outer epidermis undergo expansion (Fig. 5 D). The seed coat is six or seven layers thick at mature embryo sac stage (Fig. 5 E, F). Cells between the two epidermes show scanty cytoplasm and are highly vacuolated. Development of the endothelium does not keep pace with the expansion of the embryo sac and hence does not fully cover the micropylar and the chalazal ends. At about the two-cell stage of the proembryo, cells comprising testa remain unchanged but the endothelial cells undergo unequal expansion forming larger and smaller cells causing thus rumination of the endosperm (Fig. 5 G, H). Subsequently the cell layers between the inner and outer epidermes degenerate. The outer tangential wall of the endothelial cells is devoid of thickenings whereas the inner tangential wall shows thickenings which almost occupy two-thirds of the cell space. The endosperm cells bordering the endothelium also develop thickenings (Fig. 5 H). Histochemical studies are necessary to ascertain the nature of the thickenings in the endothelium and endosperm. The cells of the outer epidermis show degenerating nuclei. In the mature seed the testa is represented

Fig. 4. *Celsia coromandeliana* (co, initials of root cap; cot, cotyledon; de, dermatogen; iec, initials of root cortex; pe, periblem; pl, plerome; phy, hypocotyledonary region; pvt, epicotyledonary region; s, suspensor; vs, vascular strand). — A: Zygote. — B: Two-celled proembryo. — C—D: Three- and four-celled proembryos; terminal cell (ca) segments with a vertical wall whereas the basal cell (cb) divides transversely. — E—F: Quadrant stages of proembryos. — G—H: Octant stages of proembryos. Note the precocious division in the tier 1' in G. — I: Proembryo showing demarcation of dermatogen (de) with the onset of periclinal divisions in tiers 1 and 1'. — J—L: Stages leading to the formation of globular embryos. The periblem and plerome are demarcated. Note the initiation of epicotyl (pvt) and cotyledonary loci (cot) in J and K. — M—N: Dicotyledonous embryos. The procambium is well developed in N. — A—L ×680, M ×415, N ×170.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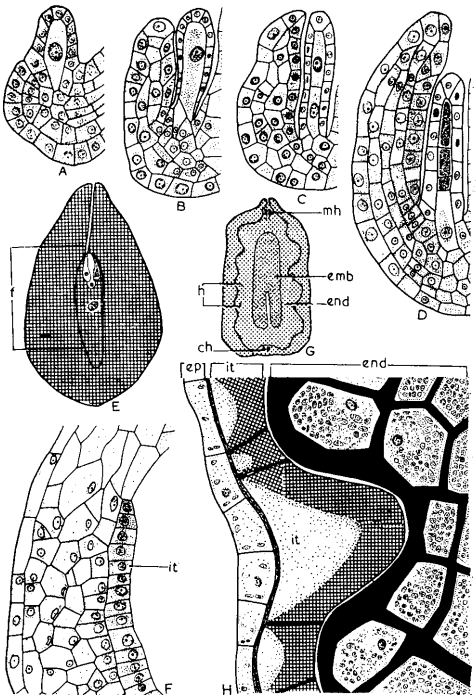

Fig. 5. *Celsia coromandeliana* (ch, chalazal haustorium; ep, epidermis; emb, embryo; end, endosperm; it, integumentary tapetum; mh, micropylar haustorium). — A: Longitudinal section of ovule showing the initiation of integument at the archesporial cell stage. — B—C: Longitudinal sections of ovules at megaspore mother cell and dyad stages; integument is 3- or 4-layered. The endothelium is well differentiated at dyad stage. — D: Five-layered testa at functional megaspore stage. The outer epidermis shows cell expansion. — E—G: Median longitudinal sections of ovules at embryo sac and dicotyledonous embryo stages. — F: Magnified view of portion marked f in E showing epidermis with elongated cells containing meagre cytoplasm. Cells of middle layers also present poor cytoplasm whereas the cells of endothelium reveal dense cytoplasm with prominent nuclei. — H: Magnified view of the region marked h in G showing tenuous epidermis, crushed middle layers, thickened and prominent integumentary tapetum. The inner tangential and radial walls of endothelium show thickenings. Note that endosperm cells (end) bordering the endothelium also show prominent thickenings. — A—D, F, H, ×350, E ×140, G ×35.

by a tenuous epidermis, degenerated middle layers and a well developed but irregular endothelium (Fig. 5 H).

DISCUSSION

Megasporangium and Megasporogenesis

The ovule in *Celsia coromandeliana* is unitegmic, anatropous and tenuinucellate as in many genera of the Scrophulariaceae. This is in contrast to the hemianatropous condition met with in *Euphrasia arctica* (Arekal 1963 a), *Melampyrum arvense* and *M. nemorosum* (Tiagi 1965); campylotropous in *Torenia fournieri* (Guilford & Fisk 1952), *Pedicularis sylvatica* (Berg 1954), *Orthocarpus luteus* (Arekal 1963 a), *Rhinanthus major* and *R. serotinus* (Tiagi 1966). Arekal (1963 a) states that in *Melampyrum lineare* the inner epidermis of integument around the micropylar part of the embryo sac breaks down and the hypodermis takes over the function of integumentary tapetum. In *Celsia coromandeliana* however, the innermost layer of the integument functions as endothelium and does not entirely surround the micropylar and chalazal parts of the embryo sac.

In *Celsia coromandeliana*, the mode of female gametophyte development is monosporic, Polygonum type. This holds true for *Alectorolophus hirsutus, A. minor, Lathraea squamaria,* and *Tozzia alpina* (Schmid 1906), *Centranthera hispida* and *Rhamphicarpa longiflora* (Krishna Iyengar 1942 b), *Pedicularis sylvatica* (Berg 1954), *Euphrasia arctica* and *Orthocarpus luteus* (Arekal 1963 a). In *Linaria ramosissima* occurrence of bisporic Allium type (Arekal & Raju 1964), in *Alectra thomsoni* coexistence of both monosporic, Polygonum and bisporic Allium types of embryo sacs (Vijayaraghavan & Ratnaparkhi 1972) are reported. Schmid (1906) reported monosporic Polygonum type in *Melampyrum pratense* and *M. silvaticum* but Arekal (1963 a) observed tetrasporic 7-nucleate embryo sac in *M. lineare.*

Interestingly in *M. pratense, M. silvaticum* (SCHMID 1906) and *M. lineare* (AREKAL 1963 a), fusion of polar nuclei does not occur. The antipodal cells in *C. coromandeliana* degenerate before fertilization. This is in contrast to *Pedicularis palustris* (BALICKA-IWANOWSKA 1899), where they persist even after fertilization. SCHMID (1906) observed two antipodal cells in *Pedicularis caespitosa* one of which is larger and binucleate. In *Lathraea squamaria* (GLIŠIĆ 1932) and *Orthocarpus luteus* (AREKAL 1963 a), the antipodal cells are large and persist even during seed development whereas in *Melampyrum lineare*, degenerated nuclei constitute the antipodals (AREKAL 1963 a).

The embryo sac extends towards the micropyle in *Alectorolophus minor, Lathraea squamaria* (SCHMID 1906), *Pedicularis zeylanica* (KRISHNA IYENGAR 1942 b), *P. sylvatica* (BERG 1954) and *Euphrasia arctica* and *Orthocarpus luteus* (AREKAL 1963 a) while it becomes extra-micropylar in *Vandellia hirsuta, Torenia cordifolia* and *T. hirsuta* (KRISHNA IYENGAR 1940 a, 1941). *Celsia coromandeliana* presents no tendencies of an extra-micropylar development of female gametophyte.

Endosperm and Haustoria

The endosperm in the Scrophulariaceae is cellular resulting in two superposed chambers — micropylar and chalazal. The sequence of the further divisions however, varies in different genera of this family. The next division in the micropylar chamber is transverse in *Anticharis linearis* (JOSHI & VARGHESE 1963), but vertical in *C. coromandeliana* as in *Pedicularis sylvatica* (BERG 1954) and *Alectra thomsoni* (VIJAYARAGHAVAN & RATNAPARKHI 1972). Another vertical division occurs in the micropylar chamber in *C. coromandeliana*. Such a condition is reported in *Isoplexis canariensis, Verbascum thapsus* (KRISHNA IYENGAR 1939, 1942 a), *Lindernia hyssopioides* and *Scoparia dulcis* (AREKAL et al. 1970, 1971).

The micropylar chamber then undergoes transverse division in *C. coromandeliana* and four cells of the upper tier develop into the 4-celled micropylar haustorium. The micropylar haustorium is, however, two-celled but each cell is binucleate in *Striga orobanchoides* and *S. euphrasioides* (TIAGI 1956) and *Alectra thomsoni* (VIJAYARAGHAVAN & RATNAPARKHI 1972). In *Euphrasia arctica, Orthocarpus luteus* and *Melampyrum lineare* (AREKAL 1963 a), division in the micropylar chamber is by an incomplete vertical wall. The micropylar haustorium in *Melampyrum arvense* and *M. nemorosum* (TIAGI 1965) and *M. lineare* (AREKAL 1963 a) produces many tubular extensions which pass through the micropyle whereas in *Alectorolophus hirsutus* (SCHMID 1906) and *Orthocarpus luteus* (AREKAL 1963 a) the micropylar haustorium extends in the direction of the funiculus. The micropylar haustorium usually exhibits elaborate features as compared to the chalazal haustorium. It is highly branched in *Alonsoa* sp., bulbous in *Isoplexis canariensis,* club-shaped in *Bonnaya tenuifolia* (KRISHNA IYENGAR 1937, 1939, 1940 b), tubular and filiform in *Melampyrum silvaticum* (SCHMID 1906) and U-shaped in *Orthocarpus luteus* (AREKAL 1963 a), but simple and non-aggressive in *Celsia coromandeliana* (present work).

The chalazal chamber develops directly into the chalazal haustorium. Variations are reported regarding the number of cells and nuclei taking part in the formation of chalazal haustorium. Uninucleate, single-celled haustorium is recorded in *Chaenorrhinum minus* (AREKAL 1963 c), binucleate, single-celled in *Orthocarpus luteus, Gerardia pedicularia, Veronica serpyllifolia* (AREKAL 1963 a, 1964, 1966), *Melampyrum arvense, M. nemorosum, Rhinanthus major, R. serotinus* (TIAGI 1965, 1966), two-celled in *Vandellia hirsuta* (KRISHNA IYENGAR 1940 a), *Calceolaria mexicana* (AREKAL & RAJU 1971), incompletely two-celled in *Chelone glabra* (AREKAL 1963 b) but four-celled, each cell

being uninucleate in *Verbascum thapsus* (KRISHNA IYENGAR 1942 a), *Microcarpaea* (AREKAL & SWAMY 1974) and *Celsia coromandeliana* (present work).

Occurrence of secondary haustoria is an important feature met with in some members of the family. The haustoria arise from the micropylar end in *Centranthera hispida* (KRISHNA IYENGAR 1942 b) and *Alectra thomsoni* (VIJAYARAGHAVAN & RATNAPARKHI 1972) but no such secondary haustoria develop in *Celsia coromandeliana*. COOK (1924), PERSIDSKY (1934) and AREKAL (1963 c), have reported absence of micropylar haustorium in *Linaria vulgaris, L. genistaefolia* and *Chaenorrhinum minus* respectively, whereas CRÉTÉ (1950 a, b), reported that the chalazal chamber never develops into the chalazal haustorium in *Nemesia floribunda* and *N. melissaefolia*.

The endosperm cells in *C. coromandeliana* adjacent to the haustoria are small when compared to those in the middle region, but in *Verbascum thapsus* the endosperm cells adjacent to the micropylar and chalazal haustoria are larger and exhibit rich protoplasm (unpublished observations).

Embryogenesis and Testa

The present investigation on *Celsia coromandeliana* is the first report on embryogeny in this plant. The development follows the Crucifer type (MAHESHWARI 1950) as in *Euphrasia arctica* (AREKAL 1963 a), *Pedicularis sylvatica* (BERG 1954), *Striga orobanchoides* (TIAGI 1956), *Mimulus ringens* (AREKAL 1965) and *Scoparia dulcis* (AREKAL et al. 1971). In *Ellisiophyllum pinnatum* it follows the Solanad type (YAMAZAKI 1957).

In *Anticharis linearis* (JOSHI & VARGHESE 1963), hypodermal integumentary cells undergo periclinal divisions and all layers of the integument except the endothelium form the testa. In *Pedicularis sylvatica* (BERG 1954), the seed has in its micropylar end a white spongy 'elaiosome' derived from the micropylar haustorium and a dark warty outgrowth at the chalazal end. The testa in *Melampyrum arvense* (TIAGI 1965) is made up of the thickened epidermis and a few degenerated hypodermal layers, whereas in *Euphrasia arctica* and *Orthocarpus luteus* (AREKAL 1963 a) it comprises cuticularized epidermis and thickened endothelium. In *Celsia coromandeliana* (present work), the epidermal cells undergo elongation, the middle layers are crushed and thickened endothelial cells elongate radially and tangentially at many places causing unevenness in the testa.

RELATIONSHIP OF CELSIA COROMANDELIANA WITH VERBASCUM THAPSUS

The morphological, anatomical and embryological features of *Celsia coromandeliana* are compared with the available data on *Verbascum thapsus* in Table 1 (for literature see FERGUSON 1971, HÅKANSSON 1926, KAPOOR 1975, KRISHNA IYENGAR 1939, 1942 a, METCALFE & CHALK 1957, SANTAPAU 1950, VISHNU-MITTRE & ROBERT 1969 and present work).

Table 1 indicates that *Celsia coromandeliana* differs from *Verbascum thapsus* especially in: (1) trichomes on bract and calyx being peltate and uniseriate; (2) absence of trichomes on the carpel; (3) presence of crystal idioblasts in the mesophyll; (4) absence of uniseriate medullary rays; (5) presence of four stamens; (6) the functional megaspore forming an L-shaped contour; (7) endosperm cells abutting the chalazal and micropylar haustoria are smaller in size and (8) unequal random expansion of the integumentary cells.

The morphological and embryological data on *Verbascum thapsus* are meagre. The data on development of wall layers, anther tapetum, tapetal dimorphism, anther dehiscence, embryogenesis, testa and pericarp of this taxon are totally lacking.

Table 1. A comparison of *Celsia coromandeliana* and *Verbascum thapsus*. * points of difference; ** unpublished observations.

Features	*Celsia coromandeliana*	*Verbascum thapsus*
Habit	Erect, pubescent, short herb	Erect, woolly, usually tall herb
Trichomes on:		
*Bract	Peltate, uniseriate	**Branched
*Calyx	Peltate, uniseriate	**Branched
Corolla	Nil	Nil
Stamens	Unicellular	**Unicellular
*Carpel	Nil, or a few	**Numerous, heavily clothed with branched hairs
*Crystals	Crystals occur in the mesophyll and the vascular bundles of the veins	Absent
*Pericyclic fibres	Arranged in a loose ring	Arranged in isolated strands
*Uniseriate medullary rays	Absent	Present
*Stamens	Four	Five
Anther development	**Dicotyledonous type	Data not available
Wall layers	**Four, including epidermis	Data not available
Endothecial thickenings	**Present in endothecium and connective region	Data not available
Anther tapetum	**Dual origin, being derived partly from the parietal layer and partly from the cells of the connective	Data not available
Tapetal dimorphism	**Present, the tapetal cells are radially elongated towards the connective, and small towards the outside	Data not available
Stomium	Present	Data not available
*Gynoecium	Bicarpellary, bilocular at the base and unilocular at the top	Bicarpellary, bilocular
*Placentation	Axile at the base and parietal at the summit	Axile
Ovule	Anatropous, unitegminal, tenuinucellate	Anatropous, unitegminal, tenuinucellate
*Megaspore tetrads	The functional megaspore undergoes curvature to form an L-shaped contour	**Straight
Embryo sac	Polygonum type	Polygonum type
Endosperm	Cellular, ruminated	Cellular, ruminated
*Micropylar haustorium	Four-celled, endosperm cells** next to the haustorial cells are smaller in size than other cells of endosperm	Four-celled, endosperm cells** next to the haustorial cells are larger than other cells of endosperm
Chalazal haustorium	Four-celled; endosperm cells** abutting the haustorium are small and rich in protoplasm	Four-celled; endosperm cells** abutting the haustorium are large and radially elongated
Embryogeny	Onagrad type; cells of mature embryo are full of reserve food materials	Data not available
Seed coat	Initially 6- or 7-layered but only epidermis and the endothelium persist	Data not available
	Endothelium is the prominent layer and its cells elongate at random and have thickenings on inner tangential and radial walls	Endothelial cells** show a row of alternating larger and smaller cells
Pericarp	Sub-epidermal cavities present	Data not available

The available information indicates that *Celsia coromandeliana* is not *pro parte Verbascum thapsus* and maintenance of these two taxa as independent genera is justified on morphological and embryological grounds.

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Syngenesious Anthers of Helianthus annuus – a Histochemical Study

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In *Helianthus annuus* L. the outer epidermes of the two adjacent anther lobes secrete a cementing substance in the form of a hyaline membrane, prior to the microspore mother cells entering meiosis. Gradually, the neighbouring anthers become bound together by the hyaline membrane. They remain in this stage only for a short period (up to meiosis I). The membrane then disorganises and at dehiscence the five anthers are almost free again. The histochemical studies have shown that the hyaline cementing membrane is PAS-negative and does not seem to contain cellulose or pectin. Tests for lignin, cutin, suberin and lipids are also negative. Furthermore it is not resistant to acetolysis which suggests that sporopollenin is absent.

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The occurrence of syngenesious anthers in the Compositae has been known for nearly a century. As early as 1917, SMALL wrote "... the stamens are five in number, and usually have the anthers syngenesious". As described by CASSINI (1826, cited in SMALL 1917), the stamen is composed of a filament, anther, connective, apical and basal appendages, pollen and a prolongation of the connective below the anther to form the 'article anthérifère'. Though this structure is an additional one, but its exact nature is not clear from the description. SAUNDERS (1931) writes that "... anthers as they develop become loosely coherent (syngenesious)". LAWRENCE (1951) thinks that the stamens are connate by their anthers to form a cylinder around the style in the Compositae. According to PORTER (1959), the syngenesious condition refers to stamens or anthers united by the anthers in a ring. WILLIS (1960) defines the syngenesious condition as united anthers.

Syngenesious anthers are found in most of the genera of the Compositae and forms a unique characteristic feature of the family. Though the anthers have been invariably referred to as syngenesious, only a few have been investigated from this point of view. While studying the life-history of *Podolepis jaceoides* DAVIS (1961) mentioned that "the young anthers are free from each other and their apparent fusion at maturity results from the adhesion of epidermal cuticle on adjacent anthers. There is never an organic fusion between the five anthers as, it appears, they remain distinct entities throughout their life-cycle" (see also DAVIS 1962 a, b, 1966).

The present investigation was undertaken to elucidate the ontogeny with special emphasis on the histochemical nature of the membrane which brings about this temporary cohesion of the anthers.

MATERIAL AND METHODS

Young capitula as well as individual disc florets of *Helianthus annuus* L. were fixed in formalin-acetic-alcohol for 24 hours at 30—31° C during July 1970 and later stored in 70 % ethanol. The voucher specimens KANAN 22—24 are deposited in the Delhi University Herbarium.

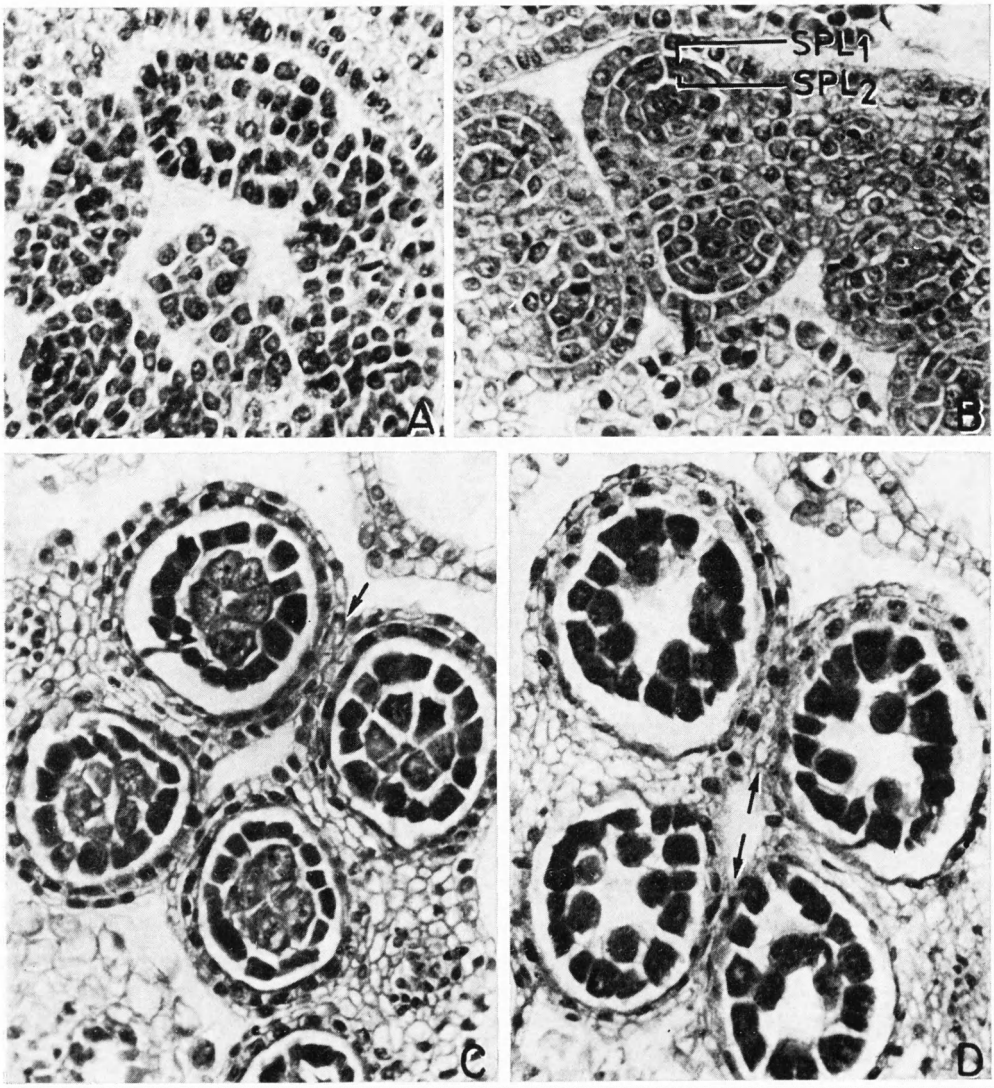

Fig. 1. *Helianthus annuus.* — A: T.s. disc floret, showing undifferentiated but free anthers. — B: Same, secondary parietal layers (SPL 1, 2) differentiated on the epidermal side; note that the anthers are still free. — C: Same, showing anthers at premeiosis, and the two adjacent microsporangia adpressed on lateral sides. — D: Same, at meiosis II. — All ×200.

After dehydration in alcohol-xylene series, the material was embedded in paraffin. Sections were cut at 3—10 microns and stained with safranin-fast green for ontogenetic studies, and for histochemical investigations they were put to various tests as detailed in Table 1.

RESULTS AND DISCUSSION

Ontogeny

The disc florets of *Helianthus annuus* have five stamens alternating with the

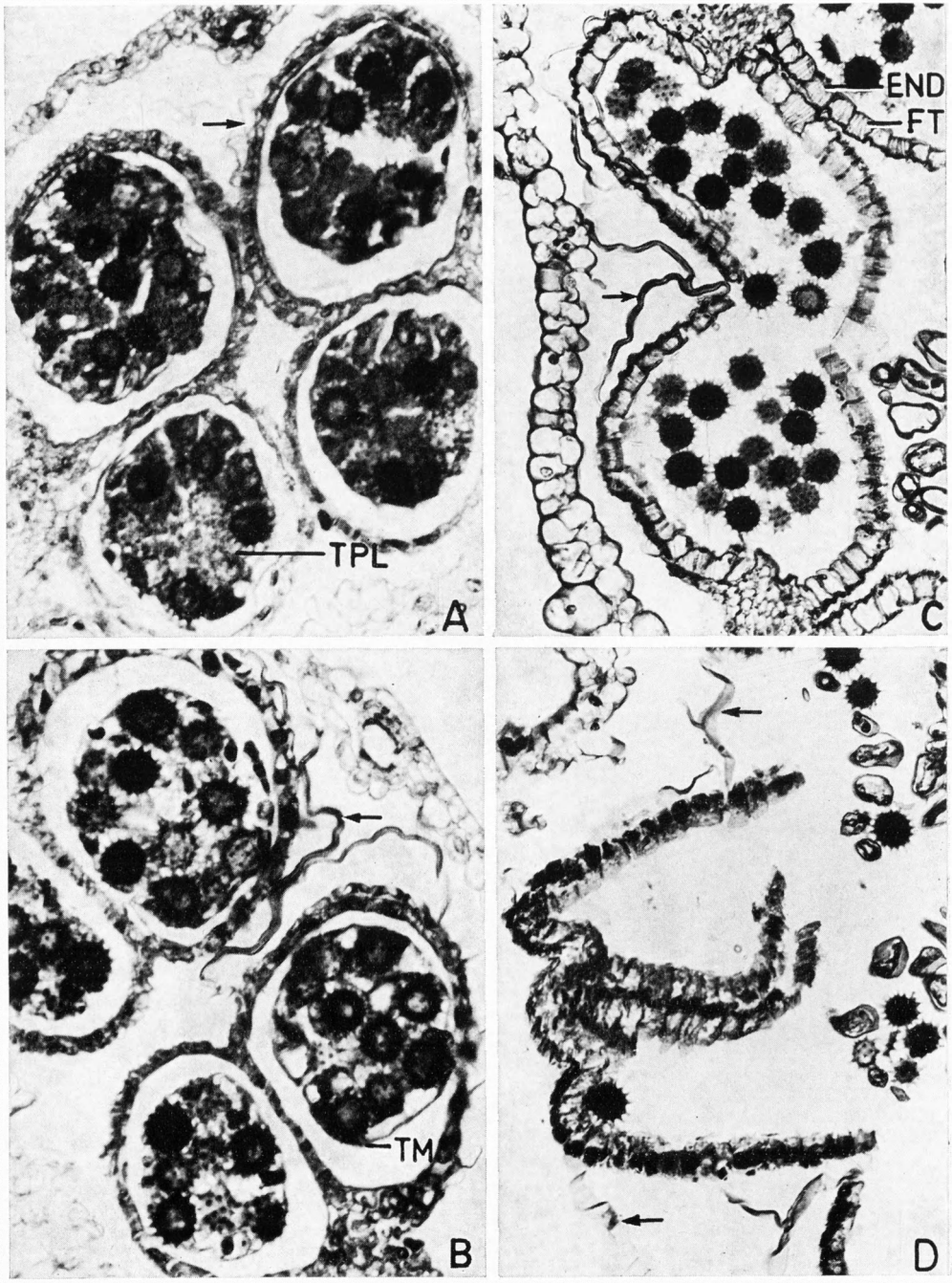

Fig. 2. *Helianthus annuus.* — A: T.s. disc floret at uni-nucleate pollen stage with tapetal periplasmodium (TPL); the membrane ruptured at places (marked by arrow) to separate the anthers. — B: Same, at 2-celled pollen stage (the cells are not clear due to highly

Table 1. Histochemical techniques.

Metabolite	Technique employed	Control	Reference
Total carbohydrates of insoluble polysaccharides	(a) PAS reaction	Acetylation	JENSEN 1962
Cellulose	(a) Zinc-chlor-iodide test	Cellulase treatment	JENSEN 1962, MEPHAM & LANE 1969
	(b) IKI-H_2SO_4	Cellulase treatment	JENSEN 1962, MEPHAM & LANE 1969
Pectin	(a) Ruthenium red technique	Pectinase treatment	JENSEN 1962, MEPHAM & LANE 1969
Lignin	(a) Maule's test	—	FOSSARD 1969
	(b) Phloroglucinol test	—	JENSEN 1962, FOSSARD 1969
Cutin	(a) KOH-chlorzinc-iodide test	—	JOHANSEN 1940
Suberin	(a) KOH-chlorzinc-iodide test	—	JOHANSEN 1940
Total lipids	(a) Sudan dyes	—	JENSEN 1962

petals and are said to be syngenesious. Anthers are dithecous and terminally appendiculate. The anther wall development in *Helianthus* (Fig. 1 A—C) follows the Dicot type of ontogeny and its details are being published elsewhere. It has been observed that initially the anthers are free and they remain so until the differentiation of the various wall layers occurs (Fig. 1 A, B). Subsequently, the two adjacent anthers gradually become adpressed (Fig. 1 C). During meiosis the epidermes of the two adpressed adjacent anther lobes secrete a hyaline cementing substance which leads to apparent fusion of the five anthers.

The two thecae of the adjacent anthers become adpressed along their entire length during meiosis I. Then they start stretching away from the central part at the septum region (Fig. 1 D). As the anthers mature, the separation continues, both towards the lateral and the dorsal sides (Fig. 2 A) until the anthers have completely separated from each other (Fig. 2 B—D). Thus, it is observed that the cementing substance is secreted by the epidermal cells of anthers on the lateral as well as dorsal sides. As the anthers mature (2-celled stage), this substance forms a hyaline membrane which later starts peeling off from the epidermal cells (Fig. 2 A, B). In this process, the otherwise free anthers remain coherent for only a very short period during ontogeny. At maturity anthers have been described as syngenesious, but histologically speaking they are completely free from each other (Fig. 2 C, D). At times, however, they might appear united at places if the cementing membrane has not completely separated from the epidermal cells.

Histochemistry

When tested histochemically, the cementing membrane has been found to be PAS-negative. It does not stain with aqueous ruthenium red for pectin. With zinc-chloriodide, it takes a brown colour similar to that of pollen exine but not the characteristic blue of cellulose. Further with IKI-H_2SO_4 test a negative reaction for

ornamented thich exine). The tapetal membrane (TM) and the periplasmodium in free anthers (arrow marked). — C: Same, at dehisced anther stage showing the degenerated epidermis and endothecial cells (END) with thickenings (FT). The membrane has almost peeled off from the epidermis (marked by arrow). — D: Same, after pollen shedding with remnants of the membrane seen at places (marked by arrow). — All ×200.

cellulose is obtained. Thus, the membrane does not contain any insoluble polysaccharide, pectin or cellulose. When tested for cutin and suberin by JOHANSEN'S (1940) method, using concentrated potassium hydroxide, it gives a very feeble reaction (indicated by a very pale yellow colour) for suberin. Therefore, the presence of suberin is possible although the results of more specific tests are required before a definitive statement is possible. The membrane gives a negative result for cutin on interaction with KOH-chlorzinciodide. The Maule's and phloroglucinol tests for lignin are negative. The membrane is non-resistant to boiling acetolysis mixture (9 parts acetic anhydride: 1 part conc. H_2SO_4), indicating that its composition does not include sporopollenin.

When the fresh membrane is stained with Sudan Black B (in 70 % ethanol) for total lipids, it gives a light pink colouration indicating absence of lipids. DAVIS (1961, 1962 b) has suggested that in *Podolepis jaceoides* and *Ammobium alatum* the membrane is cuticular in nature, however, our histochemical investigations do not confirm her remarks. The present studies, however, do not indicate the nature of the membrane although many of the typical components of plant cell walls appear not to be present, with the possible exception of suberin. Further investigation is in progress. On the basis of present ontogenic investigations, it is suggested that the earlier concept of "syngenesious" anthers, characteristic of the Compositae, should be modified.

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Isoenzyme Studies in Members of the Genus Brassica

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DENFORD, K. E. 1976 05 06. Isoenzyme studies in members of the genus Brassica. — Bot. Notiser 128: 455—462. Lund. ISSN 0006-8195.

A gel electrophoretic study has been carried out on the seed isoenzymes of 10 members of the genus *Brassica*. Eleven isoenzyme systems have been studied and the distribution of the isoenzymes used to indicate a possible historical relationship between the major recognized taxa. Three basic centres of the complex have been indicated; Indo-European, China and Mediterranean as exemplified by *B. rapa* (turnip, turnip-rape), *B. chinensis* (Pak Choi), and *B. tournefortii* (wild turnip) respectively.

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In recent years much work has been carried out in biochemical relationships with respect to plant, animal and bacterial taxonomy. The usefulness of such studies has been discussed by several workers including ALSTON and TURNER (1963), SWAIN (1963) and HAWKES (1968). Volatile oil investigations have been made by ETTLINGER and KJAER (1969) on some *Brassica* species, using seeds, roots and shoots, whilst other naturally occurring compounds, such as phenols have been investigated by DASS and NYBOM (1967) and DURKEE and HARBORNE (1973). Investigations of the genus have been carried out with respect to the use of seed proteins as taxonomic characters (VAUGHAN et al. 1966, VAUGHAN & DENFORD 1968, VAUGHAN et al. 1970), with results supporting the previous morphological studies of SCHULZ (1919). Further work has been carried out on certain enzymes in the seeds (VAUGHAN and WAITE 1967 a, b, VAUGHAN et al. 1968) such as, β-galactosidases, β-glucosidases, esterases and myrosinase.

The genus includes certain polymorphic species, and this tends to complicate the taxonomy of its members (BAILEY 1930, 1940). Such an example is found in the ten chromosome complex comprising *B. rapa* L., its allies, and *B. tournefortii* GOUAN (Table 1). This group of plants shows a wide range of polymorphy and hence rather special problems concerning the establishment of specific characters relating to its taxonomy. The members of the ten chromosome complex do have characters distinguishing them from other taxa present in the genus, and hence are essentially as follows:

Annual or biennial plants possessing tap roots; stems erect, branching; basal leaves petiolate; stem leaves sessile, lyrate and pinnatipartite with lateral alternate lobes, the terminal lobe being obovate or ovate.

The stem leaves are also deeply caudate and clasp the stem at their bases, distinguishing the species from *B. oleracea*, generally accepted as its nearest taxonomic relative, whose stem leaves are only slightly clasping. The lowest leaves of *B. rapa* L. are always more or less bristly, and the open flowers of the raceme overtop the unopened flower buds. The filaments of the outer stamens are distinctly curved at their base (cf. the straight stamens of *B. oleracea*), and the petals are bright yellow. It is interesting to note that a combination of characters, rather than absolutely specific ones, separate close relatives from one

Table 1. *Brassica rapa* and its allies investigated.

Taxon	Trivial name
B. rapa L. ssp. *rapa*	Turnip
B. rapa L. ssp. *sylvestris* (L.) JANCHEN	Wild turnip-rape
B. rapa L. ssp. *oleifera* DC.	Cultivated turnip-rape
B. rapa L. ssp. *sarson* (PRAIN) DENFORD comb. nov. Basionym *B. campestris* L. var. *sarson* PRAIN, Agr. Ledger 5: 27—28 (1898)	Sarson
B. rapa L. ssp. *toria* (PRAIN) DENFORD comb. nov. Basionym *B. campestris* L. var. *toria* PRAIN, Agr. Ledger 5: 23—25 (1898)	Toria
B. chinensis L.	Pak Choi
B. pekinensis RUPR.	Petsai
B. perviridis BAILEY	Tendergreen
B. tournefortii GOUAN	Wild turnip, Jangli-rai

another, an example of this can be found in *B. napus* which has characters in common with both *B. rapa* L. (with respect to clasping stem leaves) and *B. oleracea* (glaucous nature of the leaves, and an inflorescence similar to *B. oleracea*).

To avoid making too many new combinations in this preliminary paper, *B. chinensis*, *B. pekinensis* and *B. perviridis* are treated as species, although they should better be reduced to some lower rank.

Within the complex, work has been carried out on the seed coat, and its surface features (MUSIL 1948), however because of variability in seed size and surface markings very little has been accomplished in distinguishing between the races present, except in the case of *B. rapa* ssp. *sarson* which produces mucilage when placed in water (ALAM 1936). Seed coat pigmentation appears to be variable and of no real use in distinguishing between varieties as PRAIN (1898) has noted varying coloured seeds on the same plants of *sarson*. The genetic control of colour was investigated by SUN (1945) who found that a homozygous dominant gene gave rise to purple seeds; homozygous recessive produced yellow seeds, and the heterozygous state gave rise to intermediate forms. The histology of the testa has also been investigated by VAUGHAN et al. (1963) on certain ten chromosome taxa, for example, *B. rapa* L. and *B. chinensis*, with little distinction between them being found.

ALAM (1936) studied meiotic chromosome associations in certain races of *B. rapa* (*sarson* and *toria*) concluding that the basic chromosome number to have been 5. Various crosses were carried out by MOHAMMAD et al. (1931) between *sarson*, *toria* and turnip giving fertile offspring, indicating close relationship. SIKKA (1940) indicated that segmental interchanges and inversions may well have played an important part in separating *B. tournefortii* from the other ten chromosome members of the complex as crosses produced by him, using *sarson*, gave hybrids which at meiosis showed rings of 4 chromosomes. Further attempts to repeat this line of investigation by MOHAMMAD and SIKKA (1940) did not succeed. OLSSON (1954) also attempted to cross *B. tournefortii* with *B. rapa* subspecies (*sarson*, *toria*, *oleifera*), *B. chinensis* and *B. pekinensis*, but was not successful. The work indicated a discontinuity between *B. tournefortii* and the remaining members of the complex.

Studies of the volatile oils and glucosides present in the seeds of the *B. rapa* complex have been carried out by DELAVEAU (1959), and VAUGHAN et al. (1963). The glucosides

of certain members of the complex were examined using paper chromatography to identify the isothiocyanates produced. DELAVEAU (1959), using turnip-rape showed that the glucosides present produced butanyl, pentenyl and phenylethyl isothiocyanates. VAUGHAN (1963) and co-workers examined a larger selection of ten chromosome species including varieties of *B. rapa, B. chinensis* and *B. pekinensis*, showing the glucosides present produced 3-butanyl isothiocyanates in varying quantities. No distinction between these taxa was made in this investigation.

In all classifications the most important factor involved is the use of stable and non-trivial characters. As has previously been mentioned, the characters used in the ten chromosome *Brassica* species: leaf shape, growth habit, hairiness, glaucous nature of leaf, and root shape, are all subject to environmental alteration (BAILEY 1940, SUN 1946) and hence are of questionable value in classification.

Previous preliminary work on *Brassica* species has been carried out with the aid of serological and electrophoretic techniques by VAUGHAN et al. (1966), VAUGHAN and WAITE (1967 a, b) and VAUGHAN and DENFORD (1968).

The present investigation is a continuation of this work to evaluate the seed isoenzyme profiles of the major taxa recognized as allies of *B. rapa* and to determine the possible phylogenetic relationships, such a study might indicate.

MATERIAL AND METHODS

Wherever possible, seeds were obtained from research stations using authenticated seed from their crop breeding programme, as most of the varieties used were of commercial use. The wild species were collected by the author and authenticated accordingly. Unless all other seed samples were accompanied by an acceptable certificate of authentication, they were grown at the University of London Botanical Supply Unit (Egham., England).

Voucher specimens of all material are lodged at the Atkins Laboratories, Queen Elizabeth College, University of London, England.

Table 2. Enzyme systems studied using gel electrophoresis.

Enzyme	Method
Acid phosphatase	HALL et al. 1969
Alkaline phosphatase	EVERSON-PEARSE 1960
α-amylase	OLERED & JÖNSSON 1970
Catalase	THORUP et al. 1961
Esterase	HALL et al. 1969
β-galactosidase	VAUGHAN & WAITE 1967 a
β-glucosidase	COHEN 1952
Glutamic dehydrogenase	LAYCOCK et al. 1965
Leucine aminopeptidase	NACHLAS et al. 1957
Myrosinase	VAUGHAN et al. 1968
Peroxidase	HALL et al. 1969

Protein extracts, purification and electrophoresis were carried out as in previous studies using acrylamide gel electrophoresis (ORNSTEIN & DAVIS 1961, VAUGHAN & DENFORD 1968). Enzyme staining techniques were carried out using specific methods as in Table 2. All tests were carried out at 30° C and pH 7.0 using a tris-glycine buffered medium.

Rp (×100) were calculated from fresh gels and given to the centre of each band. No distinction was made as to intensity or rate of reaction. All estimations were made on a presence or absence basis.

ENZYME DISTRIBUTION AND TAXONOMIC RELATIONSHIPS

The presence of all the enzymes to be investigated was first of all established using agarose gel before a detailed investi-

Table 3. Enzymes occurring in all the ten chromosome *Brassica* species examined.

Enzyme	Rp
β-galactosidase	34
acid phosphatase	17
Leucine aminopeptidase	55
Peroxidase	52
Glutamic dehydrogenase	43
Glutamic dehydrogenase	60
Esterase	17
Esterase	83
Esterase	87

Table 4. Isoenzymes only found in one of the two ten chromosome "groups" of *Brassica*.

Group (1) Turnip/turnip-rape complex		Group (2) *B. chinensis* complex	
Enzyme	Rp	Enzyme	Rp
β-galactosidase	11	β-galactosidase	17
	73		63
Acid phosphatase	47		87
Leucine aminopeptidase	15	Alkaline phosphatase	67
	47	Leucine aminopeptidase	20
Peroxidase	15	Peroxidase	27
β-glucosidase	47	β-glucosidase	43
	63		67
Glutamic dehydrogenase	70	Catalase	15
Catalase	11		34
	30		43
	52		57
Esterase	93	Esterase	77

gation on acrylamide gel was carried out (VAUGHAN et al. 1970). The results of the enzyme analysis were tabulated according to Rp (Tables 3—6), each pattern being the result of ten different seed samples of each taxon (ten gels for each variety used). It was found that within each variety investigated, the enzyme pattern was constant with respect to Rp value, even though intensity of staining varied. Between varieties there appeared to be distinct differences in the patterns of certain enzymes, but within each variety the enzyme patterns were constant. It was also found that certain Rps were constantly shared between two varieties. Turnip and turnip-rape always shared the following Rps between themselves and only rarely with other taxa: Rp 15, β-glucosidase; Rp 52, β-glucosidase, also shared with *B. perviridis*; Rps 27 and 70, β-galactosidase, the former being found in *B. perviridis*; Rp 38, catalase; Rp 20, esterase; Rp 50, esterase, also found in *B. chinensis*.

Sarson and *toria* appeared to have a much smaller number of bands unique to themselves, only the catalase enzyme was found to be unique, giving bands as follows: Rps 17, 40 and 50, also found in *B. perviridis*.

The largest group of shared enzyme bands appeared to fall in the *B. perviridis*, *B. pekinensis* and *B. chinensis* complex. These bands were as follows: Rp 70, β-glucosidase shared between *B. chinensis* and *B. pekinensis* (also found in *toria*); Rp 50, acid phosphatase. All the following were found shared between *B. perviridis*, *B. pekinensis* and *B. chinensis*: Rps 15, 34, 45 and 57, catalase; Rps 38 and 77, esterase.

B. tournefortii shares one enzyme band Rp 25, catalase, with turnip, and Rp 15, ß-glucosidase, with turnip-rape. All other enzyme bands present in *B. tournefortii* are found to some extent in all the other taxa investigated, or they are only found in *B. tournefortii* (see Tables 3 and 6).

The relationships between the various

Table 5. Isoenzymes unique to *Brassica tournefortii* GOUAN.

Enzyme	Rp
β-galactosidase	60
Leucine aminopeptidase	77
Glutamic dehydrogenase	87
Catalase	50
	60
α-amylase	70
	77

Table 6. "Unique" isoenzymes.

Enzyme	Rp	Taxon
β-galactosidase	60	*B. tournefortii*
α-amylase	70	*B. tournefortii*
	77	
Leucine aminopeptidase	30	*Sarson*
	38	*B. pekinensis*
	57	*B. perviridis*
	77	*B. tournefortii*
Peroxidase	60	*Sarson*
Glutamic dehydrogenase	63	Turnip
	73	Turnip
	87	*B. tournefortii*
Catalase	08	*B. perviridis*
	50	*B. tournefortii*
	60	*B. tournefortii*
	63	Turnip-rape
Esterase	30	*B. chinensis*
	60	*B. pekinensis*

taxa based on enzyme Rps were tabulated as percentage similarities (Table 7) and a three-dimensional model was constructed using this information (Fig. 1). It was found that the similarity coefficients between turnip and turnip-rape; *sarson* and *toria*; *B. chinensis* and *B. pekinensis*, were very high (75 %). Also there appeared to be two distinct groups within the complex, the first containing turnip, turnip-rape, *sarson* and *toria*, and the other containing *B. perviridis*, *B. pekinensis* and *B. chinensis*. The other taxon investigated, *B. tournefortii*, seemed to fall somewhere between these two groups (see Fig. 1) nearer to *sarson* and *toria* than the other taxa.

Isoenzyme distributions in this complex were of four types: (1) Those occurring throughout all the taxa investigated; (2) Those occurring in one of the two groups mentioned; (3) Those found in one taxon alone, and never in any of the other taxa; and (4) Those distributed in a "random" manner.

It is interesting to note that *B. tournefortii*, a 'weed' has the greatest number of specific enzyme bands.

Within each taxon investigated the isoenzyme pattern remained constant and hence at the varietal level the taxa were indistinguishable (on the basis of presence or absence). This situation is shown in a three-dimensional manner indicating the presence of three basic 'groups' of ten chromosome taxa. One 'group' is made up of *B. chinensis*, *B. pekinensis* and *B. perviridis*, the second group is formed by the *B. rapa* complex (*sarson*, *toria*, turnip and turnip-rape) and the third 'group' is formed by the species *B. tournefortii*. Morphologically this latter separation is in agreement with all the major classifications of the *Brassica* species (SCHULZ 1919, MUSIL 1948). The grouping of garden turnip, turnip-rape, *sarson* and *toria* is in agreement with PRAIN (1898), SCHULZ (1919) and MUSIL (1948), but not with LINNAEUS (1753) and DE CANDOLLE (1821, 1824). The former workers placed all the turnips and turnip-rapes under the one species, *campestris*, whereas the latter described a separate species for the garden turnip. The other 'group' incorporates the oriental ten chromosome species described by BAILEY

Table 7. Percentage similarity between the ten chromosome *Brassica* species, using isoenzyme data.

	Tr	S	To	Pv	Ch	Pk	Tf
T	75	60	60	22	22	20	30
	Tr	60	60	21	20	20	30
		S	75	21	24	23	42
			To	28	25	24	44
				Pv	60	60	31
					Ch	75	35
						Pk	30

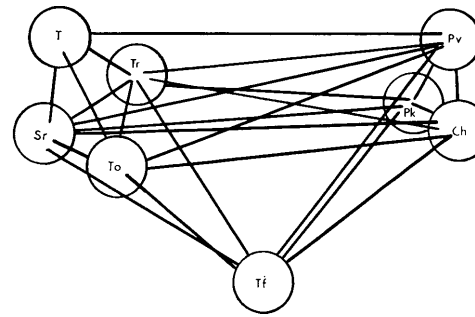

Fig. 1. Spatial taxonomic relationships between 10 taxa of *Brassica* based on isoenzyme data.

(1930), KRAUS (1940), SUN (1946) and MUSIL (1948). However, this work indicates the presence of only one species, and not three, which contradicts these workers. Such a conclusion is arrived at very readily on the grouping of the taxa in the three-dimensional model with the enzyme data (Fig. 1).

From these studies it is postulated that in my material there are three basic ten chromosome species in the genus *Brassica*:

(1) *B. rapa* which includes turnip, turnip-rape, *sarson* and *toria.*

(2) *B. chinensis* which includes *chinensis*, *pekinensis* and *perviridis.* The inclusion of *perviridis* under the species *B. chinensis* opposes the classification of BAILEY (1940) who originally gave it varietal status under *B. rapa* L., and later gave it species status as *B. perviridis.*

(3) *B. tournefortii*, a wild ten chromosome *Brassica* species.

Support for this hypothesis is found in the distribution of enzymes. There would appear to be several categories:

(i) Those only present in the turnip-turnip-rape complex (Table 4).

(ii) Those found in the *B. chinensis* complex (Table 4).

(iii) Those unique to *B. tournefortii* (Table 5).

Two other categories are present incorporating those enzymes present in all the taxa (Table 3), and those which are unique to a particular taxon (Table 6).

It is of interest to note that each of the three complexes postulated are found in three distinct geographical areas. *B. tournefortii* grows wild in the Mediterranean (endemic to this area, SCHULZ 1919). *B. rapa* and its races are found distributed throughout the Indo-European regions, and *B. chinensis* and its relatives are found in China.

It has been suggested (SUN 1946) that there are two races of *B. rapa*, an eastern and a western race. From this present study it is concluded that there are two distinct Eastern and Western species (Fig. 1). Furthermore, it would be of interest to know how these two species arose and from where they originated, with special reference to their relationship to *B. tournefortii*. One explanation for this three species situation could be that one of the species (*B. tournefortii*) gave rise to the other two. As *B. tournefortii* (of Mediterranean origin) is a weedy ten chromosome species it could be the nearest species to the original archetype suggested by SIKKA (1940) with a basic chromosome number of five. If this were true then the ten chromosome polyploid may have arisen in the Mediterranean region and spread to India/Europe and then China.

Another explanation for this situation is that there were three centres of origin for

the five chromosome archetype which eventually died out after the polyploid was formed. Possibly at each centre of origin the plants developed along their own lines, as in the case of *B. tournefortii*, or came under different selection pressures by man, as in the case of *B. rapa* and its varieties, and *B. chinensis* and its varieties. Ultimately such a process would give rise to three different groups of plants.

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Scandinavian Species of the Genus Brachythecium (Bryophyta)

I. Modification and Biometric Studies in the B. rutabulum — B. rivulare Complex

Kai Wigh

WIGH, K. 1976 05 06. Scandinavian species of the genus Brachythecium (Bryophyta). I. Modification and biometric studies in the B. rutabulum — B. rivulare complex. — Bot. Notiser 128: 463—475. Lund. ISSN 0006-8195.

Brachythecium rutabulum and *B. rivulare* have been experimentally cultivated in controlled environments to study the constancy of morphological characters. The humidity, temperature and light factors have been varied.

The variations of quantitative characters have been biometrically analysed in the cultivated mosses as well as in samples from spontaneous populations. The diagnostic value of the characters studied have been estimated for taxonomic purposes.

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Many species of mosses are extremely variable. The purpose of this investigation is to study which characters become modified thus being of little taxonomic value, and which characters are relatively constant. The morphology, taxonomy and cytology of the polymorphic complex including the two species *Brachythecium rutabulum* and *B. rivulare* will be discussed in a forthcoming paper (WIGH 1976).

The two species have been taxonomically delimited in different ways, and several varieties have been described. Some of these subspecific taxa are presumed to be modifications only. In order to assess their taxonomic value modification experiments have been carried out.

Biometric analysis revealed that certain quantitative characters are useful in distinguishing between *Brachythecium rutabulum* and *B. rivulare*.

METHODS

The modification experiments have been carried out in 9 different environments (Table 1) where the material was grown for some months. Samples grown under dry conditions grew rather slowly and were therefore kept in culture for a longer period than the others.

No nutritive was added during the experiments as it has previously been observed that these mosses can go on growing for at least two years without any additional nutritive. After the period of cultivation the plants were dried and used for the modification studies.

Measurements of leaves, nerves, cells and spores have been made under a light microscope. The magnitudes used were ×30 for the leaves and nerves, ×400 for the cells and ×1,000 for the spores. The accuracy of the measurements was 40 μ, 3 μ and 1.2 μ respectively.

The length of the leaves was measured from the insertion of the nerve on the stem to the tip of the leaves, and the length of the nerves from the insertion to the tip of the nerves. The length of the cells was measured from cells near the middle of the leaves, apart from the nerves. From each sample 30 leaves and cells were measured, and 20 spores.

MATERIAL

The investigations are based on the material previously analysed cytologically and on herbarium material. The live material of *B. ruta-*

Table 1. Climatic conditions for cultivated material.

Environment	Light		Temperature		Humidity	
	Lux	Hours	°C	Hours	%	Hours
I a	5,000	15.5	14	15	40	15
	0	8.5	14→11	2	40→60	2
			11	5	60	5
			11→14	2	60→40	2
I b	as I a	as I a	as I a	as I a	100	24
I c	2,000	15.5	as I a	as I a	as I a	as I a
	0	8.5				
I d	as I c	as I c	as I a	as I a	100	24
II	4,600	12	14	10	100	24
	0	12	14→12	2		
			12	10		
			12→14	2		
III a	9,200	15	19	12	60	12
	0	9	19→10	2	60→90	2
			10	8	90	8
			10→19	2	90→60	2
III b	7,200	15	as III a	as III a	as III a	as III a
	0	9				
III c	as III a	as III a	as III a	as III a	100	24
III d	as III b	as III a	as III a	as III a	100	24

bulum is represented by the n=12 cytotype and *B. rivulare* by the n=6 cytotype. The reference numbers are listed in WIGH (1976).

Voucher specimens are deposited at the Botanical Museum of Göteborg (GB), Sweden.

MODIFICATION EXPERIMENTS

Many intraspecific taxa in the *Brachythecium rutabulum* — *B. rivulare* complex have been described on such characters as the size and colour of the plant, length of seta, shape of lid, etc. These taxa are often modifications only. If corresponding studies were to be carried out in other species complexes also, many taxa would probably prove to be modifications only.

It seems likely that a given character can display a high degree of modifiability in one species, whereas in another species the same character is more constant, an example being the shape of the lid in the family Brachytheciaceae. This character is variable in certain species such as *Brachythecium rutabulum*, but in other genera it is probably more constant.

Some populations of *Brachythecium rutabulum* and *B. rivulare* have been cultivated in 9 different environments in climate chambers. The climatic conditions are given in Table 1. The environments have been called I a—d, II and III a—d, three climate chambers having been used.

The modification experiments have been divided into two separate investigations, one biometric, discussed on p. 469 and one in the main qualitative. In the latter some characters have also been measured but the results have not been analysed statistically.

Modificative Characters

GAMETOPHYTIC CHARACTERS

Both species become extensively modified. This was anticipated as they are also highly variable under natural conditions.

PLICATION OF LEAVES. Plication is highly modificative in both species which may give rise to problems of identification, as in several keys species with plicated leaves have been separated from species without plications. The reduced plications in *B. rutabulum* may cause trouble when distinguishing between this species and, for instance, *B. mildeanum* and *B. curtum* (WIGH 1976).

COLOUR OF PLANT. There is an obvious difference in the colour of plants cultivated in light with an intensity of 2,000 lux and those cultivated in 5,000 lux. Those grown in less light are a darker green than those cultivated in 5,000 lux. This is true of both species.

BRANCHING. The number of branches per cm of the shoot stands in direct relation to the humidity. Under conditions of saturated humidity both species produce only a few branches.

ANGULAR CELLS. In all 9 environments *B. rivulare* produces large and well-developed angular cells (Fig. 1 E, F), the size of these cells being somewhat variable, but they are always fairly large and well-delimited.

B. rutabulum displays greater variation in the development of angular cells when cultivated. Under dry conditions the angular cells do not become enlarged or more clearly delimited (Fig. 1 B). Under conditions of saturated humidity the variation, both within a sample and between samples from different populations, is more extensive, plants in some samples then producing large and well-delimited angular cells as in *B. rivulare*. Plants in other samples only produce somewhat larger angular cells. In Fig. 1 C the angular cells are somewhat enlarged.

The structure of the angular cells has been regarded by several authors as the most important diagnostic character for separating *B. rutabulum* and *B. rivulare*. This investigation shows that this character is highly modifiable in *B. rutabulum*. Natural populations of this species with large and well-delimited angular cells are also found, such forms being extremely difficult to distinguish from *B. rivulare*.

DECURRENCY OF LEAVES. The decurrent part of the leaves in cultivated samples is shown in Fig. 2. In *B. rivulare* the leaves are always longly and broadly decurrent. In *B. rutabulum* the decurrency increases with humidity, both with regard to length and breadth. This character has been accorded the same taxonomic importance as the angular cells, and it must be observed that the decurrency is extremely modifiable in *B. rutabulum*.

LENGTH OF INTERNODES. In both species the internodes attain a greater length in 2,000 lux than in 5,000 lux both where humidity is saturated and under drier conditions. The differences are marked. In 2,000 lux there are about 25 leaves per cm of the shoot and in 5,000 lux about 33. When grown in 7,200 lux or 9,000 lux there are no differences, either where the humidity is saturated or under drier conditions.

There are quite obvious differences between samples cultivated when the humidity is saturated and under drier conditions as regards length of internodes, the internodes being shorter under drier conditions. This is true of both species and with all light intensities.

NUMBER OF RHIZOIDS. The number of rhizoids is related to light intensity and to humidity, but also to the degree of contact the shoots have with the substratum. When grown in contact with the substratum the shoots produce far more rhizoids than when growing erect with no contact.

If the influence of light and of humidity are compared as regards number of rhizoids, it seems that humidity has the greater effect. Under conditions of lower humidity the number of rhizoids increases.

SPOROPHYTIC CHARACTERS

Brachythecium rutabulum only has been investigated.

LENGTH OF SETA. The length of the seta is highly modifiable and varies with hu-

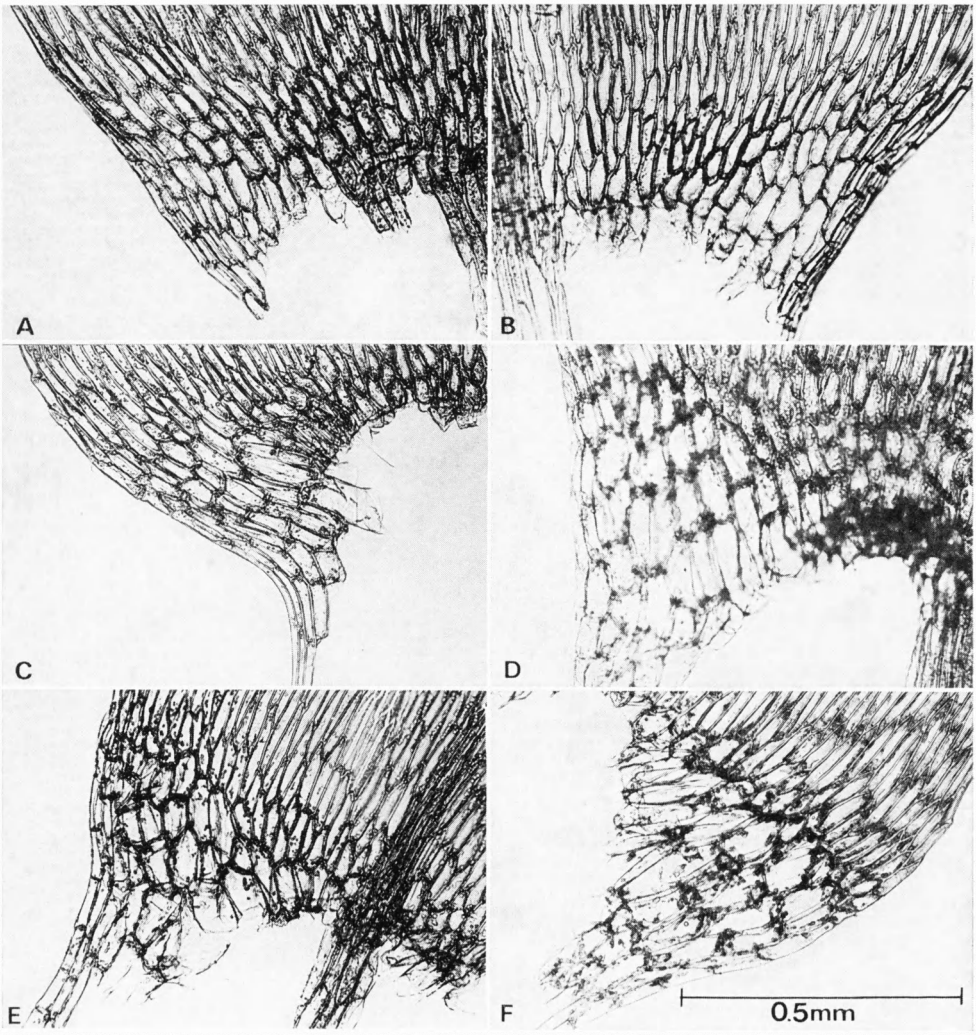

Fig. 1. Photographs of angular cells. — A—C: *Brachythecium rutabulum*. — D—F: *B. rivulare*. — A: 71-90 (spontaneous population). — B: 71-90 (environment IIIb). — C: 71-90 (environment IIId). — D: 71-169 (spontaneous population). — E: 71—127 (environment Ib). — F: 71-127 (environment Id). — The climatic conditions are given in Table 1.

midity. The differences between spontaneous material and samples cultivated under conditions of saturated humidity are marked. The length of the seta in cultivated samples is often more than twice or three times that found in spontaneous material. In one population the mean of the length of the seta in spontaneous samples was 1.5 cm and the new sporophytes produced when humidity was saturated was 4.5 cm. This observation is important since there are varieties of *B. rutabulum* described which differ from the nomenclatural type material in having longer seta.

LENGTH AND SHAPE OF LID. Under conditions of saturated humidity some

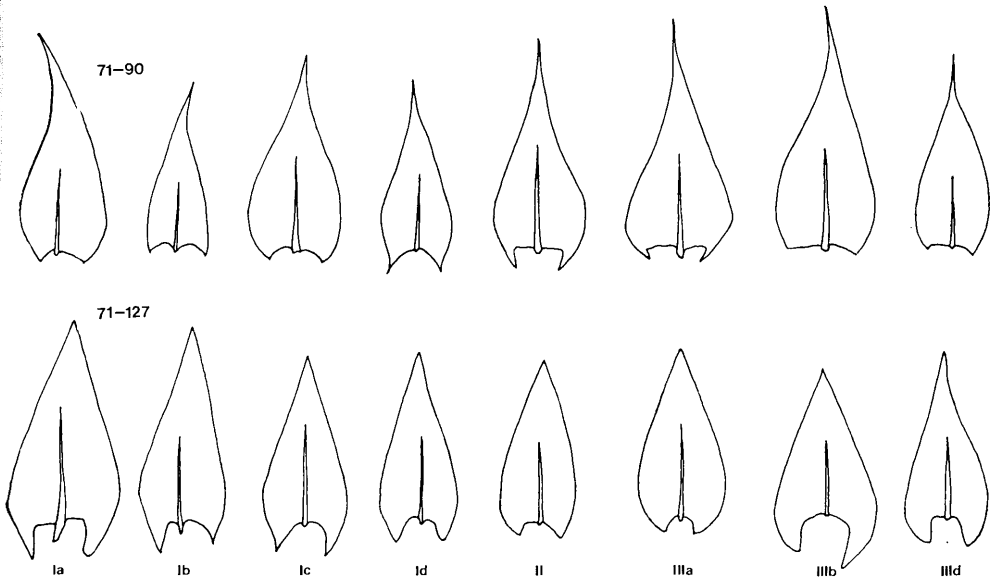

Fig. 2. Leaves of cultivated samples of *Brachythecium rutabulum* (71-90) and *B. rivulare* (71-127). The climatic conditions are given in Table 1.

populations of *B. rutabulum* produce longer lids than those found in the corresponding spontaneous material. The lid is not conical, but more or less oblique. Plants displaying this modification have been described as a variety and have also been treated as a good species.

LAZARENKO et al. (1971) investigated the chromosomes in *B. eurhynchioides* (LIMPR.) LOESKE, a taxon diverging from *B. rutabulum* in the long oblique lid only. They reported two chromosome numbers, n=6 and n=12. The chromosome complement of the n=6 and n=12 cytotypes agreed with that of the corresponding cytotypes of *B. rutabulum* which supports the statement that *B. eurhynchioides* is only a modification of *B. rutabulum*.

The long oblique lid is a character found in some genera in the family Brachytheciaceae, e.g. *Rhynchostegiella, Rhynchostegium, Cirriphyllum* and *Eurhynchium*, whereas *Brachythecium* has a short conical lid. The lid in the first-mentioned genera is probably less modifiable than in *Brachythecium rutabulum*.

Difference in shape of lid has often been the only character given in keys in separating *Brachythecium* from other genera. It must be noted that *B. rutabulum* at least could key out wrongly using such keys.

Not Modificative Characters

GAMETOPHYTIC CHARACTERS

SHAPE OF LEAVES. Neither in *B. rutabulum* nor in *B. rivulare* is the shape of the leaves modifiable (Fig. 2). This character is one of the most useful for separating the two species. In all 9 environments the leaves of *B. rutabulum* are long and pointed in contrast with the acute leaves of *B. rivulare*. Fig. 2 also gives an indication of the size of the leaves in the different environments. Leaves from 8 environments only are illustrated as no material of population 71—90 cultivated in III c was available.

DENTICULATION OF LEAVES. Neither in *B. rutabulum* nor in *B. rivulare* does the denticulation of the leaves vary

Table 2. Modificative and non-modificative characters in *Brachythecium rutabulum* and *B. rivulare*. Gametophytic characters have been studied in both species and sporophytic characters in *B. rutabulum* only. — Modificative characters: +, non-modificative characters: —. — Modification depends on humidity: H, on light: L.

Gametophytic characters		
Growth	+	H
Plication	+	H
Colour	+	L
Branching	+	H
Angular cells	+	H
Decurrency of leaves	+	H
Internodes	+	H, L
Rhizoids	+	H, L
Shape of leaves	—	
Denticulation of leaves	—	
Length of leaves	+	H, L
Length of nerves	+	H, L
Length of cells	+	H, L
Sporophytic characters		
Length of seta	+	H
Lid	+	H
Size of spores	—	
Papillae on seta	—	
Form of capsule	—	
Size of capsule	—	
Exothecial cells	—	
Peristome	—	
Stomata	—	

in any of the environments. This character is of no value for separating these two species, but is of importance in distinguishing *B. rutabulum* from *B. mildeanum* (WIGH 1976).

SPOROPHYTIC CHARACTERS

Brachythecium rutabulum only has been investigated.

PAPILLATION OF SETA. When cultivated samples were compared with spontaneous populations no differences in the papillae of the seta were observed. This is important since the papillae is one of the most widely used diagnostic characters in the genus *Brachythecium*. Whether or not these papillae are modifiable in other species has not yet been investigated.

SHAPE AND SIZE OF CAPSULE. There are no obvious differences in the shape and size of capsules of cultivated and spontaneous specimens except for the lid as stated above.

EXOTHECIAL CELLS. If natural and cultivated material are compared as regards size and arrangement of exothecial cells no differences are observed. In cultivated samples the exothecial cells are arranged in rows and have longitudinal walls that are more incrassate than the transverse walls.

PERISTOME. In cultivated samples there are no observable modifications in either the outer or inner peristome. The cilia of the inner peristome are papillose and nodose precisely as in natural populations.

STOMATA. As there are only a few stomata on each capsule no extensive biometric investigation has been undertaken. There were no differences in the shape and size of stomata in natural and cultivated material.

Summary of the Modification Experiments

The modification experiments can be summarized as follows (Table 2):

(1) Gametophytic characters display a higher degree of modification than sporophytic characters.

(2) Variations in humidity give rise to more extensive modification than do variations in light intensity. Temperature probably has little influence on the plants, at least within the range of temperatures used in this experiment.

(3) Some morphological characters are modified by humidity, others by light, whereas still others are modified by both humidity and light.

(4) In most cases the gametophytic characters of *B. rutabulum* and *B. rivulare* modify in the same way, but there are some exceptions, such as length of cells, p. 471.

(5) The most important modificative characters of taxonomic value are: size of

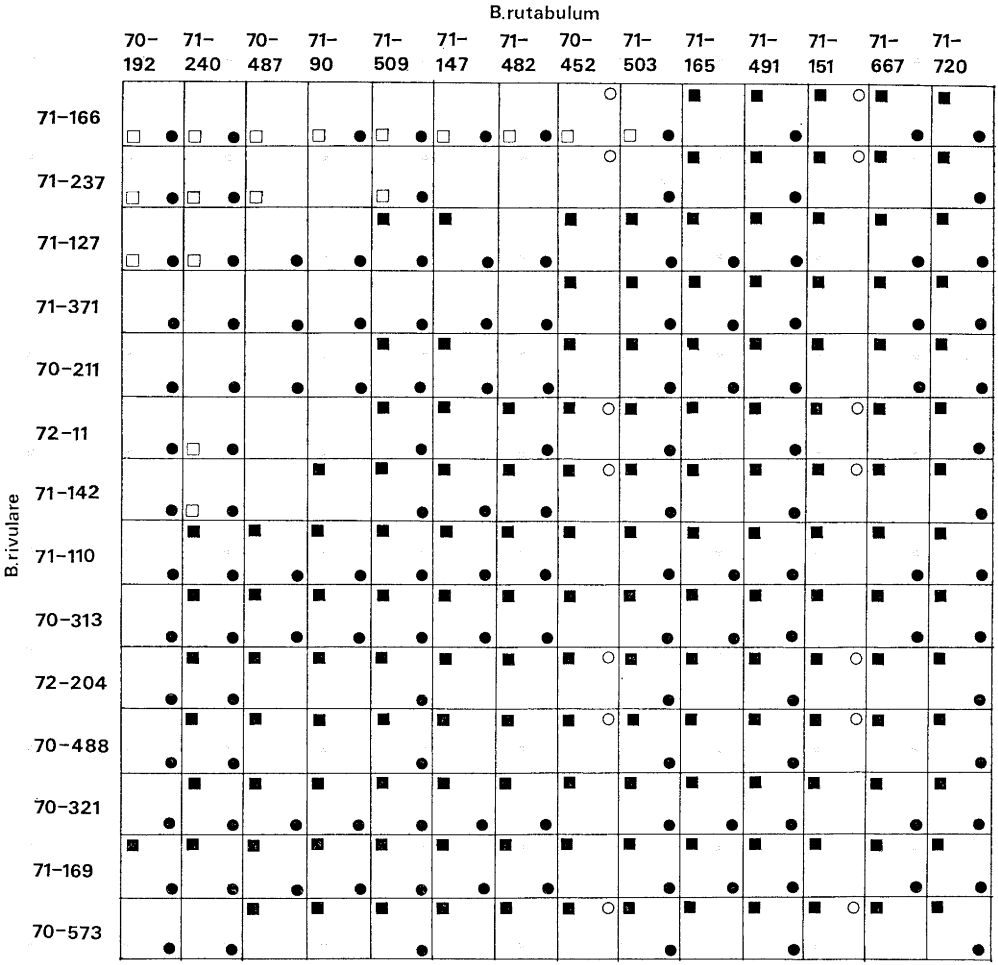

Fig. 3. Statistical analysis of biometric characters in spontaneous samples of *Brachythecium rutabulum* and *B. rivulare*. — Squares show that the leaves are longer in *B. rutabulum*, open squares that the leaves are longer in *B. rivulare*, dots that the relative length of the nerves is greater in *B. rivulare* and rings that relative length of the nerves is greater in *B. rutabulum*.

plants, length of internodes, angular cells, decurrency of leaves, colour of plant, plication of leaves, length of seta and length and shape of lid.

(6) The most important non-modificative characters are: shape of leaves, denticulation of leaves, papillation of seta, size and shape of capsules and peristome.

BIOMETRIC STUDIES

Spontaneous Populations

The length and shape of the leaves, two of the most important morphological characters for separating *Brachythecium rutabulum* from *B. rivulare* have been studied biometrically as well as other characters of possible diagnostic value.

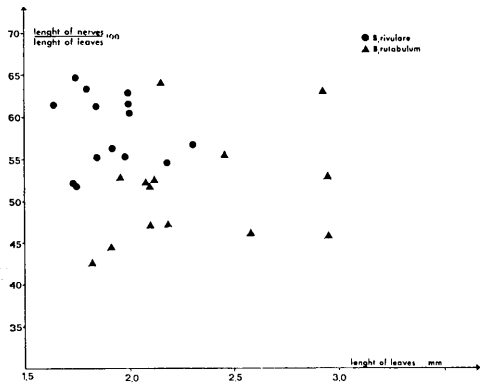

Fig. 4. Variations in length of leaves and relative length of nerves in spontaneous samples of *B. rutabulum* (triangles) and *B. rivulare* (dots).

SIZE OF SPORES

There is no statistically significant difference between the size of the spores in *B. rutabulum* and *B. rivulare*. The mean value in the populations studied is 17—21 ±1—2 μ in both species.

LENGTH OF LEAVES, NERVES AND CELLS

In both species 14 populations have been selected at random (Figs. 3, 4). The length of the leaves, nerves and cells has been measured. *B. rutabulum* and *B. rivulare* do not differ with regard to length of cells.

The shortly pointed leaves in *B. rivulare* can be expressed biometrically as the ratio of the length of the nerves to the length of the leaves. The length of the leaves and the relative length of the nerves are very useful distinguishing characters. There is, however, great variation between populations within both species. In most populations of *B. rivulare* the leaves are shorter and the nerves relatively longer than in the populations of *B. rutabulum*. The variations in these characters are shown in Fig. 4. The differences have been estimated by means of a t-test significant at the 5 % level.

Table 3. Differences significant at the 5 % level between spontaneous populations of *B. rutabulum* and *B. rivulare* with reference to length of leaves and relative length of nerves. For explanation see text and Fig. 3.

Characters	Number of combinations	%
Leaves longer in *B. rutabulum* (+character)	147	75.0
Leaves longer in *B. rivulare* (— character)	20	10.2
No differences	29	14.8
Rel. length of nerves greater in *B. rivulare* (+character)	133	67.9
Rel. length of nerves greater in *B. rutabulum* (— character)	14	7.1
No differences	49	25.0
2+characters	94	48.0
1+character	63	32.1
2 — characters	1	0.5
1 — character	3	1.5
1+ and 1 — character	29	14.8
No differences	6	3.1

In Fig. 3 the squares show that the leaves are significantly longer in *B. rutabulum* (a + character) and the dots that the relative length of the nerves is significantly greater in *B. rivulare* (a + character). The open squares show that the leaves are significantly longer in *B. rivulare* (a — character) and the rings that the relative length of the nerves is significantly greater in *B. rutabulum* (a — character).

In Table 3 the results for the population studied are summarized. In 75.0 % of the combinations the leaves of *B. rutabulum* are longer than those of *B. rivulare* (a + character). In only 10.2 % of the combinations are the leaves of *B. rivulare* longer (a — character). In 67.9 % of the combinations the relative length of the nerves is greater in *B. rivulare* (a + character) and in only 7.1 % of the combinations is the relative length of the nerves greater in *B. rutabulum* (a — character).

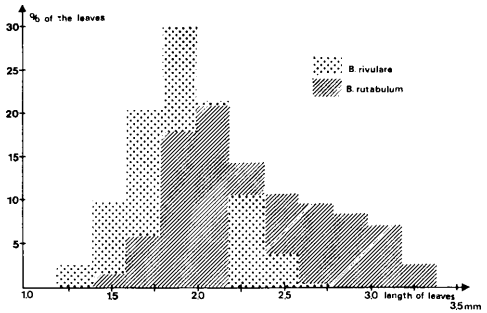

Fig. 5. Length of leaves in spontaneous samples of *Brachythecium rutabulum* and *B. rivulare*.

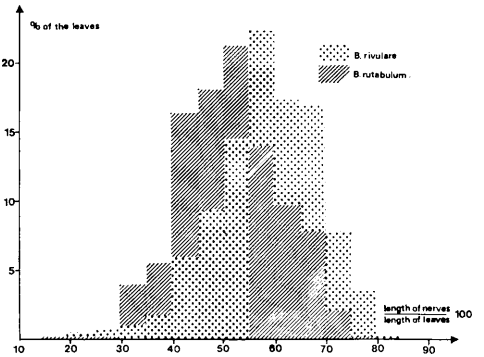

Fig. 6. Relative length of nerves in spontaneous samples of *Brachythecium rutabulum* and *B. rivulare*.

The lower half of Table 3 shows that in 48.0 % of the combinations there are two + characters and that in 0.5 % only are there two — characters. One + character occurs in 32.1 % of the combinations and one — character in 1.5 %.

Thus in 80.1 % of the combinations there are either one or two + characters (in such cases the biometric information will be helpful in identifying the species). In 14.8 % of the combinations there is one + character and one — character (the one character indicates *B. rutabulum* and the other *B. rivulare*). In 3.1 % of the combinations no differences are found and in only 2 % are one or two — characters found (here the biometric information will lead to an erroneous identification of the species).

It should be noted that these populations have been selected at random from the populations studied cytologically and that *B. rutabulum* is represented by the n=12 cytotype and *B. rivulare* by the n=6 cytotype.

The 14 populations of each species cannot cover the whole morphological variation of the species. This is the case in the length of the leaves at least.

Variation in length of leaves is shown in Fig. 5 and the relative length of the nerves in Fig. 6. These figures are very useful for separating the two species. This biometrical test should always be correlated with qualitative characters.

Cultivated Material

The same characters that were measured in natural samples have been studied in the cultivated samples. Only a limited amount of cultivated material has been available for this investigation so that the statistical analyses are based on a smaller number of samples than in the natural populations.

SIZE OF SPORES

When natural and cultivated material of *Brachythecium rutabulum* is compared no differences in size of spores is observed. *B. rutabulum* is an autoecious species often producing sporophytes when cultivated, in contrast with *B. rivulare* which is dioecious and of which no sporophytes have been available for study.

LENGTH OF LEAF CELLS

The length of the cells in cultivated material in relation to spontaneous populations is given in Table 4.

In *B. rutabulum* the cells in cultivated material are always longer than in spontaneous material. When cultivated in drier habitats the cells are longer, except in environments I c and I d.

In cultivated material of *B. rivulare* the cells are longer in the environments I a—d

Table 4. Comparison between length of cells in spontaneous and cultivated material of *Brachythecium rutabulum* and *B. rivulare*. Length of cells in cultivated samples is calculated as percentage of length of cells in the corresponding natural populations. The environmental conditions are given in Table 1.

Lux	Humidity	Environment	*B. rutabulum*	*B. rivulare*
2,000	<100 %	I c	105.7	104.4
2,000	100 %	I d	107.4	104.2
5,000	<100 %	I a	113.5	100.4
5,000	100 %	I b	108.7	107.5
7,200	<100 %	III b	114.0	93.4
7,200	100 %	III d	108.1	95.3
9,200	<100 %	III a	111.1	92.6
9,200	100 %	III c	102.7	96.5

than in the corresponding spontaneous populations. In environments III a—d the reverse is true. This difference is probably due to intensity of light. In environments III a—d light intensity is 7,200 lux or 9,200 lux and in I a—d 2,000 lux or 5,000 lux.

In drier environments there is a tendency for the cells to be somewhat smaller than where humidity is saturated. The opposite holds for *B. rutabulum*. This difference can probably be explained by the fact that *B. rivulare* is a hydrophilous species and *B. rutabulum* mesophilous.

LENGTH OF NERVES AND LEAVES

In Table 5 the mean values of absolute and relative lengths of the nerves in cultivated samples and the corresponding natural material is given.

In cultivated samples of *Brachythecium rutabulum* and *B. rivulare* both the absolute and relative length of the nerves is less than in the corresponding spontaneous material.

The relative length of the nerves has decreased more in *B. rivulare* than in *B. rutabulum*, but is greater in *B. rivulare* just as in the natural populations. The mean value of all relative lengths in cultivated samples is 47.7 % in *B. rivulare* and 44.9 % in *B. rutabulum*. In the corresponding spontaneous material the relative length of the nerves is 58.7 % in *B. rivulare* and 53.1 % in *B. rutabulum* (see also Table 7).

Table 5. Length of nerves in cultivated material (Mod.) of *Brachythecium rutabulum* and *B. rivulare* and length of nerves in corresponding spontaneous material (Spon.).

Environment	Humidity	*B. rutabulum*				*B. rivulare*			
		Absolute length mm		in % of leaf length		Absolute length mm		in % of leaf length	
		Mod.	Spon.	Mod.	Spon.	Mod.	Spon.	Mod.	Spon.
I a	<100 %	0.78	1.19	42.0	53.0	0.68	1.17	43.7	59.4
I b	100 %	0.67	1.22	42.4	53.7	0.69	1.10	48.8	59.2
I c	<100 %	0.88	1.09	46.8	51.6	0.74	1.20	48.8	60.8
I d	100 %	0.71	1.09	47.6	51.9	0.67	1.10	51.5	59.2
III a	<100 %	1.05	1.26	46.3	52.7	0.76	1.15	46.8	57.3
III c	100 %	0.81	1.38	44.3	55.7	0.70	1.21	48.4	58.0
III b	<100 %	0.92	1.25	43.3	53.2	0.88	1.11	48.2	58.3
III d	100 %	0.85	1.25	46.2	52.8	0.74	1.15	45.3	57.3

Table 6. Length of leaves in cultivated material of *Brachythecium rutabulum* and *B. rivulare* calculated as percentage of length in corresponding spontaneous populations. — In the upper half of the table the lengths are arranged according to variation in humidity. In the lower half the lengths are arranged according to variation in light intensity.

Lux	Humidity	Environment	*B. rutabulum*	*B. rivulare*
2,000	<100 %	I c	89.2	78.4
2,000	100 %	I d	70.7	71.2
5,000	<100 %	I a	80.5	79.5
5,000	100 %	I b	70.2	75.7
7,200	<100 %	III b	87.1	85.3
7,200	100 %	III d	80.7	75.9
9,200	<100 %	III a	95.2	81.1
9,200	100 %	III c	79.5	75.6
2,000	<100 %	I c	89.2	78.4
5,000	<100 %	I a	80.5	79.5
2,000	100 %	I d	70.7	71.2
5,000	100 %	I b	70.2	75.7
7,200	<100 %	III b	87.1	85.3
9,200	<100 %	III a	95.2	81.1
7,200	100 %	III d	80.7	75.9
9,200	100 %	III c	79.5	75.6

The absolute length of the nerves is greater in drier environments than where humidity is saturated. This holds for both species but the difference is more pronounced in *B. rutabulum*.

In both species the nerves are longer in environments III a—d than in I a—d. In *B. rutabulum* the mean values are 0.91 mm and 0.76 mm respectively, and in *B. rivulare* the corresponding values are 0.77 mm and 0.70 mm.

The length of the nerves is thus modified both by degree of humidity and light intensity.

Table 7. Differences significant at the 5 % level in biometric characters in cultivated samples of *B. rutabulum* and *B. rivulare*. — The climatic conditions are given in Table 1. For explanation see text.

Samples	Number of combinations	Leaves longer in *B. rutabulum*		Nerves relatively longer in *B. rivulare*	
		Number of combinations	%	Number of combinations	%
I c	25	22	88.0	11	44.0
Spon.	25	14	56.0	21	84.0
II	45	35	77.8	7	15.6
Spon.	45	22	48.9	24	53.3
III a	25	25	100.0	8	32.0
Spon.	25	21	84.0	11	44.0
III b	20	18	90.0	11	55.0
Spon.	20	15	75.0	8	40.0
III c	25	23	92.0	16	69.6
Spon.	25	13	52.0	20	80.0
III d	20	17	85.0	6	30.0
Spon.	20	13	65.0	11	55.0

In most cases the leaves are shorter in cultivated material than in spontaneous populations. In Table 6 the length of the leaves in cultivated material is calculated as percentage of the length in spontaneous populations.

In both *B. rutabulum* and *B. rivulare* the leaves are shorter in saturated humidity than in drier environments (Table 6, upper half).

If the length of the leaves is related to intensity of light, (Table 6, lower half) there are almost no differences between samples cultivated in environments I d and I b, and in III d and III c. This demonstrates that humidity modifies the length of the leaves to a greater extent than intensity of light does.

In drier habitats intensity of light has little or no influence on length of leaves in *B. rivulare* (compare I c with I a, and III b with III a). In *B. rutabulum* intensity of light modifies the length of the leaves to a greater extent.

The length of the leaves is thus modified by both humidity and intensity of light.

The statistical analysis of biometric characters in cultivated samples has been carried out in the same way as in the spontaneous material, p. 470.

In the corresponding study of spontaneous populations 14 populations of each species were used, the number of combinations thus being 196. Unfortunately much fewer cultivated samples were available but the tendency is quite clear.

The procedure followed for statistical analysis was such that the biometric results for cultivated material have been compared with the results for the corresponding spontaneous samples. The results are summarized in Table 7. For conditions of saturated humidity environments II, III c and III d have been used, and for drier habitats I c, III a and III b. These environments were chosen as the number of samples available was greater in them than in the other environments.

As regards length of leaves there is always a greater number of combinations in cultivated material than in spontaneous material which show statistically significant differences. The opposite is true of the relative length of the nerves except in environment III b.

These investigations show that biometric methods are diagnostically useful in separating *Brachythecium rutabulum* from *B. rivulare*.

Summary of the Biometric Investigations

SPONTANEOUS SAMPLES

(1) *Brachythecium rutabulum* and *B. rivulare* do not differ in size of spores and length of cells in the leaves.

(2) The leaves are significantly longer in *B. rutabulum*.

(3) The relative length of the nerves is significantly greater in *B. rivulare*.

(4) These last two characters are useful in separating the species.

CULTIVATED MATERIAL

(1) The cells in cultivated material of *B. rutabulum* are longer than in spontaneous populations. When *B. rivulare* is cultivated in lower intensities of light the cells are longer than in spontaneous populations, in lighter environments the cells are shorter.

(2) In *B. rutabulum* the cells are shorter under conditions of saturated humidity than in drier environments but longer in *B. rivulare*.

(3) Both the absolute and relative length of nerves is less in cultivated samples of both species.

(4) In lower intensities of light the nerves are shorter in both species.

(5) In drier environments the nerves are longer in both species.

(6) In both species the leaves are shorter in cultivated samples.

(7) In both species the leaves are shorter under conditions of saturated humidity than in drier habitats.

(8) Under conditions of saturated humidity the length of the leaves of both species is little influenced by light intensity or not at all.

(9) Humidity modifies the quantitative characters more than light intensity does.

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The climate chambers of the Department of Physiological Botany, the University of Göteborg, have kindly been put at my disposal for which I am most obliged to Professor HEMMING VIRGIN and Dr STIG FALK.

LITERATURE CITED

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Scandinavian Species of the Genus Brachythecium (Bryophyta)

II. Morphology, Taxonomy and Cytology in the B. rutabulum — B. rivulare Complex

Kai Wigh

WIGH, K. 1976 05 06. Scandinavian species of the genus Brachythecium (Bryophyta). II. Morphology, taxonomy and cytology in the B. rutabulum — B. rivulare complex. — Bot. Notiser 128: 476—496. Lund. ISSN 0006-8195.

Chromosome numbers in 264 gatherings of *B. rutabulum* and 42 gatherings of *B. rivulare* have been established. The cytological information obtained has formed the basis for the taxonomic treatment of the complex. In *B. rutabulum* the only chromosome number observed was n=12 and in *B. rivulare* n=6.

Some taxa in the complex have been typified and some new synonyms are given. The distribution and habitats of the species in Scandinavia are commented on.

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The section *Rutabula* of the genus *Brachythecium* has been delimited in different ways by different authors. The two species *Brachythecium rutabulum* (HEDW.) B.S.G. and *B. rivulare* B.S.G. can be said to constitute the centre of this section. Other species presumed to be related to these two species have been grouped in the section *Rutabula* (WIGH 1974). The taxonomic treatment of these latter species in the section has, however, been discussed and the delimitation of the section varies between different bryologists. Only a few controversial species will be mentioned here, e.g. *Brachythecium latifolium* KINDB., *B. ryanii* KAUR. and *B. mildeanum* (SCHIMP.) SCHIMP.

In Scandinavia the *Brachythecium rutabulum — B. rivulare* complex is relatively well delimited comprising only these two species. They are characterized by the chromosome number n=12 and n=6 respectively in contrast with the species mentioned above, *B. latifolium* and *B. ryanii* having the chromosome number n=11 and *B. mildeanum* n=13.

MATERIAL

This study is based on live material and herbarium material. The gatherings that have been studied cytologically were collected between 1970 and 1973. The localities are given in the appendix. The names of some collaborators who have contributed with some of the gatherings are shown in parentheses after the gatherings concerned. 264 gatherings of *B. rutabulum* and 42 of *B. rivulare* have been studied cytologically and voucher specimens have been deposited at the Botanical Museum of Göteborg (GB), Sweden. Reference numbers are given in the appendix.

About 2,000 herbarium specimens of each species have been studied from the following herbaria: AAU, B, BG, C, G, GB, H, LD, O, OULU, S, TRH, TROM, TUR and UPS. The abbreviations used are as in LANJOUW and STAFLEU (1964).

METHODS

The cultivation techniques used for the populations that have been studied cytologically are as in WIGH & STRANDHEDE (1971).

Two different cytological methods have been used: The Feulgen method used by WIGH & STRANDHEDE (1971) and the aceto-orcein methods used by WIGH (1972 a). Both methods

give equally good staining results. The first method is to be recommended for permanent preparations but is more difficult to standardize. The importance of pretreatments is stressed. Only with suitable pretreatment is it possible to count mitotic chromosomes in a great number of populations. Cold treatment has been used in this study (WIGH & STRANDHEDE 1971, WIGH 1972 a).

The chromosomes have been photographed as in WIGH (1973 a).

The drawings of morphological details have been made with the aid of a camera lucida.

DELIMITATION OF THE BRACHYTHECIUM RUTABULUM — B. RIVULARE COMPLEX

Brachythecium rutabulum and *B. rivulare* can be distinguished from the other Scandinavian species of the genus with the aid of the following simplified key. The key comprises all species recognized by NYHOLM (1954—1969) except for *B. geheebii* which has been transferred to the genus *Homalothecium* (WIGH 1973 b).

1. Seta ± smooth. (*B. collinum, B. curtum, B. populeum, B. plumosum, B. erythrorrhizon, B. albicans, B. groenlandicum, B. mildeanum, B. campestre, B. salebrosum, B. glareosum, B. turgidum*).
1. Seta rough throughout the whole length 2
2. Cilia of the inner peristome appendiculate, leaves often plane, as a rule not plicate. (*B. glaciale, B. velutinum, B. trachypodium, B. reflexum, B. starkei, B. latifolium*).
2. Cilia of the inner peristome nodose, leaves concave, plicate 3
3. Autoecious species ..... *B. rutabulum*
3. Dioecious species 4
4. Angular cells inflated ..... *B. rivulare*
4. Angular cells not inflated. (*B. ryanii*).

Brachythecium rutabulum (HEDW.) B.S.G.

BRUCH, SCHIMPER & GÜMBEL, Bryol. Eur. 6: 15 543 (1853) (fasc. 52—54 Mon. 11: 9). — *Hypnum rutabulum* HEDWIG, Spec. Musc. 276 (1801). Lectotype: sheet 3106/87 in the HEDWIG—SCHWAEGRICHEN herbarium (G). Coll. no. 12.

Brachythecium rutabulum var. *aureo-virens* BRID.) BROCKMÜLLER, Arch. Ver. Freund. Naturg. Mecklenburg 23: 122 (1870). — *Hypnum rutabulum* var. *aureo-virens* BRIDEL, Spec. Musc. 2: 184 (1812). Lectotype: sheet 3001/94 in the BRIDEL herbarium (B). The specimen in the lower right corner. Coll. no. 21. Collected by DEJEAN.

Brachythecium rutabulum var. *brevisetum* (FIEDL.) BROCKMÜLLER, Arch. Ver. Freund. Naturg. Mecklenburg 23: 122 (1870). — *Hypnum rutabulum* var. *brevisetum* FIEDLER, Syn. Laubm. Mecklenburg 111 (1844).

Brachythecium rutabulum var. *crassum* LANGE, Bot. Tidsskr. 2: 248 (1868) nom. nud.

Brachythecium rivulare var. *cuspidatum* JENSEN, Danm. Moss. 2: 141 (1923). Lectotype: (C). Collected by C. JENSEN in Denmark, Zealand, Allindelille Fredskov in 1882.

Brachythecium rutabulum var. *dumetorum* JENSEN, in BAUER Musci Eur. Exs. ser 14 nr. 693 (1910). Lectotype: (C). Collected by C. JENSEN in Denmark, Zealand, Hvalsö in 1904.

Brachythecium rutabulum var. *eurhynchioides* LIMPRICHT, Laubm. Deutschl. 3: 109 (1896). — *B. eurhynchioides* (LIMPR.) LOESKE, Moosfl. Harz. 273. (1903) nom. inval. prov.

Brachythecium rutabulum var. *explanatum* (BRID.) BROCKMÜLLER, Arch. Ver. Freund. Naturg. Mecklenburg 23: 122 (1870). — *Hypnum rutabulum* var. *explanatum* BRIDEL, Spec. Musc. 2: 184 (1812). — *B. starkei* (BRID.) B.S.G. var. *explanatum* (BRID.) MÖNKEMEYER, Laubm. Eur. 819 (1927). Lectotype: Sheet 3001/97 in the BRIDEL herbarium (B). The specimen in the upper left corner. Collected by BLANDOW in 1803 in Neubrandenburg. Coll. no. 25.

Hypnum rutabulum var. *flaccidum* BRIDEL, Spec. Musc. 2: 184 (1812). Lectotype: sheet 3001/4 in the BRIDEL herbarium (B). The specimen on the lower half of the sheet. Collected in 1797.

Brachythecium rutabulum var. *flavescens* (BRID.) BRUCH, SCHIMPER & GÜMBEL, Bryol. Eur. 6: 16 544 (1853) (fasc. 52—54 Mon. 12: 10). — *Hypnum rutabulum* var. *flavescens* BRIDEL, Bryol. Univ. 2: 488 (1827). — *Hypnum flavescens* BRIDEL, Spec. Musc. 2: 185 (1812) nom. illeg. — *Brachythecium rivulare* ssp. *flavescens* (BRID.) KINDB. Canad. Rec. Sc. 6(2): 73 (1894). Lectotype: sheet 3001/2 in the BRIDEL herbarium (B). The specimen in the upper left corner. Coll. no. 5.

Hypnum rutabulum var. *laxifolium* BRIDEL, Bryol. Univ. 2: 488 (1827). — *Brachythecium plumosum* (HEDW.) B.S.G. cf. LIMPRICHT, Laubm. Deutschl. 3: 87 (1896). Lectotype: sheet 3001/6 in the BRIDEL herbarium (B). Collected in 1825 by PYLAIE.

Brachythecium rutabulum var. *laxum* ROTH, Eur. Laubm. 2: 244 (1904).

Brachythecium rutabulum var. *longisetum* (BRID.) BRUCH, SCHIMPER & GÜMBEL, Bryol. Eur. 6: 16 544 (1853) (fasc. 52—54 Mon. 12: 10). — *Hypnum rutabulum* var. *longisetum* BRIDEL, Musc. Rec. 2(2): 161 (1801). Lectotype: sheet 3001/15 in the BRIDEL herbarium (B). The specimen in the upper right corner. Collected in 1798.

Brachythecium rutabulum var. *lutescens* WARNSTORF, Verh. Bot. Ver. Brandenburg 41: 73 (1899).

Brachythecium rutabulum var. *plumulosum* BRUCH, SCHIMPER & GÜMBEL, Bryol. Eur. 6: 16 544 (1853) (fasc. 52—54 Mon. 12: 10).

Brachythecium rutabulum var. *robustum* BRUCH, SCHIMPER & GÜMBEL, Bryol. Eur. 6: 16 544 (1853) (fasc. 52—54 Mon. 11: 10). — *B. robustum* (B.S.G.) LOESKE, Moosfl. Harz 273 (1903).

Hypnum uliginosum DEJEAN in BRIDEL, Bryol. Univ. 2: 487 (1827). nom. nud. Orig. coll.: sheet 3001/15 in the BRIDEL herbarium (B). The specimen in the lower left corner. Coll. no. 45. Collected by DEJEAN.

Robust plants with creeping stems and ± erect branches (Fig. 2 E), often growing in extensive green or yellowish mats. *Autoecious. Leaves* 1.8—3.0 mm, erect—spreading, more or less decurrent in a ± narrow band, slightly or strongly plicated, gradually narrowing to an acuminate point (Fig. 1 B). *Margin* denticulate, as a rule slightly recurved at base of leaf. *Nerve* reaching to about middle of leaf. *Cells* in middle of leaf 70 to more than 100 µ, towards the base near the nerve porose. *Angular cells* rectangular, ± well delimited and occasionally inflated. *Seta* as a rule 1.5—3 cm, rough throughout (Fig. 1 G). *Capsule* ± horizontal (Fig. 1 F). *Exothecial cells* in middle and upper part of capsule in rows, ± rectangular with longitudinal walls thicker than transverse walls (Fig. 1 D) at the base of capsule exothecial cells more irregular, not in rows and more incrassate (Fig. 1 E). *Stomata* large, 31—39×28—35 µ. *Inner peristome* with nodose and strongly papillose cilia (Fig. 1 A). *Lid* short and conical (Fig. 1 F). *Spores* papillose, about 17—21 µ.

VARIATION. The plants show considerable variation in size and colour. Sometimes the stems are ± ascending in a way characteristic of *Brachythecium rivulare*. When growing in wet habitats the angular cells are more clearly defined and longly and broadly decurrent. These forms are very similar to *B. rivulare*. The leaves are always acuminate but the degree of plication and the denticulation is variable. In small forms of the species the leaves are often without any plication, but there are also forms with strongly plicated leaves resembling *B. salebrosum* (WEB. & MOHR) B.S.G. (Table 3). The leaves are often denticulate along the whole margin, but the denticulation is sometimes restricted to the upper part of the leaves, and there are also forms with no denticulation at all, resembling *B. mildeanum* (SCHIMP.) SCHIMP. (Table 3). The length of the seta varies. Shape and length of lid also vary. These last two characters are considered to be of great importance for separating the genera in the family Brachytheciaceae.

EXCLUDED NAMES

Specimens of a number of varieties of *Brachythecium rutabulum* have been studied. The following varieties cannot be maintained as taxa and are regarded by the author as synonyms of *B. rutabulum*: var. *aureo-virens*, var. *brevisetum*, var. *crassum*, var. *dumetorum*, var. *eurhynchioides*, var. *explanatum*, var. *flaccidum*, var. *flavescens*, var. *laxifolium*, var. *laxum*, var. *longisetum*, var. *lutescens*, var. *plumosum* and var. *robustum* (cf. list of synonyms).

B. rivulare var. *cuspidatum* is also regarded as a synonym of *B. rutabulum*. The longly pointed leaves clearly show that it is a form of *B. rutabulum*. This statement is also supported by the fact that the specimens are autoecious.

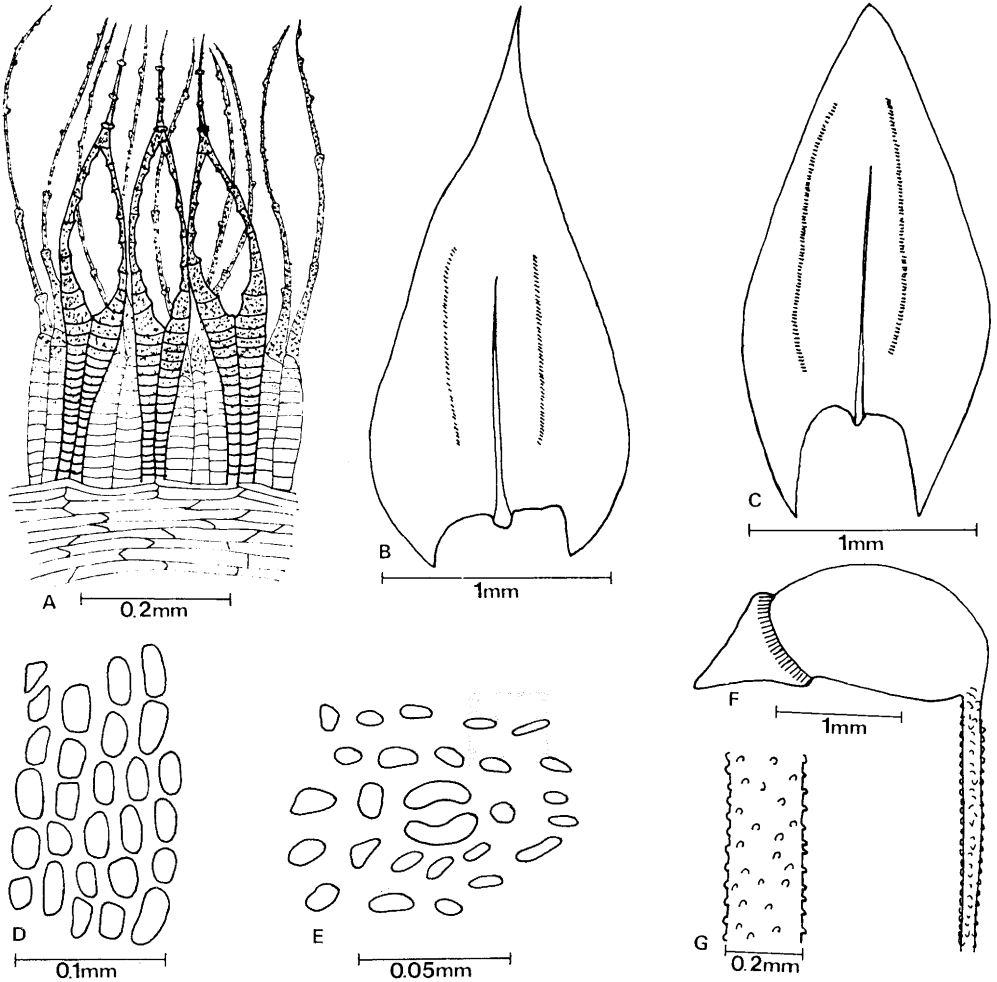

Fig. 1. A, B, D—G: *Brachythecium rutabulum*. — C: *B. rivulare*. — A: Inner peristome. — B, C: Leaves. — D: Exothecial cells from the middle of the capsule. — E: Exothecial cells from the base of the capsule. — F: Sporophyte. — G: Part of seta.

B. rutabulum var. *cavifolium* LINDB. belongs to the *B. turgidum* complex as has been pointed out by ARNELL & MÅRTENSSON (1959).

The specimens of *B. rutabulum* var. *rivulare* LANGE belong to *B. rivulare* (cf. list of synonyms under this species).

Material of *B. rutabulum* var. *viviparum* BRYHN from the type locality has been studied. According to the author this taxon does not belong to the genus *Brachythecium* but to the genus *Drepanocladus* in the family Amblystegiaceae. The differences between this taxon and *B. rutabulum* can be summarized as follows: it grows submerged (not common in *B. rutabulum*), it seems to be dioecious, the angular cells are inflated and almost reaching the nerve

Table 1. Varieties of *Brachythecium rutabulum* regarded as synonyms of *B. rutabulum* s. str. The characters listed are those diverging from the taxonomic type of *B. rutabulum*. — Characters modificative +, non-modificative —.

Taxon	Characters	
var. *aureo-virens*	± yellowish	+
	abundant rhizoids	+
	abundantly branched	+
	seta long	+
var. *brevisetum*	internodes short	+
	seta short	+
var. *crassum*	leaves long	+
	leaves strongly plicate	+
var. *dumetorum*	few branches	+
	branches elongated	+
	internodes long	+
	leaves longly decurrent	+
var. *eurhynchioides*	lid long, oblique	+
var. *explanatum*	leaves ± arranged in 2 rows	?
var. *flaccidum*	± yellowish	+
	branches elongated	+
	abundantly branched	+
var. *flavescens*	stem elongated	+
	± yellowish	+
	robust	+
var. *laxifolium*	internodes long	+
	seta long	+
	seta ± smooth	—
var. *laxum*	branches elongated	+
	internodes long	+
	lid ± long	+
var. *longisetum*	seta long	+
	stem elongated	+
var. *lutescens*	slightly plicate	+
	± yellowish	+
	nerve thin	+
var. *plumulosum*	small	+
var. *robustum*	dark green—green	+
	robust	+
	internodes short	+

(inflated angular cells are uncommon in the autoecious species *B. rutabulum*), in habit it agrees much more with species in the genus *Drepanocladus* than with species of *Brachythecium*, leaves not denticulate (this is uncommon in *B. rutabulum*), leaves not plicate (in most cases the leaves in *B. rutabulum* are more or less plicate). The author regards *B. rutabulum* var. *viviparum* as being conspecific with *Drepanocladus pseudostramineus* (C. MÜLL.) ROTH. Characters supporting this statement are: probably dioecious, leaves not plicate or denticulate, angular cells inflated, almost reaching the nerve, leaves rather shortly pointed with a recurved point, nerve rather thin.

In Table 1 taxa regarded by the author as synonyms of *Brachythecium rutabulum* s. str. are listed. The most important characters diverging from the taxonomic type specimen of *B. rutabulum* are shown in

the table. The diverging characters are denoted modificative (+), not modificative (—), and (?) (WIGH 1976).

DISTRIBUTION IN SCANDINAVIA

B. rutabulum is common in Denmark and in the southern and central parts of Sweden. It is also reported from a few localities in the northernmost parts of the country, where reports have been controlled they have proved to be incorrect, *B. rutabulum* having been confused with *B. rivulare* or species in the *B. salebrosum* complex. In a broad sense this complex can be said to comprise the following taxa: *B. salebrosum* (WEB. & MOHR) B.S.G., *B. turgidum* (HARTM.) KINDB., *B. groenlandicum* (C. JENS.) SCHLJAK and *B. mildeanum* (SCHIMP.) SCHIMP. var. *udum* (HAG.) MÖNK.

In Norway *B. rutabulum* is a common coastal species to about the province of Sör-Tröndelag. It is rather uncommon inland and does not occur in the high mountains.

In the southernmost parts of Finland it is common, rapidly decreasing in frequency towards the north.

As in Sweden *B. rutabulum* has been reported from the northern parts of Norway and Finland. Along the coast of Norway it is found in the far north, but in Finland it is uncommon in the north and in the northernmost parts of the country probably absent. Reports of *B. rutabulum* from these districts are erroneous, due to confusion with the above-mentioned species.

HABITATS

B. rutabulum grows on different kinds of substrata, for example calcareous and siliceous stones, bare soil, logs, etc. It is an apophytic species and often grows along roads, in ditches, in gardens, etc.

In ditches it sometimes grows together with *B. mildeanum* and on logs together with *B. salebrosum*. Occasionally in wet habitats it can grow together with *B. rivulare*.

Brachythecium rivulare B.S.G.

BRUCH, SCHIMPER & GÜMBEL, Bryol. Eur. 6: 17 546 (1853) (fasc. 52—54 Mon. 13: 12). Type material not seen.

Brachythecium rivulare var. *cataractarum* SAUTER, Fl. Herzogth. Salzburg 3: 60 (1870).

Brachythecium rivulare var. *gracile* JENSEN, Danm. Moss. 2: 141 (1923). Lectotype: (C). Collected by C. JENSEN in Denmark, Juteland, Norring Uhre in 1894.

Brachythecium rivulare var. *nitidum* SAUTER, Fl. Herzogth. Salzburg 3: 60 (1870).

Brachythecium rivulare var. *umbrosum* LIMPRICHT, Laubm. Deutschl. 3: 130 (1896).

Brachythecium rutabulum var. *rivulare* (B.S.G.) LANGE, Bot. Tidsskr. 3: 30 (1869).

Robust plants with creeping stem and ascending secondary stems which are more or less branched (Figs. 2 B, F). *Dioecious. Leaves* 1.6—2.3 mm, erect—spreading, longly and broadly decurrent, usually plicate, with an acute point (Fig. 1 C). *Margin* ± recurved at the base of the leaf, ± denticulate. *Nerve* reaching beyond the middle of the leaf. *Cells* in the middle of the leaf 70 to more than 100 µ, towards the base near the nerve porose. *Angular cells* rectangular, large, well-delimited, ± inflated. *Sporophyte* similar to that of *B. rutabulum*.

VARIATION. The most obvious variation is in habit. There are sometimes no secondary stems, but the stem is regularly branched (Figs. 2 A, C). When growing submerged in streams it has an elongated stem with secondary stems, differentiated or not, and without leaves at the base of the main stem (Fig. 2 D). The degree of plication and denticulation varies as in *B. rutabulum*. The size of the plants ranges from a few cm to more than 20 cm.

Some varieties of *B. rivulare* have been investigated. The following are regarded as synonyms of *B. rivulare* s. str.: var. *cataractarum*, var. *gracile*, var. *nitidum* and var. *umbrosum* (cf. list of synonyms).

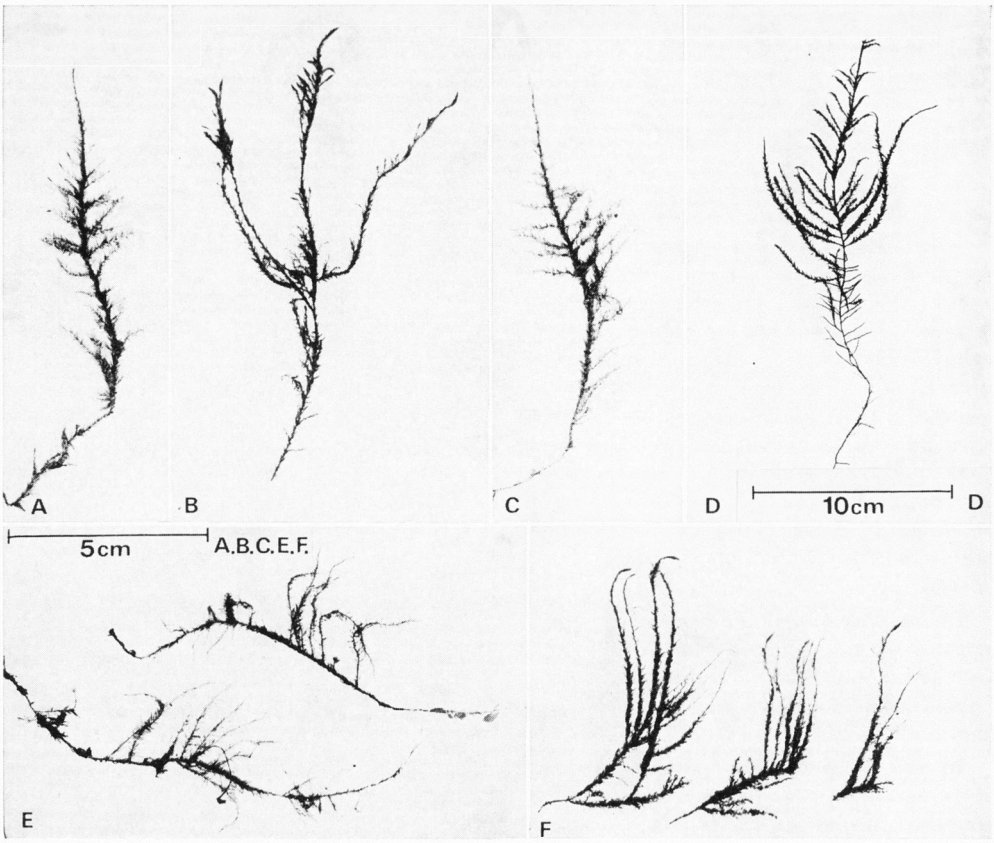

Fig. 2. A—D, F: *Brachythecium rivulare*. — E: *B. rutabulum*. — A, C: Regularly branched, secondary stems not differentiated. — B: Secondary stems differentiated. — D: Regularly branched, secondary stems poorly differentiated. Without leaves at the base of the primary stem. — E: Creeping stem with ± erect branches. — F: Creeping primary stem and erect secondary stems.

As has already been pointed out under *B. rutabulum*, *B. rivulare* var. *cuspidatum* is a synonym of *B. rutabulum*.

B. rivulare var. *longifolium* does not belong to the *B. rutabulum—B. rivulare* complex but to the *B. salebrosum* complex, which has already been pointed out by WARNSTORF (1906) who treated it as a form of *B. mildeanum* (SCHIMP.) SCHIMP. This form will be discussed in a forthcoming paper.

Brachythecium rivulare can easily be confused with *B. rutabulum*.

B. rivulare has also often been confused with *Rhynchostegium riparioides* (HEDW.) CARD. This confusion is probably largely of ecological origin as the two species often grow together in streams. They are not morphologically alike and *B. rivulare* is readily distinguished from *R. riparioides* on the inflated, longly and broadly decurrent angular cells. Another distinguishing character is the shape of the leaves. In the latter species they are ± rounded and in the former somewhat elongated. *R. riparioides* is an autoecious species often producing sporophytes, in contrast with *B. rivulare* which is dioecious and rarely

Table 2. Differences between *Brachythecium rutabulum* and *B. rivulare*.

Characters	*B. rutabulum*	*B. rivulare*	Characters modificative (+) or not (—)
Leaves	± longly pointed, Fig. 1 B.	± acute, Fig. 1 C.	—
Angular cells	rectangular, rather small, usually not well delimited or inflated	rectangular, large, ± inflated, always well delimited	+
Decurrent part of leaf	as a rule narrow and not longly decurrent	broadly and longly decurrent	+
Length of nerve	to middle of leaf	somewhat beyond middle of leaf	+
Sex condition	autoecious	dioecious	
Sporophytes	common	rare	
Habitats	often in dry habitats, but also in wet	always in wet habitats	
Type of branching	as a rule strongly branched	often poorly branched	+
Secondary stems	not often differentiated	often differentiated	+
Rhizoid bundles	often produced	not often produced	+
Chromosome number	n=12, Figs. 3, 4	n=6, Fig. 3.	
Number of large heteropycnotic bodies	2, Fig. 5	1, Fig. 5	

produces sporophytes. The seta is smooth in the former and rough in the latter.

DISTRIBUTION IN SCANDINAVIA

B. rivulare is widely distributed in the whole of Scandinavia but it is not common except in a few districts, e.g. the west coast of Norway.

HABITATS

B. rivulare always grows in wet habitats, often on stones in or beside streams. It often grows together with *Rhynchostegium riparioides* and *B. plumosum*.

Differences Between B. rutabulum and B. rivulare

The differences between the two species are given in Table 2. The most useful characters are the shape of the leaves, the angular cells and the decurrent part of the leaf. The first character is not modifiable whereas the development of the angular cells and the decurrent part of the leaves in *B. rutabulum* are characters highly dependent of humidity (WIGH 1976). The type of branching can sometimes be of diagnostic value (Fig. 2), but in some forms of *B. rutabulum* the habit is that otherwise characteristic of *B. rivulare*, just as there are forms of *B. rivulare* which have the type of branching characteristic of *B. rutabulum*.

In *B. rivulare* sporophytes if present are few, whereas *B. rutabulum* often produces abundant sporophytes. A character also of some diagnostic value is the number of rhizoids produced by the plant. *B. rutabulum* often produces bundles of rhizoids, in contrast to *B. rivulare*. This very modifiable character is dependent on humidity, light intensity and whether the shoot has grown in contact with the substratum (WIGH 1976).

If the above-mentioned characters cannot be used for diagnosis it is sometimes necessary to determine whether the plant is autoecious or dioecious. Some authors hold that *B. rivulare* can be both autoecious and

Table 3. Differences between *Brachythecium rutabulum* and other species in the genus.

Characters	Characters in *B. rutabulum*	Characters in the other species
		B. salebrosum
Seta	rough throughout	smooth
Plication	as a rule not strongly plicated, plications ± restricted to middle of leaf	strongly and regularly plicate with plications beginning from the base of the leaf
Apex of leaf	acuminate	more longly pointed
Chromosome number	n=12	n=13
		B. mildeanum
Denticulation	usually ± denticulate	not denticulate
Angular cells	mostly ± well developed	not well developed
Shape of leaf	rounded—ovate	regularly triangular
Seta	rough throughout	± smooth
Plication	± plicate	often without plication
Chromosome number	n=12	n=13
		B. curtum
Leaf	concave, exceptionally plane	plane
Nerve of branch leaf	not ending in a spine-like projection	often ending in a spine-like projection at back of leaf
Branch leaf	denticulate	dentate
Size of plant	robust—medium	medium—small
End of branches	without bundles of rhizoids	often with bundles of rhizoids
Habitat	usually not in pine forests	often in pine forests
Seta	rough throughout	often partly less papillose
Cilia of inner peristome	nodose	appendiculate
Capsule	often more than 2 mm	usually smaller
Chromosome number	n=12	n=22
		B. plumosum
Seta	rough	± smooth
Length of cells in middle of leaf	70—100 μ	often shorter than 70 μ
Leaf	erect—spreading	often secund
Nerve of branch leaf	not ending in a spine-like projection	often ending in a spine-like projection
Angular cells	rectangular, not incrassate, ± well developed	incrassate, not well developed, rectangular or quadrate
Habitat	usually not submerged in streams	often submerged in streams
Chromosome number	n=12	n=10

dioecious, but autoecious plants have not been observed by the author.

The leaves are longer in *B. rutabulum* and the relative length of the nerves longer in *B. rivulare* (WIGH 1976).

Differences Between B. rutabulum and Some Other Brachythecium Species

Brachythecium rutabulum has often been confused with other species in the genus, e.g. *B. salebrosum* (WEB. & MOHR) B.S.G., *B. mildeanum* (SCHIMP.) SCHIMP., *B. curtum* (LINDB.) LIMPR. and *B. plumosum* (HEDW.) B.S.G. The differences between *B. rutabulum* and these species are given in Table 3.

The most obvious difference between *B. rutabulum* and *B. salebrosum* is the seta. Where no sporophytes are available the plication of the leaves is a useful diagnostic character.

B. mildeanum and *B. rutabulum* sometimes grow together on clayey soil in ditches etc. These two species are similar in habit, but under the microscope there is usually no difficulty in separating the two species. The denticulation and the shape of the leaves are the two most useful distinguishing characters.

Apart from *B. rivulare*, *B. curtum* can sometimes be the most difficult species to distinguish from *B. rutabulum*, small forms of which have often been confused with *B. curtum*. These forms often have more or less plane leaves so that this character is of less value. In such cases all the other characters listed must be taken into consideration. The best distinguishing characters are the end of the nerve in the branch-leaves and the presence or absence of rhizoid bundles at the tip of the branches. Too much reliance must, however, not be placed on the latter character.

B. plumosum has also often been confused with *B. rutabulum* but it is generally easy to distinguish between the two species. As a rule it is sufficient to note whether the leaves are secund or not, but in some forms of *B. plumosum* the leaves are more or less erect and in such cases the other distinguishing characters must be used.

CYTOLOGY OF BRACHYTHECIUM RUTABULUM

Chromosome Complement

In all the gatherings studied the chromosome number was found to be identical, viz. n=12 which is remarkable since several other chromosome numbers have been reported for this species (Fig. 6).

In a few gatherings one of the chromosomes has a negatively heteropycnotic end segment (Fig. 3 E, H). This segment appears to vary in size in different populations and even within a population. In a few cases it is quite conspicuous, whereas in others it is very small and in most populations no end segment is observed at all. This indicates that the size is partly due to the degree of contraction caused by the pretreatment. The same phenomenon has been observed by the author in *Mnium undulatum* HEDW. (WIGH 1972 b).

Several hundreds of metaphases have been studied, but in none have the centromeres in all the chromosomes been observed in one single metaphase plate. This makes it difficult to construct an idiogram for the species.

It was sometimes observed that the chromosomes were built up of lightly and darkly staining blocks (Figs. 3 A—C, E, G, I, 4 A, B). The lightly staining segments are presumed to be built up of heterochromatin and are the possible sites of kinetic activity, perhaps in the same way as reported by VAARAMA (1954) for *Pleurozium schreberi*.

If different populations are compared as to the distribution of eu- and heterochromatic segments in the chromosomes, it is sometimes possible to find the same pattern of eu- and heterochromatic blocks in the presumably corresponding chromosomes from different populations. In other cases, however, the chromatic patterns were observed to differ. Such comparisons are rendered difficult as in no cases do all the chromosomes of a metaphase plate show this differentiation. This may, of course, be due to the fact that some chromosomes are wholly built up of euchromatin or almost so. Such a chromosome is observed to be darkly staining in its whole length. Thus it cannot yet be proved whether corresponding chromosomes always have identical chromatic patterns, but this investigation indicates the possibility that chromosomes often have the same chromatic pattern, but in other cases they may have different patterns, possibly due to structural changes such as translocations or inversions.

Heteropycnosis

In the resting nuclei of this species the number of positively heteropycnotic bodies

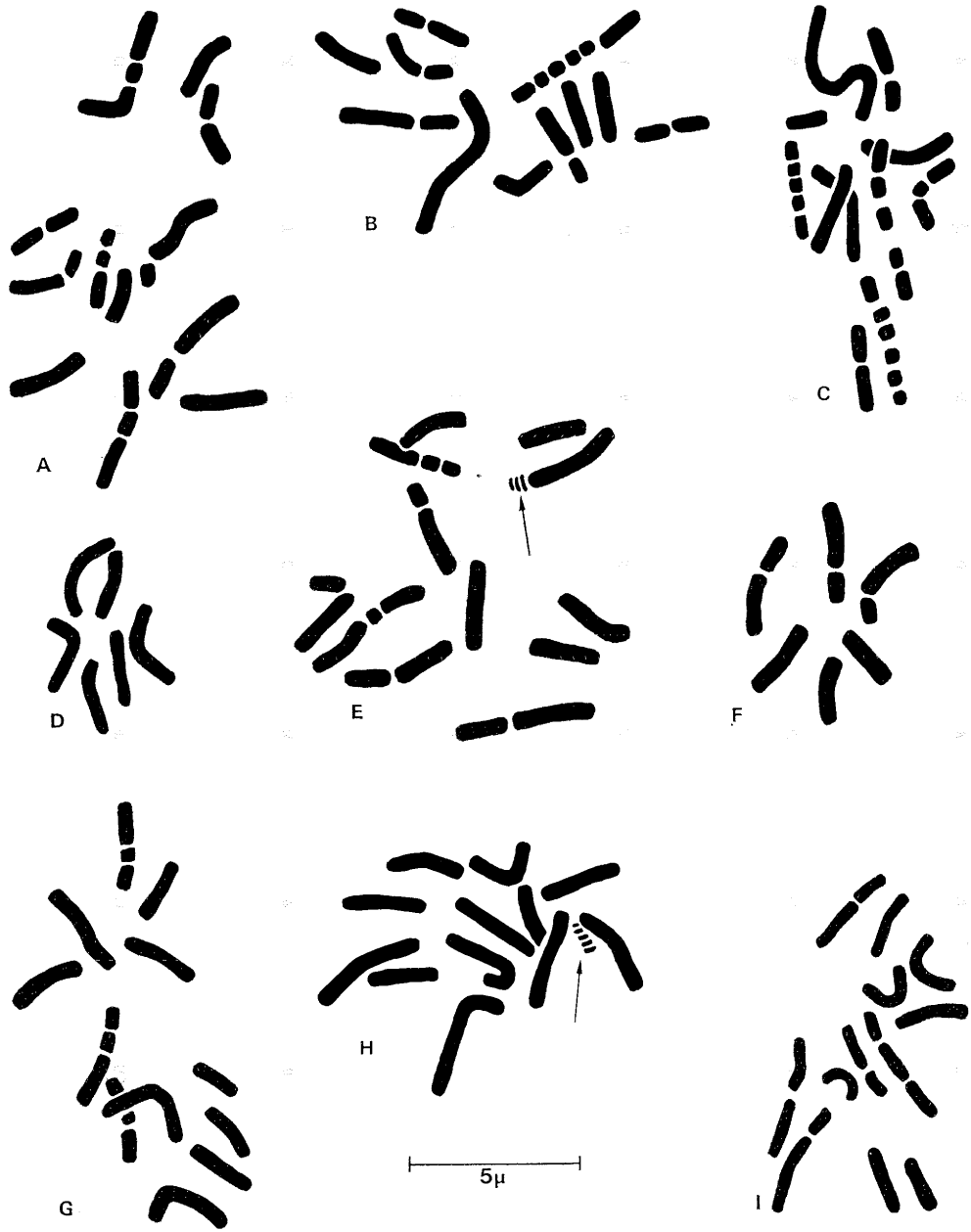

Fig. 3. Mitotic chromosomes. — A—C, E, G—I: *B. rutabulum* (n=12). — D, F: *B. rivulare* (n=6). — A: 72-528 (cf. Fig. 5 B). — B: 71-505. — C: 71-509. — D: 71-171. — E: 72-285. — F: 71-371. — G: 71-665 (cf. Fig. 5 A). — H: 71-491. — I: 71-441. — The arrows show negatively heteropycnotic end segment.

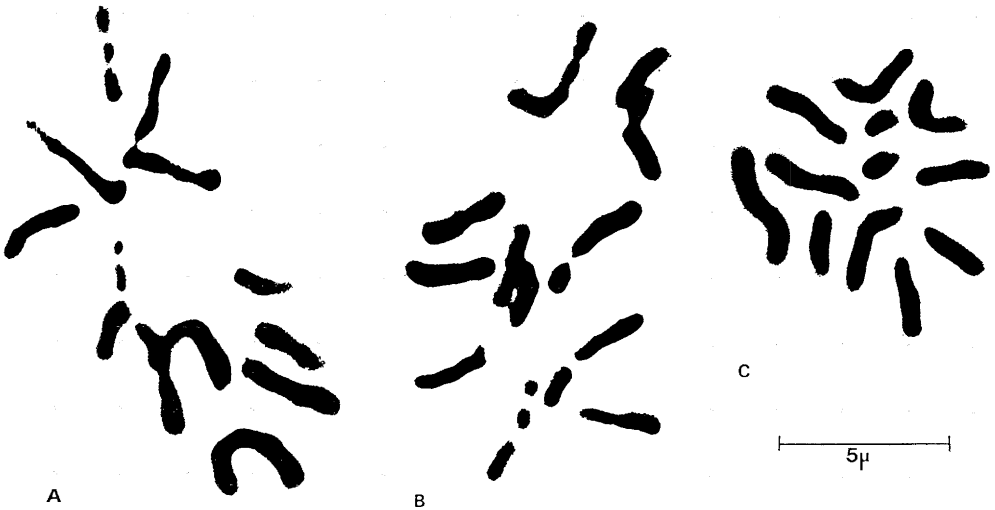

Fig. 4. Photomicrographs of mitotic chromosomes of *Brachythecium rutabulum*. — A: 71-665 (cf. Fig. 3 G). — B: 72-528 (cf. Fig. 3 A). — C: 72-481.

varies. Each nucleus contains one or two large bodies and a varying number of small bodies (Fig. 5 A—C). As a rule there are two large bodies but these sometimes fuse (Fig. 5 C), so that there appears to be only one. All stages in this fusion can be studied. These large heteropycnotic bodies are often designated H by Japanese cytologists. H stands for a large heteropycnotic body and h for the small ones. In the *Brachythecium rutabulum—B. rivulare* complex one large body denotes that the species is haploid and two large bodies that it is diploid. Moreover one body occurs in dioecious species and two in autoecious species.

The differences between heteropycnotic bodies in *B. rutabulum* and *B. rivulare* is discussed on p. 491.

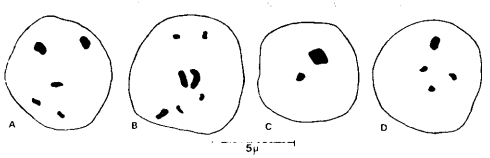

Fig. 5. Heteropycnotic bodies in resting nuclei. — A—C: *Brachythecium rutabulum*. — D: *B. rivulare*. — A: Two large bodies and three small ones. — B: The two larger bodies just before fusion, together with five small bodies. — C: The two large bodies have fused. One additional small body. — D: One large body and three small ones.

Chromosome Numbers Previously Published

n= 5 HOLMEN (1958) Denmark.

n= 6 VISOTSKA (1967) and LAZARENKO et al. (1971) the Ukrainian SSR (as *B. eurhynchioides*). — LAZARENKO et al. (1971) the Latvian SSR and the Estonian SSR, 2 populations.

n=10 MOUTSCHEN (1955) Belgium. — HOLMEN (1958) Denmark.

n=11 SINOIR (1952) probably France. — CHOPRA & KUMAR (1967) India. — BRYAN (1973) Austria.

n=12 WILSON & BURNETT (1961) Scotland. — SMITH & NEWTON (1967) the British Isles, 29 populations. — VISOTSKA (1967) and LAZARENKO et al. (1971) Ukrainian SSR, 4 populations (one population as *B. eurhynchioides*). — RAMSAY (1969) the British Isles. — VYSOTSKAYA & FETISOVA (1969) and LAZARENKO et al. (1971) the Latvian

SSR. — VYSOTSKAYA (1970) and LAZARENKO et al. (1971) the Georgian SSR. — WIGH & STRANDHEDE (1971) Denmark and Sweden, 9 populations (two of the populations as *B. rivulare*). — LAZARENKO et al. (1971) the Estonian SSR.

n=13 VISOTSKA (1967) and LAZARENKO et al. (1971) the Ukrainian SSR, 2 populations.

n=20 RAMSAY (1969) the British Isles, 2 populations.

n=22 LAZARENKO et al. (1971) the Byelorussian SSR, 2 populations.

Some of the above-mentioned populations have been studied by the author. The gathering studied by SMITH & NEWTON (1967) and RAMSAY (1969) with the chromosome number n=12 are all typical *B. rutabulum*. The two gatherings with the chromosome number n=20 reported by RAMSAY (1969) diverge somewhat from the nomenclatural type of the species, particularly in the small size of the plants and leaves. In the most important characters the two populations agree with *B. rutabulum*. As only limited material of this cytotype has been available it cannot be stated with certainty whether it belongs to another taxon in the *B. rutabulum* — *B. rivulare* complex until further material of the cytotype has been found. Until then the two gatherings must be treated as a form of *B. rutabulum*. This cytotype has not been observed elsewhere and it is with all certainty uncommon, at least in Scandinavia.

The Latvian and Estonian gatherings with the chromosome number n=6 proved to be a mixture of *B. rutabulum* and *B. rivulare* so that it seems likely that the chromosome numbers refer to *B. rivulare*. The population with n=6 published under the name of *B. eurhynchioides* has not been available for study.

Two of the Ukrainian populations with n=12 have been studied and they are both typical *B. rutabulum* as are the populations from the Latvian SSR, the Georgian SSR and the Estonian SSR.

One population of *B. rutabulum* with n=13 has also been studied and is in all characters wholly in accordance with the nomenclatural type of the species.

As the other non-Scandinavian populations that have been cytologically studied have not been available to the author, it is not possible to comment on the chromosome numbers. It is evident that the dominating cytotype in *B. rutabulum* has the chromosome number n=12. Chromosome races probably exist in this species, p. 492, but it seems most likely that some of the chromosome counts are incorrect and that some populations have been erroneously determined or that the chromosome numbers refer to mixed gatherings.

There can sometimes be difficulties in spreading and staining which may explain erroneous counts. This may also be due to the bivalents sticking together or to meiotic irregularities, p. 489.

Two European species of *Brachythecium*, *B. salebrosum* and *B. mildeanum* have the chromosome number n=13. As forms of these species can sometimes be difficult to distinguish from *B. rutabulum*, p. 484 this may perhaps explain the chromosome count n=13 reported for *B. rutabulum*. The chromosome count n=22 may have arisen from confusion with *B. curtum* as small forms of *B. rutabulum* can be difficult to distinguish from that species, p. 485.

The chromosome numbers reported for *B. rutabulum* are given in Fig. 6.

Chromosome Numbers in Scandinavian Populations

In Scandinavian populations of *B. rutabulum* three chromosome numbers have been reported, viz. n=5, 10 and 12. The first numbers have been published by HOLMEN (1958) in two Danish populations with the reference numbers 636 and 702 respectively, the latter referring to an autoecious population and the number 636

to a probably dioecious one. The population with n=10 (no. 702) has larger leaves, longer leaf cells and larger spores, 13 μ instead of 10 μ as found in the other gathering (no. 636). The seta is also longer and the capsule smaller in no. 702. According to HOLMEN population 702 is morphologically closely related to *B. curtum*.

The small size of the capsule indicates such a relationship (Table 3) but this is contradicted by the chromosome number. All populations of *B. curtum* that have been studied cytologically by the author have the chromosome number n=22.

No dioecious form of *B. rutabulum* has been observed by the author. In the probably dioecious population, no. 636, the leaves are smaller indicating that it may be a form of *B. rivulare*. This is, however, contradicted by the size of the spores which is only 10 μ.

As these two populations have not been available to the author it is difficult to discuss the morphology in any detail. In Scandinavia some dioecious species of *Brachythecium* are known but none with n=5 has been found by the author. The lowest numbers known are n=6 in *B. rivulare* and n=7 in some species of the *B. albicans* complex (WIGH 1974). This complex is, however, morphologically very divergent from the *B. rutabulum* — *B. rivulare* complex and can thus be excluded from the discussion.

The chromosome numbers in these two populations are thus problematic. The cytological methods used (the sporophytes were embedded in paraffin and cut on a microtome) can perhaps cause the loss of one or more chromosomes so that the chromosome number would be higher than reported. Of course there is a possibility that cytotypes of *B. rutabulum* exist in Scandinavia with n=5 and n=10. It seems, however, more likely that the chromosome numbers are due to erroneous counts, p. 492.

WIGH & STRANDHEDE (1971) reported the chromosome number n=12 in two Scandinavian populations of *B. rivulare*. These reports, however, refer to *B. rutabulum*. The taxonomic determinations were based on the rather well-delimited angular cells, a character that must not be overemphasized. The leaves of two populations are longly pointed in a manner wholly characteristic of *B. rutabulum* and the two populations are autoecious which also supports this latter determination. The other 7 populations studied by the authors are typical *B. rutabulum*.

Meiotic chromosomes in Scandinavian populations of *B. rutabulum* have been studied by VAARAMA (unpubl.) who observed 12 bivalents in a Finnish population.

Meiotic Irregularities

Several meiotic irregularities have been observed in particular in the n=12 cytotype of *B. rutabulum*. RAMSAY (1969) reported for example non-synchronous separations of bivalents, laggards at telophase I and II, micronuclei and irregular spore tetrads. SMITH & NEWTON (1967) reported irregularities such as failure of pairing, bridges, fragments, lagging bivalents or semi-bivalents. LAZARENKO et al. (1971) observed 12 and 13 bivalents in one single sporophyte. In mitotic divisions in the capsule they observed 24 and 26 chromosome bodies, each body consisting of two chromosomes, the chromosome number thus being 2n=48 or 52. Unfortunately they did not study the chromosomes in the gametophyte so that it is difficult to explain this mixoploidy. These irregularities, together with the sticky bivalents, can easily give rise to erroneous chromosome counts.

Origin

According to WILSON & BURNETT (1961) and other authors *B. rutabulum* is an autoploid species. SMITH & NEWTON (1967) did not agree with this as they found neither trivalents nor quadrivalents and as

no cytotype with n=6 is known it must at least be very uncommon. They thought that there would be selection against an autopolyploid species since it would imply the occurrence of tri- and quadrivalents which would give rise to unbalanced spores.

As so few cytological experiments have been carried out in mosses it is difficult to discuss autopolyploidy and allopolyploidy. Through experimental apospory it is possible to produce a polyploid series in mosses, for instance from n=6 to 12 etc. In a number of species it is fairly easy to obtain these polyploids, as the regenerative capacity is very high. It is thus possible to generate a gametophyte with the double chromosome number from a sporophyte, if the sporophyte is cultivated in a suitable nutritional medium.

In the classic work by MARCHAL (1912) a diploid form of *Amblystegium*, *A. serpens bivalens*, was produced through apospory. According to him the basic chromosome number in this species is n=12, and the *bivalens* form thus had n=24. The behaviour of the chromosomes was studied during meiosis. In no sporophyte was a regular pairing of the chromosomes observed. In every sporophyte there was a mixture of quadri-, bi- and univalents, resulting in unbalanced chromosome numbers in the spores. Such a diploid form would thus not be able to compete in nature with the haploid form of the species.

Brachythecium rutabulum may be an autopolyploid species, but if so, the formation of quadri- and trivalents has been suppressed in some way. The species may have originated through autopolyploidy a long time ago and the formation of quadri- and trivalents been suppressed by natural selection. It seems probable that diploid forms of mosses arise in nature through apospory but that these forms presumably have difficulty in establishing themselves if they cannot multiply vegetatively, and thus cannot become widespread if there is no mechanism to ensure more regular meiosis. Autopolyploid species can also arise through endomitosis.

It seems, however, more likely that *B. rutabulum* is an allopolyploid species that has evolved from cytotypes with n=6.

Euploidy and Aneuploidy

The polyploid series n=5, 10 and 20 in *B. rutabulum* has been much discussed. The cytotypes with n=5 and n=10 are discussed here on p. 488. The author cannot support this theory of the basic number n=5 in the species (Fig. 6).

As has been already mentioned some of the chromosome numbers reported in *B. rutabulum* are probably erroneous and others probably refer to other taxa, but this does not explain all the diverging chromosome numbers. Although chromosome races have not been observed by the author in the Scandinavian populations of *B. rutabulum* studied, their existence is supported by the interesting investigation carried out by MOUTSCHEN (1955). Through irradiation of the sporophytes a series of viable aneuploid mutants was obtained. The irradiation resulted in a number of fusions and the number of chromosomes was thus reduced. This investigation shows that *B. rutabulum* can survive radical chromosome mutations. Such changes may occur in nature and it seems likely that the chromosome number can be lower than n=12 as a result of translocations or fusions of whole or almost whole chromosomes.

Only one detailed investigation of the centromere conditions in mosses has been carried out. In a most important investigation VAARAMA (1954) studied the kinetic activity of one easily identifiable chromosome in *Pleurozium schreberi* (BRID.) MITT. This study shows that the particular chromosome has more than one site of active mobility.

As no other investigations of the centromere conditions in mosses have been carried out it is not possible to say if there

is the same type of centromeric activity in other moss chromosomes. In the family Brachytheciaceae accessory chromosomes are known in three genera comprising five species, viz. *Homalothecium lutescens* (HEDW.) ROBINS., *H. sericeum* (HEDW.) B.S.G., *Brachythecium glareosum* (SPRUCE) B.S.G., *B. velutinum* (HEDW.) B.S.G. and *Rhynchostegium megapolitanum* (WEB. & MOHR) B.S.G. (WIGH 1973 a, NYHOLM & WIGH 1973). The accessory chromosomes in all these species behave in the same way as the A-chromosomes. They undergo divisions quite normally and they are never eliminated in mitosis, which denotes kinetic activity.

Chromosome fragmentation or fusion has been observed by VAARAMA (1953) in *Orthotrichum tenellum* BRUCH. In one sporophyte a large bivalent with a subterminal constriction was observed. In another there was no such bivalent but instead there was an additional small bivalent presumed to have derived from the large bivalent. VAARAMA did not exclude the possibility of the large bivalent having arisen through the fusion of two smaller bivalents.

Available information points to the likelihood in certain mosses at least of one or more of the chromosomes having more than one centromere. Furthermore the chromosome number in a population of a species can apparently increase as the result of fragmentation and decrease through translocations or fusion of whole or almost whole chromosomes.

CYTOLOGY OF BRACHYTHECIUM RIVULARE

Chromosome Complement

Only one chromosome number, n=6 has been observed in this species (Fig. 3 D, F). Unlike *B. rutabulum* no chromosome with a negatively heteropycnotic end segment has been observed. This may be due to the fact that fewer gatherings of this species have been studied.

The centromeres are seldom observed in this species, but in one metaphase plate the centromeres in three chromosomes were seen (Fig. 3 F). These three chromosomes have submedian centromeres. All six chromosomes are of about equal size as observed by HOLMEN (1958).

Heteropycnosis

In this dioecious species only one large positively heteropycnotic body is present in the resting nuclei (Fig. 5 D). Apart from this body a varying number of smaller bodies can be observed.

Resting nuclei of *B. rutabulum* and *B. rivulare* can be readily distinguished. Only when the large heteropycnotic bodies in the former species have fused can it sometimes be problematic if only a few cells are available.

Chromosome Numbers Previously Published

n= 6 HOLMEN (1958) Denmark. — SMITH & NEWTON (1968) the British Isles. — VYSOTSKAYA & FETISOVA (1969) and LAZARENKO et al. (1971) the Latvian SSR and the Estonian SSR 3 populations. — WIGH & STRANDHEDE (1971) Denmark. — WIGH (1972 a) Spain, 2 populations.

n=11 INOUE (1967) Japan.

n=12 FETISOVA & VYSOTZKAYA (1970) and LAZARENKO et al. (1971) the Estonian SSR and the Latvian SSR, 2 populations. — The report by WIGH & STRANDHEDE (1971) is erroneous because of incorrect taxonomical determination. The two populations belong to *B. rutabulum*.

n=13 VISOTSKA (1967, 1970) and LAZARENKO et al. (1971) the Ukrainian SSR and Georgian SSR, 4 populations.

n=16 ANDERSON & BRYAN (1958) North Carolina, USA.

The population with n=6 investigated by SMITH & NEWTON (1968) has been studied by the author. It is a typical form of *B. rivulare*, as are the two Spanish populations studied by WIGH (1972 a).

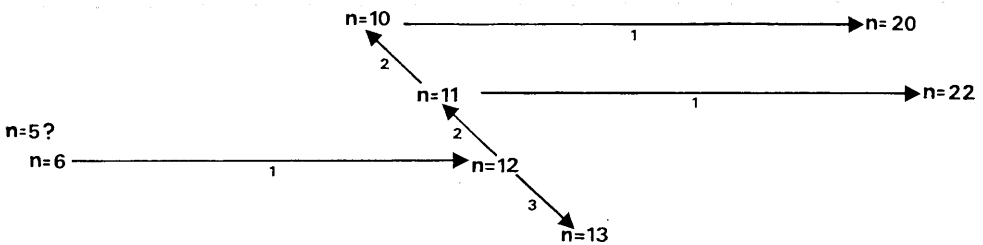

Fig. 6. Chromosome numbers published for *Brachythecium rutabulum*. — Arrow 1 indicates chromosome doubling. — Arrow 2 indicates reduction of chromosome number. — Arrow 3 indicates increase in chromosome number. — For explanation see text.

One of the Latvian populations with n=6 has been investigated and was found to belong to *B. rivulare*. The populations with the chromosome number n=12 from the Latvian SSR and the Estonian SSR both proved to be mixed gatherings of *B. rivulare* and *B. rutabulum* so that the chromosome number presumably refers to *B. rutabulum*.

One of the Ukrainian populations with n=13 has been available. It combines characters typical of both *B. rivulare* and *B. rutabulum*. In the habit, shape and length of leaves and length of nerves it agrees with *B. rivulare*, but in the poorly developed angular cells and the shortly decurrent leaves it resembles more closely *B. rutabulum*. Archegonia only have been found indicating that it may be a dioecious specimen which supports regarding it as a divergent form of *B. rivulare* until additional material is available.

Chromosome Numbers in Scandinavian Populations

Chromosome numbers in *B. rivulare* have been published by HOLMEN (1958) who reported n=6 in a Danish population and WIGH & STRANDHEDE (1971) who published n=6 in a Danish population and n=12 in two other populations. The taxonomic determinations of these last two populations are erroneous and the report refers to *B. rutabulum*.

The chromosome number n=6 has also been observed by ALMGREN (unpubl.) in a Swedish population of *B. rivulare*. In all characters this population is typical of *B. rivulare* as is the population studied by WIGH & STRANDHEDE (1971). It seems thus likely that there is only one cytotype of *B. rivulare* in Scandinavia or at least that the other cytotypes are uncommon.

A WORKING HYPOTHESIS FOR EXPLANATION OF CHROMOSOME NUMBERS IN B. RUTABULUM AND RIVULARE

In Figs. 6 and 7 the chromosome numbers reported in *B. rutabulum* and *B. rivulare* are given.

In *B. rutabulum* n=5 has been published by HOLMEN (1958). At first meiotic metaphase 5 large bivalents of about the same size are shown. In the same species LAZARENKO et al. (1971) reported n=6. At first meiotic metaphase they found 6 large bivalents about equal in size. If the n=5 cytotype has arisen through the fusion of two chromosomes in the n=6 cytotype, one of the chromosomes in the n=5 cytotype would be conspicuously larger than the others. As this is not the case the author presumes that the chromosome number n=5 is an erroneous count. It does not seem likely that it is due to misdetermination as no morphologically related species is known with the chromosome number n=5, p. 489.

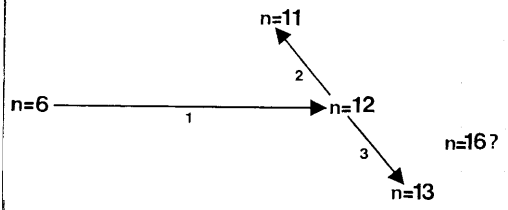

Fig. 7. Chromosome numbers published for *Brachythecium rivulare*. — Arrow 1 indicates chromosome doubling. — Arrow 2 indicates reduction in chromosome number. — Arrow 3 indicates increase in chromosome number. — For explanation see text.

It must be noted that two of the populations of *B. rutabulum* with n=6 published by LAZARENKO et al. (1971) are mixed populations, p. 492.

B. rutabulum probably originates from a cytotype with n=6. This hypothetical cytotype would probably be dioecious and the doubling of the chromosome number would have caused a change from the dioecious to the autoecious state. The n=12 cytotype dominates in this species and structural chromosome changes of this cytotype have given rise to the other cytotypes. Such changes can cause an increase in the chromosome number through fragmentation, if the fragments are centric and display no tendency to fuse with the other chromosomes. This would indicate that the n=13 cytotype could be karyologically heterogeneous and polyphyletic as it seems likely that fragmentation may arise several times and in different chromosomes.

Through translocation of whole or almost whole chromosomes the chromosome number could be lower than n=12. Such changes could comprise one or more chromosomes and also give rise to different karyotypes.

Chromosome doubling of the n=11 and n=10 cytotypes have given rise to the n=22 and n=20 cytotypes respectively.

These chromosome changes have evidently not given rise to any great morphological difference as the cytotypes are still identifiable as belonging to the species *B. rutabulum*. The cytotypes with chromosome numbers other than n=12 are probably not so widespread nor so common as the n=12 cytotype. This is so in Scandinavia at least.

In *B. rivulare* the basic number is n=6. The chromosome number n=12, 13 and 11 can be explained in the same way as in *B. rutabulum*. The chromosome number n=16, however, does not seem to fit into the pattern and its origin is difficult to explain. This chromosome number is uncommon in the genus *Brachytheicum* and exists in a few species only (WIGH 1974).

It must be stressed that this is merely a hypothesis and that perhaps some of the chromosome numbers reported are erroneous. The only cytotypes seen by the author, except for mixed populations with n=6, are n=12, n=13 and n=20 in *B. rutabulum* and n=6 and n=13 in *B. rivulare*.

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APPENDIX. Localities of Cytologically Studied Material

Brachythecium rutabulum

FINLAND. Nyland. Ingå, Fagervik (70—213, 70—215, 70—217, 70—218); Karjalohja, Pyöli (70—191, 70—192, 70—197); Lohja, Ahtiala (70—177, 70—178, 70—181, 70—184), Outamo (70—67); Tenala, Lindö (70—228). — Regio Aboënsis. Salo, Viitta (70—153); Särkisalo, Bastböle (70—85, 70—89), Förby (70—78, 70—163); Turku, Kaarina, Tuorla (70—110).

NORGE. Hordaland. Arna (70—329). — Rogaland. Bryne, Nordheim (71—186, 71—187, 71—188), Orre (71—181, 71—182, 71—184); Eigersund, Helleland (71—135, 71—137, 71—138); Gjestal, Dirdal (71—156); Hå, Ogna (71—147); Karmöy, Avaldsnes (70—427), Stokkastrand (70—416); Kleppe (71—151, 71—152, 71—153); Sandnes, Ålgård (71—164, 71—165); Sauda, 4 km S of Saudasjöen (70—378, 70—392); Stavanger, near the church (71—91), Rennesöy (71—105, 71—106, 71—107, 71—111). — Östfold. Fredrikstad, Veumengen (72—127); Onsöy, Hurröd (72—108, 72—110), Kjölberg (71—124, 72—136, 72—137), Krökeröy, Enhus (72—163, 72—164, 72—166, 72—167), Krökeröy, the quarry near Femdal (72—189), Kråkeröy, Holte (72—196, 72—197), Kråkeröy, Röd (72—44, 72—55, 72—56, 72—63, 72—64, 72—65, 72—142, 72—144, 72—146, 72—150), Kråkeröy, Tangen (72—169, 72—170, 72—171, 72—172), Torgauten (72—38, 72—39, 72—41), Trondalen (72—72, 72—74, 72—77, 72—78, 72—83), Åle (72—90, 72—91), Örebekk (72—119, 72—120, 72—121).

SVERIGE. Bohuslän. Backa, Fridhem (70—479, 70—481, 70—482, 71—3), leg. M. NEUENDORF (71—3); Björlanda, Högåsa (71—12); Kungälv, Stubbhult (71—59 leg. T. HALLINGBÄCK); Skepplanda, Skår (73—01 leg. T. HALLINGBÄCK); Säve, Lindesnäs (72—4, 72—12); Tanum, Knäm (70—374); Torsby, Lilla Överön (70—510); Uddevalla, Kristinedal (71—239, 71—240, 71—244, 71—245, 71—246, 71—247, 71—248, 71—249, 71—250), Kuröd (71—90); Ytterby, Ragnhildsholmen (71—10, 72—7, 72—8). — Dalsland. Ånimskog, Skållebyn (71—15 leg. D. NILSSON). — Gotland. Gotska Sandön, Gamla gården (71—720, 71—722 leg. S. SUNHEDE), Stora Idemoren (71—719 leg. S. SUNHEDE); Västerhejde, Fridhem (72—227 leg. B. PETTERSSON); Västkinde, Nors (71—622 leg. B. PETTERSSON). — Halland. Fjärås, Tjolöholm (71—507, 71—508, 71—509, 71—510); Släp, Särö (70—25), Särö, Västerskog (71—17 leg. D. NILSSON); Skogaby, Ebbarp (70—35, 70—36). — Närke. Gällersta, Attersta (72—576); Kumla (70—272); Vintrosa, Lannafors, limestone quarry (71—457, 71—458). — Skåne. Araslöv, Ullstorp, pond (71—513, 71—514, 71—521), Ullstorp, limestone quarry (71—500, 71—501, 71—502, 71—503, 71—504, 71—505); Bromölla, Edenryd (71—730); Brönnestad, Hovdala (73—20); Fjälkinge, Ivön, limestone quarry (71—489, 71—490, 71—491, 71—492), Näsum kaolin quarry (72—639, 72—641, 72—642). — Småland. Huskvarna, Ådalsfallen (71—27, 71—28 leg. T. HALLINGBÄCK); Lagan, near the river Lagan (73—24 leg. S. SUNHEDE); Visingsö, near the harbour (72—285). — Uppland. Bogesund (71—127); Danmark, Tjocksta (72—481); Gamla Uppsala (72—430); Huddunge (71—697 leg. G. EEN); Uppsala. Röbo, the brick-yard (72—445, 72—453); Vaksala, Skälby (72—469); Vattholma, Åsby (72—412); Vaxholm, Skägga (70—274); Värmdö (70—281). — Västergötland. Askim, St. Amundön (71—19 leg. D. NILSSON); Berg, Postgården (70—517, 70—518, 70—523); Bredsäter, Lugnås (70—249, 70—255, 70—262); Broddetorp, Hornborga (70—550, 70—557, 70—558); Göteborg, Botaniska trädgården (70—461, 70—610, 71—482), Långedrag (70—452), Tynnered (70—431, 70—432); Kinnekulle, Österplana (71—538), Råbäck (73—7, 73—8 leg. S. SUNHEDE); Landvetter (70—450); Lerdala, Karlsfors (70—532, 70—542, 70—545); Skövde, Ryd, Åsen (70—487); Våmb, near the church (72—607, 72—609); Timmersdala, Stora Stolan (72—593, 72—597, 72—601, 72—602); Tuve, Stora Holm (71—16 leg. L. ARVIDSSON). — Västmanland. Guldsmedshyttan, Mårdshyttan, the marble quarry (72—544, 72—550), Fanthyttan, the limestone quarry (71—441, 71—442, 71—445, 71—450); Ljusnarberg, Ställdalen, Östra Bom limestone quarry (71—415); Norberg, Klackberg (72—518, 72—523, 72—528, 72—529, 72—530, 72—531); Sala, Skå, limestone quarry (72—511). — Öland. Algutsrum, Gråborg (71—652, 71—653); Borgholm, slottsruinen (71—80, 71—81, 71—608, 71—609, 71—610, 71—611), between Borgholm and Köping (71—563, 71—564, 71—565, 71—566, 71—567, 71—568, 71—570, 71—571, 71—572, 71—573, 71—574); Degerhamn, Albrunna (71—75, 71—77, 71—82 leg. T. HALLINGBÄCK); Högsrum, Halltorp (71—646, 71—647); Knisa, Knisa mosse (71—79 leg. T. HALLINGBÄCK); Köping, 1 km SW of Dalby (71—585, 71—589, 71—590, 71—591); Stenåsa, Frösslunda (71—626, 71—627, 71—628, 71—629, 71—631, 71—632); Torslunda, Arontorp

(71—685, 71—686), Eriksöre (71—664, 71—665, 71—666, 71—667, 71—668). — Östergötland. Borensberg, brick-yard (72—228, 72—229); Godegård, Blommedal (72—238); Krokek, marble quarry (72—255, 72—256, 72—260, 72—264, 72—265, 72—275, 72—280, 72—292); Ringarum, Sätterbo (72—324, 72—326, 72—327); Törnevalla, limestone quarry (72—244, 72—245); Vånga, Glan limestone quarry (72—304).

Brachythecium rivulare

FINLAND. Nyland. Ingå, Fagervik (70—211, 70—212).

NORGE. Akershus. Asker, Groset (72—201, 72—204), Sem (71—127); Baerum, Skui (70—309, 70—313). — Aust-Agder. Tvedestrand, Tveite (70—349). — Hordaland. Arna, Herland (70—316, 70—321, 70—324). — Rogaland. Frafjord, Brålandsforsen (71—169, 71—171); Hå, Ogna (71—146); Sandnes, Trodal (71—166); Stavanger, Rennesöy (71—109, 71—110). — Telemark. Bamle, Feset (70—354, 70—361). — Vest-Agder. Flekkefjord, Ystabö (71—142).

SVERIGE. Bohuslän. Säve, Lindesnäs (72—11); Uddevalla, Kristinedal (71—237, 71—243). — Jämtland. Åre, Åreskutan (71—367, 71—368, 71—370, 71—371, 71—372). — Skåne. Brönnestad, Hovdala (73—17, 73—18); Dalby, Fågelsångsdalen (71—72 leg. T. HALLINGBÄCK). — Västergötland. Berg, Postgården (70—521, 70—522); Broddetorp, Hornborga (70—560); Falköping, Karleby, Djupadalsbäcken (70—573, 70—579, 70—580); Lerdala, Karlsfors (70—543); Skövde, Ryd, Skåningstorp (70—569), Ryd, Åsen (70—488, 70—489). — Östergötland. Vånga, Glan, limestone quarry (72—299).

Nomenclatural Notes on Arctic Plants

Áskell Löve and Doris Löve

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Nine genera, three species and two subspecies of arctic plants are described as new, one new name is validated, and a change in rank of 49 taxa and new combinations of 124 taxa are validated.

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In connection with the compilation of a cytotaxonomical atlas and checklist of the arctic flora (LÖVE & LÖVE 1975 a), we made efforts to arrive at a uniform classification for as many as possible of the 404 genera, 1629 species and 270 additional subspecies of higher plants which are known to occur within the tundra of the circumpolar northlands. As a norm for the classification, we followed the Linnaean species concept as adopted by Scandinavian and Russian botanists working with these plants and strengthened by the biological or cytogenetical approach. According to this paradigm, the family in its traditional sense is defined as a collection of genera that are likely to have evolved from a common ancestor as far as indicated by morphological and cytological characteristics. The natural genera should show morphological and cytological evidence of linear, and therefore strictly monophyletic, evolution of their species from a single prototype. They must also have certain crossability barriers towards other such groups, although that biological requirement sometimes needs to be relaxed because of taxonomical expediency for very large genera (LÖVE & LÖVE 1974). A good biological species is reproductively isolated from other such taxa, but it is identified by aid of morphological and geographical distinctions. However, within the species miscibility is not only allowed but directly required, irrespective of the magnitude of the morphological distinction of various races. Therefore, sexual subspecies and varieties are defined as interfertile major or minor geographical races that are capable of mixing freely whenever they meet. Since these concepts are at least very close to those followed by the majority of botanists working with arctic plants, only a limited number of adjustments were found to be needed to attain a reasonable closeness to the uniformity endeavoured. They are mainly caused by redefinition of a few generic limits.

In order to save space when validating new names for the arctic taxa for which this is justified, short descriptions are given for the new taxon, or a citation only to the name-giving basionym, except when the rank-deciding combination needs to be added for clarification. Synonyms are neglected unless necessary for identification, and other information is included sparingly for particular cases.

Gymnocarpium disjunctum (RUPRECHT) LÖVE & LÖVE, comb. nov., based on *Polypodium Dryopteris* L. var. *disjunctum* RUPRECHT, in Beitr. Pflanzenk. Russ. Reiches 3 (1845), p. 52; *Dryopteris disjuncta* (RUPR.) C. V. MORTON, p. p.

This is a Pacific species with 2n=80

chromosomes, corresponding to the more widespread Atlantic taxon *G. dryopteris* (L.) NEWMAN with 2n=160 chromosomes (cf. LÖVE & LÖVE 1967).

Festuca rubra L. ssp. **fraterculae** (RASM.) LÖVE & LÖVE, comb. nov., based on *Festuca rubra* L. var. *Fraterculae* RASMUSSEN, in Nytt Mag. f. Naturvid. 66 (1927), p. 110; *F. Richardsonii* HOOK. ssp. *fraterculae* (RASM.) LÖVE & LÖVE.

This rare but very distinct taxon of birdcliffs in northern Norway, the Faeroes and Iceland and perhaps elsewhere in the North Atlantic region, was originally described as a variety only by RASMUSSEN (1927), but later elevated to subspecific rank under *F. richardsonii* HOOK. by LÖVE & LÖVE (1956). Additional observations by us and by BRYNJÓLFSSON (1974) indicate that it is correctly classified as a subspecies equivalent to but younger and therefore less widespread than ssp. *arctica* (HACK.) GOVOR., which is an older name for ssp. *richardsonii* (HOOK.) HULTÉN of the *F. rubra* complex.

Poa supina SCHRAD. ssp. **ustulata** (FRÖHNER) LÖVE & LÖVE, stat. & comb. nov., based on *Poa ustulata* FRÖHNER, in Bot. Jahrb. 88 (1968), p. 437.

This is the widespread Asiatic race of *Poa supina,* rather than a species in its own right as maintained by FRÖHNER (1968), differing most clearly from the European typical race by its lack of long stolons so it grows in tufts, by its dark spikes and the dark-violet anthers, and in its later and longer flowering time, its distinctly shorter lifespan, and several other characters which together make it an easily distinguishable taxon. Naturally, both races are characterized by the same diploid chromosome number, and, in our experience, they are easily hybridized and then give rise to later generations in which their distinguishing characters show a clearly Mendelian segregation, as could be expected of well-defined races at this level of classification.

Phippsia R. BR.

It was pointed out by LÖVE (1970 a), that the morphological characters traditionally employed to distinguish the large grass genus *Puccinellia* PARL. from the small arctic-subarctic genus *Phippsia* R. BR. are of little significance for the separation of taxa at that level. Biologically still more important is the fact, observed by several students in recent decades, that the crossability between these two taxa is no more inhibited than between the species of *Puccinellia* itself. Therefore, following either the classical and purely morphological standard (cf. HARTMAN 1832) or the biological definition of the generic category, these groups must be regarded as being congeneric, as earlier concluded by LÖVE (1970 a, b) and LÖVE & LÖVE (1975 b). The name *Phippsia* has priority and so must be accepted as the valid name for the united group. The following new transfers, changes in rank, and descriptions are required for the taxa occurring in the Arctic:

Phippsia agrostoidea (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia agrostoidea* TH. SÖRENSEN, in PORSILD in Natl. Mus. Canada Bull. 135 (1955), p. 78.

Phippsia anderssonii (SWALLEN) LÖVE & LÖVE, comb. nov., based on *Puccinellia anderssonii* SWALLEN, in Journ. Wash. Acad. Sci. 34 (1944), p. 21.

Phippsia angustata (R. BR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia angustata* R. BROWN, Chloris Melvilliana (1823), p. 29.

Phippsia angustata ssp. **palibinii** (TH. SÖR.) LÖVE & LÖVE, stat. & comb. nov., based on *Puccinellia palibinii* TH. SÖRENSEN, in Medd. om Grönl. 136,3 (1953), p. 74.

Phippsia arctica (HOOK.) LÖVE & LÖVE, comb. nov., based on *Puccinellia arctica* W. J. HOOKER, Fl. Bor. Amer. 2 (1840), p. 248.

Phippsia borealis (SWALLEN) LÖVE & LÖVE, comb. nov., based on *Puccinellia*

borealis SWALLEN, in Journ. Wash. Acad. Sci. 34 (1944), p. 19.

Phippsia borealis ssp. **neglecta** (TZVELEV) LÖVE & LÖVE, comb. nov., based on *Puccinellia borealis* ssp. *neglecta* TZVELEV, in Arkt. Fl. SSSR 2 (1964), p. 206.

Phippsia bruggemannii (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia bruggemannii* TH. SÖRENSEN, in PORSILD in Natl. Mus. Canada Bull. 135 (1955), p. 80.

Phippsia capillaris (LILJEBL.) LÖVE & LÖVE ssp. **pulvinata** (FR.) LÖVE & LÖVE, stat. & comb. nov., based on *Glyceria distans* (L.) WG. var. *pulvinata* FRIES, Mant. 2 (1839), p. 11, pro parte; *Atropis pulvinata* V. KRECZETOVICH, Fl. SSSR 2 (1934), p. 761.

Phippsia deschampsioides (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia deschampsioides* TH. SÖRENSEN, in Medd. om Grönl. 136,3 (1953), p. 73.

Phippsia fragiliflora (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia fragiliflora* TH. SÖRENSEN, in Medd. om Grönl. 136,3 (1953), p. 73.

Phippsia gorodkovii (TZVELEV) LÖVE & LÖVE, comb. nov., based on *Puccinellia gorodkovii* TZVELEV, in Arkt. Fl. SSSR 2 (1964), p. 199.

Phippsia groenlandica (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia groenlandica* TH. SÖRENSEN, in Medd. om Grönl. 136,3 (1953), p. 37.

Phippsia hauptiana (V. KRECZ.) LÖVE & LÖVE, comb. nov., based on *Atropis Hauptiana* V. KRECZETOVICH, in Fl. SSSR 2 (1934), p. 763.

Phippsia interior (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia interior* TH. SÖRENSEN, in HULTÉN, Fl. Alaska & Yukon X (1950), p. 1713.

Phippsia langeana (BERL.) LÖVE & LÖVE, comb. nov., based on *Glyceria Langeana* BERLIN, Öfvers. Kongl. Vet.-Akad. Förh. 1884, No. 7, p. 79.

Phippsia langeana ssp. **alaskana** (SCRIBN. & MERR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia alaskana* SCRIBNER & MERRILL, in Contrib. U. S. Natl. Herb. 13,3 (1910), p. 78; *Puccinellia Langeana* ssp. *alaskana* (SCRIBN. & MERR.) TH. SÖR.

Phippsia langeana ssp. **asiatica** (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia Langeana* ssp. *asiatica* TH. SÖRENSEN, in HULTÉN, Flora Alaska & Yukon X (1950), p. 1710.

Phippsia laurentiana (FERN. & WEATH.) LÖVE & LÖVE, comb. nov., based on *Puccinellia laurentiana* FERNALD & WEATHERBY, in Rhodora 18 (1916), p. 14.

Phippsia lenensis (HOLMB.) LÖVE & LÖVE, comb. nov., based on *Puccinellia sibirica* HOLMB. var. *lenensis* HOLMBERG, in Bot. Not. 1927, p. 207; *Puccinellia lenensis* (HOLMB.) TZVELEV.

Phippsia neoarctica LÖVE & LÖVE, spec. nov.

Planta perennis, caespitosa, foliis glaucescentibus, stolonifera, stolonibus epigeis. Culmi 10—15 cm longi, procumbentes. Folia caulinaria duo, longivaginata; lamina stricta, plicata, 1—3 cm longa, 1.5—2.0 mm lata, apice acuta, glabra. Ligula 1.0—1.3 mm longa, acuta, vel abrupte acuminata. Panicula macilenta, diluto-purpurascens, 3—6 cm longa; rami e nodo inferiore 2—3, tenues, rigidi ascendentes, demum reflexi, spiculis 1—3; pedicelli non incrassati. Spiculae oblongae, 6—11 mm longae, 3—6-florae. Gluma inferior 1.5—2.0 mm longa, lanceolata, obtusa, 3-nervia. Lemmata 3.5—4.5 mm longa, obtusa vel plus minusve emarginata. Palea bifida, lemmatis longitudinis, carinis sine spiculis. Antherae 1.5—2.0 mm longae, sterilis, non dehiscentes. Sine granis.

Chromosomatum numerus 2n=21.

Holotypus: West Greenland, Sydostbugt, leg. N. HARTZ, July 1880, in Herb. Copenhagen, cf. SÖRENSEN, in Medd. om Grönland 136,3 (1953), p. 51—52.

A perennial and caespitose plant with glaucescent leaves and with epiterranean stolons. The flowering culms are procumbent, 10—15 cm long, with two leaves; the upper sheath is elongated; the blades are rigid, folded, 1—3 cm long and 1.5—2.0 mm broad, abruptly pointed at the apex, and glabrous. The ligule is 1.0—1.3 mm long, acute or abruptly pointed. The panicle is meager, dilute-purple, 3—6 cm

long; branches 2—3 from the lower node, slender, stiffly ascending, later on reflexed, bearing 1—3 spikelets; the pedicels are scarcely thickened. Spikelets oblong, 6—11 mm long, 3—6-flowered. The first glume is 1.5—2.0 mm long, lanceolate, obtuse or slightly emarginate, glabrous at the base. The palea is bifid, as long as the lemma or a little longer, the keels are without spinules. The anthers are 1.5—2.0 mm long, sterile and not dehiscent. No seeds develop. Chromosome number 2n=21.

This taxon, which is the socalled "Greenland type" of *P. phryganodes* sensu TH. SÖRENSEN, is distributed throughout arctic North America from Greenland to eastern Alaska. It is apparently a completely sterile and triploid hybrid of unknown parentage that is capable of effective vegetative reproduction, although its wide distribution also may be the result of that it is produced frequently and in many places and survives for a long time.

Phippsia nutkaënsis (K. PRESL) LÖVE & LÖVE, comb. nov., based on *Poa nutkaënsis* K. PRESL, Reliq. Haenk. 1 (1830), p. 272; *Puccinellia nutkaënsis* FERN. & WEATH.

Phippsia nutkaënsis ssp. **borealis** (HOLMB.) LÖVE & LÖVE, comb. nov., based on *Puccinellia retroflexa* (CURT.) HOLMB. ssp. *borealis* HOLMBERG, Bot. Not. 1926, p. 182; *Puccinellia coarctata* FERN. & WEATH.

The new combination at the subspecies level is required because hybridization experiments, still unpublished, between the Beringian taxon and the Atlantic plant have confirmed the suggestion by SÖRENSEN (1953) that these taxa are conspecific, since the hybrids are fully fertile and their meiotic divisions without even the slightest disturbance so a reproductive barrier is absent. Since some slight morphological differences are connected with the geographical separation, however, we find it reasonable to accept the Atlantic taxon as a subspecies in its own right, although its distinction is, admittedly, not always very obvious. It is our belief that this and some other plants and animals that are common to the North Atlantic region and the Beringian area have dispersed over the still open Polar Sea by aid of ocean currents after the formation of the Bering Strait in the Pliocene (cf. EINARSSON, HOPKINS & DOELL 1967).

Phippsia phryganodes (TRIN.) LÖVE & LÖVE, comb. nov., based on *Poa phryganodes* TRINIUS, in Mém. Acad. Pétersb., sér. 6, 1 (1830), p. 389; *Puccinellia geniculata* V. KRECZETOVICH.

This taxon, in its strict sense, is a diploid and sexual species of the Beringian region. Its epithet should not be misapplied as a collective name for the circumpolar arctic complex which here is included in *P. vilfoidea* and *P. neoarctica,* although this has been done by SÖRENSEN (1953) and others.

Phippsia poacea (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia poacea* TH. SÖRENSEN, in PORSILD, in Natl. Mus. Canada. Bull. 135 (1955), p. 78.

Phippsia porsildii (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia porsildii* TH. SÖRENSEN, in Medd. om Grönl. 136,3 (1953), p. 35.

Phippsia rosenkrantzii (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia rosenkrantzii* TH. SÖRENSEN, in Medd. om Grönl. 136,3 (1953), p. 33.

Phippsia sibirica (HOLMB.) LÖVE & LÖVE, comb. nov., based on *Puccinellia sibirica* HOLMBERG, in Bot. Not. 1927, p. 206, excl. var.

Phippsia svalbardensis (RÖNNING) LÖVE & LÖVE, comb. nov., based on *Puccinellia svalbardensis* RÖNNING, in Kgl. Norske Vidensk. Selsk. Skrifter 1961, Nr. 4 (1962), p. 10.

Phippsia tenella (LGE) LÖVE & LÖVE, comb. nov., based on *Glyceria tenella* LANGE, in KJELLMAN & LUNDSTRÖM, Vega-Exp. Vetensk. Iakttag. 1 (1882), p. 313.

Phippsia vaginata (LGE) LÖVE & LÖVE, comb. nov., based on *Glyceria vaginata*

LANGE, Flora danica, fasc. 44 (1858), tab. 2583.

Phippsia vahliana (LIEBM.) LÖVE & LÖVE, comb. nov., based on *Poa Vahliana* LIEBMANN, Flora danica, fasc. 41 (1845), tab. 2401.

Phippsia vahliana ssp. **byrrangensis** (TZVELEV) LÖVE & LÖVE, stat. & comb. nov., based on *Puccinellia byrrangensis* TZVELEV, in Novit. Syst. Plant. Vasc. 8 (1971), p. 80.

Phippsia vahliana ssp. **colpodioides** (TZVELEV) LÖVE & LÖVE, stat. & comb. nov., based on *Puccinellia colpodioides* TZVELEV, in Arkt. Flora SSSR 2 (1964), p. 194.

Phippsia vahliana ssp. **jenisseiensis** (ROSHEV.) LÖVE & LÖVE, stat. & comb. nov., based on *Atropis jenisseiensis* ROSHEVICH, in Izv. Bot. Sada Akad. Nauk SSSR 30 (1932), p. 300.

Phippsia vilfoidea (ANDERSS.) LÖVE & LÖVE, comb. nov., based on *Catabrosa vilfoidea* ANDERSSON, in MALMGREN, in Öfvers. Kgl. Vet.-Akad. Förhandl. 19 (1862), p. 254; *Puccinellia vilfoidea* (ANDERSS.) LÖVE & LÖVE.

This is the variable tetraploid circumpolar taxon which has frequently but erroneously been identified with the diploid eastern Asiatic and Beringian species *P. phryganodes*. It includes three subspecies of which ssp. *vilfoidea* occupies the European arctic area.

Phippsia vilfoidea ssp. **beringensis** LÖVE & LÖVE, ssp. nov.

Planta stolonifera, stolones foliiferae superficiales praesunt. Palearum carinae papillosae. Cellulae epidermale folii in pagina superiore semper tumidae, saepe guttiforme, interdum item inconspicue papillosae.

Chromosomatum numerus 2n=28.

Holotypus: Bering Sea district, Qiqertariaq, A. E. PORSILD 1069, in Herb. Mus. Canada.

A stoloniferous plant, the stolons with superficial leaves. The keels of the palea are papillose. The cells of the epidermis of the upper leaf surface are always tumid and often dropshaped, sometimes also inconspicuously papillose. Chromosome number 2n=28.

This race, which is the "Beringian type" of *P. phryganodes* sensu SÖRENSEN, grows on the coasts around the Bering Sea and the Bering Strait.

Phippsia vilfoidea ssp. **sibirica** (HADAČ & LÖVE) LÖVE & LÖVE, comb. nov., based on *Puccinellia vilfoidea* ssp. *sibirica* HADAČ & LÖVE, in Bot. Not. 114 (1961), p. 36; *P. phryganodes* ssp. *asiatica* TZVELEV, in Arkt. Fl. SSSR 2 (1964), p. 186.

Phippsia wrightii (SCRIBN. & MERR.) LÖVE & LÖVE, comb. nov., based on *Colpodium Wrightii* SCRIBNER & MERRILL, in Contrib. U.S. Natl. Herb. 13,3 (1910), p. 74.

Bromopsis FOURR.

As recently shown by HOLUB (1973), the generic name *Bromopsis* FOURR. is the correct name for the perennial group of the collective genus *Bromus,* when separated as a distinct genus, and not the frequently used but invalid name *Zerna* PANZER. The following taxa of the eastern Asiatic or western North American Arctic are in a need of transfer to this name, some at a new rank:

Bromopsis dicksonii (MITCH. & WILT.) LÖVE & LÖVE, stat. & comb. nov., based on *Bromus Pumpellianus* SCRIBN. ssp. *dicksonii* MITCHELL & WILTON, in Brittonia 18 (1966), p. 163.

Bromopsis ircutensis (KOM.) LÖVE & LÖVE, comb. nov., based on *Bromus ircutensis* KOMAROV, in Bot. Mat. Herb. Petersb. Bot. Sada 2 (1921), p. 130.

Bromopsis pumpelliana (SCRIBN.) HOLUB ssp. **arctica** (SHEAR) LÖVE & LÖVE, stat. & comb. nov., based on *Bromus arcticus* SHEAR, in SCRIBNER & MERRILL, Grass. Alaska (1910), p. 83.

Bromopsis vogulica (SOCZ.) HOLUB. By an oversight, LÖVE & LÖVE (1975 a) re-

placed the name of the latter author of this combination with their own. It is also worth noting, that TZVELEV (1974) regards this taxon as a subspecies only of *B. pumpelliana,* perhaps a likely proposition which then might logically also require that level for *B. ircutensis.* Lacking experimental evidence, we prefer to keep these taxa at the species level, despite their cytological similarity to the also octoploid *B. pumpelliana.*

Elymus L.

Following numerous experimental observations of the Triticeae group, LÖVE & LÖVE (1961, 1965), LÖVE (1970 a, b), TZVELEV (1973) and DEWEY (1974) have advocated the acceptance of the generic name *Elymus* L. for most of the perennial taxa that have been traditionally included in that genus or in *Agropyron* s. l., *Anthosachne, Clinelymus, Hystrix, Roegneria* and *Sitanion,* excluding as distinct genera *Elytrigia, Leymus* and *Agropyron* s. str. and some annual genera. This proposal has been accepted also in part by RUNEMARK & HENEEN (1968), although they included also *Elytrigia* and *Leymus* in their then much more collective genus *Elymus.* The great majority of arctic taxa of the genus so circumscribed have already been transferred to this group by TZVELEV (1973 and earlier) and others. However, a change in rank or new combinations are required for the following entities:

Elymus alaskanus (SCRIBN. & MERR.) LÖVE & LÖVE ssp. **borealis** (TURCZ.) LÖVE & LÖVE, comb. nov., based on *Triticum boreale* TURCZANINOV, in Bull. Soc. Nat. Moscou 29 (1856), p. 58; *Elymus kronokensis* (KOM.) TZVELEV ssp. *borealis* (TURCZ.) TZVELEV; non *Elymus borealis* SCRIBN.

Elymus alaskanus ssp. **hyperarcticus** (POLUNIN) LÖVE & LÖVE, comb. nov., based on *Agropyron violaceum* HORNEM. var. *hyperarcticum* POLUNIN, in Bull. Natl. Mus. Canada 92 (1940), p. 95; *Roegneria borealis* (TURCZ.) NEVSKI ssp. *hyperarcticum* (POLUNIN) LÖVE & LÖVE; *Elymus sajanensis* (NEVSKI) TZVELEV ssp. *hyperarcticus* (POLUNIN) TZVELEV.

Elymus alaskanus ssp. **islandicus** (MELD.) LÖVE & LÖVE, comb. nov., based on *Roegneria borealis* var. *islandica* MELDERIS, in Svensk Bot. Tidskr. 44 (1950), p. 163; *Roegneria borealis* ssp. *islandica* (MELD.) LÖVE & LÖVE.

Elymus alaskanus ssp. **subalpinus** (L. NEUM.) LÖVE & LÖVE, comb. nov., based on *Triticum violaceum* HORNEM. f. *subalpinum* L. NEUMAN, Sveriges Flora (1901), p. 726; *Agropyron latiglume* (SCRIBN. & SM.) RYDB. ssp. *subalpinum* (L. NEUM.) VESTERGREN.

Elymus alaskanus ssp. **villosus** (V. VASSIL.) LÖVE & LÖVE, comb. nov., based on *Roegneria villosa* V. VASSILIEV, in Bot. Mat. 16 (1954), p. 57; *Elymus sajanensis* (NEVSKI) TZVELEV ssp. *villosus* (V. VASSIL.) TZVELEV; non *Elymus villosus* MUEHL.

Elymus trachycaulus (LINK) GOULD ssp. **andinus** (SCRIBN. & SM.) LÖVE & LÖVE, comb. nov., based on *Agropyron violaceum* (HORNEM.) LGE var *andinum* SCRIBNER & SMITH, in U. S. Dept. Agric., Div. Agrostol. Bull. 4 (1897), p. 30; *Agropyron violaceum* ssp. *andinum* (SCRIBN. & SM.) MELD.

Elymus trachycaulus ssp. **subsecundus** (LINK) LÖVE & LÖVE, stat. & comb. nov., based on *Triticum subsecundum* LINK, Hort. Berol. 2 (1833), p. 190.

Elymus trachycaulus ssp. **stefanssonii** (MELD.) LÖVE & LÖVE, comb. nov., based on *Roegneria Doniana* (WHITE) MELD. var. *Stefanssonii* MELDERIS, in Svensk Bot. Tidskr. 44 (1950), p. 158; *Roegneria Doniana* ssp. *Stefanssonii* (MELD.) LÖVE & LÖVE.

Elymus trachycaulus ssp. **violaceus** (HORNEM.) LÖVE & LÖVE, stat. & comb. nov., based on *Triticum violaceum* HORNEMANN, Flora danica, fasc. 35 (1832), tab. 2044.

Elymus trachycaulus ssp. **virescens** (LGE) LÖVE & LÖVE, comb. nov., based on *Agro-*

pyron violaceum ß *virescens* LANGE, in Medd. om Grönl. 3 (1880), p. 155; *Roegneria Doniana* ssp. *virescens* (LGE) LÖVE & LÖVE.

Critesion RAFIN.

It is our settled belief based on studies by numerous authors and also on our own, still unpublished, cytogenetical experiments, that the genus *Hordeum* L. in its traditional circumscription is an unnatural assemblage of taxa which are composed of haplomes (LÖVE & LÖVE 1975 c) that are too distantly related to be united in a single genus, even at the subgeneric or sectional levels as accepted by TZVELEV (1973). This view is especially supported by the observation that hybridization between these taxa is absent even under ideal experimental conditions, and also by the fact that both annual and perennial taxa are involved, differing morphologically in numerous characters that have been found to be of utmost importance for separating groups at higher levels in other taxa of the Triticeae. Therefore, we find it logical to accept the generic name *Hordeum* L. in a restricted sence, including only the annual species of the subgenus *Hordeum* of TZVELEV (l.c.) or of the section *Crithe* DOELL., typified by *Hordeum vulgare* L. We are not ready to propose what is the correct generic name for the two perennial sections *Hordeastrum* DOELL. and *Bulbohordeum* NEVSKI, hybrids between which seem to indicate haplomic relationships of a congeneric significance (LÖVE & LÖVE, unpubl.), but the section *Stenostachys* NEVSKI differs so substantially from all these groups in its haplomic arrangement that a generic separation is well substantiated, as it also seems to be on purely morphological grounds. At that level, its valid name is *Critesion* RAFIN. Only the single species *C. jubatum* (L.) NEVSKI reaches the Arctic, where it is represented by the following race:

Critesion jubatum (L.) NEVSKI ssp. **breviaristatum** (BOWDEN) LÖVE & LÖVE, comb. nov., based on *Hordeum jubatum* L. ssp. *breviaristatum* BOWDEN, in Canad. Journ. Bot. 40 (1962), p. 1691.

Leymus HOCHST.

The most widespread species of the genus *Leymus* is the tetraploid *L. mollis* (TRIN.) PILGER, which with its subspecies is circumpolar both in the boreal and arctic regions. In the Arctic that species is represented by its typical race and also by the two following races:

Leymus mollis (TRIN.) PILGER ssp. **interior** (HULTÉN) LÖVE & LÖVE, comb. nov., based on *Elymus interior* HULTÉN, Flora of Alaska and Yukon II (1942), p. 270; *Elymus mollis* TRIN. ssp. *interior* (HULTÉN) BOWDEN.

Leymus mollis ssp. **villosissimus** (SCRIBN.) LÖVE & LÖVE, comb. nov., based on *Elymus villosissimus* SCRIBNER, in U. S. Dept. Agric., Div. Agrostol. Bull. 17 (1899), p. 326; *Elymus mollis* ssp. *villosissimus* (SCRIBN.) Á. LÖVE.

Leymus velutinus (BOWDEN) LÖVE & LÖVE, stat. nov., based on *Elymus innovatus* BEAL ssp. *velutinus* BOWDEN, in Canad. Journ. Bot. 37 (1959), p. 1146.

Since this taxon is octoploid with 2n=56 chromosomes, as contrasted to the tetraploid *L. innovatus* from which it is, thus, separated by a reproductive barrier in addition to clear morphological and geographical differences, it is hardly logical to regard it as a subordinate race of the latter. Therefore this change of rank.

Deschampsia caespitosa (L.) PB. ssp. **anadyrensis** (V. VASSIL.) LÖVE & LÖVE, stat. & comb. nov., based on *Deschampsia anadyrensis* V. VASSILIEV, in Bot. Mat. 8 (1940), p. 68.

Calamagrostis maltei (POLUNIN) LÖVE & LÖVE, stat. & comb. nov., based on *Calamagrostis purpurascens* R. BR. var. *Maltei* POLUNIN, in Natl. Mus. Canada Bull. 92

(1940), p. 51; *Calamagrostis purpurascens* ssp. *Maltei* (POLUNIN) A. E. PORSILD.

We are unable to propose a natural division of the very variable and collective taxon *Calamagrostis purpurascens* R. BR. into species that conform with various degrees of polyploidy, mainly because the chromosome reports have not been accompanied by close morphological comparisons of the material. However, we find it to be a step in the right direction to distinguish as separate species those units that are most clearly recognizable. One of these is the taxon above, which has recently been closely analysed and lifted from its originally tentative level of variety to that of subspecies (PORSILD 1975), although that is certainly no improvement in the understanding of its distinctness, which certainly is greater than that of a major geographical race.

Agrostis scabra WILLD. ssp. **septentrionalis** (FERN.) LÖVE & LÖVE, stat. nov., based on *Agrostis scabra* var. *septentrionalis* FERNALD, in Rhodora 35 (1933), p. 209.

The variety category as used by FERNALD for this and many other taxa is clearly that of a major geographical race, or a subspecies in our definition.

Hierochloë orthantha TH. SÖR. We find it difficult to follow WEIMARCK (1971) in placing the strictly apomictic 63-chromosome North American taxon as a subspecies of the predominantly sexual 56-chromosome circumpolar *H. alpina* (SW.) R. & S. LÖVE & LÖVE (1965) found this taxon to be identical with a plant described from Mt Washington by BIGELOW (1816) as *Holcus monticola* and transferred this name to *Hierochloë* (in LÖVE & SOLBRIG 1964). The taxon is listed as *Hierochloë monticola* (BIGEL.) LÖVE & LÖVE by LÖVE & LÖVE (1975 a). We overlooked, however, that this is a homonym of the Australian *H. monticola* MEZ, which in turn is a synonym of *H. submutica* F. MUELL. (cf. VICKERY 1975). Therefore, the correct name for the taxon at the level of species must be *H. orthantha* TH. SÖR., or the same name as applied at the subspecific level by WEIMARCK (1971).

Carex capillaris L. ssp. **fuscidula** (V. KRECZ.) LÖVE & LÖVE, stat. & comb. nov., based on *Carex fuscidula* V. KRECZETOVICH, in EGOROVA, in Novit. Syst. Plant. Vasc. 1 (1964), p. 36.

We are of the opinion that EGOROVA (1964) errs in identifying the southern Eurasiatic-North American tall-grown race ssp. *chlorostachys* (STEV.) LÖVE, LÖVE & RAYMOND with the typical Atlantic-Scandinavian ssp. *capillaris,* but she is evidently correct in distinguishing a low-grown arctic-alpine Eurasiatic-North American taxon from the typical boreal race, since the species was obviously described from the lowlands of Central Sweden to where neither ssp. *chlorostachys* nor the arctic-alpine race reach. However, there is no reason to believe that the taxon in question is a species in its own right, as proposed by EGOROVA (l.c.) with reference to a nomen nudum on a map by KRECZETOVICH (1952), but we find it reasonable to accept it as a major geographical race at the subspecific level.

Carex gaudichaudiana KÜK. ssp. **appendiculata** (TRAUTV. & MEY.) LÖVE & LÖVE, stat. & comb. nov., based on *Carex acuta* L. var. *appendiculata* TRAUTVETTER & MEYER, Flor. Ochot. phaen. (1856), p. 100; *Carex appendiculata* (TRAUTV. & MEY.) KÜK.

We follow KOYAMA (1959) in regarding this northern taxon as a race only of the Asiatic *C. gaudichaudiana*; however, we find it warranted to transfer it to a higher level, since we prefer to distinguish between varieties and subspecies on basis of their geographical distinction.

Carex nigra (L.) REICHARD

The cytological similarities between the morphologically distinguishable races of this widespread species are corroborated

by the ease with which they hybridize where they come together and also under experimental conditions (LÖVE & LÖVE, unpubl.). Therefore, we find it reasonable to accept the three taxa reaching the Arctic only at the subspecific level, to which two need to be transferred:

Carex nigra ssp. **juncea** (FR.) LÖVE & LÖVE, comb. nov., based on *Carex vulgaris* FR. * (ssp.) *juncea* FRIES, Mant. 3 (1842), p. 154.

Carex nigra ssp. **wiluica** (MEINSH.) LÖVE & LÖVE, comb. nov., based on *Carex wiluica* MEINSHAUSEN, in MAAK, Vilyusk. Okr. Yakutsk. Obl. 2 (1886), p. 308; *Carex juncella* (FR.) TH. FR. ssp. *wiluica* (MEINSH.) EGOROVA.

Calla L.

The genus *Calla* is usually regarded as a monotypic taxon with a circumpolar distribution. However, cytotaxonomical studies have revealed, that the north and central European populations, which certainly belong to the species *C. palustris* L. s.str., are characterized by the octoploid chromosome number 2n=72, whereas the North American plant, which is smaller in all respects, is a tetraploid with 2n=36. It was accepted as a distinct species, *brevis,* of the genus *Provenzalia* by RAFINESQUE (1836) but later ignored. In *Calla* its correct name is:

Calla brevis (RAFIN.) LÖVE & LÖVE, comb. nov., based on *Provenzalia brevis* RAFINESQUE, New Fl. North Amer. 2 (1836), p. 67.

Populus tremula L. ssp. **tremuloides** (MICHX.) LÖVE & LÖVE, stat. & comb. nov., based on *Populus tremuloides* MICHAUX, Flora Bor. Amer. 2 (1803), p. 243.

The North American taxon is morphologically very close to the typical *P. tremula* L. of Eurasia, from which it differs technically in having regularly crenate-serrulate and usually short acuminate leaves, as contrasted to the irregularly sinuate-dentate and often obtuse leaves of the Eurasiatic plant. They are ecologically and cytologically identical, and numerous experiments have shown them to be completely interfertile. Therefore, we find it illogical to retain them as distinct species despite their large and distinct geographical areas, and propose the transfer of the North American taxon to the subspecific level of the Eurasiatic species.

Salix brachycarpa NUTT. ssp. **fullertonensis** (C. K. SCHNEIDER) LÖVE & LÖVE, stat. & comb. nov. based on *Salix fullertonensis* C. K. SCHNEIDER, in Bot. Gazette 66 (1918), p. 340.

The northwestern American species *S. brachycarpa* is composed of a few races, two of which reach the arctic regions. The more widespread one of these, ssp. *niphoclada* (RYDB.) ARGUS, is rather common in arctic-alpine areas west of the Hudson's Bay, but in the northern Keewatin District it is replaced by the distinct but less widespread and more prostrate and smaller leaved *S. fullertonensis,* which certainly ought to be reduced to the subspecific level.

Betula nana L. ssp. **perfiljevii** (V. VASSIL.) LÖVE & LÖVE, stat. & comb. nov., based on *Betula Perfiljevii* V. VASSILJEV, in Novit. Syst. Plant. Vasc. 3 (1966), p. 75.

Betula nana ssp. **tundrarum** (PERF.) LÖVE & LÖVE, stat. & comb. nov., based on *Betula tundrarum* PERFILJEV, in Bot. Zhurn. 48 (1963), p. 1139.

In conformity with the acceptance of the widespread Eurasiatic and North American races of *Betula nana* as the ssp. *nana* and ssp. *exilis* (SUKACZ.) HULTÉN, we find it necessary to propose subspecific status also for the two morphologically distinct races above, both of which were originally described as species of a restricted distribution.

Alnus incana (L.) MOENCH ssp. **hirsuta** (SPACH) LÖVE & LÖVE, stat. nov., based on *Alnus incana* var. *hirsuta* SPACH, in Ann. Sci. Nat., 2 sér., 15 (1841), p. 207.

We prefer to regard the species *Alnus incana* as a complex of distinct major

geographical races, since they have been shown by numerous experimenters to be easily hybridized without a reduction in fertility and with later generations giving clearly Mendelian segregations. Of the four races reaching the Arctic, only the above one from eastern Asia has not earlier been validated as a subspecies.

Urtica gracilis AIT. ssp. **sondenii** (SIMM.) LÖVE & LÖVE, comb. nov., based on *Urtica dioica* L. var. *Sondenii* SIMMONS, in LINDMAN, Svensk fanerogamfl. (1918), p. 208; *Urtica dioica* ssp. *Sondenii* (SIMM.) HYLANDER.

Recent cytological investigations have demonstrated beyond doubt that the mainly eastern North American *Urtica gracilis* and its far northern outposts in Scandinavia differ not only morphologically and geographically from the Eurasiatic *Urtica dioica* L. and from other dioecious North American species, but also cytologically, since the latter are distinctly tetraploid with 2n=52 chromosomes (we have reason to doubt records of 2n=48 because reexamination of the slides on which our own reports of this number were based showed that these numbers were caused by a too low estimation of crowded metaphase plates), and the former taxon is diploid with 2n=26. The diploid species reaches the Arctic only in northern Scandinavia and the adjacent Soviet Union, where it is represented by the above race.

Rumex L.

We see no reason to retain the genus *Rumex* in its traditionally very collective sense, and so accept for the dioecious arctic plants the generic names *Acetosella* FOURR. and *Acetosa* MILL. Only the following recently described species need to be transferred to these genera, since valid combinations are available for the other taxa of the northlands:

Acetosella beringensis (JURTSEV & PETROVSKY) LÖVE & LÖVE, comb. nov., based on *Rumex beringensis* JURTSEV & PETROVSKY, in YURTSEV, SYTIN & SEKRETAREVA, in Bot. Zhurn. 58 (1973), p. 1745 (note).

Acetosella krausei (JURTSEV & PETROVSKY) LÖVE & LÖVE, comb. nov., based on *Rumex Krausei* JURTSEV & PETROVSKY, in YURTSEV, SYTIN & SEKRETAREVA, in Bot. Zhurn. 58 (1973), p. 1745.

Acetosa oblongifolia (TOLM.) LÖVE & LÖVE, comb. nov., based on *Rumex oblongifolius* TOLMACHEV, in Arkt. Flora SSSR 5 (1966), p. 154.

Koenigia hadacii LÖVE & LÖVE, spec. nov., based on *Koenigia islandica* L. var. *arctica* HADAČ, in Studia Bot. Čechica 5 (1942), p. 3.

This small diploid taxon is apparently an Asiatic plant that reaches Svalbard. It is distinguished from typical and tetraploid *K. islandica* by being diploid and having smaller flowers and smaller achenes but since this is a modifiable character requiring completely ripe seeds for secure identification, other less modifiable characters need to be searched for. When compared under controlled experimental conditions, the floral and fruit size differences are always reliable, and then the diploid also ripens its seeds significantly earlier than the tetraploid. Both species seem to be almost obligately autogamous and hybridization rarely succeeds even under controlled conditions because of the difficulties of emasculating the flowers. However, triploids derived from pollinations of the tetraploid by pollen from the diploid were found to have a rather high frequency of trivalents at meiosis, perhaps indicating an autoploid origin of the tetraploid species (LÖVE & LÖVE, unpubl.).

Polygonum L.

It is our opinion based on long-time studies of various features of numerous taxa belonging to this very collective genus, that it ought to be divided into more

clearly defined genera, as proposed by many previous authors though generally ignored by authors of manuals. Cytologically, this is well substantiated by variations in chromosome morphology and by the occurrence of at least three basic chromosome numbers that coincide with the morphological characters that have been used to define the restricted genera. Following this view, *Polygonum* is restricted to the annual groups belonging to the section or subgenus *Avicularia,* whereas other genera represented in the Arctic are *Bistorta* SCOP. (not MILL. as inadvertently given by LÖVE & LÖVE, 1975 a), *Persicaria* MILL., *Aconogonon* RCHB. and *Fallopia* ADANS.

According to HULTÉN (1968), who does not subdivide the collective genus, the northern Pacific populations of the wide taxon *P. bistorta* L. all belong to the ssp. *plumosum* (SMALL) HULTÉN, which then includes the ssp. *ellipticum* (WILLD.) PETROVSKY. Recent cytological evidence, however, casts a doubt on this conclusion, since the former apparently strictly American taxon has been found to be hexaploid with 2n=72 chromosomes, whereas the latter eastern Asiatic and Alaskan plant is a tetraploid with 2n=48 chromosomes, as is also the typical race of the species. Therefore, we accept the latter as a subspecies of the Eurasiatic species in the genus *Bistorta* and the former as a species in its own right, *B. plumosa* (SMALL) GREENE (not LÖVE & LÖVE as in LÖVE & LÖVE 1975 a). Likewise, the genus *Aconogonon* is represented in the Arctic by some species, only one of which requires a transfer.

Bistorta major S. F. GRAY ssp. **elliptica** (WILLD.) LÖVE & LÖVE, comb. nov., based on *Polygonum ellipticum* WILLDENOW ex SPRENGEL, Syst. veget. ed. 16, 2 (1825), p. 253; *Polygonum bistorta* L. ssp. *ellipticum* (WILLD.) PETROVSKY.

Aconogonon laxmannii (LEPECH.) LÖVE & LÖVE, comb. nov., based on *Polygonum Laxmannii* LEPECHIN, Nova Acta Petrop. 10 (1797), p. 414.

Dichodon (BARTL.) RCHB.

The genus *Dichodon,* as recently resusciated by IKONNIKOV (1973) to accomodate the species *Cerastium dubium* (BAST.) O. SCHWARZ and *C. cerastoides* (L.) BRITTON and their close relatives, which represent the sections *Dichodon* and *Perennia* IKONN. respectively, ought also to include the section *Strephodon* SER. of the collective genus *Cerastium,* as shown by observations made by SÖLLNER (1954). Both groups are morphologically related and are characterized by the same rare basic chromosome number x=19, as contrasted to x=9 of *Cerastium* proper. This conclusion requires the following transfers:

Dichodon sect. **Strephodon** (SERINGE) LÖVE & LÖVE, comb. nov., based on *Cerastium* sect. *Strephodon* SERINGE, in DC. Prodr. 1 (1824), p. 414.

Dichodon chlorifolium (FISCH. & MEY.) LÖVE & LÖVE, comb. nov., based on *Cerastium chlorifolium* FISCHER & MEYER, in Index IV Sem. Hort. Petrop. (1837), p. 34.

Dichodon dahuricum (FISCH.) LÖVE & LÖVE, comb. nov., based on *Cerastium dahuricum* FISCHER ex SPRENGEL, Pl. minus cognit. Pug. II (1815), p. 65.

Dichodon maximum (L.) LÖVE & LÖVE, comb. nov., based on *Cerastium maximum* LINNAEUS, Spec. plant. (1753), p. 439.

Dichodon perfoliatum (L.) LÖVE & LÖVE, comb. nov., based on *Cerastium perfoliatum* LINNAEUS, Spec. plant. (1753), p. 437.

Sagina L.

Although some botanists of the last century had shown that the collective genus *Sagina* could be divided into at least three more homogeneous genera on basis of floral and fruit characters, this advise has not been heeded by later authors, probably because other technical characters for this separation are somewhat confusing. Since recent cytological evidence, however, shows that these three groups

differ also drastically in their basic chromosome numbers and chromosome morphology, there is a reason now to accept these opinions. In that case, the annual boreal species are assigned to the genus *Saginella* KOCH, s.str. which is characterized by the basic number x=6 and typified by *S. apetala* ARD. The boreal and arctic-alpine group of perennial species similar to *S. nodosa* L. are classified as representing the genus *Spergella* RCHB., s.str. which has the basic number x=7, but the perennial *S. procumbens* L. and its relatives are retained in the genus *Sagina* L., s.str. which is cytologically characterized by the basic number x=11. The acceptance of this division requires the transfer of two arctic-alpine species to the genus *Spergella:*

Spergella caespitosa (J. VAHL) LÖVE & LÖVE, comb. nov., based on *Arenaria caespitosa* J. VAHL, in Flora danica, fasc. 39 (1840), tab. 2389; *Sagina caespitosa* (J. VAHL) LGE.

Spergella intermedia (FENZL) LÖVE & LÖVE, comb. nov., based on *Sagina intermedia* FENZL, in LEDEBOUR, Flora ross. I (1842), p. 339.

Minuartia L.

The redefinition of the strictly Mediterranean genus *Minuartia* L. by HIERN (1899), which made it possible to accomodate within its limits even arctic species, certainly was caused by a misunderstanding of considerable magnitude, although later authors and even two monographers (MATTFELD 1921, 1922; MCNEILL 1962) seem to have accepted this without hesitation. The group so widely defined is highly unnatural from whatever modern point of view it is looked upon, as shown most clearly be the apparent difficulties experienced by MCNEILL (l.c.) in dividing it into subgenera, sections and even subsections and series some of which are not only morphologically heterogeneous but also characterized by distinct basic chromosome numbers and by karyomorphology different from that of their supposedly closest relatives. *Minuartia* s.str. is known to have the basic number x=15, whereas other groups within the collective genus have been reported to have basic numbers as variable as x=8, 9, 10, 11, 12, 13, and 23. We have had the opportunity to make cytotaxonomical studies, still mainly unpublished, of considerable living and herbarium material of numerous species from arctic and boreal regions in Eurasia and North America and also of populations from the Mediterranean and the southwestern Asiatic area of the collective genus. These studies, which also include detailed observations on pollen and seed coat morphology, have convinced us that this unnatural assemblage needs to be divided into groups that better fit the modern biological definition of a genus. Therefore, in the Cytotaxonomical Atlas of the Arctic Flora (LÖVE & LÖVE 1975 a) we have resusciated some long ignored but well-defined and more restricted genera that are represented in the tundra of the northlands, and proposed new names for a couple of groups for which valid names at that level were not available.

One of the most distinct groups within this unnatural assemblage is the section *Uninerviae* which in its strict sense includes a single species with two races that are distributed from southern Greenland to the mountains of Tennessee, with some outposts in South America. Since the taxon has not previously received recognition as a genus, we are pleased to be able to name it in honour of A. ERLING PORSILD, the most outstanding Canadian specialist on arctic plants who received his basic training in Greenland.

Another well-defined group requiring a new name at the generic level is named in honour of JOHANNES and DAGNY TANDE LID of Oslo, he an ardent student of arctic-alpine plants and the author of arctic floras and of the best recent manual of Scandinavian plants, and she the most

outstanding illustrator of arctic and boreal and even subtropical plants.

Additional and revived genera of this complex that reach arctic lands are *Alsinanthe* (FENZL) RCHB., *Neumayera* RCHB., *Tryphane* (FENZL) RCHB. and *Wierzbickia* RCHB., whereas the bulk of genera in need of reseparation from this confused complex are distributed in more southern mountains of the boreal zone. Instead of furnishing exact and detailed descriptions of each of the arctic genera, we provide below a key for their identification, which we have lifted out of the good comprehensive key by MCNEILL (1962), followed by validations of the new taxa of various ranks required for some of the arctic populations.

1 Annual or biennial herbs; petals more or less emarginate, twice as long as the calyx; sepals obscurely or reticulately nerved, erect at anthesis; leaves one-nerved (or almost three-nerved), slender or rather fleshy; seeds obscurely tuberculate to tuberculate, sometimes echinate ..... *Porsildia*, x=10
1 Suffruticose or herbaceous perennials; petals entire, very rarely shortly emarginate .. 2
2 Sepals rounded to obtuse at apex, linear; calyx cylindrical; sterile shoots gradually passing into flowering shoots, rarely flowering shoots distinct and then bearing large fascicles; leaves fleshy, rarely rather rigid, traversed by one more or less prominent nerve 3
2 Sepats acute or acuminate, rarely obtuse and then ovate; calyx ovoid or urceolate; leaves of the sterile rosettes closely fasciculate, or even spreading, slender 4
3 Leaves flat, lanceolate or linear-lanceolate; entire leaf, or the margin near the base, setose, bearing long acute hairs; seeds with a fimbriate crest on the dorsal ridge ..... *Wierzbickia*, x=23
3 Leaves linear-subulate, the margin near the base more or less scabrid with short and obtuse hairs, rarely glabrous; seeds obscurely reticulate to obscurely tuberculate all over ..... *Lidia*, x=13
4 Petals shorter than sepals; sepals erect at anthesis; leaves one-nerved; seeds obscurely tuberculate; perennial herbs with elongate pedicels ..... *Alsinanthe*, x=15
4 Petals longer than sepals, or if shorter, then sepals spreading at anthesis; plant perennial; sepals 3—5(—9)-nerved with a rather narrow membranous or scarious margin; calyx not hardened at the base 5
5 Sepals 5—7(—9)-nerved, rarely 3-nerved and then the seeds are fimbriate; leaves linear-subulate or setaceous; sepals spreading at anthesis; seeds obscurely tuberculate or muricate ..... *Tryphane*, x=12
5 Sepals 3-nerved, acuminate, erect at anthesis; petals obovate or oblong, gradually narrowing to the base, 1.5—2 times as long as sepals; seeds obscurely tuberculate and sometimes echinate ..... *Neumayera*, x=13

Alsinanthe rossii (R. BR.) LÖVE & LÖVE, comb. nov., based on *Arenaria Rossii* R. BROWN, in RICHARDSON, in FRANKLIN, Narr. Journ. Polar Sea, App. VII (1823), p. 738; *Minuartia Rossii* (R. BR.) GRAEBNER, s.str.; *Minuartia Rolfii* NANNF.

Alsinanthe elegans (CHAM. & SCHLECHT.) LÖVE & LÖVE, comb. nov., based on *Arenaria elegans* CHAMISSO & SCHLECHTENDAL, in Linnaea 1 (1826), p. 57; *Minuartia elegans* (CHAM. & SCHLECHT.) SCHISCHKIN.

Porsildia LÖVE & LÖVE, gen. nov.

Based on *Alsine* 12 *Uninerviae* FENZL, in ENDLICHER, Gen. plant. (1840), p. 965; *Minuartia* sect. *Uninerviae* (FENZL) MATTFELD, in Bot. Jahrb. 57, Beih. 126 (1921), p. 28, p. p., excl. *M. uniflora* (WALT.) MATTF. Type species: *Porsildia groenlandica* (RETZ.) LÖVE & LÖVE.

Porsildia groenlandica (RETZ.) LÖVE & LÖVE, comb. nov., based on *Stellaria groenlandica* RETZIUS, Flora Scand. Prodr. ed. 2 (1795), p. 107; *Minuartia groenlandica* (RETZ.) OSTENF.

Porsildia groenlandica ssp. **glabra** (MICHX.) LÖVE & LÖVE, comb. nov., based on *Arenaria glabra* MICHAUX, Flora Bor. Amer. 1 (1803), p. 274; *Minuartia groenlandica* ssp. *glabra* (MICHX.) LÖVE & LÖVE.

Lidia LÖVE & LÖVE, gen. nov.

Based on *Minuartia* sect. *Spectabilis* series *Biflorae* MATTFELD, in Feddes Repert., Beih. 15 (1922), p. 182, diagn. in clavae. Type species: *Lidia biflora* (L.) LÖVE & LÖVE.

Lidia arctica (STEV.) LÖVE & LÖVE, comb. nov., based on *Arenaria arctica* STEVEN, ex SÉRINGE, in DC. Prodr. 1 (1824), p. 104; *Minuartia arctica* (STEV.) A. & GR.

Lidia biflora (L.) LÖVE & LÖVE, comb. nov., based on *Stellaria biflora* LINNAEUS, Spec. plant. (1753), p. 422; *Minuartia biflora* (L.) SCHINZ & THELL.

Lidia obtusiloba (RYDB.) LÖVE & LÖVE, comb. nov., based on *Alsinopsis obtusiloba* RYDBERG, in Bull. Torrey Bot. Club 33 (1906), p. 132; *Minuartia obtusiloba* (RYDB.) HOUSE.

Lidia yukonensis (HULTÉN) LÖVE & LÖVE, comb. nov., based on *Minuartia yukonensis* HULTÉN, in Arkiv f. Bot. II, 7 (1967), p. 52.

Gastrolychnis RCHB.

The arctic-alpine hermaphroditic taxa that traditionally have been treated as a section of either the otherwise dioecious genus *Melandrium* ROEHL. or of the then much too inclusive genus *Silene* L. are more appropriately included in the well-defined genus *Gastrolychnis* (TOLMACHEV & KOZHANCHIKOV, in TOLMACHEV 1971), a procedure based on morphological distinctions but strongly supported by cytological observations of the behavior of haplomes and of genomic relationships in the Caryophyllaceae (LÖVE & LÖVE, unpubl.). Most of the arctic taxa have already been transferred to this genus by previous authors, but new combinations are needed for the following:

Gastrolychnis apetala (L.) TOLM. & KOZH. ssp. **arctica** (FR.) LÖVE & LÖVE, comb. nov., based on *Wahlbergella apetala* (L.) FR. ß *arctica* TH. M. FRIES, in Öfvers. Vetensk.-Akad. Förhandl. 2 (1869), p. 133; *Melandrium apetalum* (L.) FENZL ssp. *arcticum* (FR.) HULTÉN.

This race is endemic in Svalbard.

Gastrolychnis apetala ssp. **uralensis** (RUPR.) LÖVE & LÖVE, stat. & comb. nov., based on *Gastrolychnis uralense* RUPRECHT, in Beitr. Pflanzenk. Russ. Reiches 7 (1850), p. 30; *Silene uralensis* (RUPR.) BOCQUET ssp. *apetala* (L.) BOCQUET.

This circumpolar arctic-subarctic race is frequently confused with the endemic Svalbard race above, even by HULTÉN (1968, 1971).

Gastrolychnis involucrata (CHAM. & SCHLECHT.) LÖVE & LÖVE, comb. nov., based on *Lychnis apetala* L. γ *involucrata* CHAMISSO & SCHLECHTENDAL, in Linnaea 1 (1826), p. 43; *Melandrium involucratum* (CHAM. & SCHLECHT.) ROHRBACH; *Melandrium furcatum* (RAFIN.) HADAČ.

Gastrolychnis involucrata ssp. **elatior** (REGEL) LÖVE & LÖVE, comb. nov., based on *Lychnis apetala* var. *elatior* REGEL, in Bull. Soc. Imp. Nat. Moscou 34 (1862), p. p. emend. MAGUIRE, in Rhodora 52 (1950), p. 240; *Silene involucrata* ssp. *elatior* (REGEL) BOCQUET.

Gastrolychnis involucrata ssp. **tenella** (TOLM.) LÖVE & LÖVE, comb. nov., based on *Melandrium affine* J. VAHL ssp. *tenellum* TOLMACHEV, in Trud. Bot. Muz. 24 (1932), p. 258.

Gastrolychnis soczaviana (SCHISCHKIN) TOLM. & KOZH. ssp. **ogilviensis** (A. E. PORSILD) LÖVE & LÖVE, comb. nov., based on *Melandrium apetalum* ssp. *ogilviense* A. E. PORSILD, in Natl. Mus. Canada Publ. Bot. 4 (1975), p. 23.

Gastrolychnis triflora (R. BR.) TOLM. & KOZH. ssp. **dawsonii** (ROBINS.) LÖVE & LÖVE, stat. & comb. nov., based on *Lychnis triflora* R. BR. var. *Dawsonii* ROBINSON, in Proc. Amer. Acad. 28 (1893), p. 149.

Caltha minor MILL. ssp. **arctica** (R. BR.) LÖVE & LÖVE, comb. nov., based on *Caltha arctica* R. BR., Suppl. to App.

PARRY's Voy. (1824), p. 265; *Caltha palustris* L. ssp. *arctica* (R. BR.) HULTÉN.

Morphological and cytological observations support the opinion that the conventionally circumscribed collective species *Caltha palustris* actually consists of two good species, the Linnaean taxon in its strict sense, which is a plant with 2n=32 chromosomes that is represented in the Eurasiatic Arctic by its ssp. *palustris* and in northwestern Alaska by ssp. *asarifolia* (DC.) HULTÉN, and a circumpolar arctic-alpine polyploid with a variable chromosome number and perhaps partially apomictic. The latter has been given various names in the past, but the oldest valid name for the complex is *C. minor* MILL., described from the mountains of Great Britain, of which the arctic populations are best regarded as a single subspecies.

Anemone drummondii S. WATS. ssp. **heimburgeri** LÖVE & LÖVE, subsp. nov.

Stylus filiformis, firmus, non fragilis. Holotypus: Alaska, Bering Strait district, Teller; Walpole 2006 in U.S. Natl. Herb.

This northern race has a filiform style, which is firm and not fragile as in the more southern typical subspecies. We name it in honour of Dr MARGARET HEIMBURGER, an ardent student of the cytology of the collective genus *Anemone*.

Jurtsevia LÖVE & LÖVE, gen. nov.

Based on *Anemone* subgenus *Rivularidium* JANCZEWSKI, in Revue gén. Bot. 4 (1892), p. 251.

As pointed out by HOLUB (1973), the genus *Anemone* L. represents an unnatural aggregate even after the exclusion of *Hepatica* MILL. and *Pulsatilla* MILL. He defined it strictly as typified by *A. coronaria* L. (x=8) and separated from it the genera *Anemonoides* MILL. (x=8, 15) and *Anemonastrum* HOLUB (x=7). Even after this division, the genus remains heterogeneous, since the monotypic subgenus *Rivularidium* also deviates strongly in its morphology from the so restricted genus *Anemone* from which it also differs in having the basic chromosome number x=7 and morphologically different chromosomes. Its only species is a slender and delicate plant with filiform rootstocks, sparingly hirsute with deeply five-cleft basal leaves and three-cleft involucral leaves; the stems are 5—20 cm high and terminate in a solitary yellow flower which is 1.5—2.5 cm in diameter; the fruiting heads are subglobose, and the achenes are few and globose with a slender and hooked beak. It is a plant of snow-patches, herb-slopes and moist willow thickets in the northlands from Taimyr to Greenland, although LÖVE & LÖVE (1975 a) mistakingly omitted the number 6 (Greenland) from the information of its latitudinal distribution. We find it logical to propose the separation of this taxon under a new generic name. As such, we name it in honour of the very active arctic botanist, BORIS YURTSEV, and transfer its only species to the new genus:

Jurtsevia richardsonii (HOOK.) LÖVE & LÖVE, comb. nov., based on *Anemone Richardsonii* W. J. HOOKER, Flora Bor. Amer. 1 (1829), p. 6.

Anemonastrum narcissiflorum (L.) HOLUB

The widespread and variable species *Anemonastrum narcissiflorum* comprises sixteen major geographical races (HULTÉN 1944; LÖVE, LÖVE & KAPOOR 1971) of which three with outposts in the Arctic are in need of transfer:

Anemonastrum narcissiflorum ssp. **calvum** (JUZ.) LÖVE & LÖVE, stat. & comb. nov., based on *Anemone calva* JUZEPCZUK, in Flora SSSR 7 (1937), p. 279.

Anemonastrum narcissiflorum ssp. **sibiricum** (L.) LÖVE & LÖVE, comb. nov., based on *Anemone sibirica* L., Spec. plant. (1753), p. 541; *Anemone narcissiflora* L. ssp. *sibirica* (L.) HULTÉN.

Anemonastrum narcissiflorum ssp. **villosissimum** (DC.) LÖVE & LÖVE, comb. nov., based on *Anemone narcissiflora* ς

villosissima DE CANDOLLE, Prodr. 1 (1828), p. 22; *Anemone narcissiflora* ssp. *villosissima* (DC.) HULTÉN.

Atragene alpina L. ssp. **sibirica** (L.) LÖVE & LÖVE, comb. nov., based on *Atragene sibirica* LINNAEUS, Spec. plant. (1753), p. 343; *Clematis alpina* (L.) MILL. ssp. *sibirica* (L.) O. KUNTZE.

Since we favour the splitting of the genus *Clematis* L. of recent authors but agree that the Eurasiatic taxon reaching the Arctic is only a race of the alpine species, this transfer is required.

Batrachium circinatum (SIBTH.) SPACH ssp. **subrigidum** (DREW) LÖVE & LÖVE, stat. & comb. nov., based on *Ranunculus subrigidus* DREW, in Rhodora 38 (1936), p. 39.

This is the vicarious North American race of the Eurasiatic species.

Beckwithia glacialis (L.) LÖVE & LÖVE ssp. **chamissonis** (SCHLECHT.) LÖVE & LÖVE, comb. nov., based on *Ranunculus Chamissonis* SCHLECHTENDAL, Animadv. Ranunc. 1 (1819), p. 12; *Ranunculus glacialis* L. ssp. *Chamissonis* (SCHLECHT.) HULTÉN.

We agree with HULTÉN (1944) that the arctic Pacific taxon is most appropriately regarded as a subspecies of the Atlantic arctic-alpine species, which, however, we place in a distinct genus of its own. That requires the present transfer.

Cyrtorhyncha cymbalaria (PURSH) BRITT. ssp. **alpina** (HOOK.) LÖVE & LÖVE, comb. & stat. nov., based on *Ranunculus cymbalaria* PURSH var. *alpina* W. J. HOOKER, Flora Bor. Amer. 1 (1829), p. 11.

The representatives of the species in the western American mountains and in the Arctic from Alaska to Greenland clearly constitute a major rather than a minor geographical race.

Ranunculus hyperboreus ROTTB. ssp. **tricrenatus** (RUPR.) LÖVE & LÖVE, stat. nov., based on *Ranunculus hyperboreus* var. *tricrenatus* RUPRECHT, in Beitr. Pflanzenk. Russ. Reiches 2 (1845), p. 19.

This geographical race has been regarded as a variety only as recently as in the Flora Arctica USSR, although it certainly is no less distinct morphologically and geographically than are the generally accepted arctic races ssp. *hyperboreus* and ssp. *arnellii* SCHEUTZ. Therefore its validation at this level.

Ranunculus acris L.

We agree with ORLOVA (1956) that in addition to the more widespread and distinct low-grown race, ssp. *pumilus* (WG) LÖVE & LÖVE of this species of the arctic regions, two more taxa of this complex in northwestern Eurasia are worthy of recognition, although we are of the opinion that they are more correctly classified as subspecies than as species. At that level their names are:

Ranunculus acris ssp. **glabriusculus** (RUPR.) LÖVE & LÖVE, stat. & comb. nov., based on *Ranunculus glabriusculus* RUPRECHT, in Beitr. Pflanzenk. Russ. Reiches 2 (1845), p. 19.

Ranunculus acris ssp. **scandinavicus** (ORLOVA) LÖVE & LÖVE, stat. & comb. nov., based on *Ranunculus scandinavicus* ORLOVA, in Flora Murm. Obl. 3 (1956), p. 288; *Ranunculus silvaticus* FRIES, non THUILLIER; *Ranunculus acris* ssp. *stevenii* auct. scand., non ANDRZ., nec KORSH.

Papaver relictum (LUNDSTR.) NORDH. ssp. **hyperboreum** (NORDH.) LÖVE & LÖVE, comb. nov., based on *Papaver radicatum* ROTTB. ssp. *hyperboreum* NORDHAGEN, in Bergens Mus. Årbok 1931, Naturv. rekke 2, p. 48; *Papaver Nordhagenianum* Á. LÖVE ssp. *Nordhagenianum*.

This is the northern Scandinavian major race of the 70-chromosome Eurasiatic species of the genus.

Torularia (COSS.) O. E. SCHULZ

We regard it as advisable to accept the genus *Torularia* as distinct from *Braya* STERNB. & HOPPE to avoid heterogeneity of the latter. We also find it necessary to

divide the collective species *humilis* into units restricted by their morphology and single chromosome numbers. So defined, the genus includes two species in the Arctic, here validated:

Torularia arctica (BÖCHER) LÖVE & LÖVE, stat. & comb. nov., based on *Torularia humilis* (C. A. MEY.) O. E. SCHULZ ssp. *arctica* BÖCHER, in Medd. om Grönland 147,7 (1950), p. 29.

Torularia richardsonii (RYDB.) LÖVE & LÖVE, comb. nov., based on *Pilosella Richardsonii* RYDBERG, in Torreya 7 (1907), p. 159.

Boechera LÖVE & LÖVE, gen. nov.

Folia caulina integra, sagittata vel auriculata, amplectia, inferiora dense stellato-pilosa. Corolla alba ab purpurea. Pedicelli maturescentes deflexi vel appressi. Semina alata.

Numerus basicus chromosomatum x=7.

Typus generis: *Boechera holboellii* (HORNEM.) LÖVE & LÖVE.

Cauline leaves entire, sagittate or auriculate, clasping. Leaves of lower part of stem densely covered with minute stellate hairs. Corolla red-violet to white. Ripe fruiting pedicels distinctly deflexed or appressed to the rachis. Seeds winged. Basic chromosome number x=7.

This taxon, which traditionally has been included in the then very collective and heterogeneous genus *Arabis* L., is morphologically as well as cytologically (x=7 versus x=8) clearly distinct, especially when fruiting specimens are compared. We name it in honour of TYGE W. BÖCHER, an arctic botanist of great reputation who has studied this group in detail from various points of view for several decades. The genus includes several species of boreal and mountainous areas in North America, of which the following occur in the Arctic:

Boechera divaricarpa (A. NELSON) LÖVE & LÖVE, comb. nov., based on *Arabis divaricarpa* A. NELSON, in Bot. Gazette 30 (1900), p. 193.

Boechera drummondii (A. GRAY) LÖVE & LÖVE, comb. nov., based on *Arabis Drummondii* A. GRAY, in Proc. Amer. Acad. 6 (1862), p. 187.

Boechera holboellii (HORNEM.) LÖVE & LÖVE, comb. nov., based on *Arabis Holboellii* HORNEMANN, in Flora danica, fasc. 11 (1827), tab. 1879.

Boechera tenuis (BÖCHER) LÖVE & LÖVE, stat. & comb. nov., based on *Arabis Holboellii* var. *tenuis* BÖCHER, in Svensk Bot. Tidskr. 48 (1954), p. 38.

Noccaea MOENCH

The genus *Thlaspi* L. as treated in recent manuals is a heterogeneous group, and some of its socalled sections or subgenera are so distinct that their species never produce hybrids with those of other sections even under experimental pressure. Since the explanation of this lack of crossability of at least the morphologically well-defined section *Pterotropis* DC. is connected with certain features of the chromosomes that indicate a profound haplomic distinction, the separation of this section under the restricted generic name *Noccaea* seems to be well warranted. Two taxa reaching the arctic regions then require to be transferred to this genus:

Noccaea cochleariforme (DC.) LÖVE & LÖVE, comb. nov., based on *Thlaspi cochleariforme* DE CANDOLLE, Syst. nat. 2 (1821), p. 381.

Noccaea montana (L.) F. K. MEYER ssp. **arctica** (A. E. PORSILD) LÖVE & LÖVE, stat. & comb. nov., based on *Thlaspi arcticum* A. E. PORSILD, in Sargentia 4 (1943), p. 40.

Cochleariopsis LÖVE & LÖVE, gen. nov.

Plantae perennis humilis, 2—12 cm alta, multicaulis, rhizomate verticale, a basi ramosa et vix inflata, carnosa; caulibus saepius prostratis, folia radicalia longe petiolata, ovala vel ovata, obtusa, basi rotundata vel reniformi-cordata, post florationem mox emarcida. Folia caulinaria rhomboideo-elliptica, integra vel subhastato-trilobata. Racemi florentes densi, fructiferentes elongati. Flores

minores; stylus brevissimus, pedicelli patuli, capsula subglobosa vel elliptico-ovalis, laevis vel obsolete venosa, 2—3-plo longior quam lata. Siculae globosae, ellipsoideae, obovatae vel ambitu angustatae.

Numerus basicus chromosomatum x=7.

Typus generis: *Cochleariopsis groenlandica* (L.) LÖVE & LÖVE.

A low-growing perennial, 2—12 cm high, the rhizomes vertical with many stems, branched at the base and slightly inflated, fleshy; the stems are often prostrate; the basal leaves have long petioles, and are oval or ovate, obtuse, with a round or reniform-cordate base, withering soon after the flowers have fallen off. The blades of the stem leaves are shorter than the petioles, rhomboid-elliptic, entire or subhastate-trilobed. The racemes are densely covered with flowers and elongate when the fruits ripen. The flowers are small, with short styles, the pedicels spreading; the capsule is subglobose or elliptic-oval, veinless or scarcely veined and 2—3 times longer than broad. The silicules are globose, elliptic, obovate or in extreme cases also narrowed. Basic chromosome number x=7.

The collective nature of the genus *Cochlearia* L. as traditionally circumscribed has become evident through intensive cytotaxonomical studies, which have shown that the taxon actually consists of two morphologically and geographically distinct groups which also differ in their basic chromosome numbers and chromosome morphology and never hybridize, whereas crosses between taxa of each group are more easily produced and also occur in nature. Since the Linnaean genus is typified by *C. officinalis* L., the group with x=6 must be retained as *Cochlearia* s. str., whereas we propose the new name *Cochleariopsis* for the arctic taxon with x=7. The latter includes only a single diploid species with three variable subspecies, in contrast to several distinct species of a polyploid series of the restricted Linnaean genus. The following taxa need to be transferred to the new genus:

Cochleariopsis groenlandica (L.) LÖVE & LÖVE, comb. nov., based on *Cochlearia groenlandica* LINNAEUS, Spec. plant. (1753), p. 647.

Cochleariopsis groenlandica ssp. **arctica** SCHLECHT.) LÖVE & LÖVE, comb. nov., based on *Cochlearia arctica* SCHLECHTENDAL, in DC. Reg. Veg. Syst. Nat. 2 (1821), p. 367; *Cochlearia officinalis* L. ssp. *arctica* (SCHLECHT.) HULTÉN.

Cochleariopsis groenlandica ssp. **oblongifolia** (DC.) LÖVE & LÖVE, comb. nov., based on *Cochlearia oblongifolia* DE CANDOLLE, Reg. Veg. Syst. Nat. 2 (1821), p. 363; *Cochlearia officinalis* ssp. *oblongifolia* (DC.) HULTÉN.

Tolmachevia LÖVE & LÖVE, gen. nov.

Plantae perennis. Caudex crassus ramosus; caulibus plerumque paucis. Folia obovata, lanceolata vel oblonga ovata, approximata. Inflorescentia cymosa, densa, terminalis; flores polygami, pentameri raro tetrameri, purpureo-rosei vel viridi-purpurei vel flavi. Folliculi apocarpa.

Numerus basicus chromosomatum x=9.

Typus generis: *Tolmachevia integrifolia* (RAFIN.) LÖVE & LÖVE.

Perennial plants. The rootstock is thick and branched; the stems are often few. The leaves are obovate-lanceolate or oblong-ovate, close together. The inflorescences are a terminal and dense cyme. The flowers are polygamous, pentamerous or rarely tetramerous, purple-red or greenish-purple or yellow. The follicles are apocarpous. Basic chromosome number x=9.

This western North American and eastern Asiatic genus is biologically most clearly distinguished from *Rhodiola* L. by having polygamous flowers and the basic chromosome number x=9 as contrasted to the dioecious character of the Linnaean genus with its basic number x=11. Its polygamous condition also separates it from the arctic-alpine Eurasiatic *Kirpicznikovia* validated below and from the apparently monotypic Rocky Mountain *Clementsia rhodantha* (A. GRAY) ROSE, both of which have hermaphroditic flowers and

seem to be characterized by the basic chromosome number x=7. We have the pleasure of naming this beautiful arctic-alpine genus in honour of ALEKSANDR I. TOLMACHEV, the eminent master of Russian arctic botany and a longtime friend. It includes the following three species:

Tolmachevia atropurpurea (TURCZ.) LÖVE & LÖVE, comb. nov., based on *Sedum atropurpureum* TURCZANINOV, in Bull. Soc. Mosc. 1 (1840), p. 13, 70.

Tolmachevia integrifolia (RAFIN.) LÖVE & LÖVE, comb. nov., based on *Rhodiola integrifolia* RAFINESQUE, Atl. Journ. 1 (1832), p. 146.

Tolmachevia krivochzhinii (SIPL.) LÖVE & LÖVE, comb. nov., based on *Rhodiola Krivochzhinii* SIPLIVINSKY, in KRIVOCHZHIN & SIPLIVINSKY, in Novit. Syst. Plant. Vasc. 11 (1974), p. 313.

Kirpicznikovia LÖVE & LÖVE, gen. nov.

Based on *Rhodiola* sect. *Chamae-Rhodiola* BORISSOVA, in Novit. Syst. Plant. Vasc. 6 (1969), p. 114.

Typus generis: *Kirpicznikovia quadrifida* (PALL.) LÖVE & LÖVE.

This genus of seven alpine species of which the single one reaching the Arctic is transferred below, is distinguished by its hermaphroditic usually pentamerous and large white, red or rarely yellowish flowers with the stamens attached to the upper part of the petals; it has a thick and branched rootstock, the leaves are linear to oblong and entire, and the numerous stems are short, clustered and persistent. We have the pleasure of naming it after our longtime friend, M. E. KIRPICZNIKOV, who is a specialist on Asiatic plants and one of the good contributors to the Flora SSSR.

Kirpicznikovia quadrifida (PALL.) LÖVE & LÖVE, comb. nov., based on *Sedum quadrifidum* PALLAS, Reise III, Anh. (1776), p. 730.

Saxifraga monticola (SMALL) LÖVE & LÖVE, comb. nov., based on *Muscaria monticola* SMALL, in North Amer. Flora 22 (1905), p. 130.

This arctic eastern Asiatic and Canadian taxon of the group related to *S. caespitosa* L. is apparently a species in its own right, differing morphologically, geographically and cytologically from the circumpolar decaploid complex since it is only a hexaploid.

Alchemilla L.

It seems advisable to regard the apomictic microspecies of *Alchemilla* that reach the arctic regions only as subspecies of the species *A. vulgaris* L., since they are morphologically and geographically comparable to that category of other species, despite being obligately apomictic. The following three taxa are then in need of being transferred to that level:

Alchemilla vulgaris ssp. **oxyodonta** (BUSER) LÖVE & LÖVE, comb. nov., based on *Alchemilla acutidens* BUSER ssp. *oxyodonta* BUSER, in Bot. Not. 1906, p. 141.

Alchemilla vulgaris ssp. **transpolaris** (JUZ.) LÖVE & LÖVE, stat. & comb. nov., based on *Alchemilla transpolaris* JUZEPCZUK, in Bot. Mat. 16 (1954), p. 179.

Alchemilla vulgaris ssp. **vestita** (BUSER) LÖVE & LÖVE, stat. & comb. nov., based on *Alchemilla filicaulis* BUSER var. *vestita* BUSER, in Bull. Herb. Boissier 1 (1893), Appendix 2, p. 22.

Astragalus astragalinus (HOOK.) LÖVE & LÖVE, comb. nov., based on *Phaca astragalina* W. J. HOOKER, Flora Bor. Amer. 1 (1833), p. 145; *Astragalus alpinus* L. ssp. *alaskanus* HULTÉN.

This taxon was reduced to the subspecific level of *A. alpinus* by HULTÉN (1947), and two decades later, HULTÉN (1968) claimed that it and ssp. *alpinus* "form introgression". This is clearly based on the same misuse of this term for morphological indications of alloploidy as by HULTÉN (1956), since *A. alpinus* s. str. is a diploid plant, whereas ssp. *alaskanus* is a tetraploid of which *A. alpinus* may

be one of the parental species. It is evident that the taxon is a species in its own right and so we transfer its name to that level.

Oxytropis taimyrensis (JURTSEV) LÖVE & LÖVE, stat. & comb. nov., based on *Oxytropis arctica* R. BR. ssp. *taimyrensis* JURTSEV, in Bot. Mat. 19 (1959), p. 239.

Recent studies have shown that this taxon is an octoploid plant with 2n=64 chromosomes, whereas *O. arctica* is a dodecaploid with 2n=96, thus indicating that their relationship may be more remote than originally surmised and their taxonomical level similar. Therefore this transfer to a higher level.

Callitriche anceps FERN. ssp. **subanceps** (V. PETR.) LÖVE & LÖVE, stat. & comb. nov., based on *Callitriche subanceps* V. PETROV, in Izvest. Glavn. Bot. Sada 27 (1928), p. 359.

The North American species *C. anceps*, which reaches from Greenland to Alaska in the American northlands, is represented in easternmost Asia by this morphologically and cytologically very closely related vicarious taxon, which certainly is best regarded as a subspecies only.

Viola epipsiloides LÖVE & LÖVE, nom. nov., based on *Viola repens* TURCZANINOV ex TRAUTVETTER & MEYER, in MIDDENDORF, Reise Sibir. 1,2,2 (1856), p. 18; non *Viola repens* SCHWEINITZ.

A new name is required for this species of the eastern Siberian and western North American arctic-alpine regions, because of an earlier homonym. It has frequently been wrongly identified with the Eurasiatic *V. epipsila* LEDEB. to which it does not seem to be even remotely related.

Viola aduncoides LÖVE & LÖVE, spec. nov.

Planta perennis; folia longi-petiolata, subcoriacea, ovata, cordata, glabrata vel dense pubescentia, pilis brevis (minus 0.2 mm longi); stipulae lineari-lanceolatae, integrae vel spinulosi-dentatae; corolla caerulea-purpurea, 10—15 mm longa. Projectura in styli capitata globosa, 1/10 vel minus latitudo capitis; capsula 4—5 mm longa; semina atrofusca. Numerus chromosomatum 2n=40.

Holotypus: Canada, Manitoba, Árnes, meadow along poplar shrub, May 5, 1953, LÖVE & LÖVE 5744 in Herb. Winnipeg.

A perennial plant with long-petioled leaves which are subcoriaceous, ovate and cordate, glabrous or densely pubescent with short hairs (less than 0.2 mm long); the stipules are linear-lanceolate, entire or spinulose-dentate; the corolla is bluish-purple, 10—15 mm long. Projections on the upper tip of the style head are short-conical or globular, 1/10 or less the width of the style head. The capsule is 4—5 mm long; the seeds are dark-brown. Chromosome number 2n=40.

This North American tetraploid species differs from the diploid *V. adunca* SM. in the form of the style head and the smaller projections on it, the shorter hairs on the leaves when present, and in the size of guard cells and pollen grains (MCPHERSON & PACKER 1974). It is apparently an hemiautoploid (LÖVE & LÖVE 1975 c) of Pleistocene origin as indicated by its distribution.

Chamerion platyphyllum (DANIELS) LÖVE & LÖVE, comb. nov., based on *Chamaenerion angustifolium* (L.) SCOP. var. *platyphyllum* DANIELS, in Univ. Missouri Studies 2,2 (1911), p. 176; *Epilobium Danielsii* D. LÖVE; *Epilobium platyphyllum* (DANIELS) LÖVE & LÖVE, non RYDBERG.

This is the octoploid (2n=72) taxon of southern boreal mountains in eastern North America and the western mountains north to the arctic regions, corresponding to the more northern circumpolar *C. angustifolium* (L.) HOLUB. For a discussion of the genus and its correct name, see HOLUB (1972).

Chamerion subdentatum (RYDB.) LÖVE & LÖVE, comb. nov., based on *Chamaenerion subdentatum* RYDBERG, Flora Rocky Mts. (1917), p. 585.

This is the tetraploid mainly western American and eastern Asiatic alpine taxon corresponding to the more widespread and almost circumpolar arctic-alpine octoploid species *C. latifolium* (L.) HOLUB.

Coelopleurum lucidum (L.) FERN. ssp. **gmelinii** (DC.) LÖVE & LÖVE, stat. & comb. nov., based on *Archangelica Gmelinii* DE CANDOLLE, Prodr. 4 (1830), p. 170.

This is the Pacific vicarious race of the otherwise eastern North American species.

Conioselinum chinense (L.) B.S.P. ssp. **boreale** (SCHISCHKIN) LÖVE & LÖVE, stat. & comb. nov., based on *Conioselinum boreale* SCHISCHKIN, in Flora SSSR 17 (1951), p. 351.

This race is the northernmost European population of this widespread and variable species.

Pyrola rotundifolia L. ssp. **asarifolia** (MICHX.) LÖVE & LÖVE, stat. & comb. nov., based on *Pyrola asarifolia* MICHAUX, Flora Bor. Amer. 1 (1803), p. 251.

This vicarious race replaces the ssp. *rotundifolia* of Eurasia in North America and eastern Asia.

Douglasia LINDL.

This genus is closely related to *Androsace* L. from which it differs in some technical characters and also in the apparently derived basic chromosome number x=19 as contrasted to x=10. It is represented in the northlands by three taxa which we believe are most adequately classified as subspecies only of the species *D. ochotensis* (WILLD.) HULTÉN. Two of these are here transferred to this level:

Douglasia ochotensis ssp. **arctica** (CHAM. & SCHLECHT.) LÖVE & LÖVE, stat. & comb. nov., based on *Androsace arctica* CHAMISSO & SCHLECHTENDAL, in Linnaea 1 (1826), p. 220.

Douglasia ochotensis ssp. **gormanii** (GREENE) LÖVE & LÖVE, stat. & comb. nov., based on *Androsace Gormanii* GREENE, in Pittonia 4 (1900), p. 149; *Douglasia Gormanii* (GREENE) CONSTANCE.

Primula tschuktschorum KJELLM. ssp. **arctica** (KOIDZ.) LÖVE & LÖVE, stat. & comb. nov., based on *Primula arctica* KOIDZUMI, in Bot. Mag. Tokyo 25 (1911), p. 216.

We believe that the three rather distinct variations of this Beringian species are correctly classified as three subspecies, although the opinion could also be defended that they may be minor geographical races and then only varieties. A transfer is needed for one of these taxa that has even been described as a species under three different names.

Gentiana L.

The collective genus *Gentiana* needs to be divided into several more natural genera, as demonstrated by several authors during the past two decades. Of these groups, *Ciminalis* ADANS.; HOLUB, *Calathiana* DELARBRE, *Comastoma* (WETTST.) TOYOKUNI, *Gentianella* MOENCH, *Gentianodes* LÖVE & LÖVE, *Gentianopsis* MA and *Lomatogonium* R. BR. are represented in the arctic regions, but only one species and one subspecies of these are in need of a transfer:

Ciminalis prostrata (HAENKE) LÖVE & LÖVE, comb. nov., based on *Gentiana prostrata* HAENKE, in JACQUIN, Collectanea 2 (1788), p. 66.

Gentianopsis detonsa (ROTTB.) MA ssp. **raupii** (A. E. PORSILD) LÖVE & LÖVE, comb. nov., based on *Gentiana Raupii* A. E. PORSILD, in Sargentia 4 (1943), p. 60; *Gentianella detonsa* (ROTTB.) G. DON ssp. *Raupii* (A. E. PORSILD) J. M. GILLETT.

Polemonium boreale ADAMS ssp. **humile** (WILLD.) LÖVE & LÖVE, stat. & comb. nov., based on *Polemonium humile* WILLDENOW ex ROEMER & SCHULTES, Syst. Veget. 4 (1819), p. 792, non SALISBURY; *Polemonium Hultenii* HARA.

This is the northern Siberian race of the species.

Polemonium pulcherrimum HOOK. ssp. **hyperboreum** (TOLM.) LÖVE & LÖVE, stat. & comb. nov., based on *Polemonium hyperboreum* TOLMACHEV, in Feddes Repert. 23 (1927), p. 273.

This is the Siberian subspecies of the species, the typical race of which is met with in the mountains and northlands of North America.

Phlox sibirica L. ssp. **alaskensis** (JORDAL) LÖVE & LÖVE, comb. nov., based on *Phlox alaskensis* JORDAL, in Rhodora 54 (1952), p. 38; *Phlox Richardsonii* HOOK. ssp. *alaskensis* (JORDAL) WHERRY.

Pseudolysimachium OPIZ

The splitting of the collective genus *Veronica* L. has been made on basis of morphological differences only, but these are strongly supported also by differences in basic chromosome numbers, since *Veronica* L., s. str. is characterized by x=8, 9, whereas *Veronicastrum* MOENCH has x=7 and *Pseudolysimachium* OPIZ has x=17. Two of the species belonging to the last genus and occurring in the northlands require a transfer:

Pseudolysimachium maritimum (L.) LÖVE & LÖVE, comb. nov., based on *Veronica maritima* LINNAEUS, Spec. plant. (1753), p. 10.

Pseudolysimachium septentrionale (BORISS.) LÖVE & LÖVE, comb. nov., based on *Veronica septentrionalis* BORISSOVA, in Flora SSSR 22 (1955), p. 369.

Castilleja pallida (L.) KUNTH

This northern species is represented in the arctic tundra by three evidently major geographical races, which REBRISTAIA (1964) regarded as distinct species. Although they are admittedly rather distinct morphologically, this seems to be the result of an almost obligate autogamy rather than of the occurrence of reproductive isolation, so we see no reason to classify them higher than as subspecies, as here validated:

Castilleja pallida ssp. **hyparctica** (REBR.) LÖVE & LÖVE, stat. & comb. nov., based on *Castilleja hyparctica* REBRISTAIA, in Novit. Syst. Plant. Vasc. 1 (1964), p. 289.

Castilleja pallida ssp. **lapponica** (GANDOGER) LÖVE & LÖVE, stat. & comb. nov., based on *Castilleja lapponica* GANDOGER, Flora Europ. 18 (1889), p. 25.

Castilleja pallida ssp. **pavlovii** (REBR.) LÖVE & LÖVE, stat. & comb. nov., based on *Castilleja Pavlovii* REBRISTAIA, in Novit. Syst. Plant. Vasc. 1 (1964), p. 294.

Pedicullariopsis LÖVE & LÖVE, gen. nov.

Plantae perennis, humilis, superne pilosa vel glabra; foliis profunde pinnatifidis pinnatipartisve, laciniis ovatis oblongisve pinnatopinnatifidis, lobis dentatis; spicis interruptis; calycis dentibus abbreviatis integerrimis serrulatisve; corolla tubo basi infracto; galea erostrata, obtusa, labium duplo superans.

Numerus basicus chromosomatum x=6.

Typus generis: *Pedicullariopsis verticillata* (L.) LÖVE & LÖVE.

Perennial plants, erect but low growing, above pilose or glabrous. The stem leaves are in 3—4 whorls, deeply pinnatifid or pinnately partite, and the divisions are ovate-oblongish pinnato-pinnatifid, the lobes are toothed. The spikes are interrupted; the calyx has short teeth that are entire or finely serrate; the corolla tube is sharply bent at the base, the helmet is beakless and obtuse and twice the size of the lower lip. Basic chromosome number x=6.

The new genus differs from *Pedicularis* L. in several characters of the flowers, the arrangement of the spike and in leaf morphology, but the most profound difference is in its chromosome morphology and in the basic number x=6 as contrasted to x=8 of the Linnaean genus. It includes a single but not very variable species of considerable arctic-alpine distribution:

Pedicullariopsis verticillata (L.) LÖVE & LÖVE, comb. nov., based on *Pedicularis verticillata* LINNAEUS, Spec. plant. (1753), p. 846.

Chlorocrepis tristis (WILLD.) LÖVE & LÖVE, comb. nov., based on *Hieracium*

triste WILLDENOW ex SPRENGEL, Syst. veget. 3 (1826), p. 640.

This transfer is needed when the three traditionally accepted subgenera of *Hieracium* L. are elevated to generic rank.

Crepis tectorum L. ssp. **nigrescens** (POHLE) LÖVE & LÖVE, stat & comb. nov., based on *Crepis nigrescens* POHLE, in Acta Hort. Jurjev. 3 (1903), p. 231.

This taxon of northernmost Europe and western Siberia is often regarded as a synonym only of *C. tectorum,* even if some authors accept it as a species in its own right. Although some of its few characteristics are perhaps only modifications of no taxonomical importance, others seem to be genetically conditioned. Since it also has a distinct area of its own, we find it logical to accept it as a race at the subspecific level rather than to ignore it.

Antennaria canescens (LGE) MALTE ssp. **porsildii** (E. EKM.) LÖVE & LÖVE, stat. & comb. nov., based on *Antennaria Porsildii* E. EKMAN, in Svensk Bot. Tidskr. 21 (1927), p. 51.

This is an apomictic and endemic Greenland population of a rather widespread apomictic complex, which certainly was given too high a rank when described as a species. It might even be more correctly classified as a variety only or as a hybrid that has survived simply thanks to its being apomictic.

Nardosmia arctica (A. E. PORSILD) LÖVE & LÖVE, comb. nov., based on *Petasites arcticus* A. E. PORSILD, in Sargentia 4 (1943), p. 74.

The certainly good reasons for keeping this genus as separate from *Petasites* in a more strict sense, given by KUPRIYANOVA (1961), require a transfer of this arctic Canadian taxon.

Nardosmia vitifolia (GREENE) LÖVE & LÖVE, comb. nov., based on *Petasites vitifolius* GREENE, in Leafl. West. Bot. 1 (1906), p. 180.

Another Canadian taxon requiring transfer to this restricted genus.

Endocellion TURCZ.

There are valid morphological and cytological reasons to distinguish the genus *Nardosmia* CASS. from *Petasites* MILL., although both are characterized by the same basic number, x=10. However, we find it illogical to attach to the former the small Asiatic group that has been described as the genus *Endocellion,* even as a subgenus as done by KUPRIYANOVA (1961), since it is not only morphologically distinct but differs also in having the basic number x=7 in addition to a considerably different chromosome morphology. The following two of its three eastern Asiatic arctic-alpine species require a transfer:

Endocellion glacialis (LEDEB.) LÖVE & LÖVE, comb. nov., based on *Nardosmia glacialis* LEDEBOUR, Flora rossica 2,2 (1845), p. 466.

Endocellion gmelinii (TURCZ.) LÖVE & LÖVE, comb. nov., based on *Nardosma Gmelinii* TURCZANINOV, ex DC., Prodr. 7,1 (1838), p. 271.

Tephroseris (RCHB.) RCHB.

As shown by HOLUB (1973), this boreal group which is traditionally included in the then very collective genus *Senecio* L., is morphologically best distinguished by its absence of outer involucral bracts, in addition to several less obvious technical characters. Its most profound biological difference that clearly sets it apart as an evolutionary unit of considerable distinction is, however, the fact that its basic chromosome number is x=8 as contrasted to x=10 of *Senecio* proper. HOLUB (l.c.) recommends that the group be accepted as a genus of its own, an opinion which we endorse on basis of longtime observations of its European and North American representatives. The following new combinations for taxa of the northlands are required:

Tephroseris aquilonaris (SCHISCHKIN) LÖVE & LÖVE, comb. nov., based on *Senecio aquilonaris* SCHISCHKIN, in Flora SSSR 26 (1961), p. 884.

Tephroseris atropurpurea (LEDEB.) HOLUB ssp. **frigida** (RICHARDS.) LÖVE & LÖVE, stat. & comb. nov., based on *Cineraria frigida* RICHARDSON, in Bot. Appendix to FRANKLIN, Narr. of Journ. (1823), p. 748.

Tephroseris atropurpurea ssp. **tomentosa** (KJELLM.) LÖVE & LÖVE, comb. nov., based on *Cineraria frigida* f. *tomentosa* KJELLM., in Vega Exp. Vetensk. Iaktt. 2 (1883), p. 13; *Senecio atropurpureus* (LEDEB.) FEDTSCH. ssp. *tomentosus* (KJELLM.) HULTÉN.

Tephroseris lindstroemii (OSTENF.) LÖVE & LÖVE, comb. nov., based on *Senecio integrifolius* (L.) CLAIRV. var. *Lindstroemii* OSTENFELD, Christiania Vidensk. Selsk. Skr. 1909, No. 8 (1910), p. 70; *Senecio Lindstroemii* A. E. PORSILD.

Packera LÖVE & LÖVE, gen. nov.

Plantae perennis, herbaceae. Caules non rite foliosi. Caudex sine rhizoma repens vel suberectus. Folia simplicia et integra ad lyrato-pinnatifida, folia radicalia petiolata, caulinaria amilia vel minora. Plantae glabratae alteruter ab initium vel plus minusve permanentes tomentosae; pubescentia nunquam e pilis longis articulatisque.

Numerus basicus chromosomatum x=23.

Typus generis: *Packera aurea* (L.) LÖVE & LÖVE.

Herbaceous perennials. Stems not uniformly leafy to the inflorescences, arising from a horizontal to suberect caudex or rhizome. Leaves simple and entire to lyrate-pinnatifid, those at the base petiolate, gradually reduced upwards, or uniform throughout. Plants either quite glabrous from the beginning or more or less permanently tomentose; pubescence never of long jointed hairs. Basic chromosome number x=23.

This mainly North and South American genus with a few representatives in Asia comprises the groups *Aurei, Lobati* and *Tomentosi* of the collective genus *Senecio* as described by RYDBERG (1900) and GREENMAN (1916), which stand apart from the other divisions of the collective aggregate by having prolonged rhizomes, and if pubescence is present it is a tomentum of more or less arachnoid and never of long and jointed hairs, but persistent as flocculent tufts. Its morphological and geographical distinctions are enhanced by its basic chromosome number, which differs markedly from that of *Senecio* L. s. str. (x=10) and *Tephroseris* (RCHB.) RCHB. (x=8) so that its distinction as a genus is biologically well substantiated. It is our pleasure to name the new genus in honour of JOHN G. PACKER, an oldtime friend who has contributed much to the clarification of the status of the arctic-alpine North American members of the taxon. Its arctic taxa are:

Packera aurea (L.) LÖVE & LÖVE, comb. nov., based on *Senecio aurea* LINNAEUS, Spec. plant. (1753), p. 270.

Packera fernaldii (GREENM.) LÖVE & LÖVE, comb. nov., based on *Senecio Fernaldii* GREENMAN, in Ann. Missouri Bot. Gard. 3 (1916), p. 90.

Packera hyperborealis (GREENM.) LÖVE & LÖVE, comb. nov., based on *Senecio hyperborealis* GREENMAN, in Ann. Missouri Bot. Gard. 3 (1916), p. 98.

Packera indecora (GREENE) LÖVE & LÖVE, comb. nov., based on *Senecio indecorus* GREENE, Flora Franciscana (1897), p. 470.

Packera ogotorukensis (PACKER) LÖVE & LÖVE, comb. nov., based on *Senecio ogotorukensis* PACKER, in Canad. Journ. Bot. 50 (1972), p. 511; *Senecio conterminus* auct. Alaska, non GREENMAN.

Packera pauciflora (PURSH) LÖVE & LÖVE, comb. nov., based on *Senecio pauciflorus* PURSH, Flora Amer. Sept. 2 (1814), p. 529.

Packera paupercula (MICHX.) LÖVE & LÖVE, comb. nov., based on *Senecio pauperculus* MICHAUX, Flora Bor. Amer. 2 (1803), p. 120.

Packera resedifolia (LESS.) LÖVE & LÖVE, comb. nov., based on *Senecio resedifolius* LESSING, in Linnaea 6 (1831), p. 243.

Aster L.

We find it more logical to regard the five taxa of arctic *Aster* as representing three and two subspecies only of the two species *A. sibiricus* L. and *A. alpinus* L., rather than as species as accepted in recent manuals. As such the following new levels and combinations are validated:

Aster sibiricus L. ssp. **pygmaeus** (LINDLEY) LÖVE & LÖVE, stat. & comb. nov., based on *Aster pygmaeus* LINDLEY, in W. J. HOOKER, Flora Bor. Amer. 2 (1834), p. 6.

Aster sibiricus ssp. **richardsonii** (SPRENG.) LÖVE & LÖVE, stat. & comb. nov., based on *Aster Richardsonii* SPRENGEL, Syst. Veg. 3 (1826), p. 258.

Aster sibiricus ssp. **subintegerrimus** (TRAUTV.) LÖVE & LÖVE, stat. nov., based on *Aster sibiricus* var. *subintegerrima* TRAUTVETTER, in MIDDENDORF, Reise 1 (1847), p. 161.

Aster alpinus L. ssp. **serpentimontanus** (TAMAMSCH.) LÖVE & LÖVE, stat. & comb. nov., based on *Aster serpentimontanus* TAMAMSCHAN, in Flora SSSR 25 (1959), p. 108, and *Aster cyllenius* ONNO, in Bibl. Bot. 106 (1932), p. 38, p.p., non HALACSY.

Aster alpinus ssp. **tolmatschevii** TAMAMSCH.) LÖVE & LÖVE, stat. & comb. nov., based on *Aster Tolmatschevii* TAMAMSCHAN, in Flora SSSR 25 (1959), p. 107, and *Aster chryzocomoides* DE CANDOLLE, Prodr. 7 (1838), non DESFONTAINES.

Matricaria maritima L. ssp. **boreale** (HARTM.) LÖVE & LÖVE, comb. nov., based on *Tripleurospermum inodorum* SCHULZ-BIP. β *borealis* C. J. HARTMAN, Handb. i Skand. Flora, ed. 5 (1849), p. 2; *Tripleurospermum maritimum* (L.) KOCH ssp. *borealis* (HARTM.) A. PEDERSEN.

We follow the typification of the genus by RAUSCHERT (1974), and refer to HÄMET-AHTI (1967) and PEDERSEN (1972) for clarification of the North Atlantic races of *M. maritima.*

Erigeron thunbergii A. GRAY ssp. **komarovii** (BOTSCH.) LÖVE & LÖVE, stat. & comb. nov., based on *Erigeron Komarovii* BOTSCHANTSEV, in Flora SSSR 25 (1959), p. 213.

Erigeron thunbergii ssp. **koraginensis** (KOM.) LÖVE & LÖVE, stat. & comb. nov., based on *Aster koraginensis* KOMAROV, Flora Kamch. 3 (1930), p. 125.

Erigeron uniflorum L. ssp. **eriocalyx** (LEDEB.) LÖVE & LÖVE, stat. & comb. nov., based on *Erigeron alpinus* L. β *eriocalyx* LEDEBOUR, Flora Altai 4 (1833), p. 91.

Tanacetum vulgare L. ssp. **boreale** (FISCH.) LÖVE & LÖVE, stat. & comb. nov., based on *Tanacetum boreale* FISCHER, ex DC. Prodr. 6 (1838), p. 128.

This is a distinct eastern Asiatic arctic-alpine major race of this common boreal Eurasiatic species, distinguished by its more dissected leaves with narrow and sharply serrulated segments.

Oligosporus groenlandicus (HORNEM.) LÖVE & LÖVE, comb. nov., based on *Artemisia groenlandica* HORNEMANN, Flora danica, fasc. 27 (1818), tab. 1585; *Artemisia borealis* PALL. ssp. *Purshii* (BESS.) HULTÉN; *Artemisia campestris* L. ssp. *spithamea* HALL & CLEM., non *Artemisia spithamea* PURSH.

We find it logical to break up the very heterogeneous *Artemisia* L. into more natural units, as advocated by POLYAKOV (1961), and so accept the generic name *Oligosporus* CASS. for the species traditionally constituting the section or subgenus *Dracunculus.* That genus is characterized by having a smooth and not hairy receptacle and disc-flowers with both stamens and pistils but sterile because of an abortive ovary, and by having an entire or nearly entire style, in addition to other technical differences.

As shown by HULTÉN (1950), the considerable diversity of the arctic-alpine populations that are usually included in the species *Artemisia borealis,* falls nicely into two major groups, which he regarded as major geographical races and separated as the typical taxon and its ssp. *purshii.* Since these taxa have been found to differ in chromosome number so they are certainly reproductively isolated, we find it more appropriate to accept them as distinct species and adopt for the latter its old and validly published name *groenlandicus.* Typical *Oligosporus borealis* (PALL.) POLYAK., as its name must be in the restricted genus, was described from the neighborhood of the Ob river of Siberia. It is a plant with more or less densely and loosely pubescent leaves, the upper ones lobed and the lower ones small with a few broad lobes, and with relatively large (5—6 mm broad) heads with a glabrous involucrum and forming dense and usually unbranched spikes. *O. groenlandicus,* however, which was originally described from western Greenland, is a plant with densely sericeous or pubescent basal leaves which are 2—3 times pinnatifid with narrow lobes, and with smaller (3—4 mm broad) globular heads with pubescent or glabrous involucrum and forming thin spikes. The former taxon is tetraploid with 2n=36 chromosomes, but the latter is diploid with 2n=18. Both are arctic-alpine. The tetraploid reaches from northern European Russia over Siberia to Labrador and western Greenland, where it is relatively common. The diploid is met with from lower Yenissei east to Baffin Island and western Greenland, where it is rare; however, it seems to reach farther north in North America than the tetraploid and grows also in southern mountains in Asia and in Gaspé and the Rocky Mountains of Colorado in North America.

SOME CORRECTIONS

A few obvious misprints have crept in on a few pages of LÖVE & LÖVE (1975 a), but only the following omissions and oversights need to be pointed out:

p. XIV: The important reference to DOROGOSTAISKAYA (1972) has been omitted.

p. 9: The author of the family Botrychiaceae is NAKAI.

p. 320: The reference year 1969 b has fallen out after MULLIGAN & PORSILD for the chromosome report for *Saxifraga adscendens* ssp. *oregonensis.*

p. 596: Lagotis 433 has been omitted from the index.

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Botanical Literature

LÖVE, Á. & LÖVE, D.: Cytotaxonomic Atlas of the Arctic flora. — J. Cramer, Vaduz 1975. ISBN 3-7682-0976-8. xxiii+598 pp. Price (subscription) DM 160:—; (regular) DM 200:—.

The second of a projected series of cytotaxonomic atlases by Á. and D. LÖVE has appeared. (Why, it could be asked, are they called atlases?) The first is that on Slovenian plants reviewed by me in Botaniska Notiser 128: 551—553, where I stressed the significance of the Slovenian list. This in my opinion lies in its usefulness as a source of references to the literature dealing with all vascular plants found in Slovenia (using the taxonomic concept of the authors). In addition, however, I delivered a somewhat lengthy criticism of some of the basic principles presented and exemplified the disadvantages of the "critical" method employed. As the same criticism applies to this volume the reader is referred to the former review.

I have studied the new Atlas of Arctic plants with particular interest, both by reason of my experience of the first Atlas and because my own research has at times brought me into contact with Arctic botany. The book serves the dual purpose of being both a check-list of Arctic taxa and a critical review of their chromosome numbers. The area covered is rather more extensive than the term "arctic" usually implies which is scarcely a disadvantage in this context. This is, however, not the only reason why the number of genera presented has increased by 75 % and the number of species by over 80 % as compared with those dealt with by POLUNIN in his Circumpolar Arctic Flora (1959). The main reason for the discrepancy is of course the difference in taxonomic concepts adopted. POLUNIN used a somewhat collective concept whereas LÖVE and LÖVE are splitters in the extreme. They employ a "biological" or "evolutionary" concept, which implies that a taxon at generic level or lower is defined "biologically" but identified morphologically. More than one basic chromosome number is not tolerated within a single genus, and a correctly and exactly defined species must have one single chromosome number only. In most cases this does not give rise to conflict but the outcome can at times be surprising. *Minuartia*, for example, has been virtually reduced to fragments, and several other genera have been split up. There has also rarely been some lumping, an example being the merging of *Puccinellia* and *Phippsia* with the latter name having been given priority. For practical reasons it might have been wiser to have proposed the conservation of *Puccinellia*. The taxonomic and nomenclatural changes will probably provoke considerable irritation but should perhaps not be regarded as being controversial as they mainly reflect differences of personal opinion. Validations of new taxa and combinations are made in a paper appearing in this issue of Botaniska Notiser (pp. 497—523).

My own limited knowledge of the vast field of the cytotaxonomy of Arctic plants does not permit me to check the overall reliability of the information in the list. As when reviewing the first Atlas I chose to check a genus with which I am familiar, in this case the grass genus *Hierochloë*. The result was both astonishing and disturbing. There is, for instance, no reference to ZHUKOVA's report (1967) on the chromosome number 2n=56 in *H. alpina* nor to my report (1970) on 2n=66 in the same taxon, nor to my report (1971) on 2n=58 in *H. monticola* (*H. orthantha*, *H. alpina* ssp. *orthantha*), nor to my reports (1971, 1973) on 2n=72, 75, 76 and 77 in *H. alpina*. All these reports except ZHUKOVA's represent deviations from the

normal euploid conditions within the taxa. *H. odorata* has not been listed for Greenland where it has been collected from one place (voucher at C). In *H. hirta* ssp. *arctica*, 2n=56 (WEIMARCK 1971) should have been underlined as it has been determined from Arctic material as geographically delimited here. If the omissions are due to oversight there is a severe risk that there may be other accidental omissions and mistakes in the list which would diminish its value catastrophically. On the other hand I must react adversely if the authors should have omitted the information as being "apparently incorrect or inexact", "obviously wrong or taxonomically suspect" or "scientifically worthless and . . . directly misleading to those less familiar with the cytotaxonomical method" (quoted from the reasons given for the exclusion of certain references). I consider that it is the author's responsibility to decide whether the information he publishes is correct, and that no attempt at screening should be made by the compilers of a list of this type.

It is to be hoped that this one unfortunate example is not a measure of the reliability of the book as a whole. If this were so the total number of possible mistakes would be somewhere in the region of 1,500.

As to general appearance I consider that this Atlas, which is typewritten, is more attractive than the first volume, which was a crude computer outprint. It is perhaps regrettable that both volumes are not of the same format.

GUNNAR WEIMARCK

LÖVE, Á. & LÖVE, D.: Plant Chromosomes. — J. Cramer, Vaduz 1975. ISBN 3-7682-0966-0. xv+184 pp. Price DM 36: —.

This is the first of a projected series of volumes on Plant Science. First the microscopic structure of chromosomes is described and their behaviour at mitosis and meiosis surveyed. The theoretical basis of chromosome study is outlined and there is a short section dealing with tissues suitable for cytological study. The microscope and other equipment are briefly presented together with some simple techniques of observation. Practical cytotechnology is described in greater detail with a number of selected methods.

The little book is handy to use and is in general attractive. Most terms are adequately explained and their philologic derivations given. However, I should have preferred the terms "centromere" and "kinetochore" to have been kept separate, using "centromere" to denote the visual constriction and "kinetochore" for the submicroscopic organelle for chromosome movement. This is a practice that has been introduced into modern literature and is to my mind a commendable one. A short section on the submicroscopic structure and biochemistry of chromosomes would have been warranted although admittedly it is somewhat peripheral in view of the limited scope of the book. As it is now the book is predominantly descriptive with rather little of the functional aspect. Some emphasis is laid on chromosome number. Techniques for karyotype analysis, the detailed study of meiosis, etc. are more superficially treated. I admit to being astonished that sectioned material is so strongly recommended for karyotype analysis rather than squashes. In spite of the fact that much current literature is cited, the impression might be received that little has happened in the field of karyology since the 40s. In particular I find it regrettable that the new banding techniques such as the Giemsa technique are so briefly mentioned and no practical details discussed. Although only very recently taken into use by botanists these techniques will undoubtedly assume great importance. I also searched in vain for mention of certain other methods of which my own experience has been satisfactory.

I cannot agree with the statement on p. 93 that the chromosome number counted at meiosis is n. The number 2n is obtained when counting the two groups at anaphase I (they should be added together to avoid a miscount if non-disjunction has occurred) as well as at, for example, diakinesis and metaphase I where bivalents are usually counted (consisting, of course, of two chromosomes each).

Figures 15, 25 and 26 are wrongly oriented which could be misleading.

So much negative criticism is perhaps hardly fair, for what book conforms wholly with the demands of the prospective reviewer. I am convinced that this volume will serve favourably as a short introduction to chromosome study. A great advantage is that it comprises both theory and practice whereas the comprehensive textbooks usually deal with only the one or the other.

GUNNAR WEIMARCK