Drawings of Scandinavian Plants 101–102

Epilobium L. Sect. Epilobium

Alf Oredsson and Sven Snogerup

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

Alf Oredsson and Sven Snogerup, Department of Plant Taxonomy, University of Lund, Ö. Vallgatan 18—20, S-223 61 Lund, Sweden.

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.

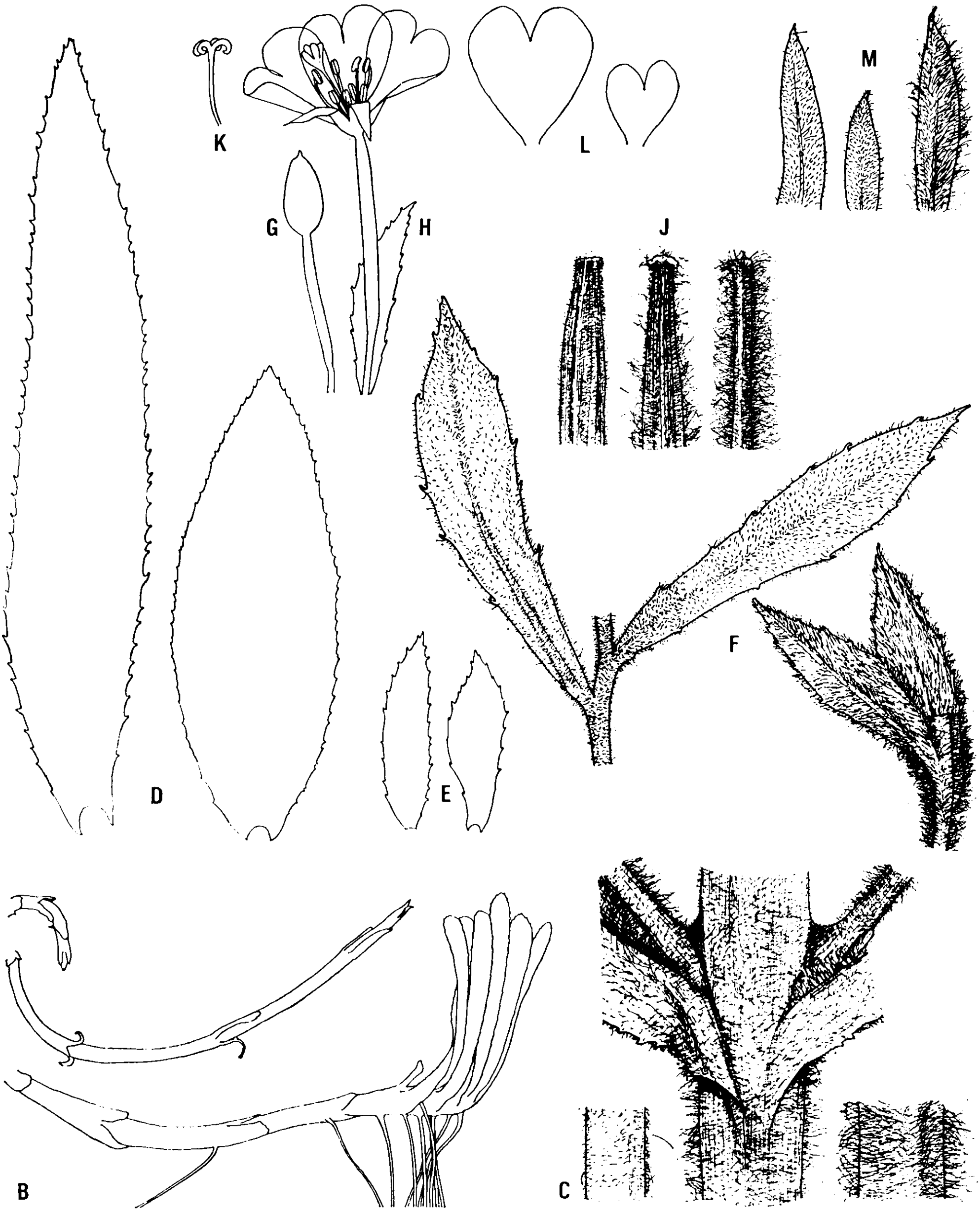

Fig. 101. *Epilobium hirsutum* L. — A: Habit, ×1/3. — B: Stolons, ×1/2. — C: Stem node and stem parts with deviating types of indumentum, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem part and leaves, ×2.5. — G: Bud, ×1. — H: Flower, ×1. — J: Apical parts of capsules, ×2.5. —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

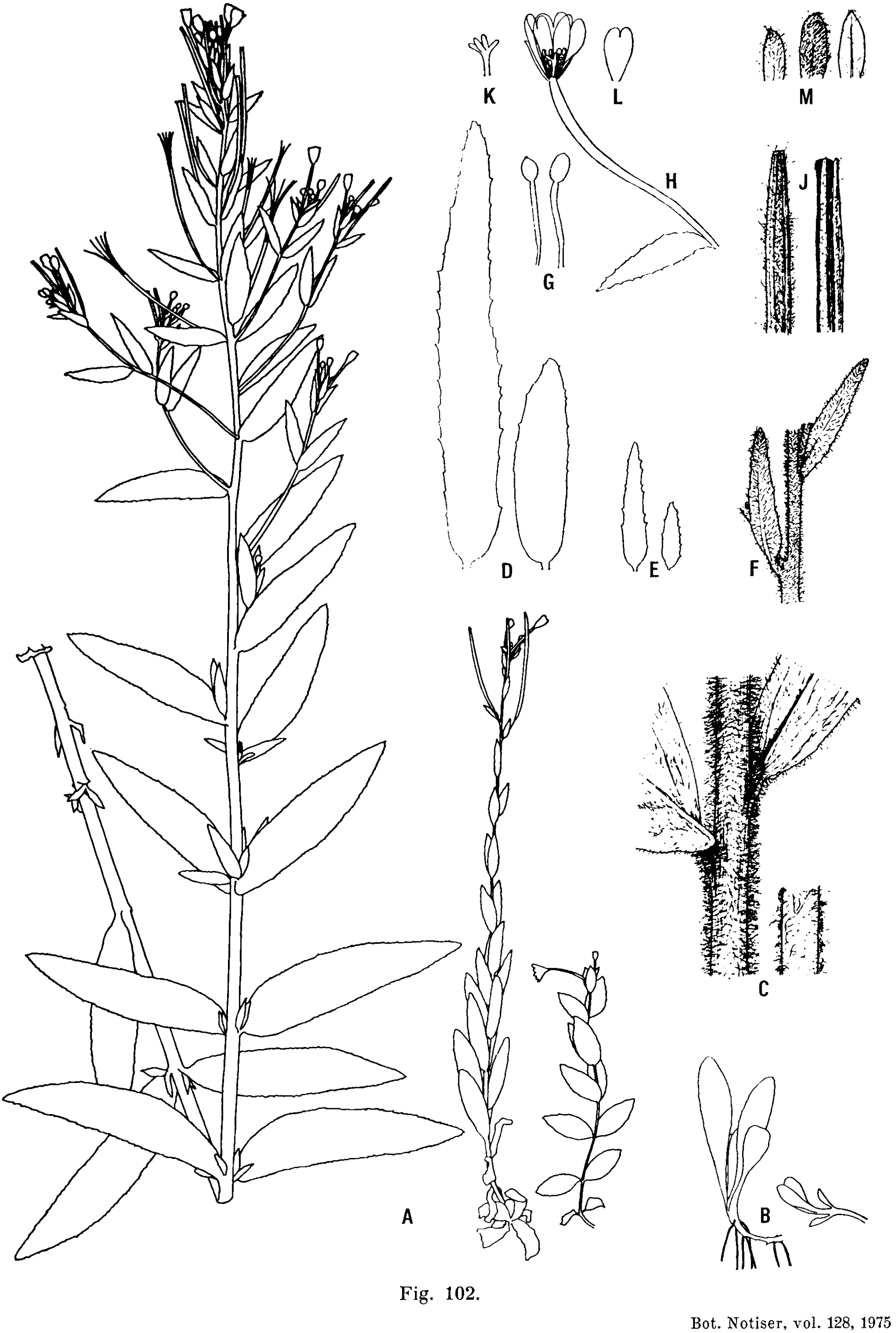

Fig. 102.

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.

Bo Sjöstedt, Agricultural College of Sweden, Division of Plant Breeding, Balsgård, S-291 90 Kristianstad, Sweden.

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

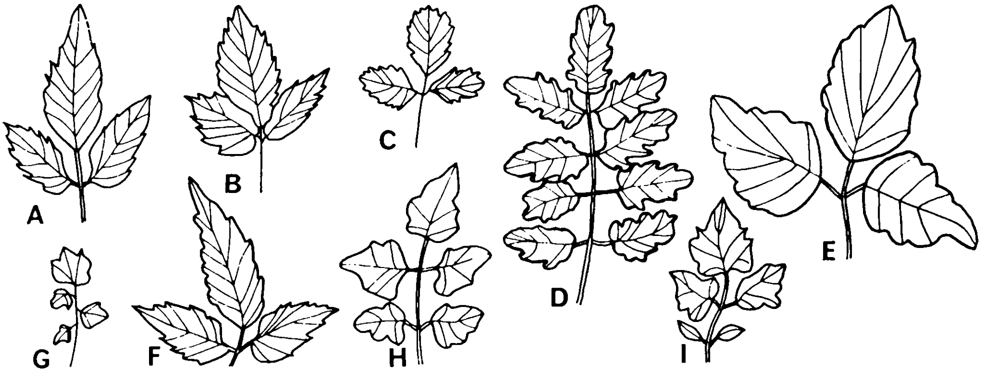

Fig. 1. Leaves of South and Central American specimens of *Cardamine africana*. — A: Ekman n. 5431. — B: Buchtien n. 455 (as *C. ovata*). — C: Aspiund n. 7554 (as *C. ovata*). — D: von Sneidern n. 1781, (as *C. Jamesonii*). — E: Mosén n. 395. — F: von Türckheim n. 3030. — G: Ekman n. 11702 (as *C. ocoana*). — 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

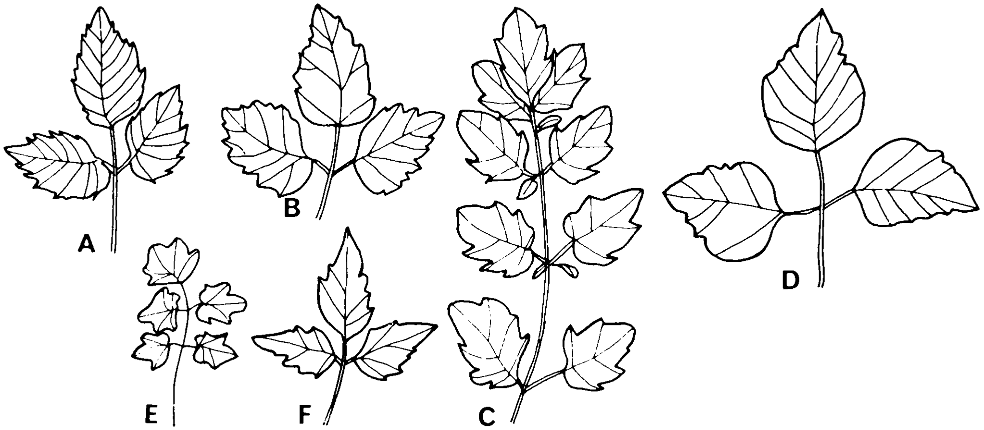

Fig. 2. Leaves of African specimens of *Cardamine africana*. — A: Hafström n. 511. — B: O. Hedberg n. 1531. — C: Fries & Fries n. 1179 (as *C. Johnstonii*). — D: Ekblom n. 106. — E: E. Schelpe n. 2718 (as *C. Johnstonii*). — F: Y. Sjöstedt (as *C. Holtziana*). — All ×0.5.

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).

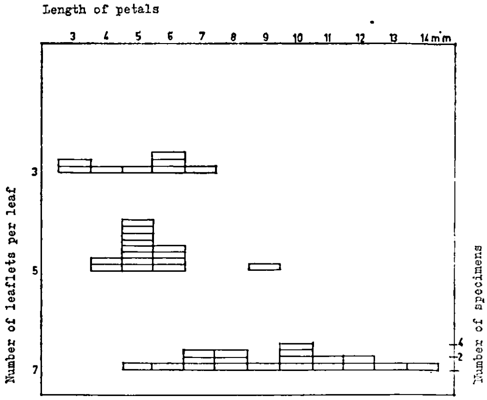

Fig. 3. Length of petals of specimens of *Cardamine africana* with varying number of leaflets on lowest stem-leaf).

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

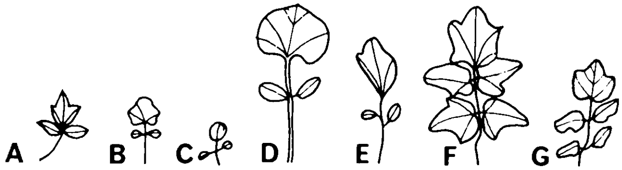

Fig. 4. Leaves of *Cardamine bonariensis.* — A: SKOTTSBERG n. 251 (as *C. flaccida*). — B: FAGERLIND n. 2040. — C: HAMMARLUND n. 156 (as *C. flaccida*). — D: SPARRE n. 348 (as *C. flaccida*). — E: FAGERLIND n. 972. — F: SKOTTSBERG n. 435 (as *C. flaccida*). — G: SPARRE n. 2260 (as *C. flaccida*). — All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

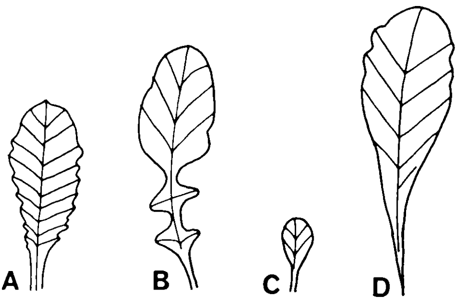

Fig. 6. Leaves of *Cardamine chenopodiifolia*. — A: Lindman n. 339. — B: Specimen cultivated in the garden "Bergianska Trädgården" in Stockholm. — C: Herter n. 62. — D: Pedersen n. 790. — All ×0.5.

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.

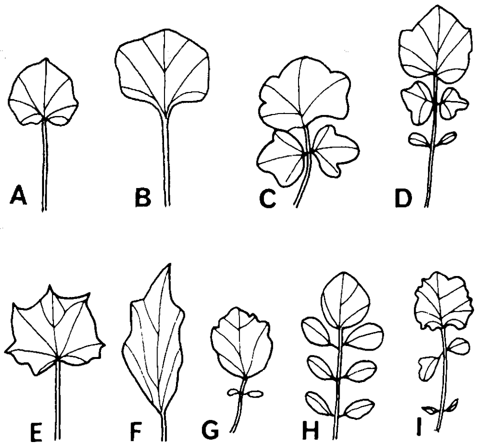

Fig. 7. Leaves of *Cardamine glacialis*. — A: C. and I. SKOTTSBERG (as *C. tuberosa* DC.). — B: WERDEMANN n. 1313 (as *C. cordata* BARN.). — C: C. GRANDJOT (as *C. tuberosa* DC.). — D: VALENTIN n. 187. — E: SPARRE n. 4887 (as *C. cordata* BARN.). — F: BUCHTIEN n. 170 (as *C. variabilis* PH.). — H: SPARRE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

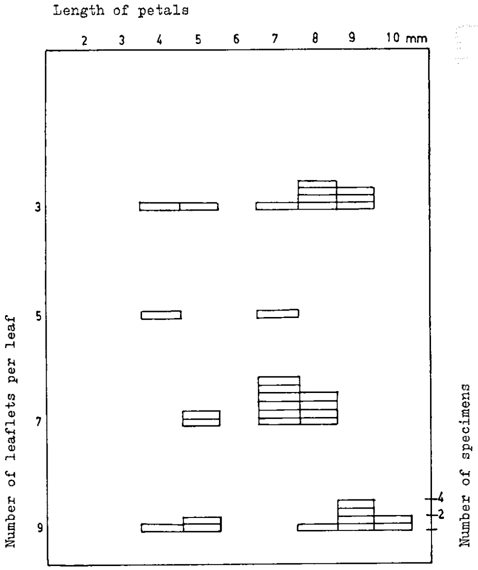

Fig. 8. Length of petals of specimens of *Cardamine glacialis* with varying number of leaflets on lowest stem-leaf.

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).

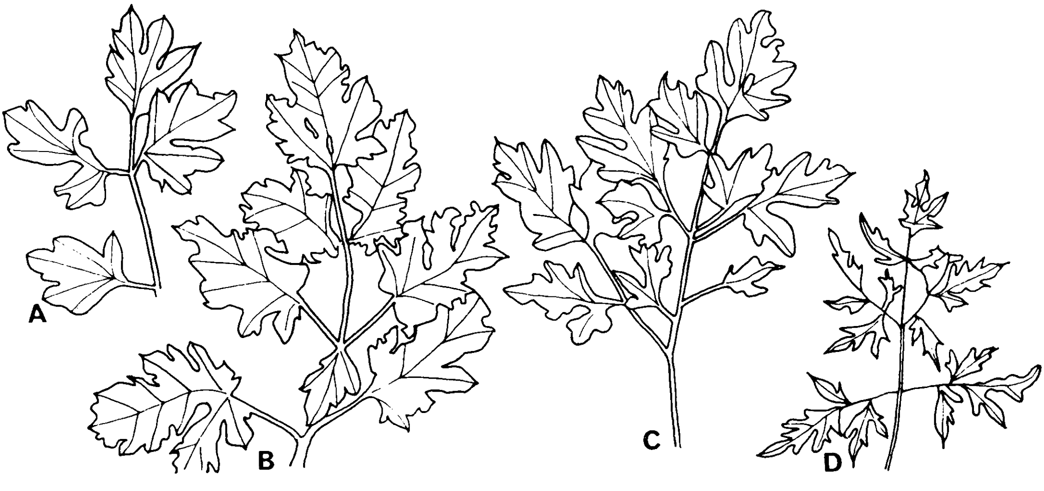

Fig. 9. Leaves of *Cardamine geraniifolia*. — A: Lechler n. 1162. — B: Dusén n. 107. — C: Andersson n. 318. — D: Skottsberg n. 194. — All ×0.5.

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

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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.

Bengt Jonsell, Institute of systematic botany, University of Uppsala, Box 541, S-751 21 Uppsala, Sweden.

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 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

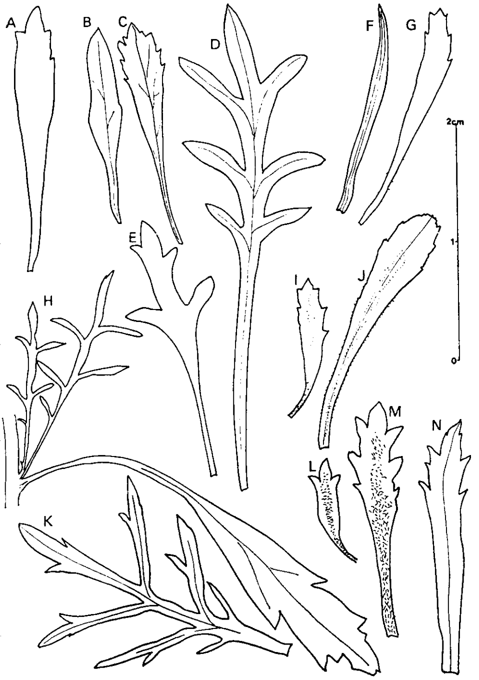

Fig. 1. Drawings of leaves. — A: *L. armoracia,* Ethiopia, DE WILDE 7026 (WAG), middle cauline leaf. — B—E: *L. africanum* subsp. *africanum,* all from Ethiopia. — B: TERRACIANO & PAPPI 971 (FI), upper primary cauline leaf. — C: TERRACIANO & PAPPI 997 (FI), middle secondary, cauline leaf. — D: TERRACIANO & 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.

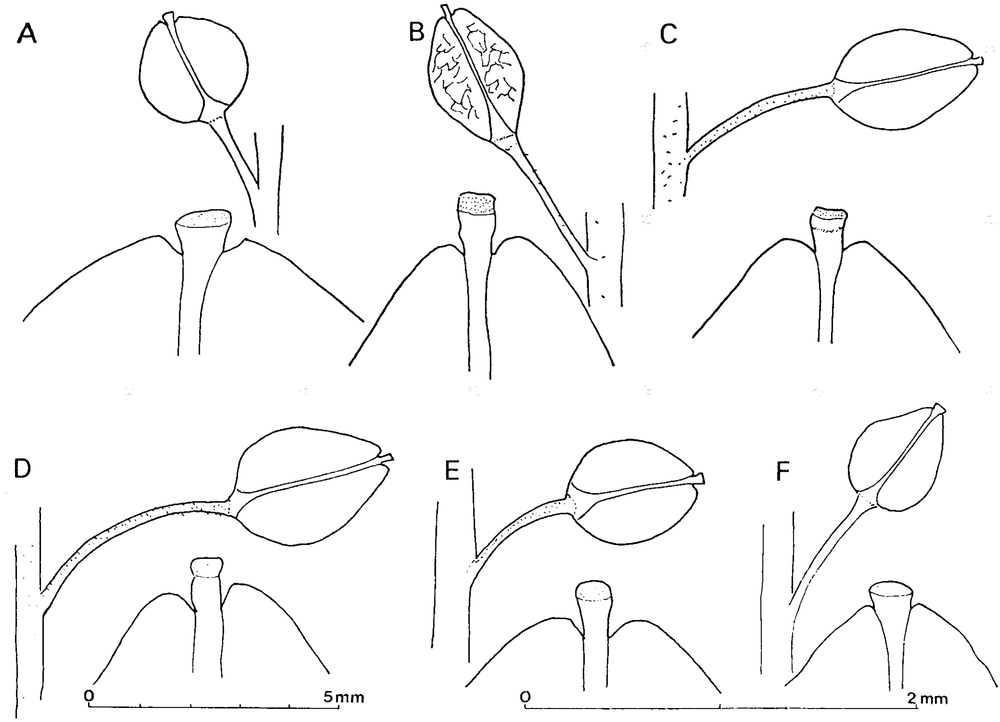

Fig. 2. Drawings of siliculae with pedicels, and apices of siliculae of the *L. armoracia*-group. — A—E: *L. armoracia*. — A: SCHIMPER II: 741 (P), type of "subsp. *abyssinicum*". — B: Tanzania, NEWBOULD 6300 (EA). — C: Ethiopia, DE WILDE 7026 (WAG). — D: QUARTIN-DILLON & PETIT s.n. (P), type of "subsp. *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

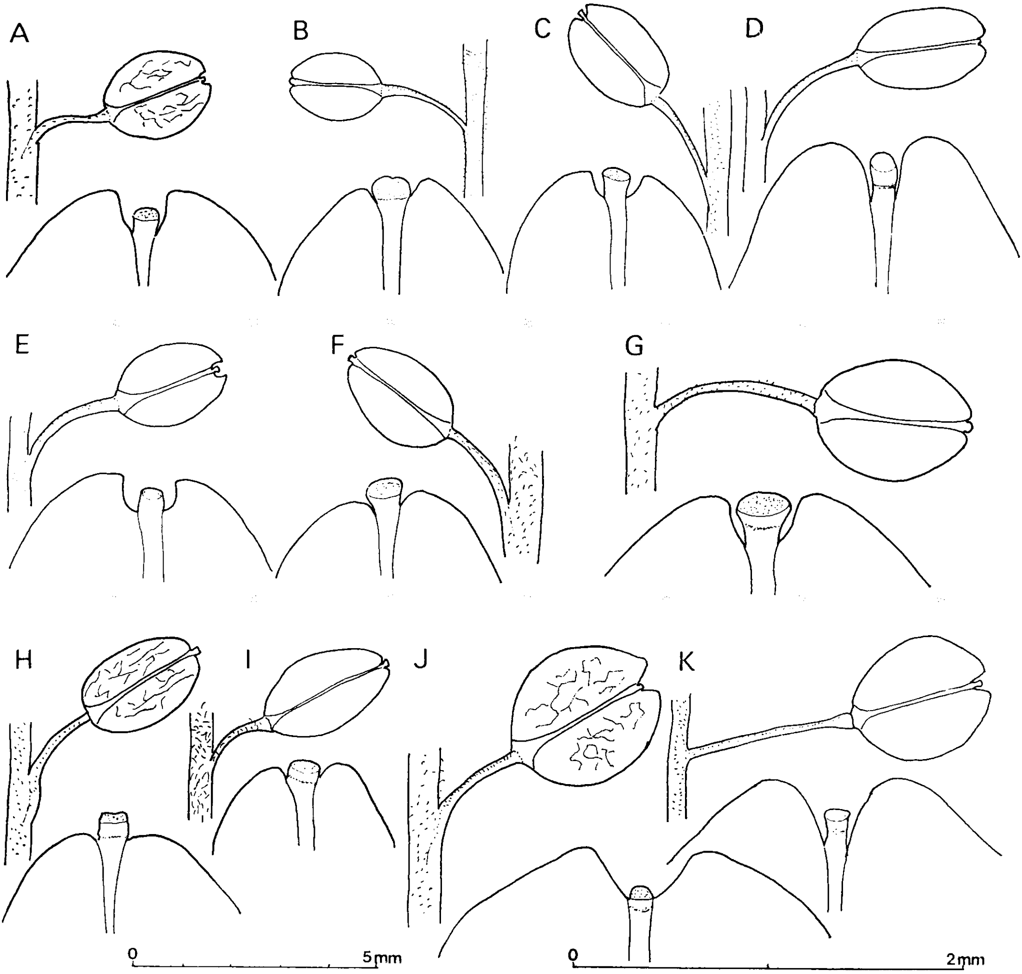

Fig. 3. Drawings of siliculae with pedicels, and apices of siliculae of the *L. africanum*-group and of the introduced species. — A—D: *L. africanum* subsp. *africanum*. — A: Ethiopia, DE WILDE 4550 (WAG). — B: Kenya, FRIES & FRIES 875 (UPS). — C: Uganda, LYE 6917 (EA). — D: Rhodesia, DRUMMOND 4933 (BR). — 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).

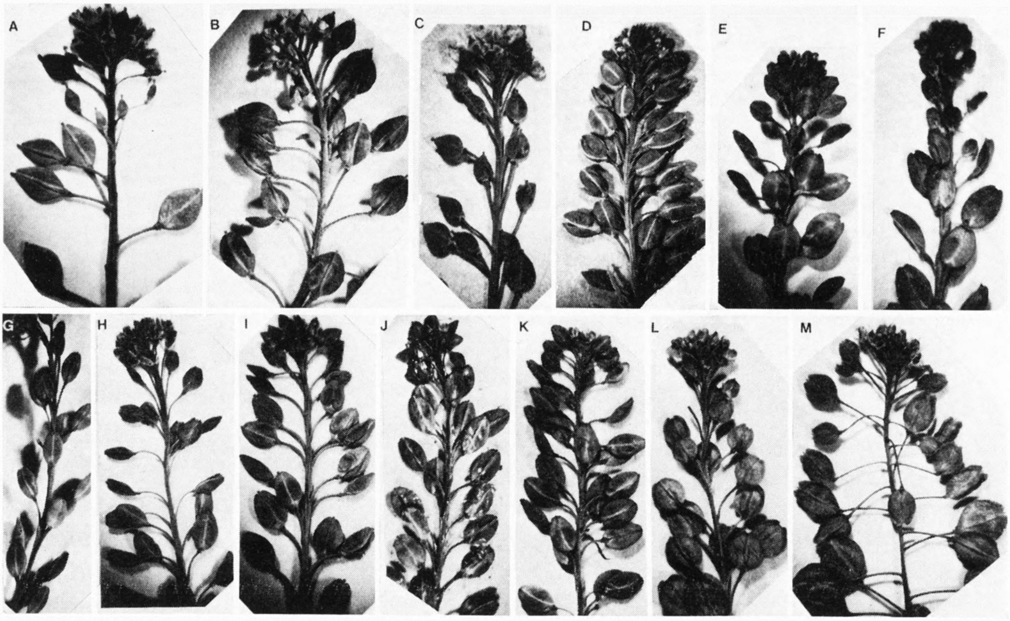

Fig. 4. Racemes with ripe fruits. — A—B: *L. armoracia.* — A: Tanzania, Newbould 6300 (EA). — B: Ethiopia, De Wilde 7026 (WAG). — C: *L. graminifolium,* O.S. 12.VII.1854 (UPS). — D—E: *L. africanum* subsp. *africanum.* — D: Kenya, Fries & Fries 875 (S). — E: Ethiopia, De Wilde 4550 (WAG). — F: *L. africanum* 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-

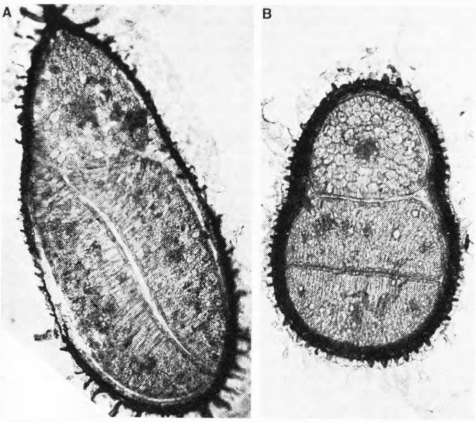

Fig. 5. Cross-sections of seeds. — A: Obliquely accumbent cotyledons, *L. virginicum,* MARQUES 2195 (LISC). — B: Incumbent cotyledons, *L. africanum,* LYE 6197 (EA). — Both ca. ×50.

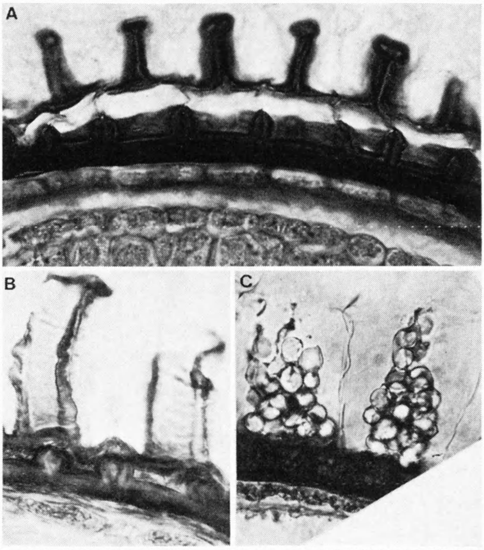

Fig. 6. Cross-sections of testa showing columns of the epidermis. — A: *L. suluense,* MENDONÇA 2797 (BR), ca. ×385. — B: *L. bonariense,* Tanzania, SHABANI 810 (EA), ca. ×385. — C: *L. virginicum,* Switzerland, SAMUELSSON 25.VI.1921 (UPS), ca. ×250.

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

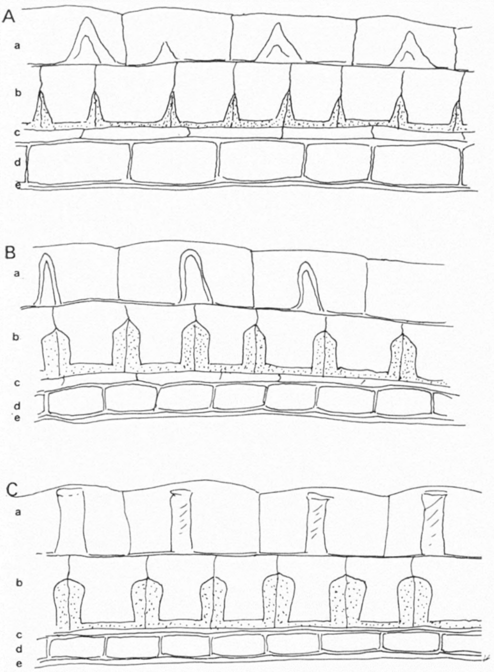

Fig. 7. Schematic drawings of testa in cross-section (a=epidermis; b=palisade layer; c=inner parenchyma; d=aleurone layer; e=hyaline layer; terminology according to Vaughan & Whitehouse 1971, cf. text). — A: Palisade layer, Type I. — B: Ditto, Type II. — C: Ditto, Type III. — See further in text. — Ca.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

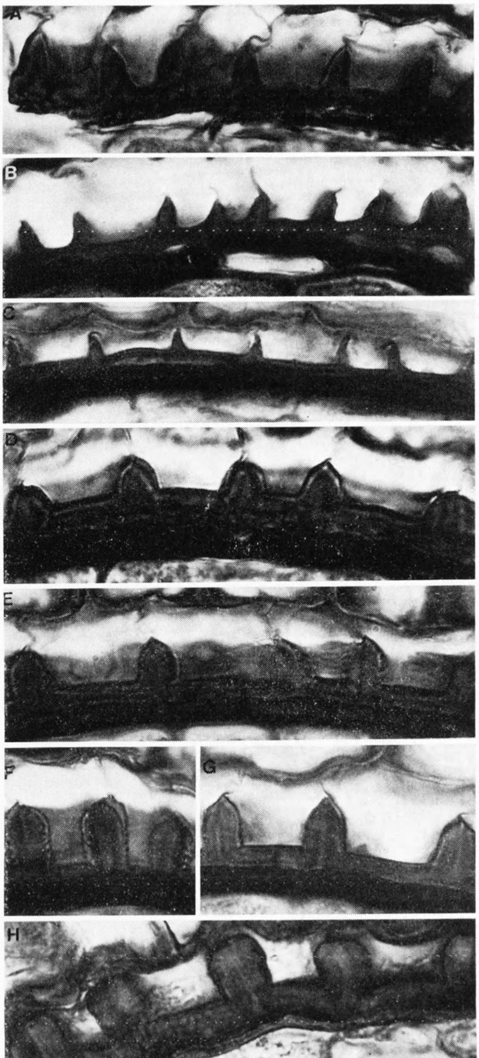

Fig. 8. Cross-sections of testa, palisade layer. — A—C: Type I. — A: *L. armoracia,* Tanzania, Newbould 6300 (EA). — B: *L. armoracia,* Ethiopia, Solleggio 19 (FI). — C: *L. inyangense,* Robinson 1969 (K). — D—G: Type II. — D: *L. africanum,* Uganda, Purseglove 3620 (EA). — E, F: *L. suluense,* Mendonça 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

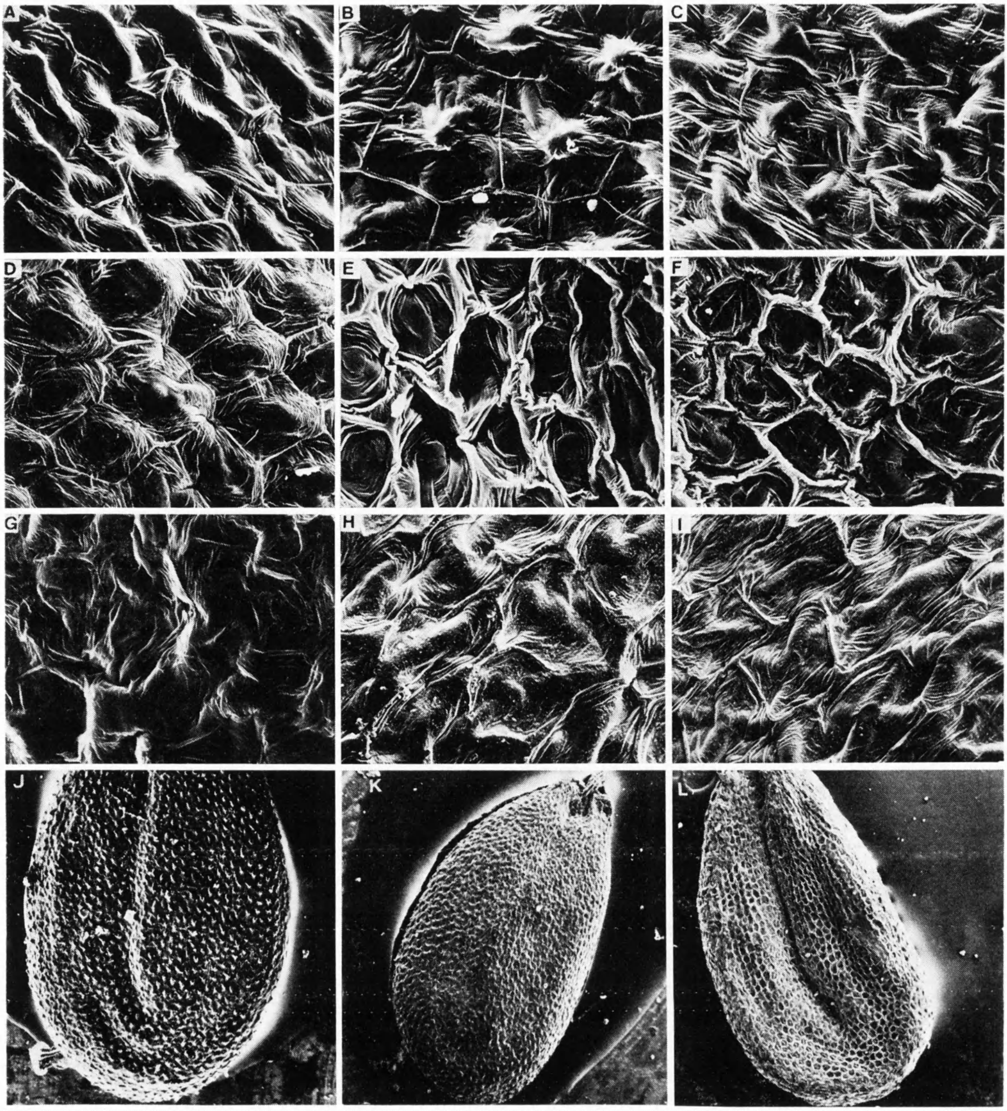

Fig. 9. Scanning electron photomicrographs of testa surface. — A—B: *L. armoracia.* — A: Tanzania, Greenway 9919 (K). — B: Ethiopia, Fiori 1033 (FI). — C—D: *L. africanum.* — C: Kenya, Ryman 173 (UPS). — D: Ethiopia, Pappi 2951 (FI). — E—F: *L. keniense.* — E: Kenya, Verdcourt 3820 (BR). — F: Ethiopia, 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

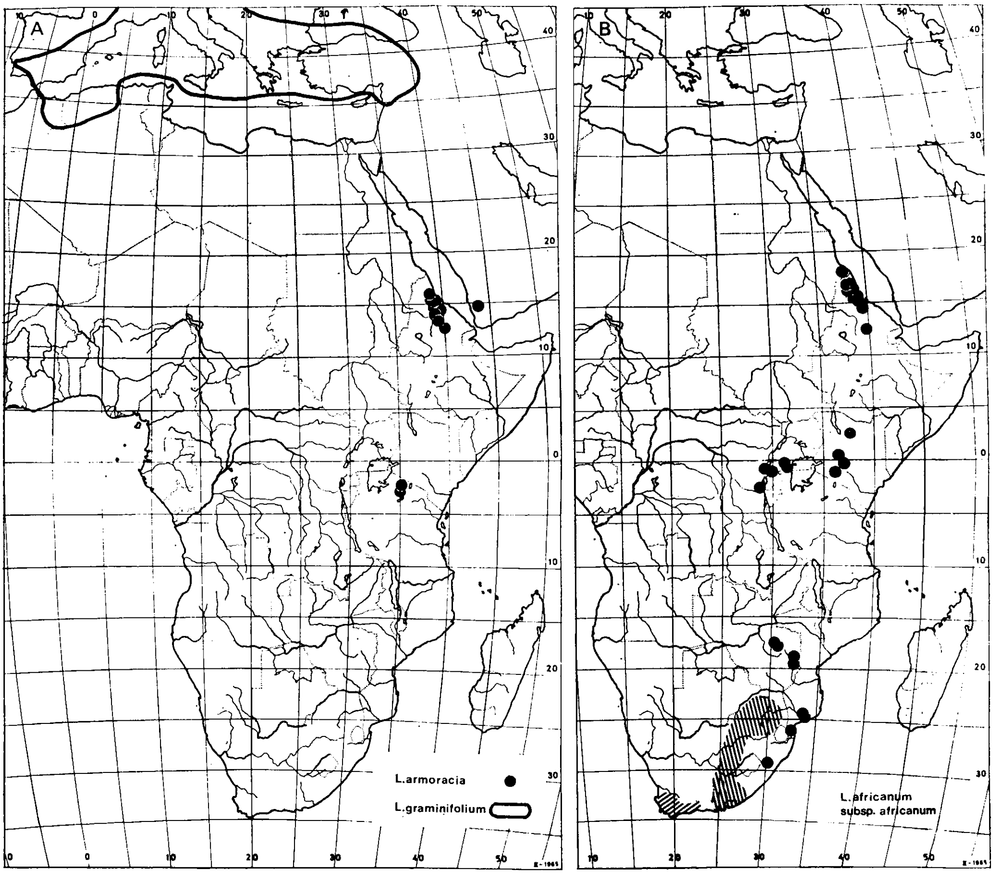

Fig. 10. A: Total distribution of *L. armoracia* and approximate distribution of *L. graminifolium* (arrow points at occurrence in the Crimea). — B: Total distribution of *L. africanum* subsp. *africanum* (within hatched areas approximate). — C: Total distributions of *L. angolense, L. inyangense, L. 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.

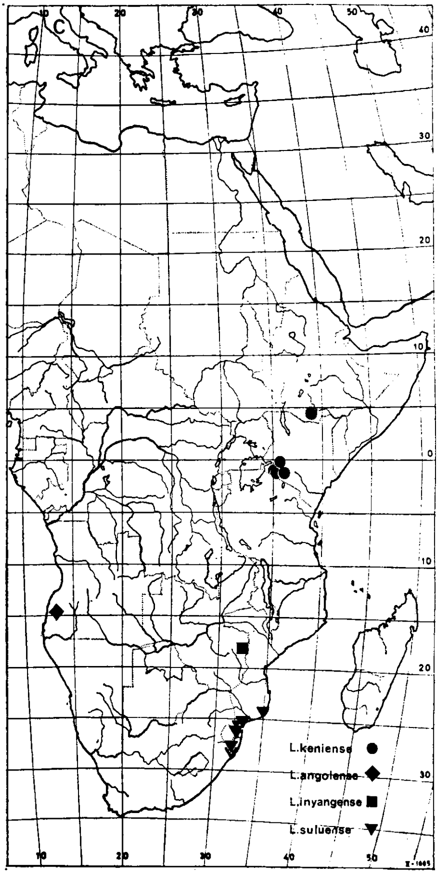

Fig. 10 C.

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 abovementioned 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 differences 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

Oredsson, A. 1975 07 08. Factors possibly influencing the range of shrubby Rubus species in Sweden. I. Severity of winter. — Bot. Notiser 128: 47—54. Lund. ISSN 0006-8195.

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.

Alf Oredsson, Department of Plant Taxonomy, University of Lund,
Ö. Vallgatan 18—20, S-223 61 Lund, Sweden.

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 ⁰/₀ (average 13 ⁰/₀).

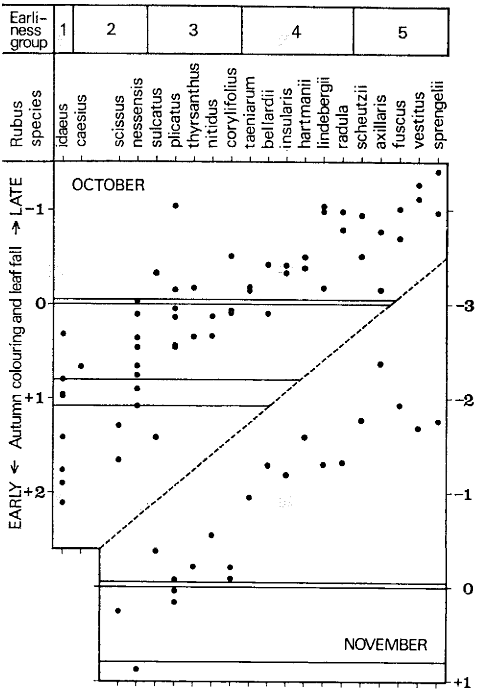

Fig. 1. Relative earliness with respect to autumn colouring and leaf fall (dots). Fixed values for the relative positions of the four (for November, three) standard species (lines).

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.

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

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

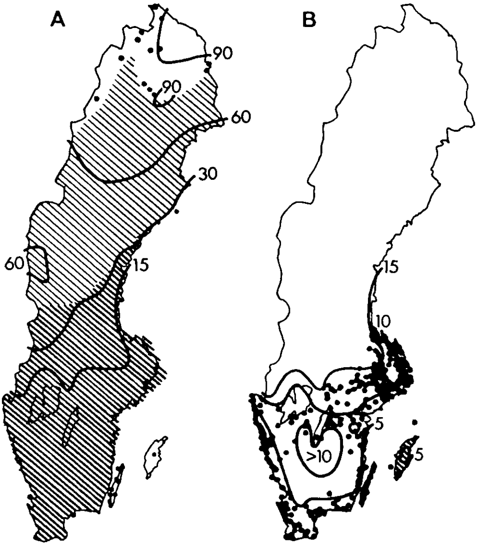

Fig. 2. Distribution of A: wild raspberry and B: dewberry in Sweden. Very common—common occurrence (thick lines), fairly common—less common (fine lines), isolated finds (dots). After HULTÉN (1971). — Length of extreme winter (p. 51) indicated by isochrones for 5—90 days. After ÅNGSTRÖM (1953).

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.

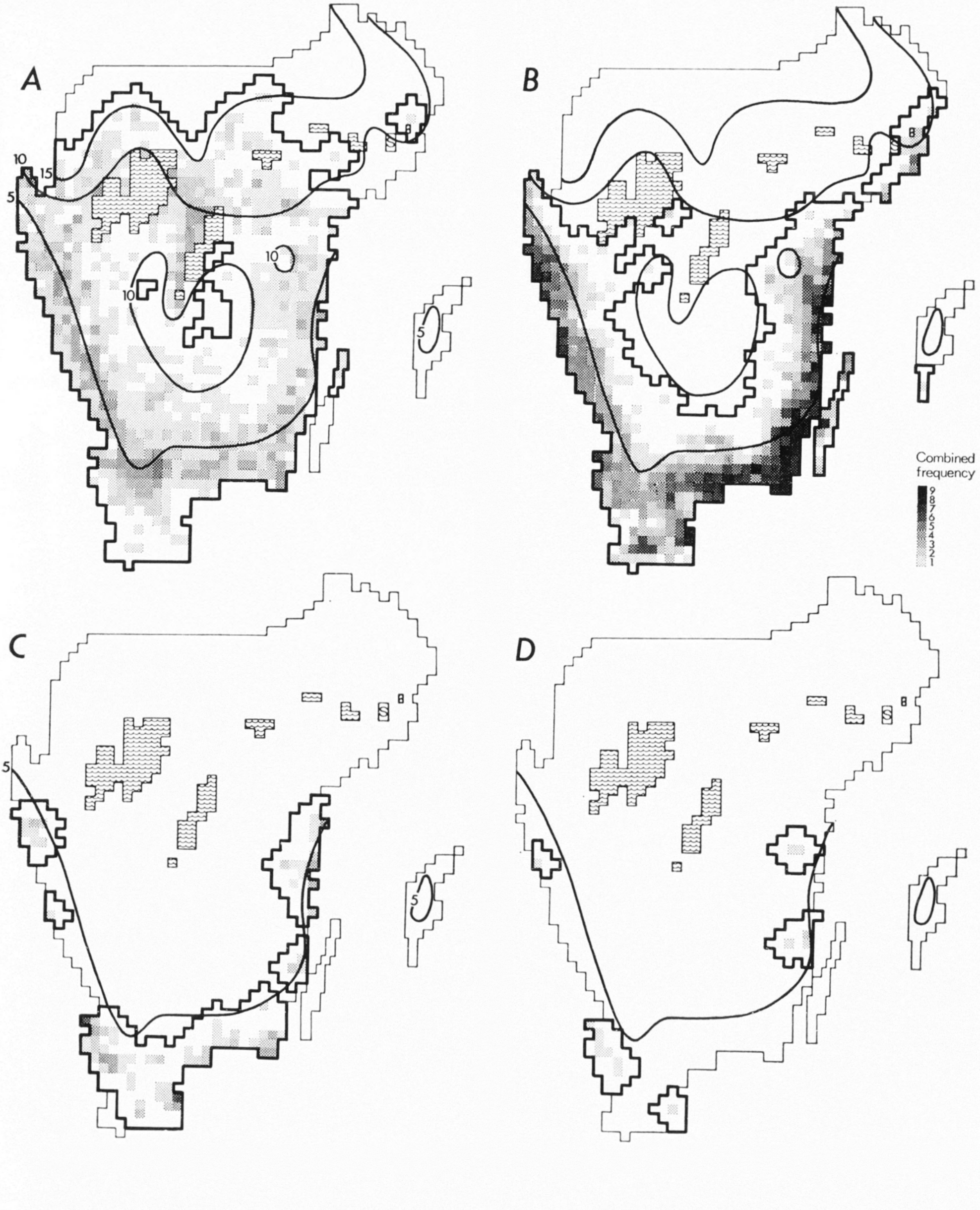

Fig. 3. Distribution of blackberry species in Sweden. Separate maps for earliness groups (see Fig. 1). — A: Group 2 (*caesius* excluded), two species. — B: Group 3, five species. — C: Group 4, six species. — D: Group 5, five species. Range (thick zigzag line) and Combined frequency (scale inset), the 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

OLSSON, U. 1975 07 08. A morphological analysis of phenotypes in populations of Quercus (Fagaceae) in Sweden. — Bot. Notiser 128: 55—68. Lund. ISSN 0006-8195.

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.

Ulf Olsson, Department of Plant Taxonomy, University of Lund, Ö. Vallgatan 18—20, S-223 61 Lund, Sweden.

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

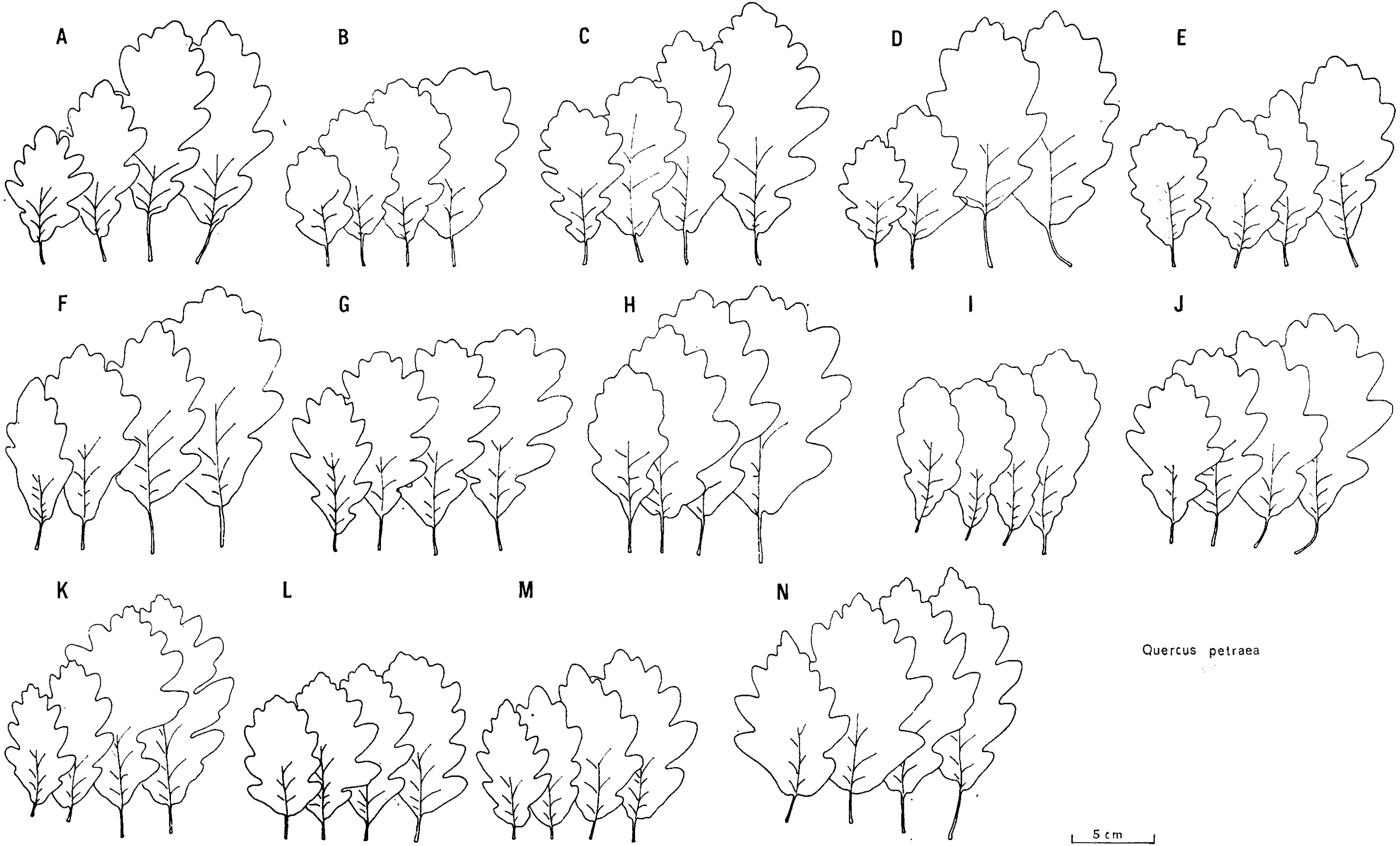

Fig. 1. *Q. petraea*. Variation in leaf shape and size within a population of sessile oak. Of each tree (A—N) four leaves of different size are taken from S—SW exposed twigs.

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.

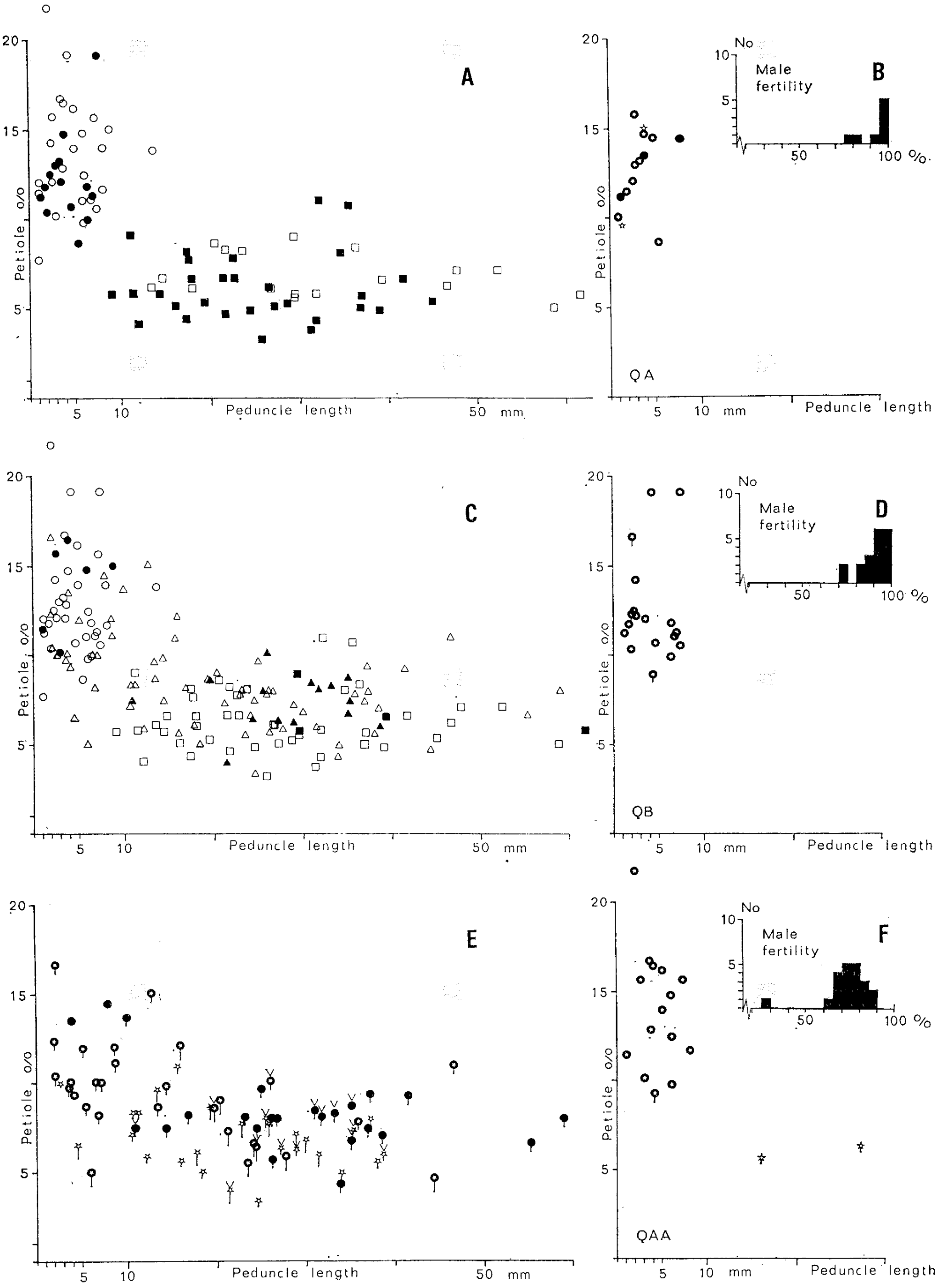
A
B
C
D
E
F
Petiole o/o
Peduncle length
5
10
50 mm
20
15
5
QA
QB
QAA
No
10
5
Male fertility
50
100 %

Fig. 3 A—F.

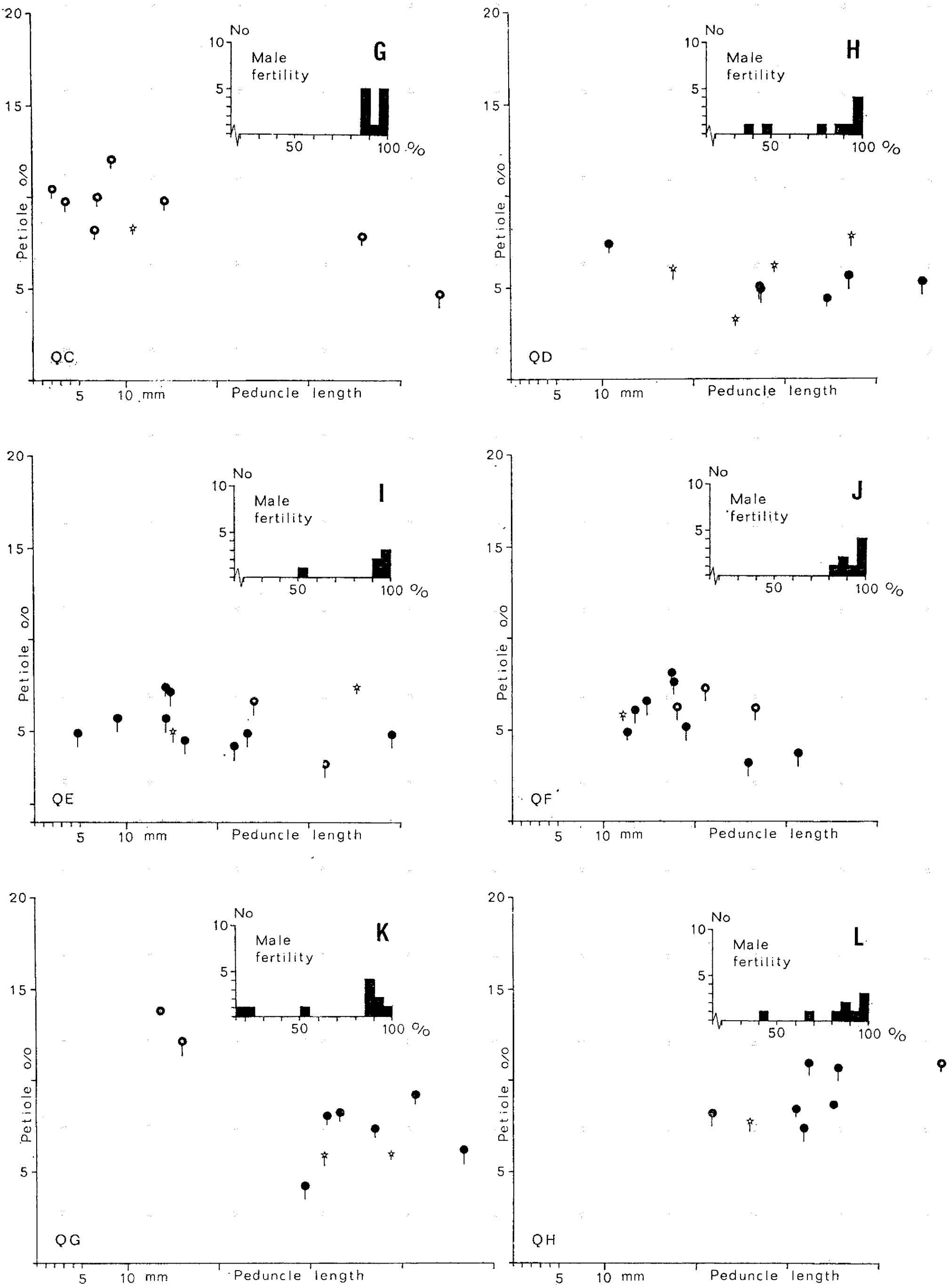
G
No
10
5
Male fertility
50
100 %
20
15
5
Petiole o/o
QC
5
10 mm
Peduncle length
H
No
10
5
Male fertility
50
100 %
20
15
5
Petiole o/o
QD
5
10 mm
Peduncle length
I
No
10
5
Male fertility
50
100 %
20
15
5
Petiole o/o
QE
5
10 mm
Peduncle length
J
No
10
5
Male fertility
50
100 %
20
15
5
Petiole o/o
QF
5
10 mm
Peduncle length
K
No
10
5
Male fertility
50
100 %
20
15
5
Petiole o/o
QG
5
10 mm
Peduncle length
L
No
10
5
Male fertility
50
100 %
20
15
5
Petiole o/o
QH
5
10 mm
Peduncle length

Fig. 3 G—L.

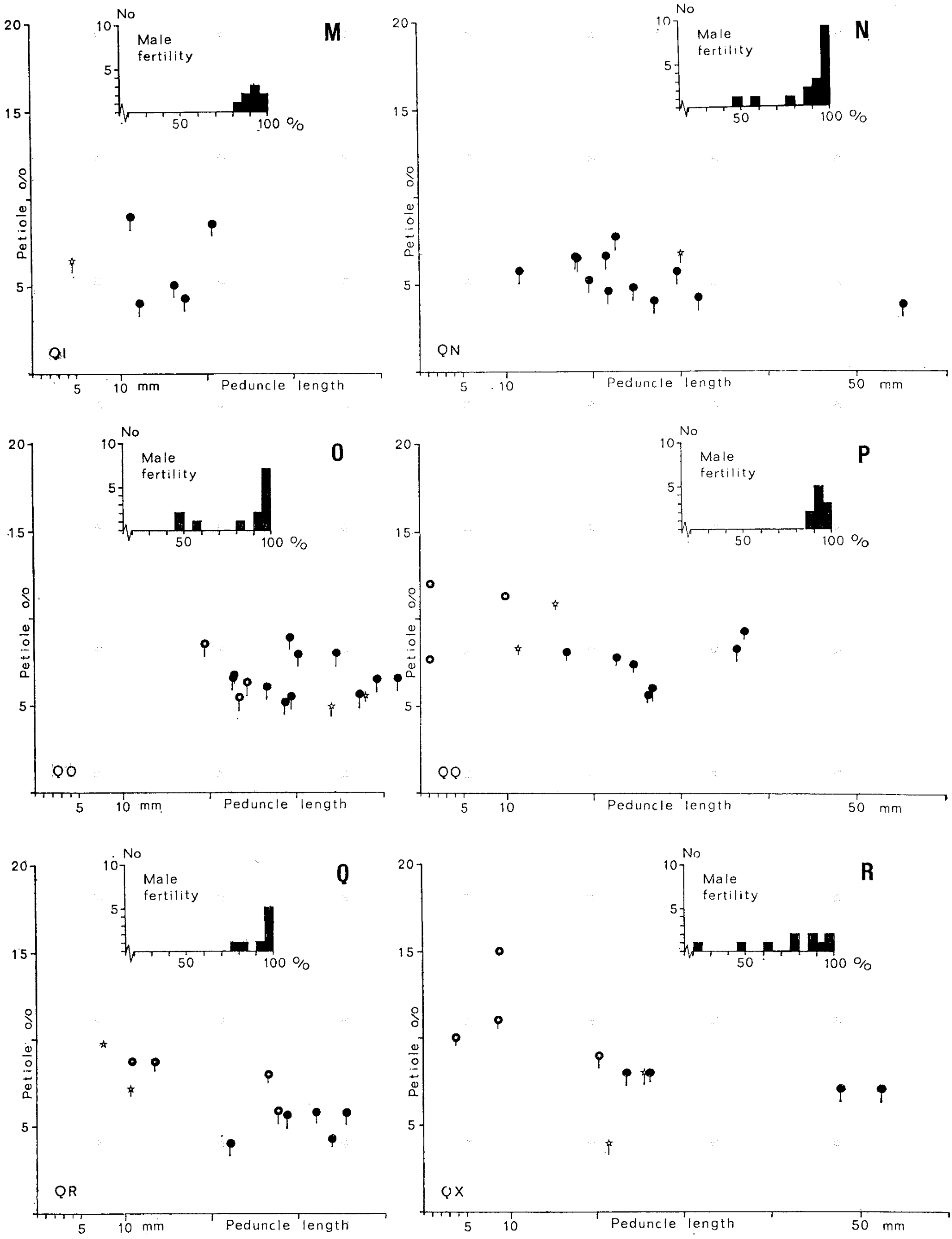
M
N
O
P
Q
R
No
10
5
Male fertility
50
100 %
20
15
5
Petiole %
Peduncle length
5
10
50
mm
QI
QN
QO
QQ
QR
QX

Fig. 3 M—R.

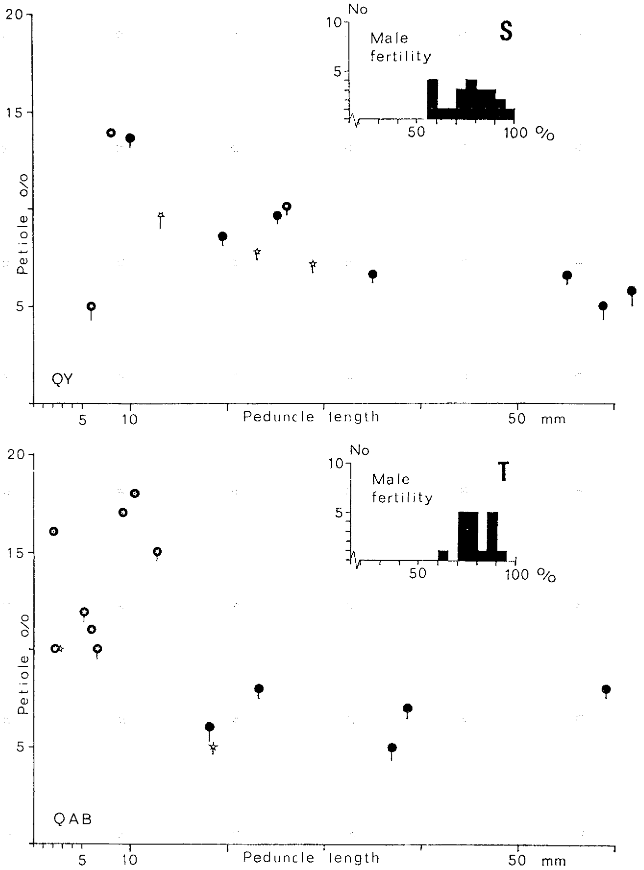

Fig. 3. Combined petiole % and peduncle length. — A: Scatter diagram for all individuals classified as theoretical species types (phenotypes *petraea (a)* and *robur (i)* respectively). Circles: individual values for "petraea"-oaks; squares: individual values for "robur"-oaks. Solid symbols represent 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

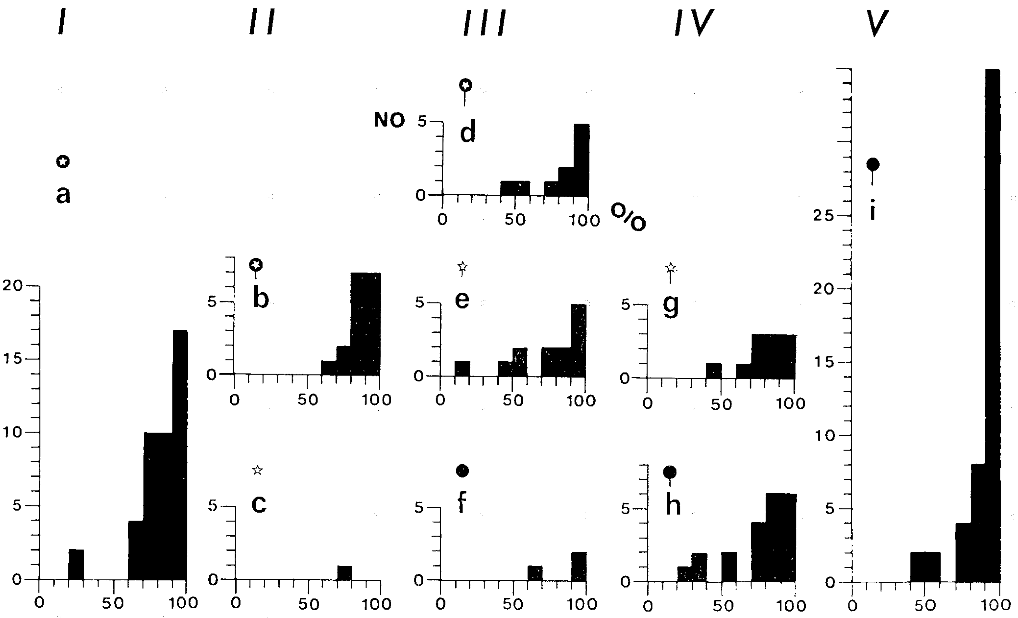

Fig. 4. Histograms showing the frequency distribution of nine phenotypes of oak in different classes of pollen stainability. The phenotypes are designated by symbols and arranged in five groups (I—V) according to Table 2.

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)	ⁱ
	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 localities 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 V. 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.

Gertrud Cronberg, Limnological Institute, S-220 03 Lund, Sweden.

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.

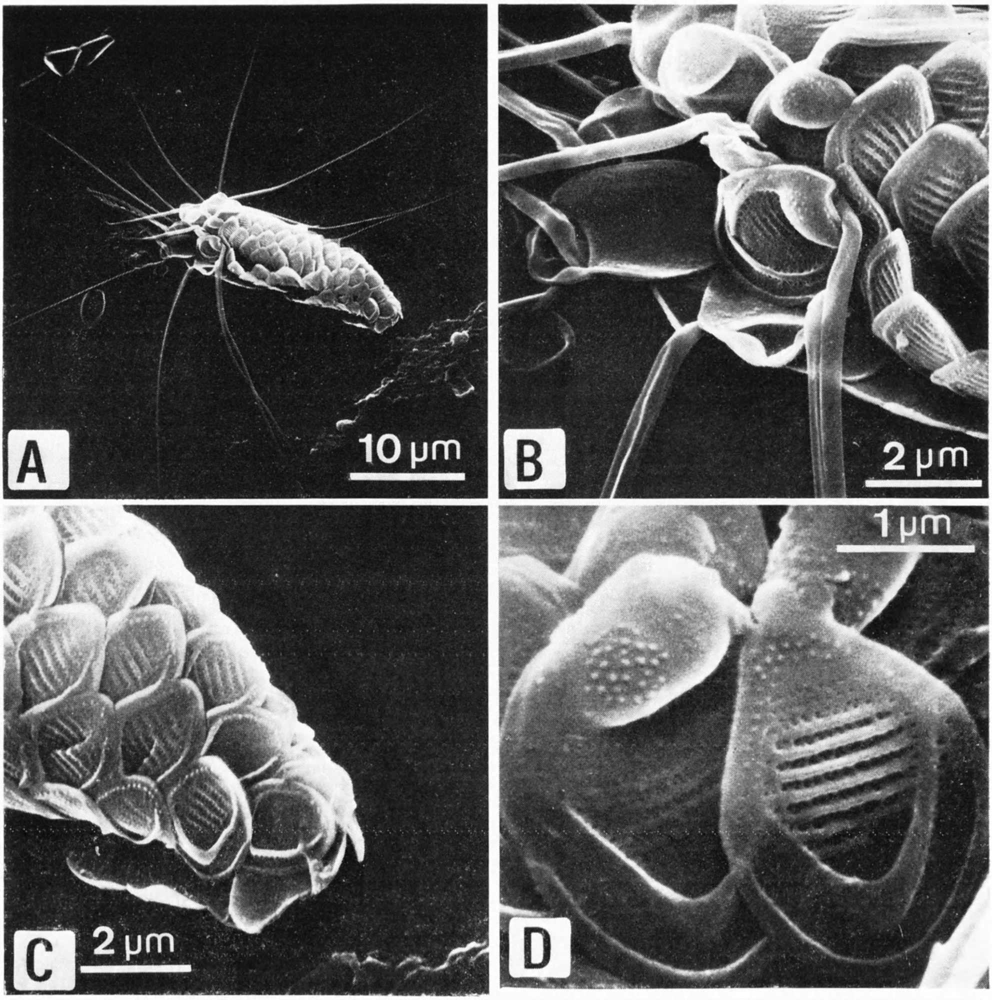

Fig. 1. *Mallomonas trummensis.*— A: A complete cell showing the apical part with short serrate bristles and long thin bristles to the left of the cell seen under the scanning electron microscope (SEM). — B: Anterior part of cell showing scales with dome and bristles loosely fastened to dome (SEM). — 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

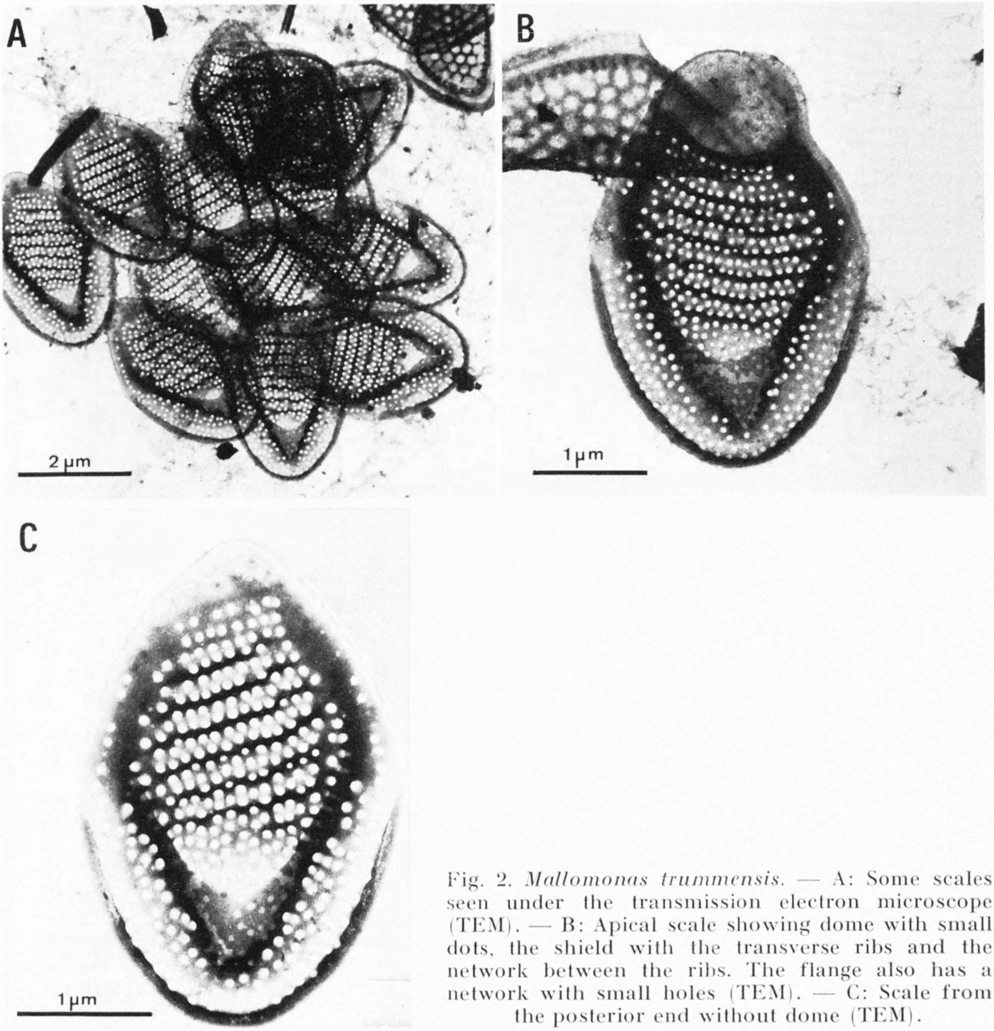

Fig. 2. *Mallomonas trummensis.* — A: Some scales seen under the transmission electron microscope (TEM). — B: Apical scale showing dome with small dots, the shield with the transverse ribs and the network between the ribs. The flange also has a network with small holes (TEM). — C: Scale from the posterior 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.

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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.

Anita Dunbar, Institute of Botany, University of Stockholm, and Swedish Museum of Natural History, S-104 05 Stockholm, Sweden.

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

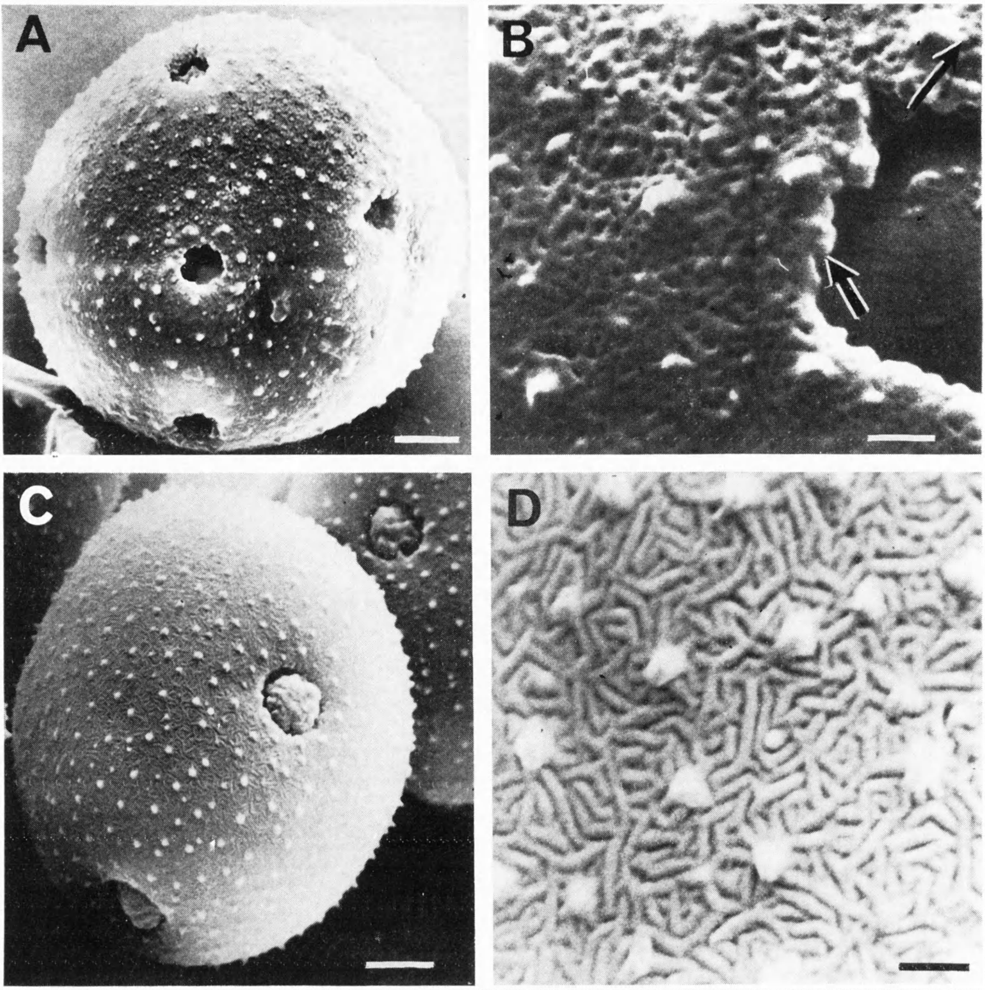
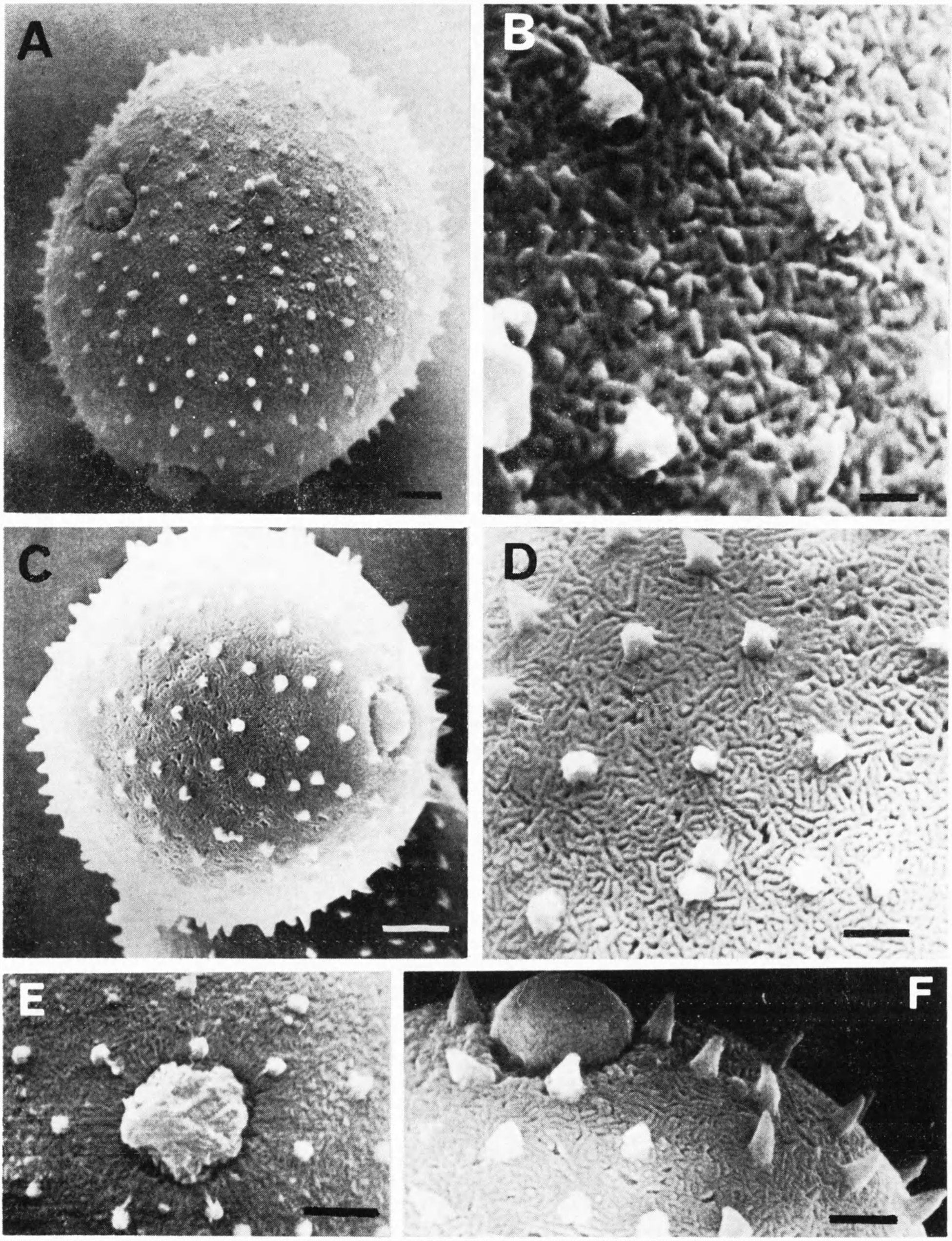


Fig. 1. *Campanula.* — A, B: *C. americana.* — A: Pantoporate pollen grain. Spinules of varying size are distributed over the surface. C. ×1,700. — B: Part of the pollen wall with a pore to the right; the margin is irregular (thick arrow). The surface of the sexine consist of a low relief reticulum with 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

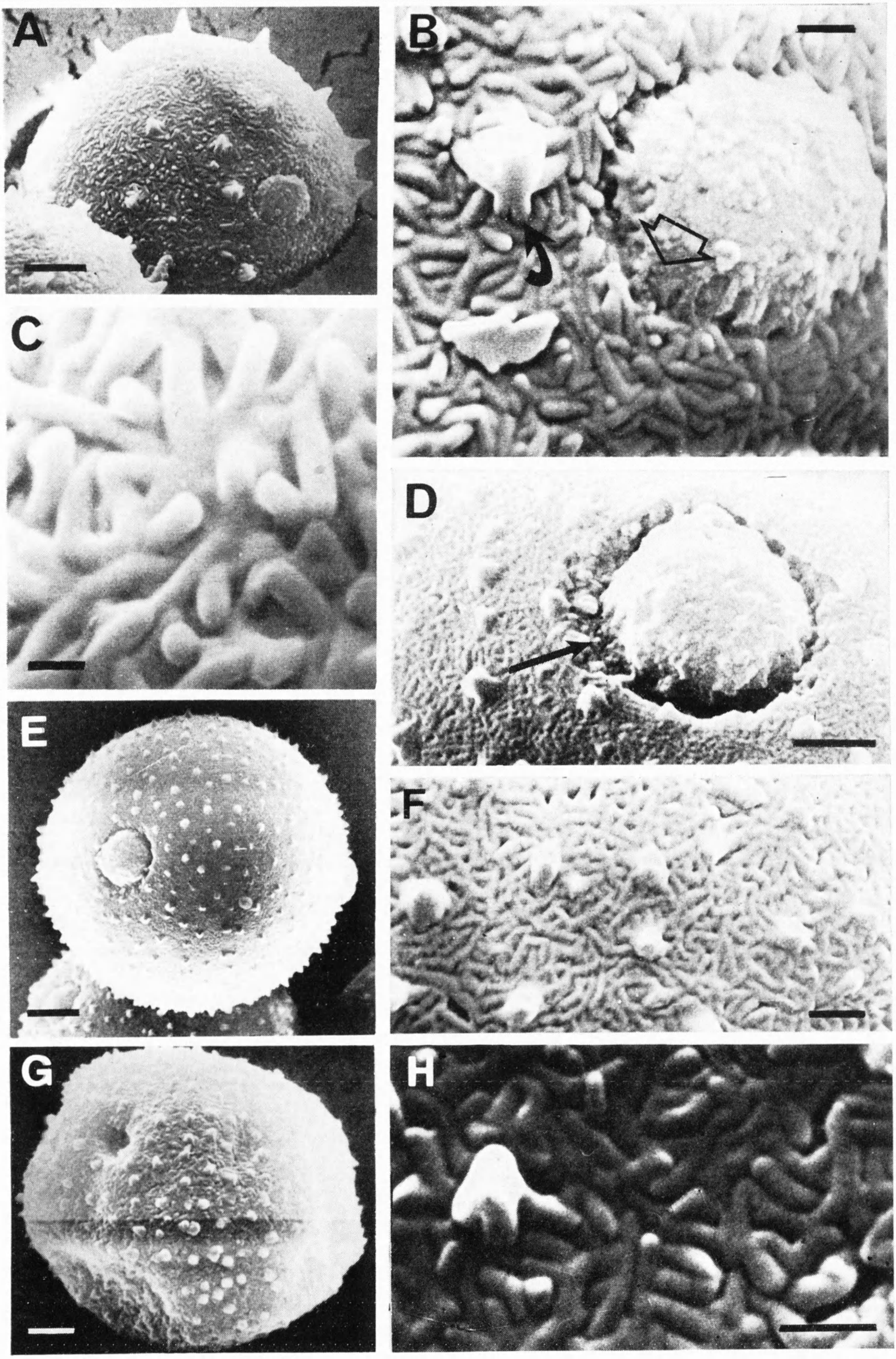
Shape: oblate-spheroidal.

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.


A
B
C
D
E
F
G
H

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.

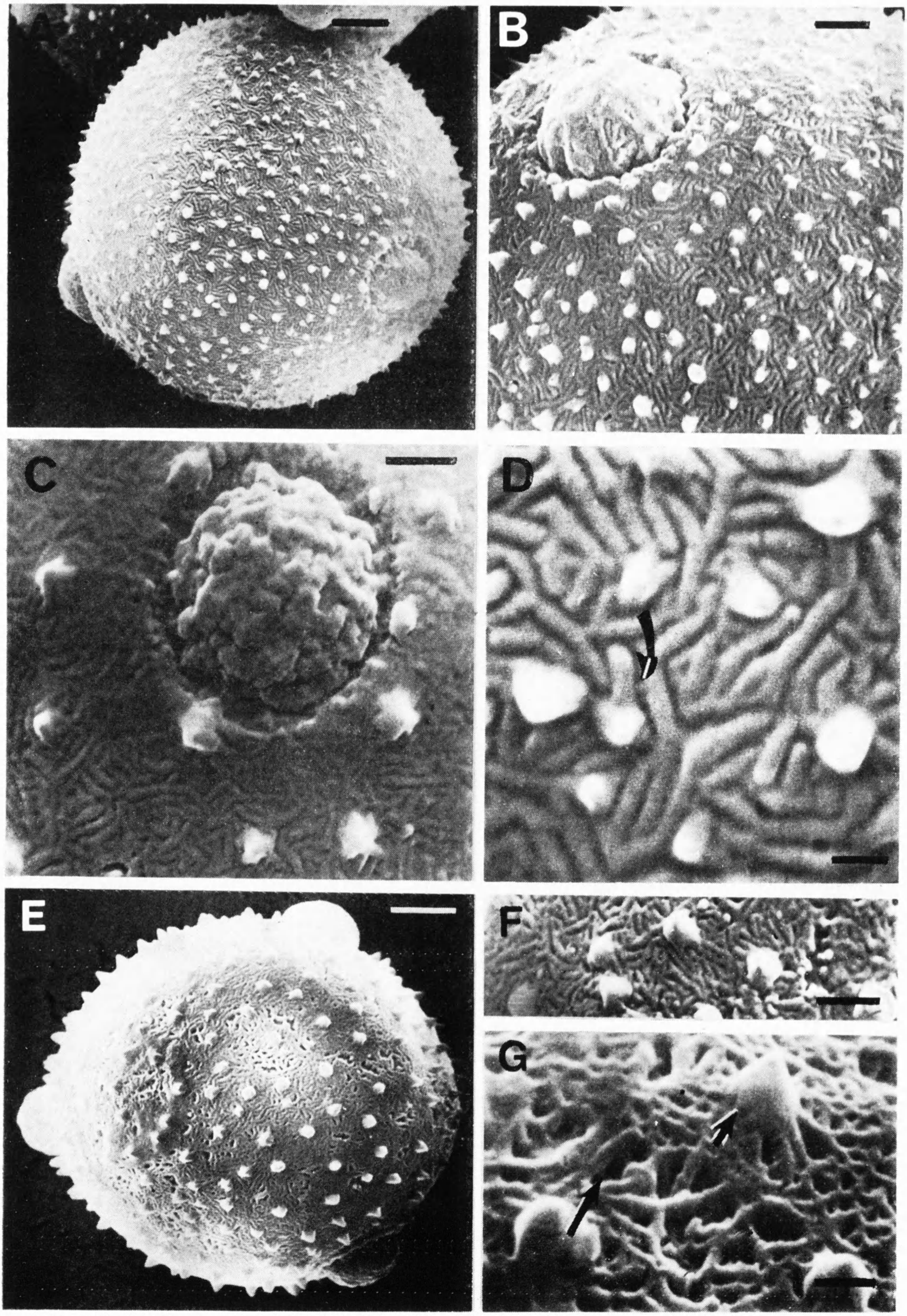
Campanula pyramidalis L. — Fig. 3 A, B, C; DUNBAR (1975 Fig. 6 D)
Shape: oblate-spheroidal.
Size: 34×36 μ.
Apertures: pollen grains 3-porate, pore diam. 4 μ, 5 μ (SEMG), surface of operculum granular (Fig. 3 B).
Exine: 2 μ thick, sexine slightly thicker than nexine, relatively few spinules, mostly 1.8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


A
B
C
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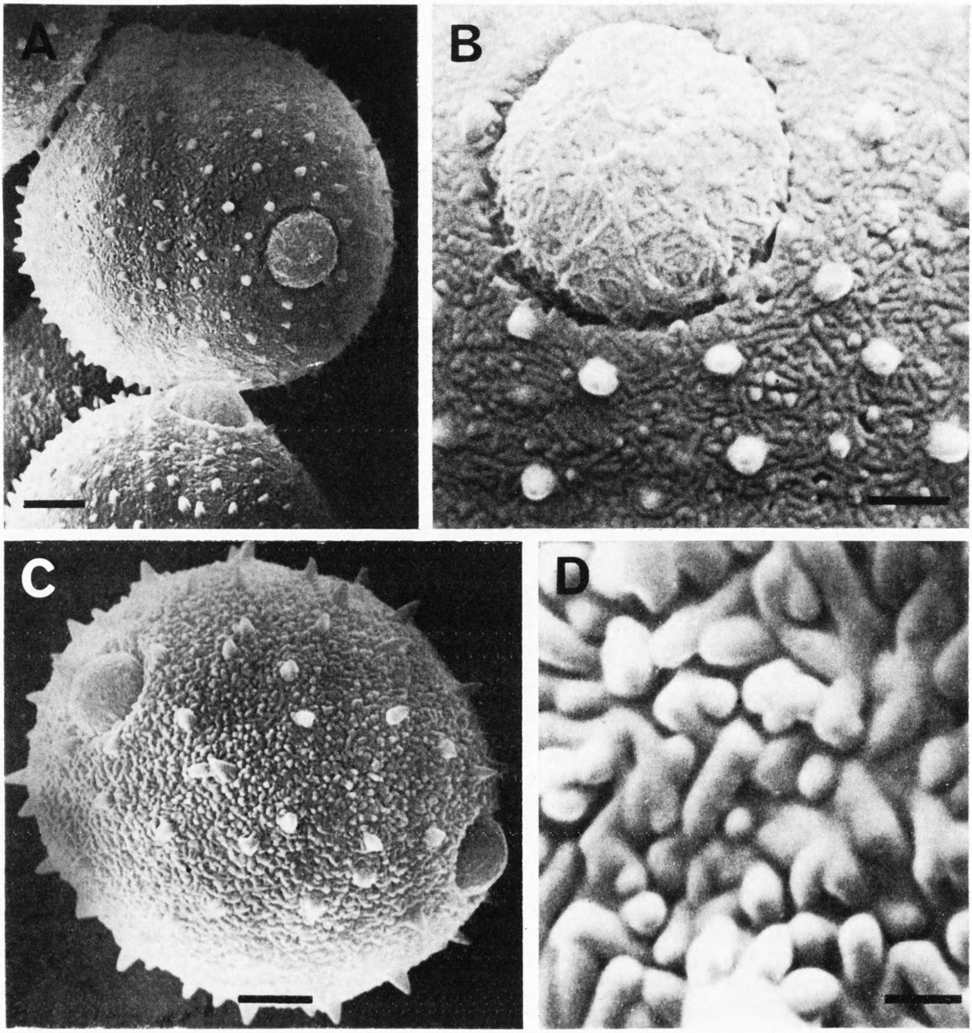


Fig. 5. *Campanula*. — A, B: *C. alliariaefolia*. — A: 3-porate pollen grain showing two pores. Spinules distributed over surface. C. ×1,700. — B: Part of pollen wall with pore and operculum. Surface of operculum shows elongated structures. Sexine between spinules consists of short ridges and protrusions. 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.

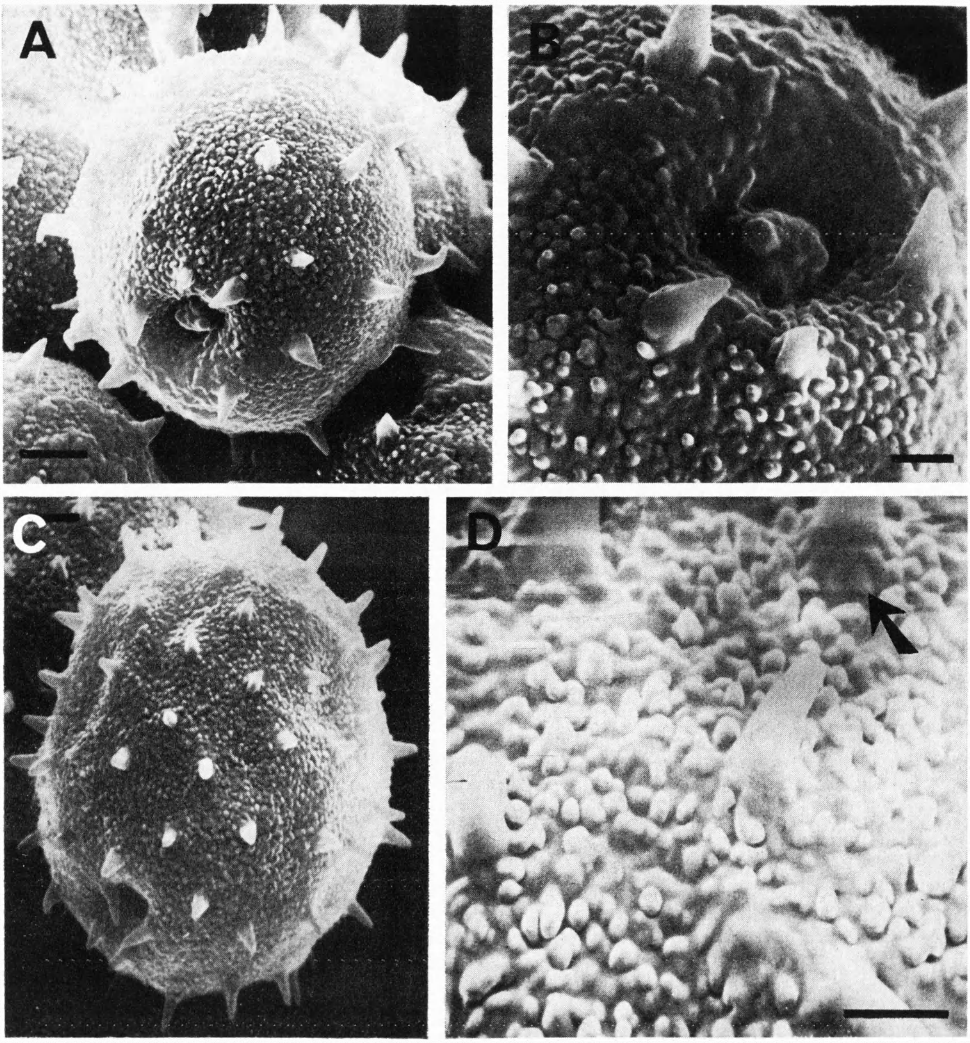


Fig. 6. *Campanula.* — A, B: *C. speciosa.* — A: 3-porate pollen grain showing one pore. Few and large spinules distributed over surface. C. ×1,800. — B: Detail of the pollen wall with a pore; operculum appears to be covered with protrusions. Verrucose-like protrusions on sexine surface. C. ×4,300. Line 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.

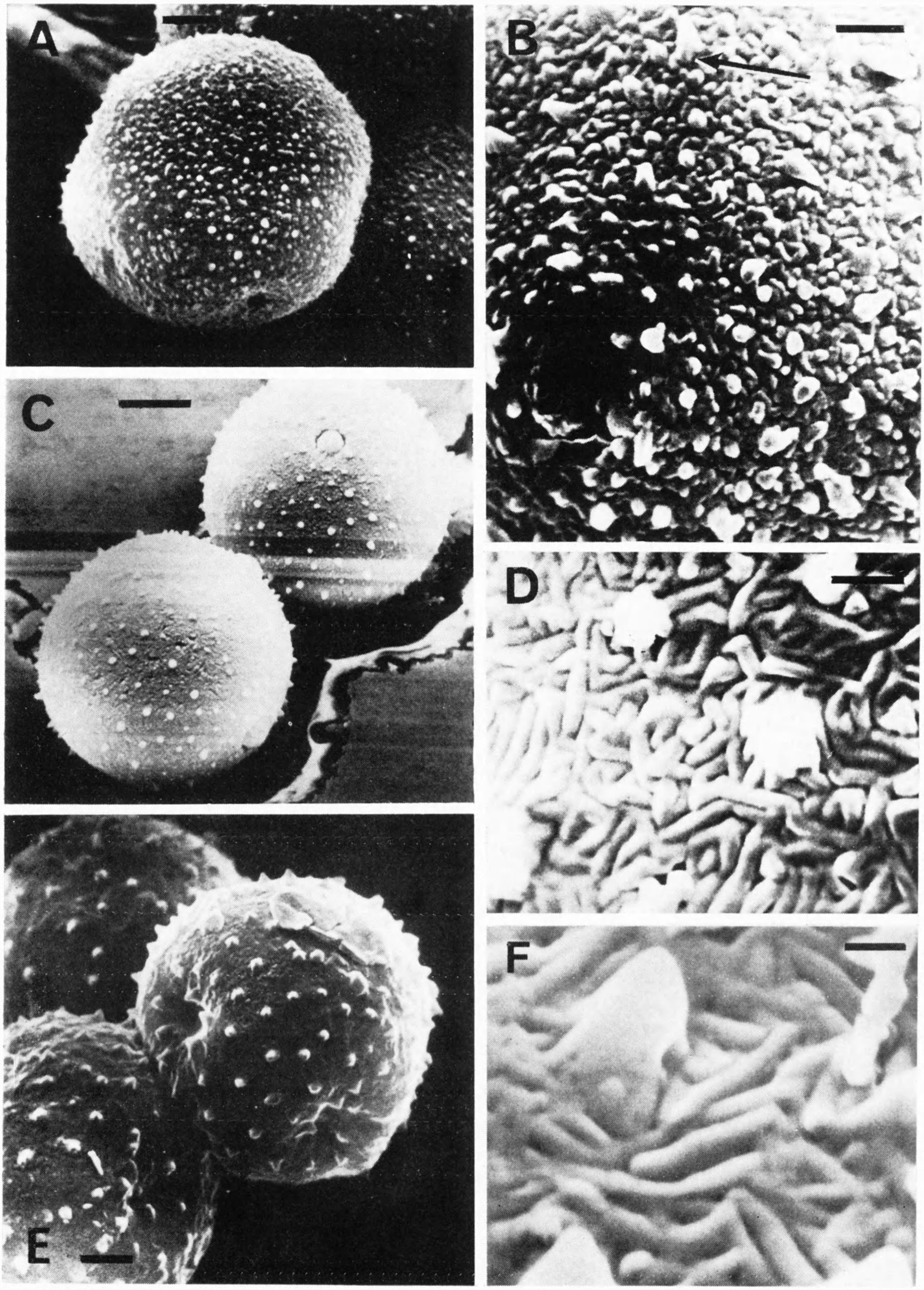


Fig. 7.

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.

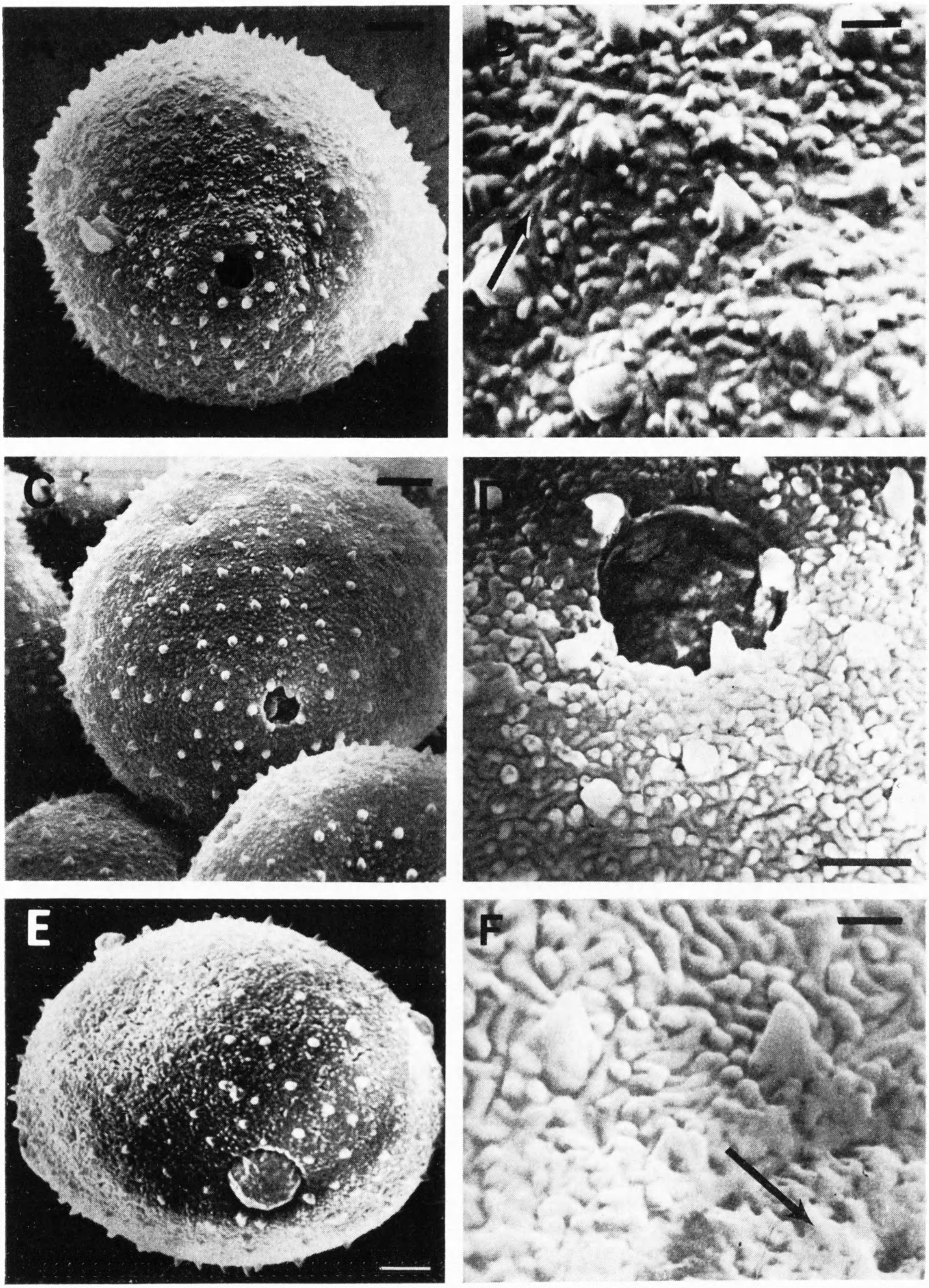


Fig. 8.

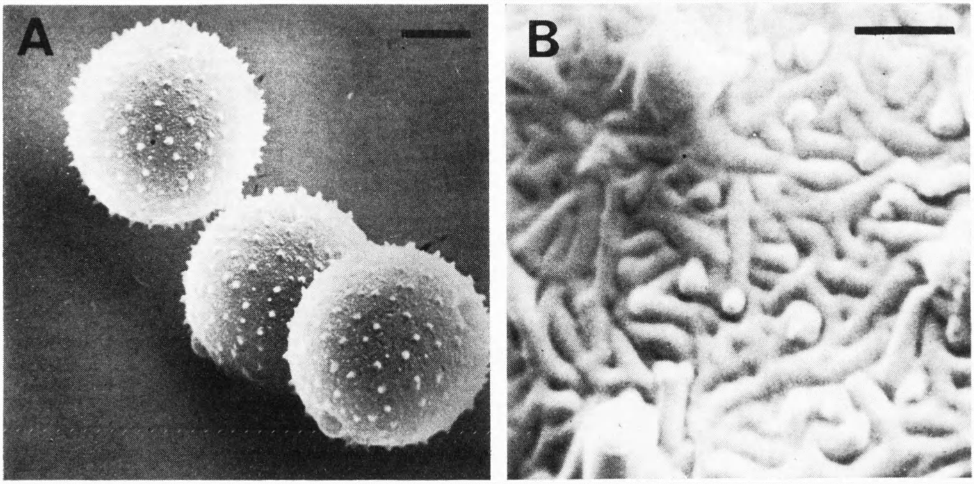


Fig. 9. *Symphyandra hofmannii.* — A: 3-porate, spinulose pollen grains with pores. C. ×940. Line c. 10 μ. — B: Part of pollen wall showing basally divided spinules, short ridges and rounded protrusions. C. ×13,000. Line c. 1 μ.

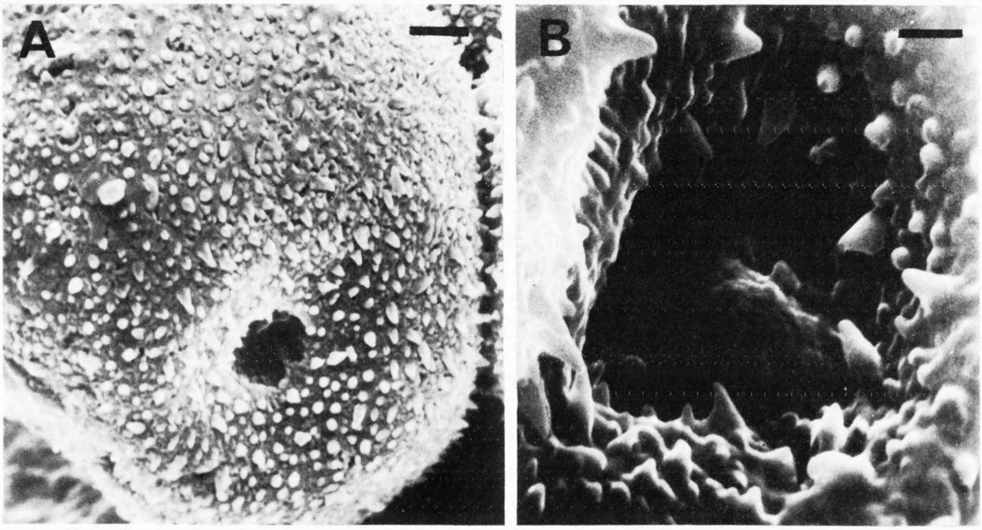
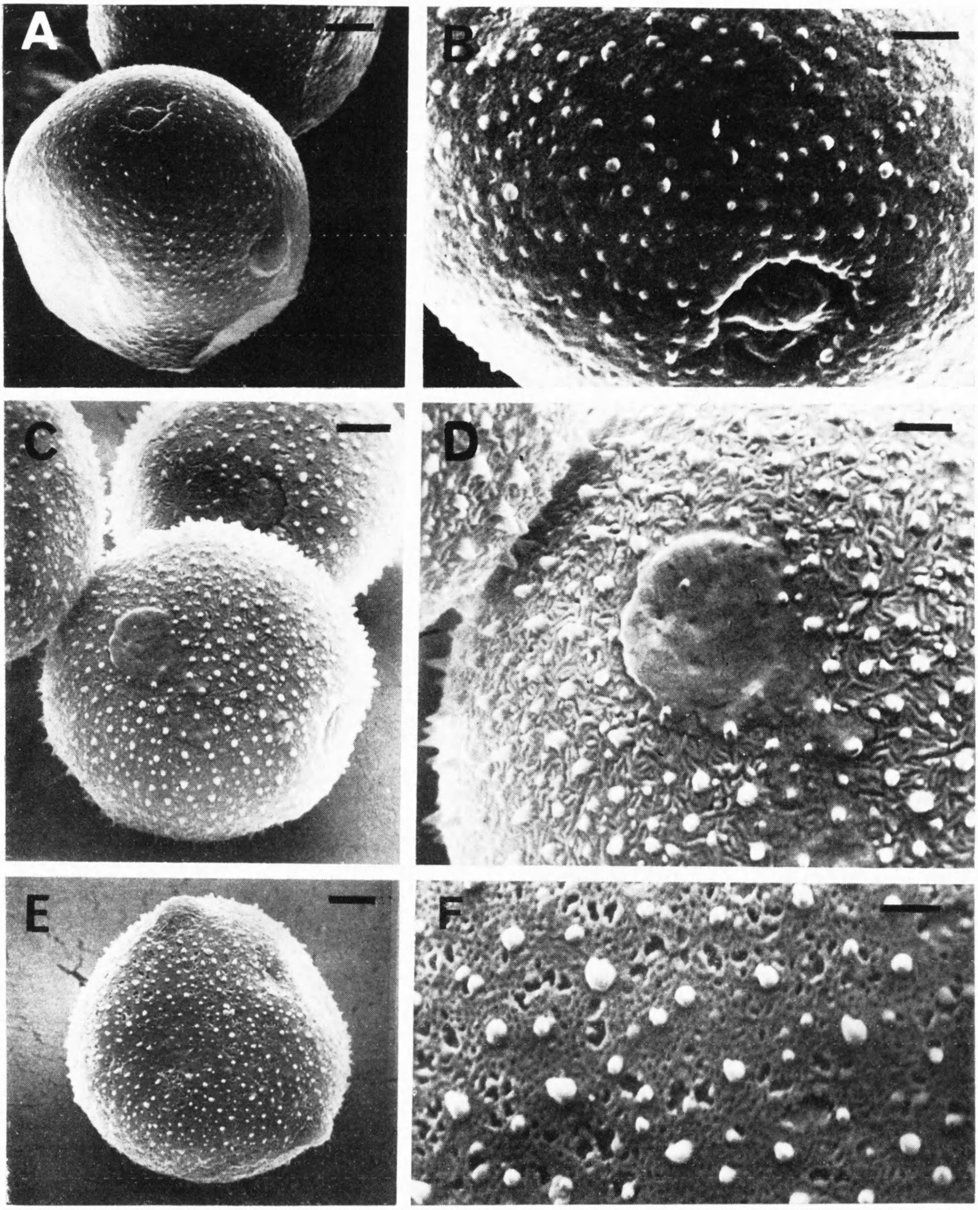


Fig. 10. *Roella muscosa.* — A: 3-porate pollen grain with pore in face view. Spinules distributed over surface. C. ×1,600. — B: Detail of pollen wall showing one pore and pore margin. Rounded protrusions between spinules. C. ×8,000. Line c. 1 μ.

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.

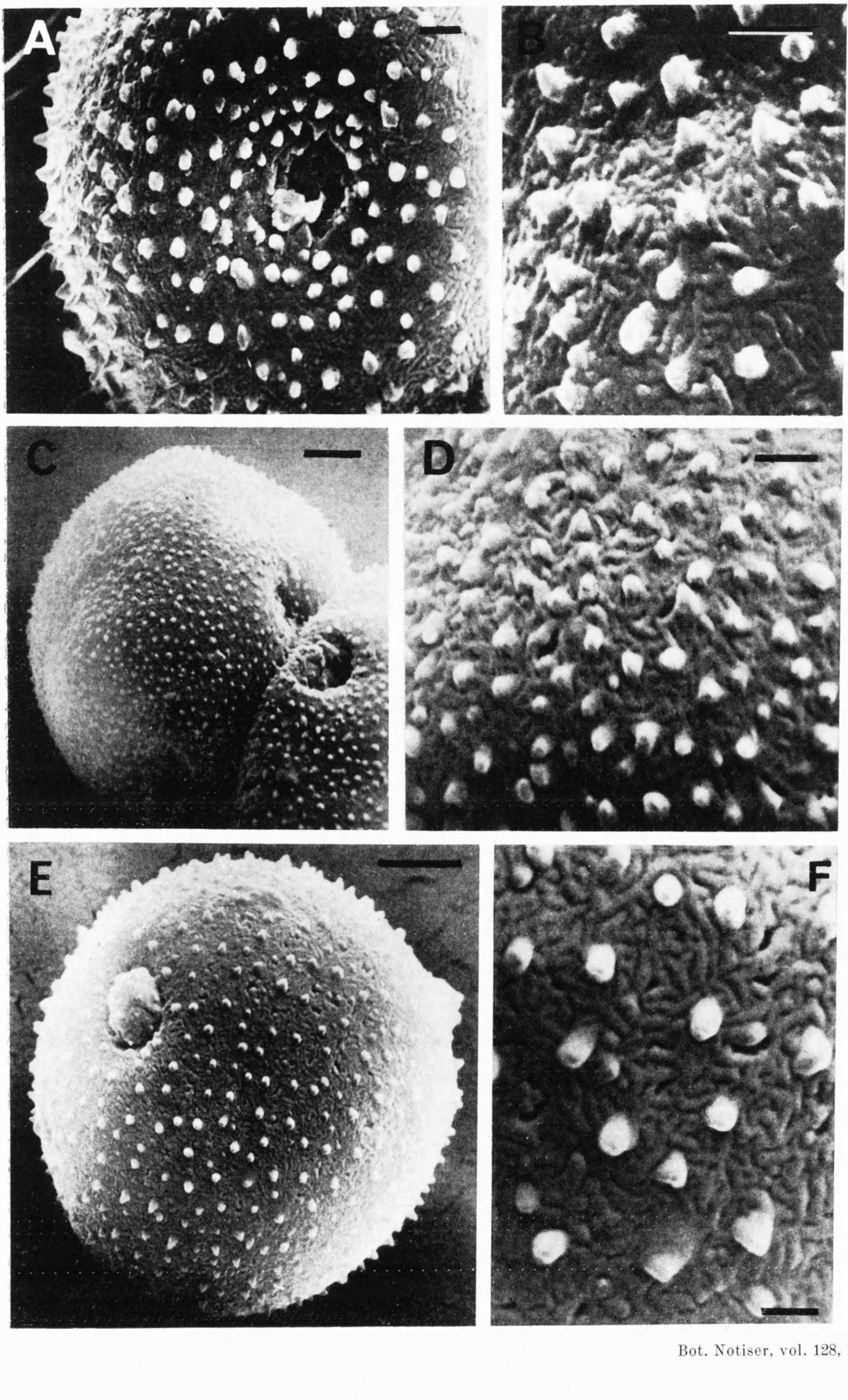
Wahlenbergia communis CAROLIN (author's observations)
Shape: oblate-spheroidal.
Size: 38×45 μ (SEMG).
Apertures: pollen grains 3-porate, pore diam. 3.8 μ (SEMG).
Exine: sexine with spinules basally divided, rather closely and irregularly spaced, mostly 1.2 μ high, lower ones also occurring; short ridges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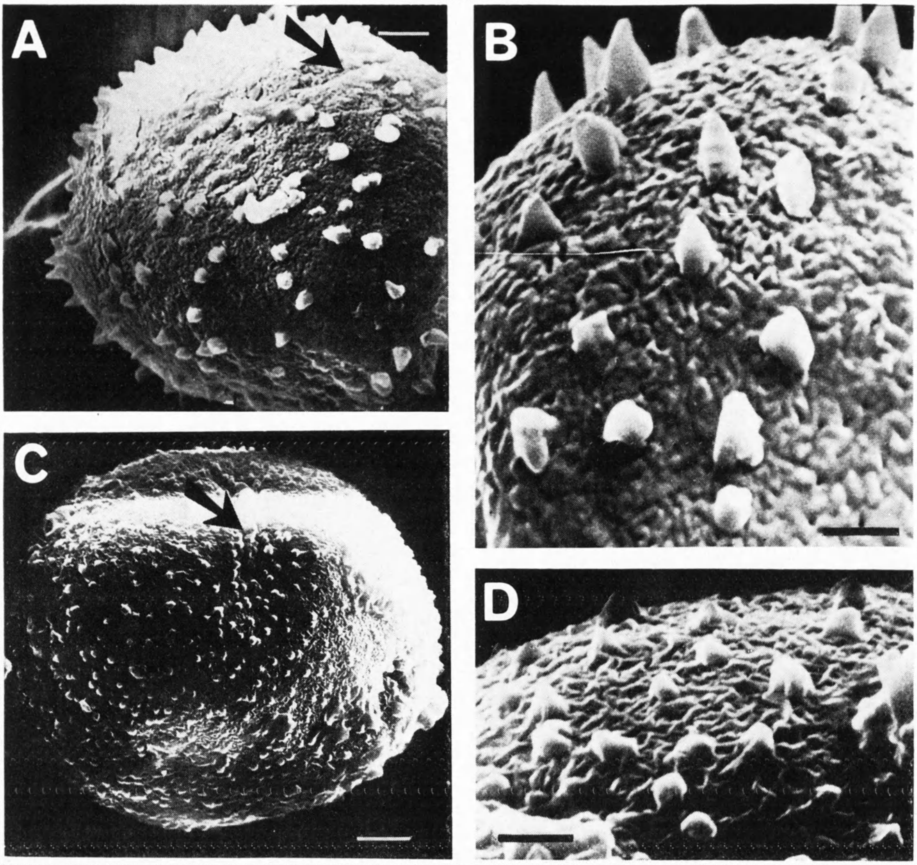


Fig. 13. *Campanumoea.* — A, B: *C. lancifolia.* — A: 3-colporate pollen grain with relatively few and large spinules. One of the compound apertures traceable (arrow). C. ×1,400. — B: Part of pollen wall with basally divided spinules and short irregular ridges. C. ×5,000. Line c. 2 μ. — C, D: *C. maximowiczii.*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

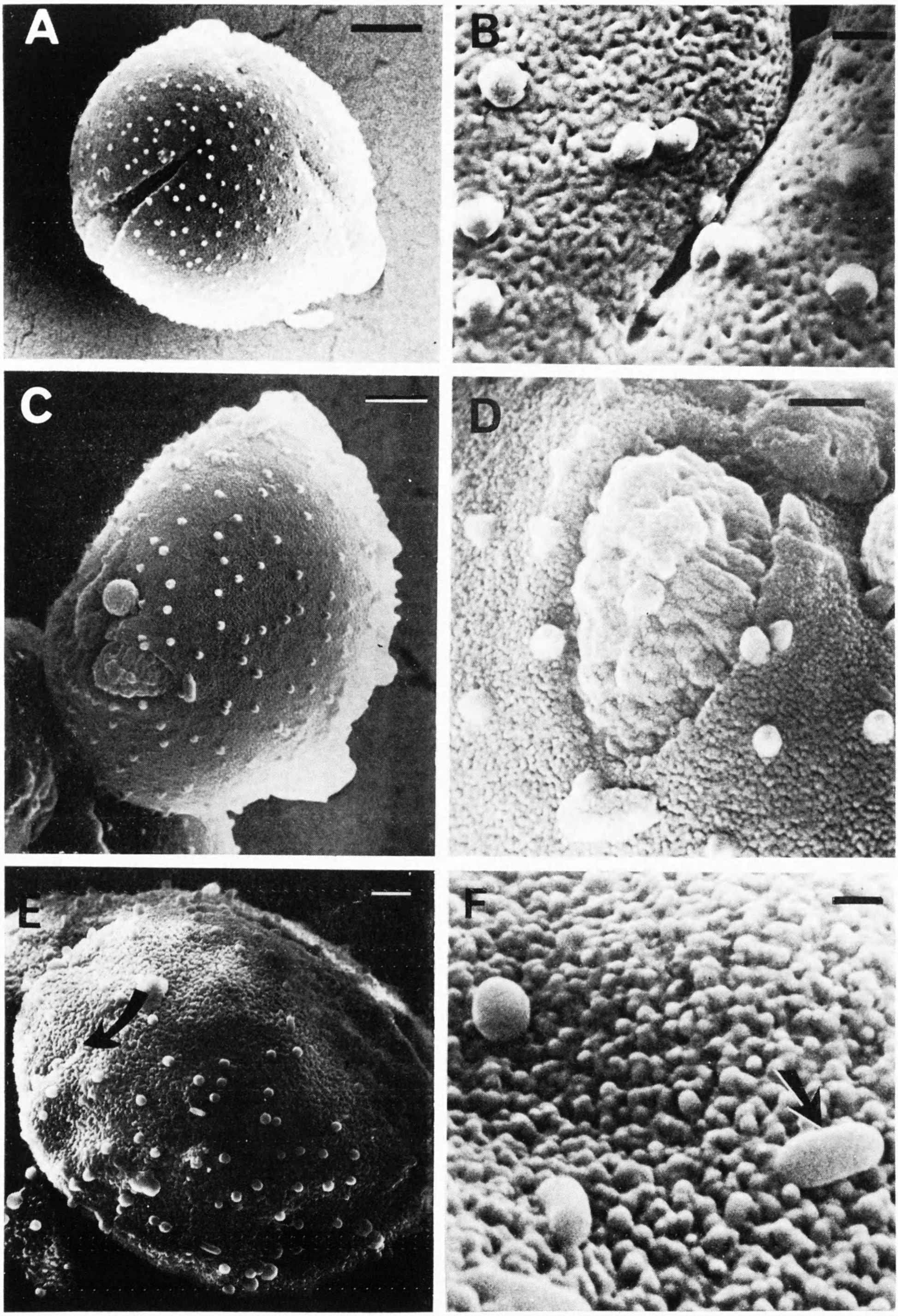
Shape: oblate-spheroidal.

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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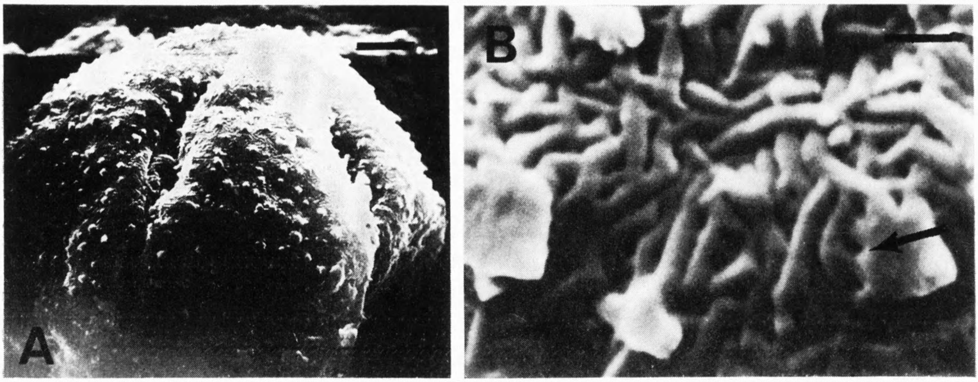


Fig. 15. *Platycodon grandiflorum.* — A: 5—6-colporate pollen grain. Two of the apertures visible. Spinules distributed over surface. C. ×1,600. — B: Detail of pollen wall showing basally divided spinules and short branched ridges forming an irregular pattern. Note connection between one ridge and more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

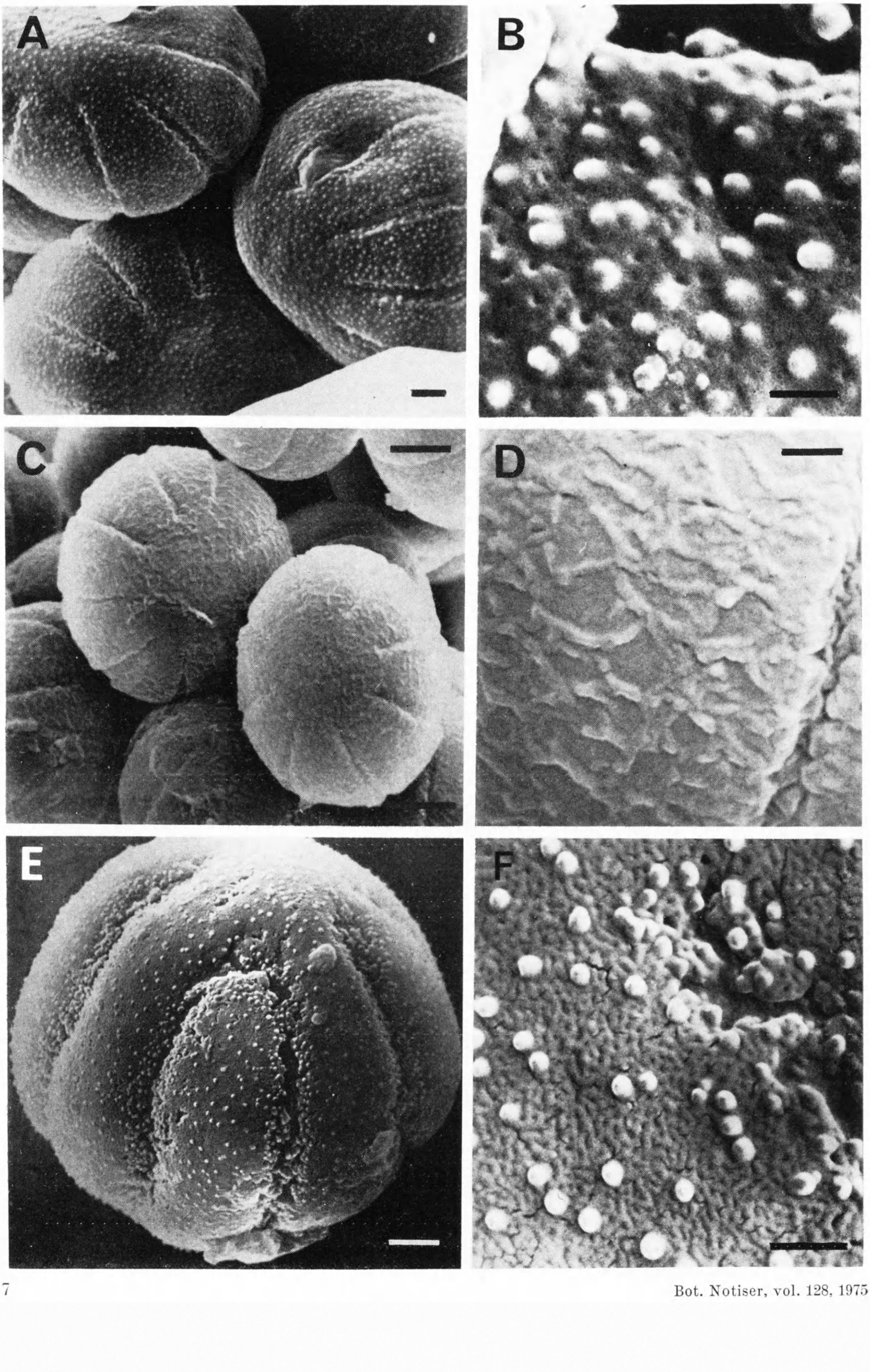
Apertures: pollen grains 4-porate, pore diam. 3 μ (SEMG).

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.


A
B
C
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E
F

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

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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).

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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

DUNBAR, A. 1975 07 08. On pollen of Campanulaceae and related families with special reference to the surface ultrastructure. II. Campanulaceae subfam. Cyphioidae and subfam. Lobelioidae; Goodeniaceae; Sphenocleaceae. — Bot. Notiser 128: 102—118. Lund. ISSN 0006-8195.

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.

Anita Dunbar, Institute of Botany, University of Stockholm, and Swedish Museum of Natural History, S-104 05 Stockholm, Sweden.

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.

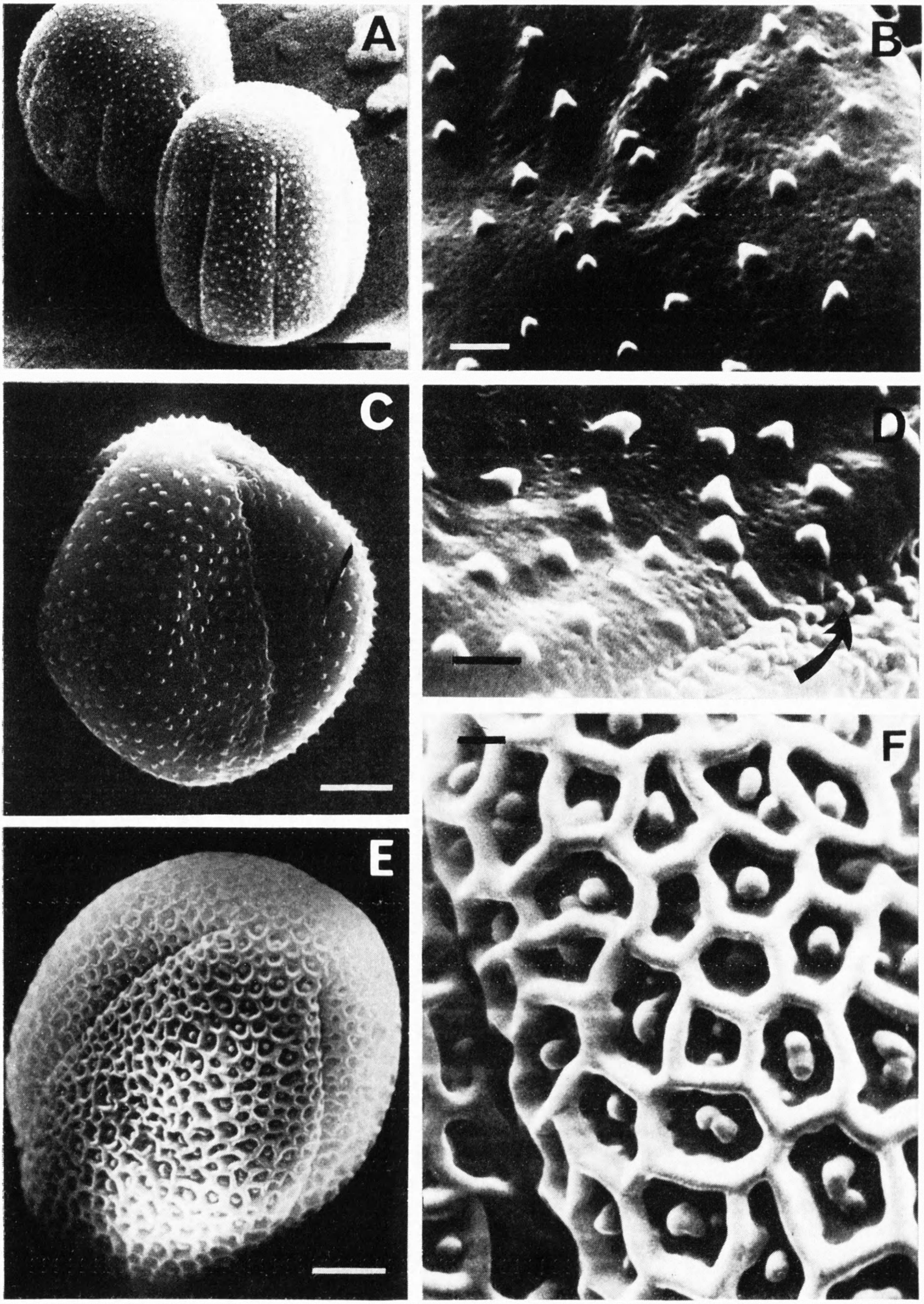

Fig. 1.

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

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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.

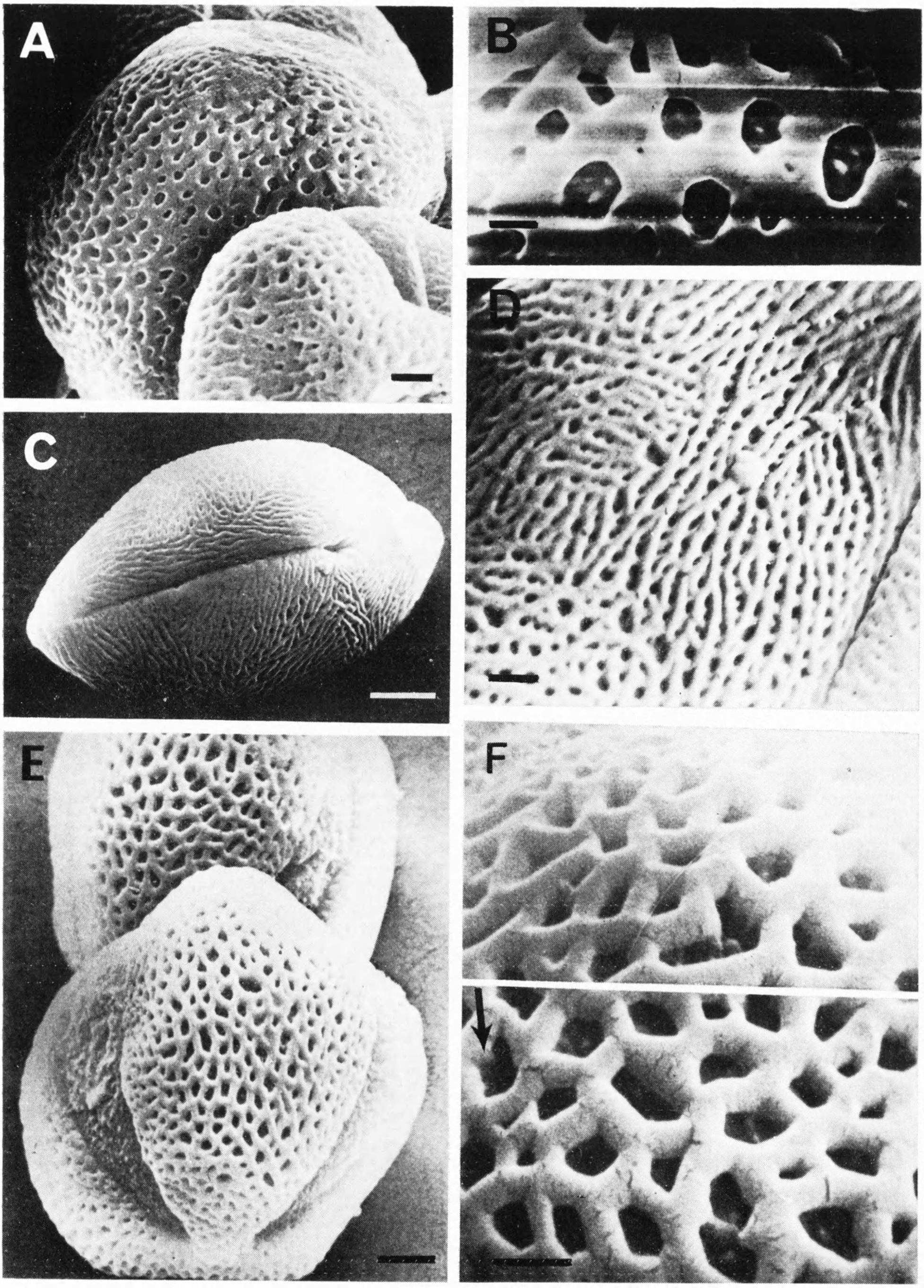


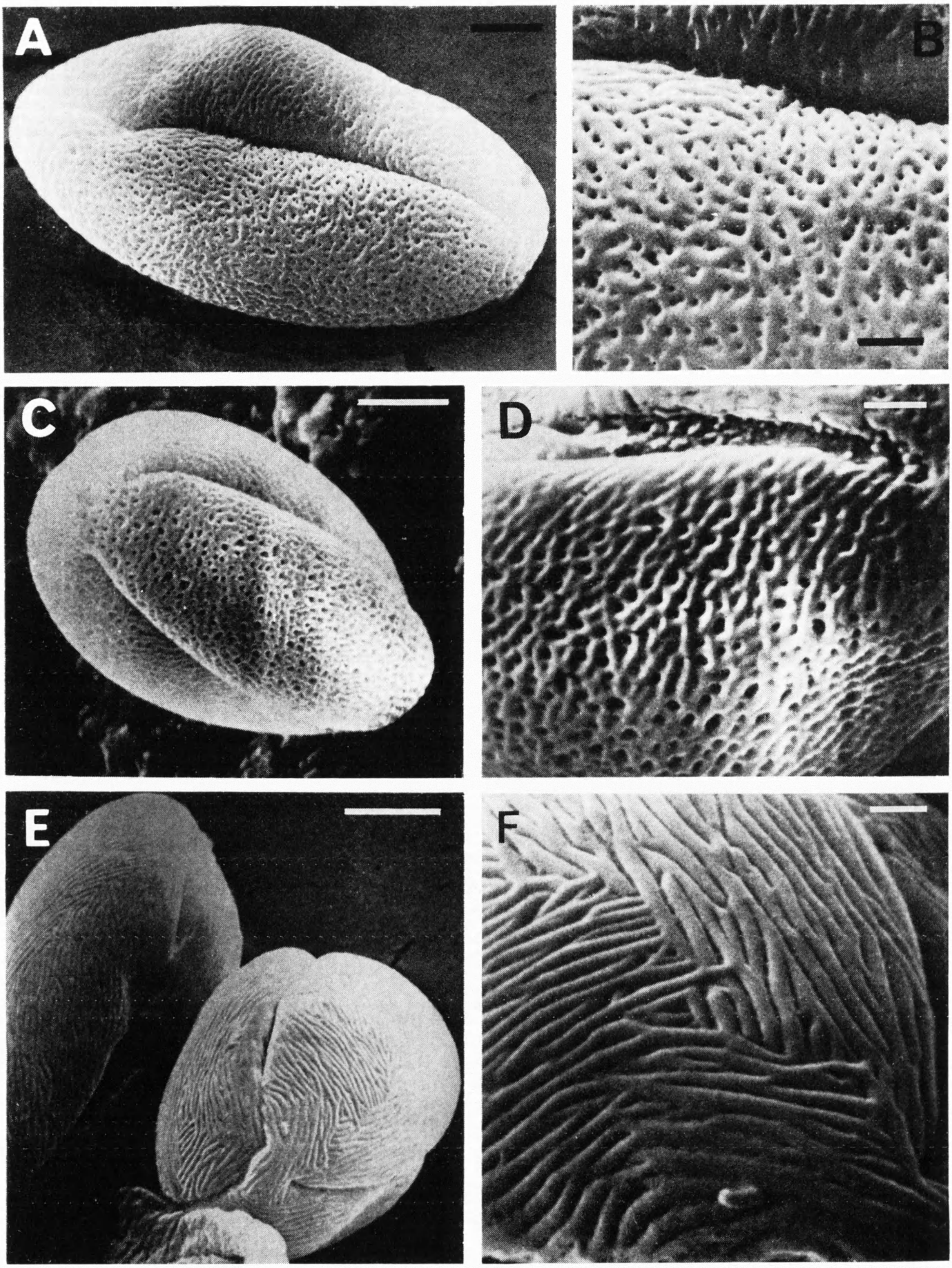
Fig. 2.

(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.

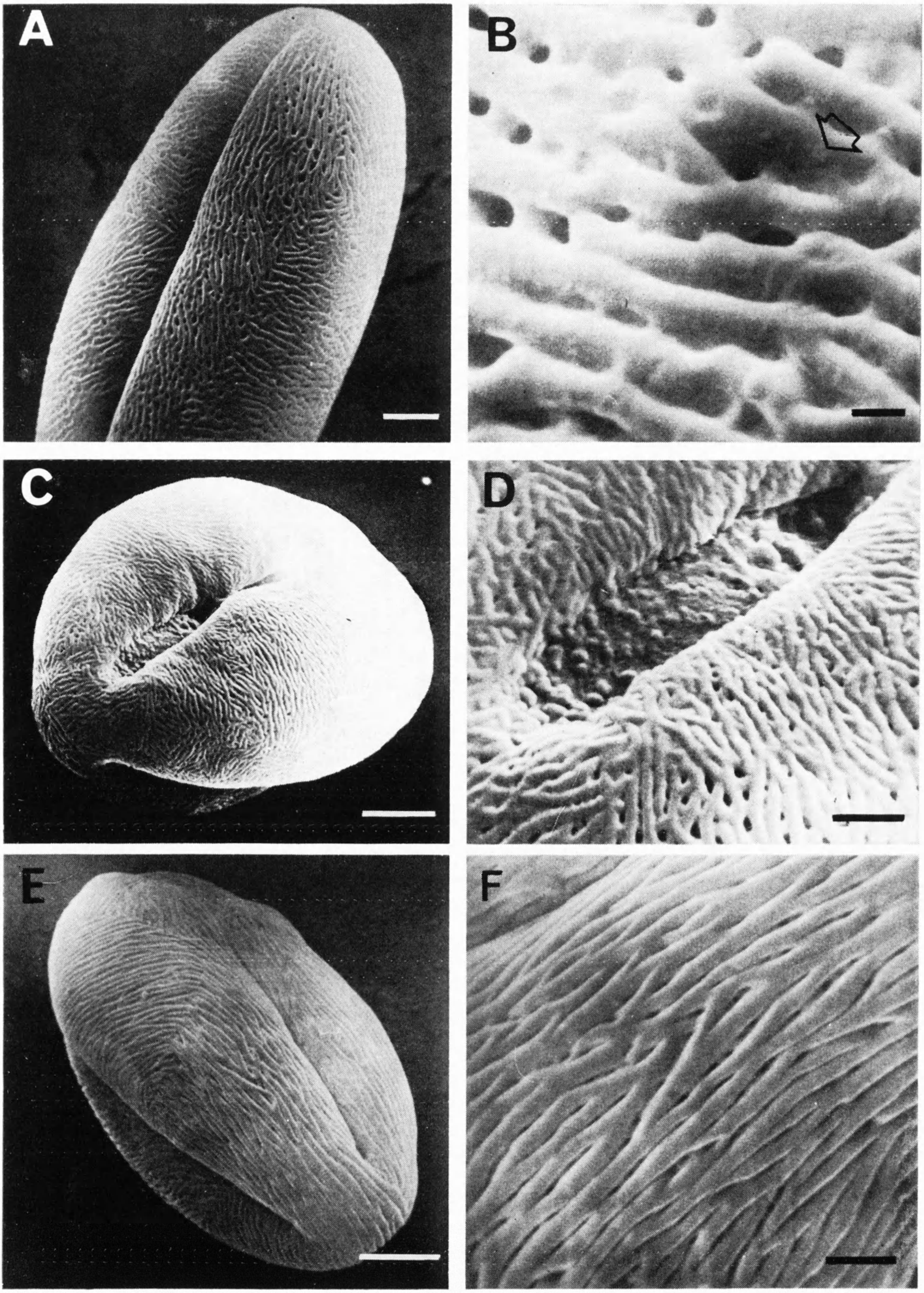


Fig. 4.

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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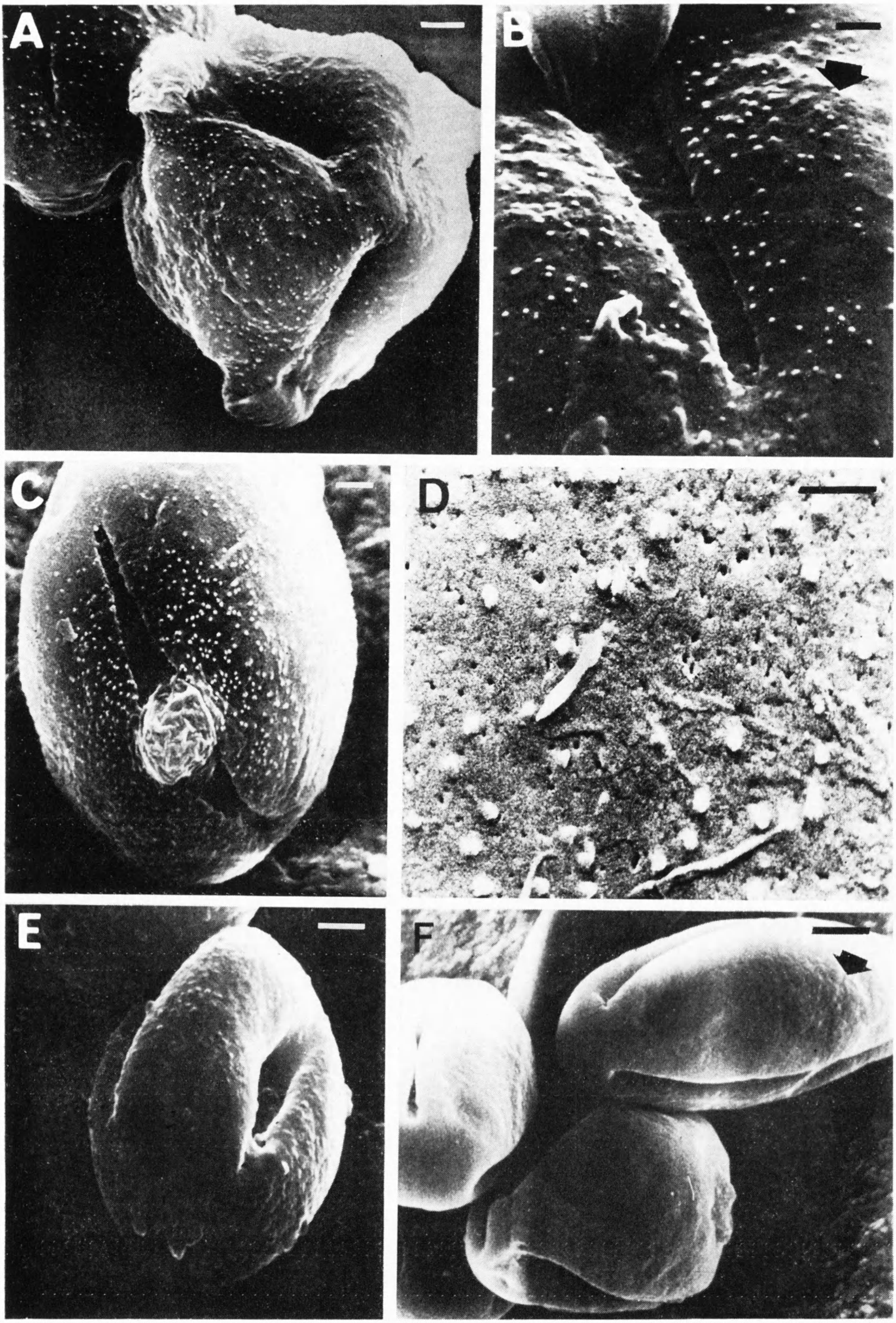
APPENDIX. SPECIMENS INVESTIGATED

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

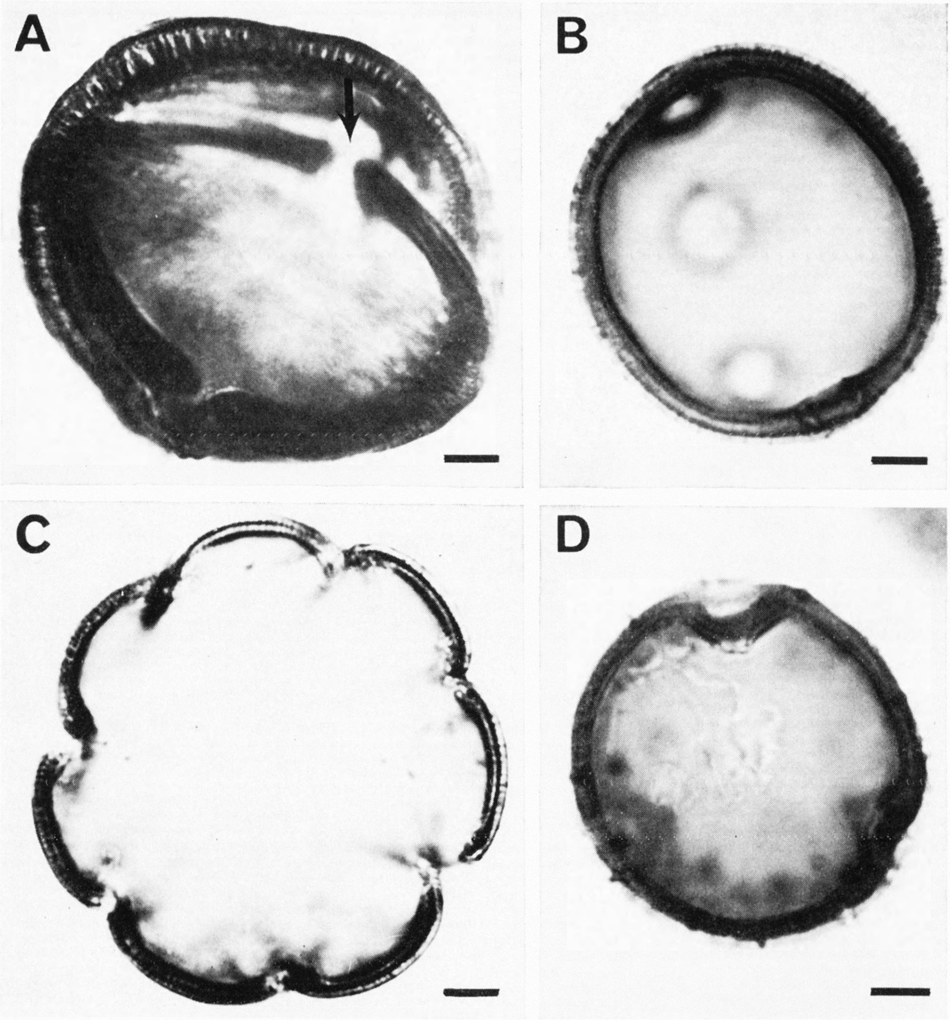


Fig. 6. A: *Scaevola koenigii*. Two of the three compound apertures are shown. Note lalongate ora (arrow), and thick layer of exine with bacula, exine varying in thickness with thickest areas below pole. C. ×1,500. — B: *Githopsis specularioides*. Four of the 6 equatorially arranged pores are shown. 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).

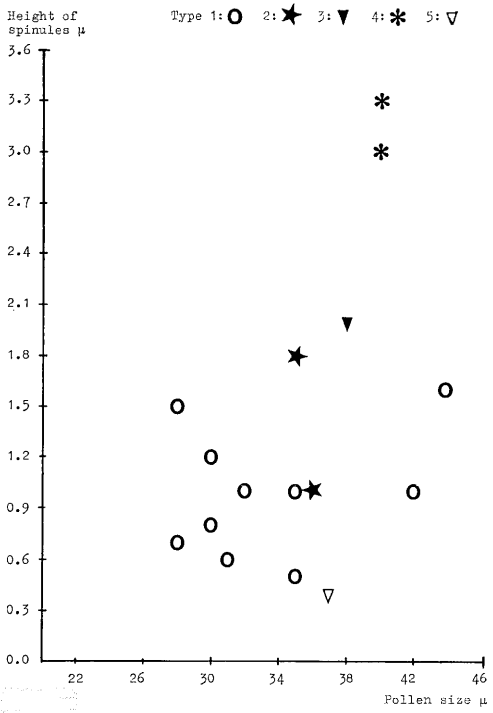


Fig. 7. Height of spinules in relation to the size of pollen grains and the pattern of sexine in *Campanula*. A change in the surface pattern along with a decrease in the height of spinules is obvious. The types of surface pattern (see Dunbar 1975 p. 76) are indicated by the symbols 1—5.

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).

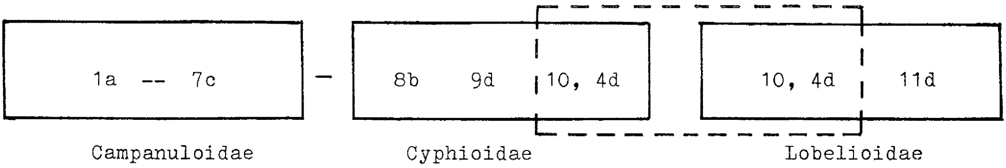


Fig. 8. Schematical, hypothetical representation of relationships between the subfamilies of Campanulaceae. For types of sexine pattern, indicated by numbers and letters, see Dunbar (1975 pp. 76, 77).

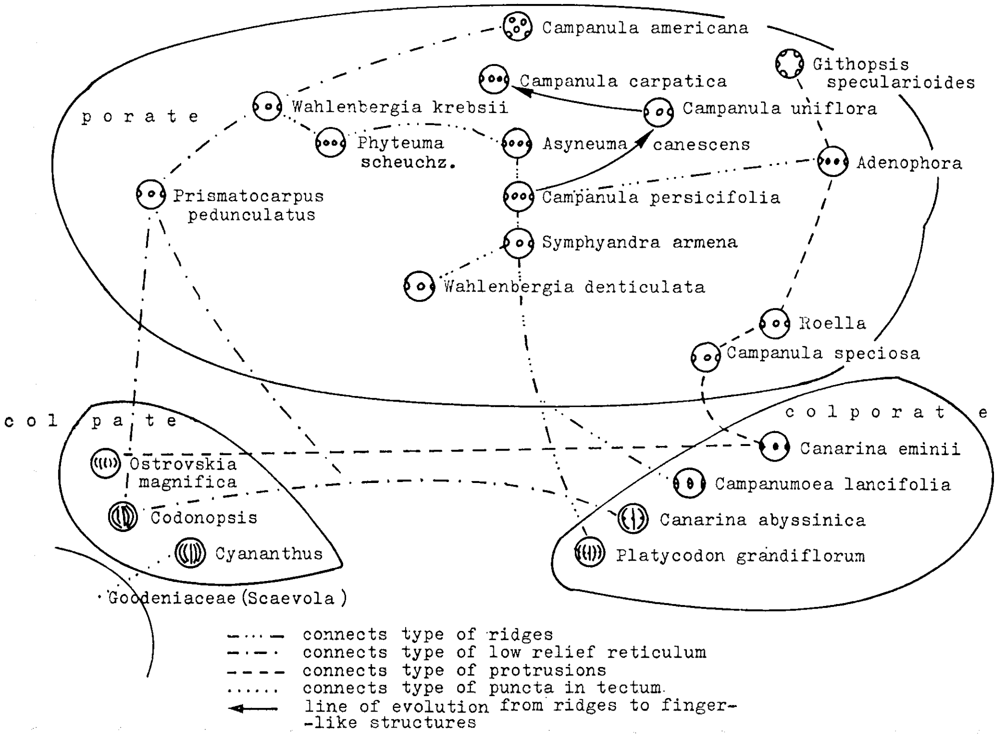


Fig. 9. Similarities between some of the genera and species of Campanuloidae (DUNBAR 1975 Table 1), and a possible line of evolution of the sexine pattern. The pollen grains are represented schematically, the porate above the colpate-colporate and the 6—12-porate above the 3—4-porate ones. One pattern 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.

Rolf Dahlgren, Botanical Museum of the University of Copenhagen, Gothersgade 130, DK-1123 Copenhagen, Denmark.

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

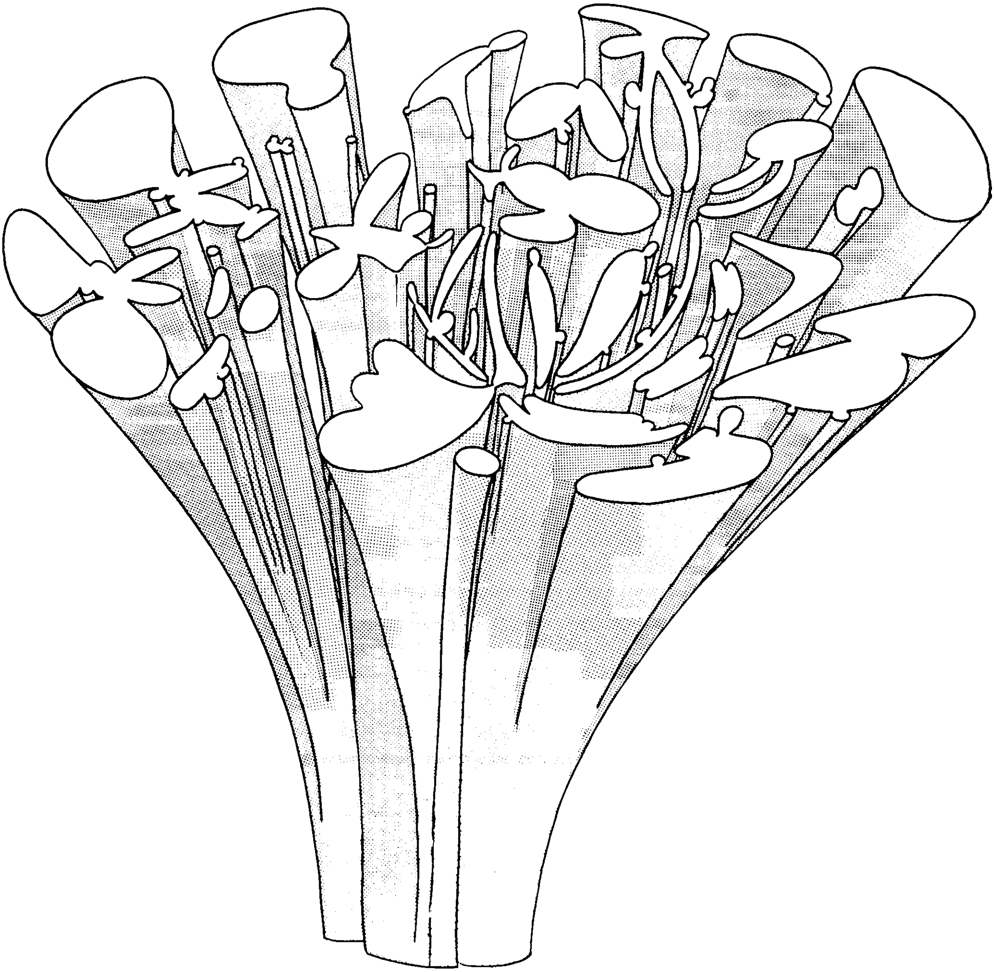


Fig. 1. The present angiosperm system pictured as the transection of an imaginary phylogenetic tree. Details of connections between branches should not be considered as having great significance.

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
esp.: especially
excl.: excluding
incl.: including
occas.: occasionally
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.*

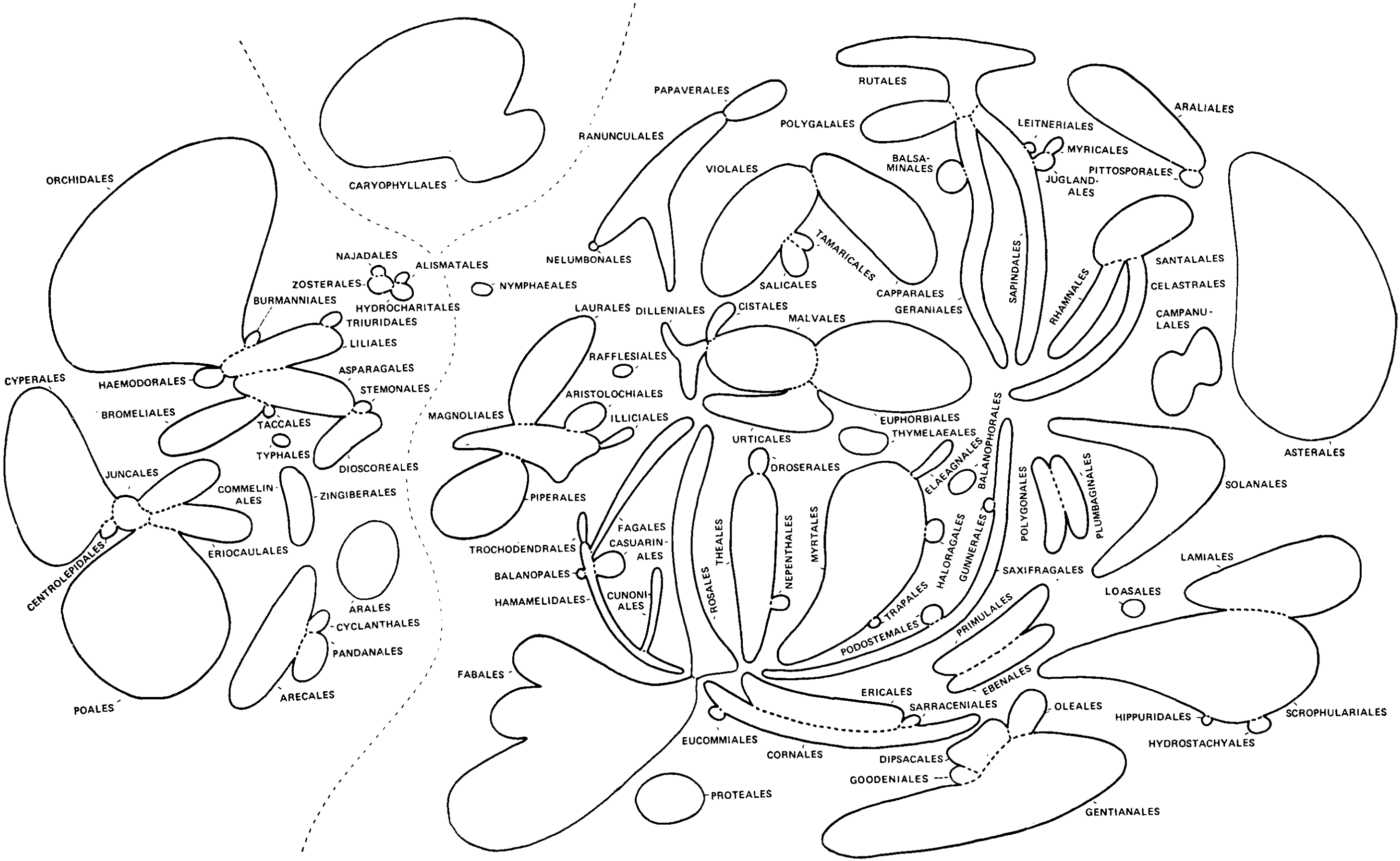


Fig. 2. The present angiosperm system (cf. Fig. 1). The size of each order roughly corresponds to its number of species. Orders with great similarity are placed next to each other as far as possible. Further explanations in the text.

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, unior 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, honey-leaves 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 derivatives 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. widened 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 Podostemales); 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; endosperm 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, Aegicerataceae, 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; gynoecium 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

Søren Rosendal Jensen, Bent Juhl Nielsen and Rolf Dahlgren

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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.

Søren Rosendal Jensen and Bent Juhl Nielsen, Department of Organic Chemistry, Technical University of Denmark, DK-2800 Lyngby, Denmark.
Rolf Dahlgren, Botanical Museum of the University of Copenhagen, Gothersgade 130, DK-1123 Copenhagen, Denmark.

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 overlapping 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

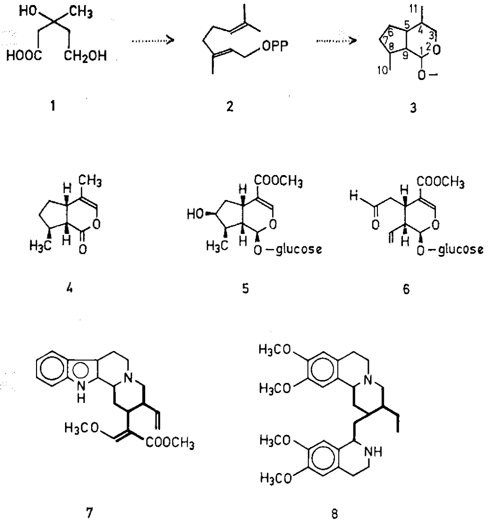

Fig. 1. Examples of iridoid structures (3—8).

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.

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.

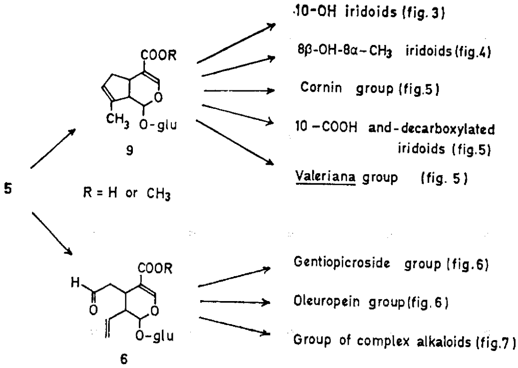

Fig. 2. Classification of carbocyclic and seco-iridoids.

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-desoxygeniposide (**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.

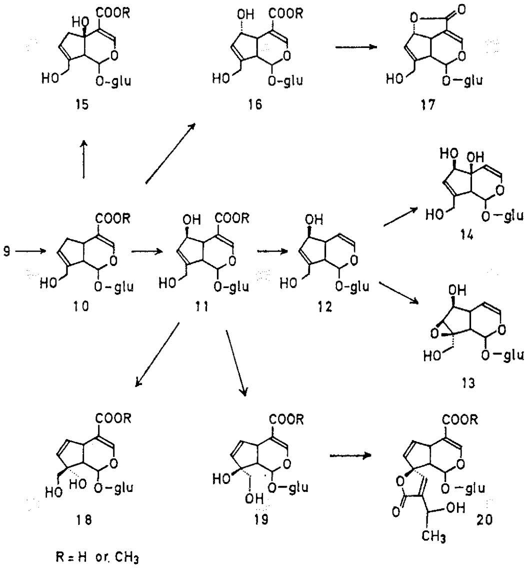

Fig. 3. Iridoids of Group I (10-hydroxylated compounds).

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 [α] 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

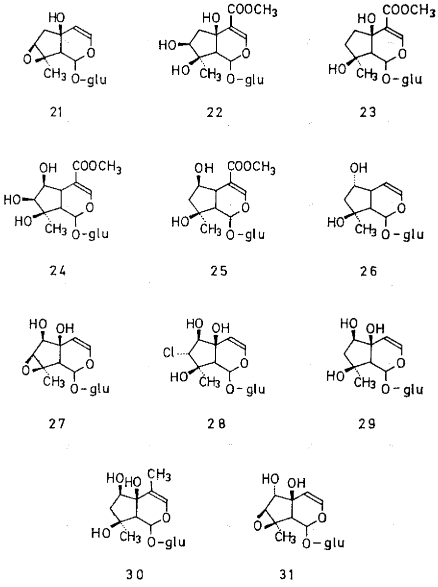

Fig. 4. Iridoids of Group II (8β-oxy-8α-methyl substituted compounds).

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).

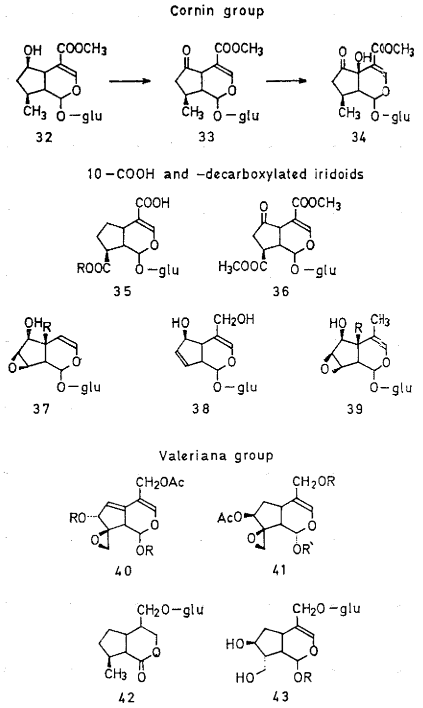

Fig. 5. Iridoids of Groups III, IV and V.

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

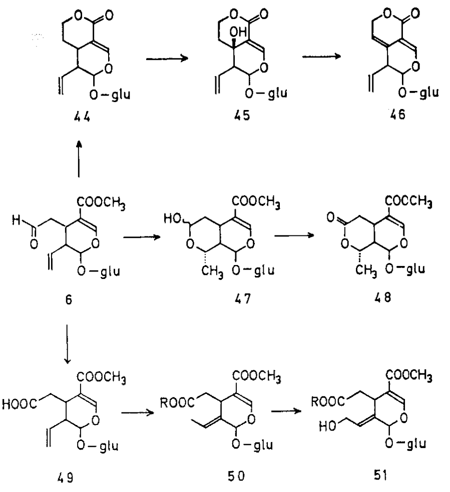

Fig. 6. Seco-iridoids of Groups VI, VII and VIII.

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-

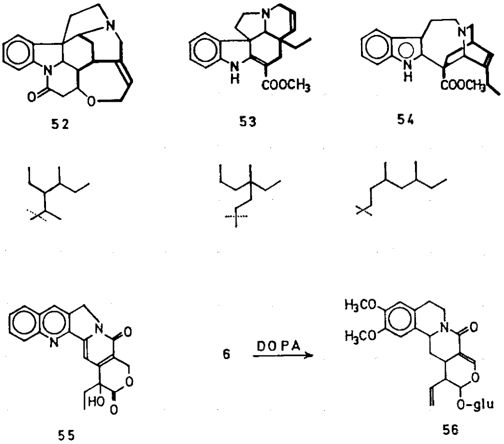

Fig. 7. Complex iridoid alkaloids. Group IX.

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

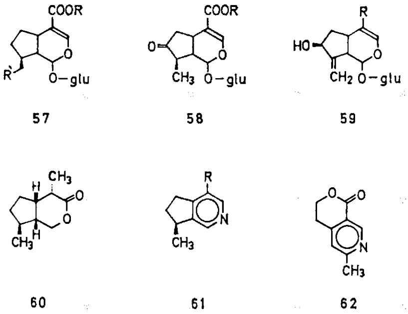

Fig. 8. Unclassified iridoids. Group X.

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.

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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 desoxygeniposide (**9**) or from secologanin (**6**), which in turn are both derived from loganin (**5**). The glucosides in the biosynthetic 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. Desoxyloganin (**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.

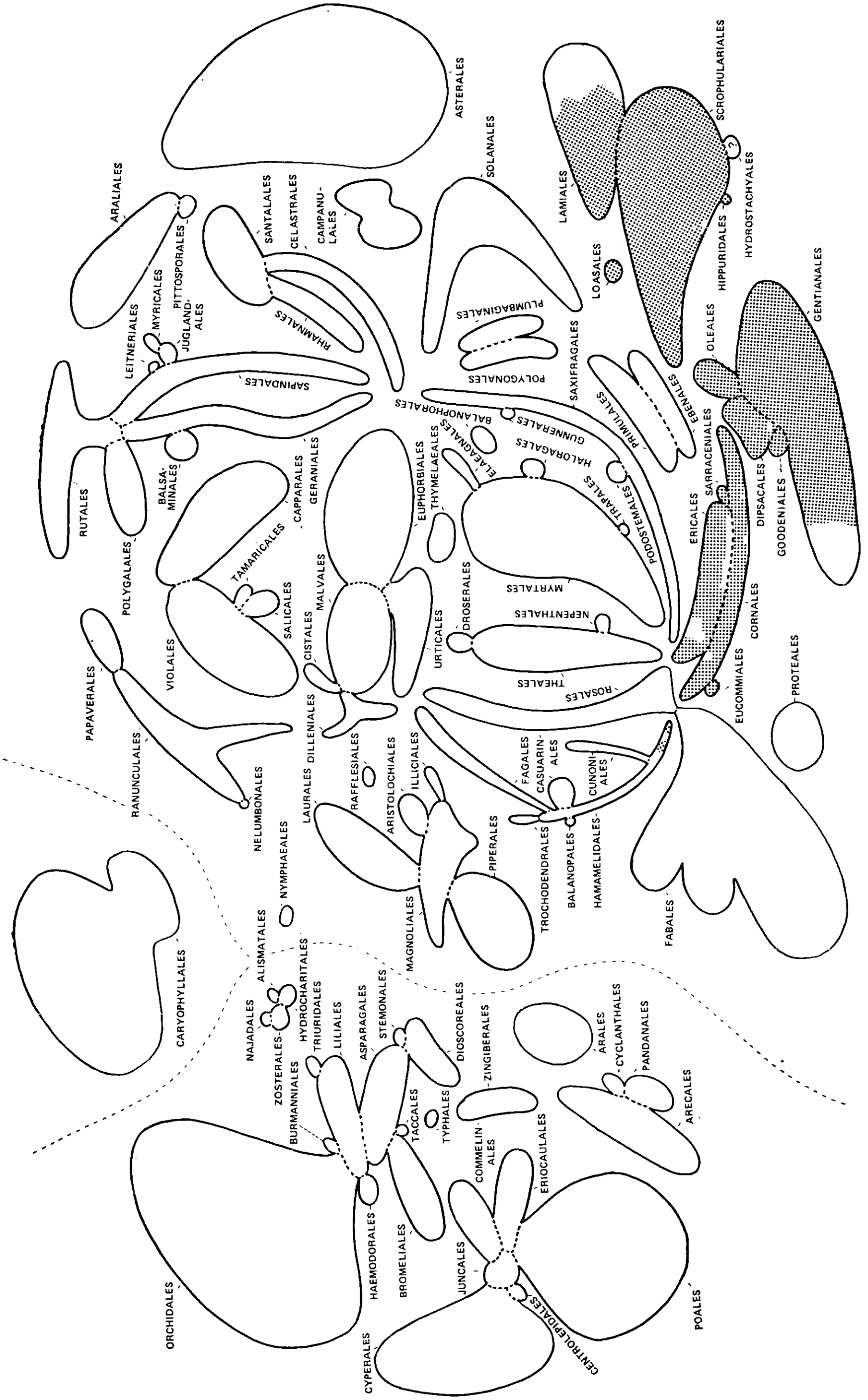

Fig. 9. Documented distribution of iridoid compounds in the angiosperm system. The area of each family from where iridoids are known has been shaded in its entirety except for Lamiaceae, where it is known that the iridoids are restricted to certain groups of genera.

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

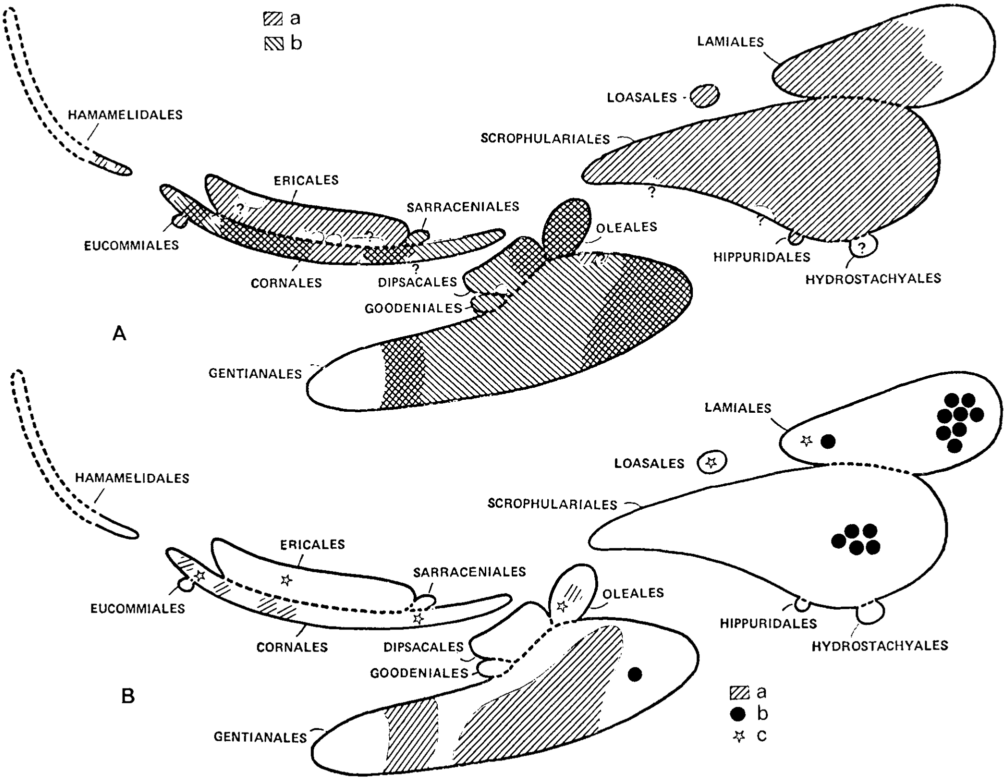

Fig. 10. — A: a: Distribution of carbocyclic iridoids (Groups I—V and X) if seco-iridoids are not present; b: Distribution of seco-iridoids (Groups VI—IX). Families where both kinds occur are checkered. — B: a: Occurrence of "complex" iridoid alkaloids (Group IX), the records are numerous in Rubiaceae 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 iridoids. 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 iridoids 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 Gentiananae. 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 usually 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.

Rolf Dahlgren, Botanical Museum of the University of Copenhagen, Gothersgade 130, DK-1123 Copenhagen, Denmark.

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), Aegicerataceae (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.

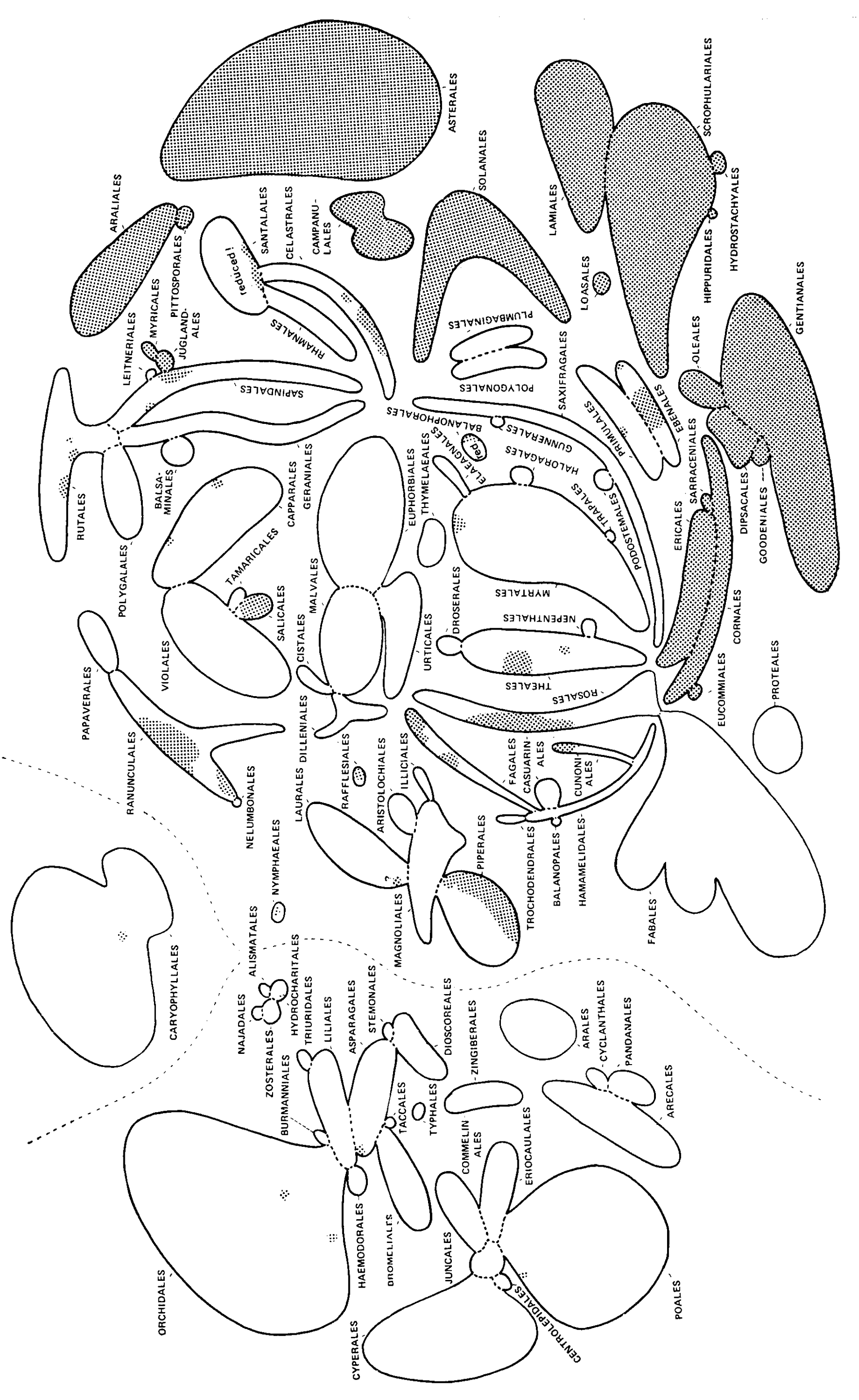

Fig. 1. Distribution of unitegmic (shaded) and bitegmic ovules in the orders of angiosperms. In Santalales and Balanophorales the ovule is greatly reduced and there is no integument at all. (N.B. Balanopales should also be shaded.)

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, Gentiananae, 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: Aegicerataceae (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-

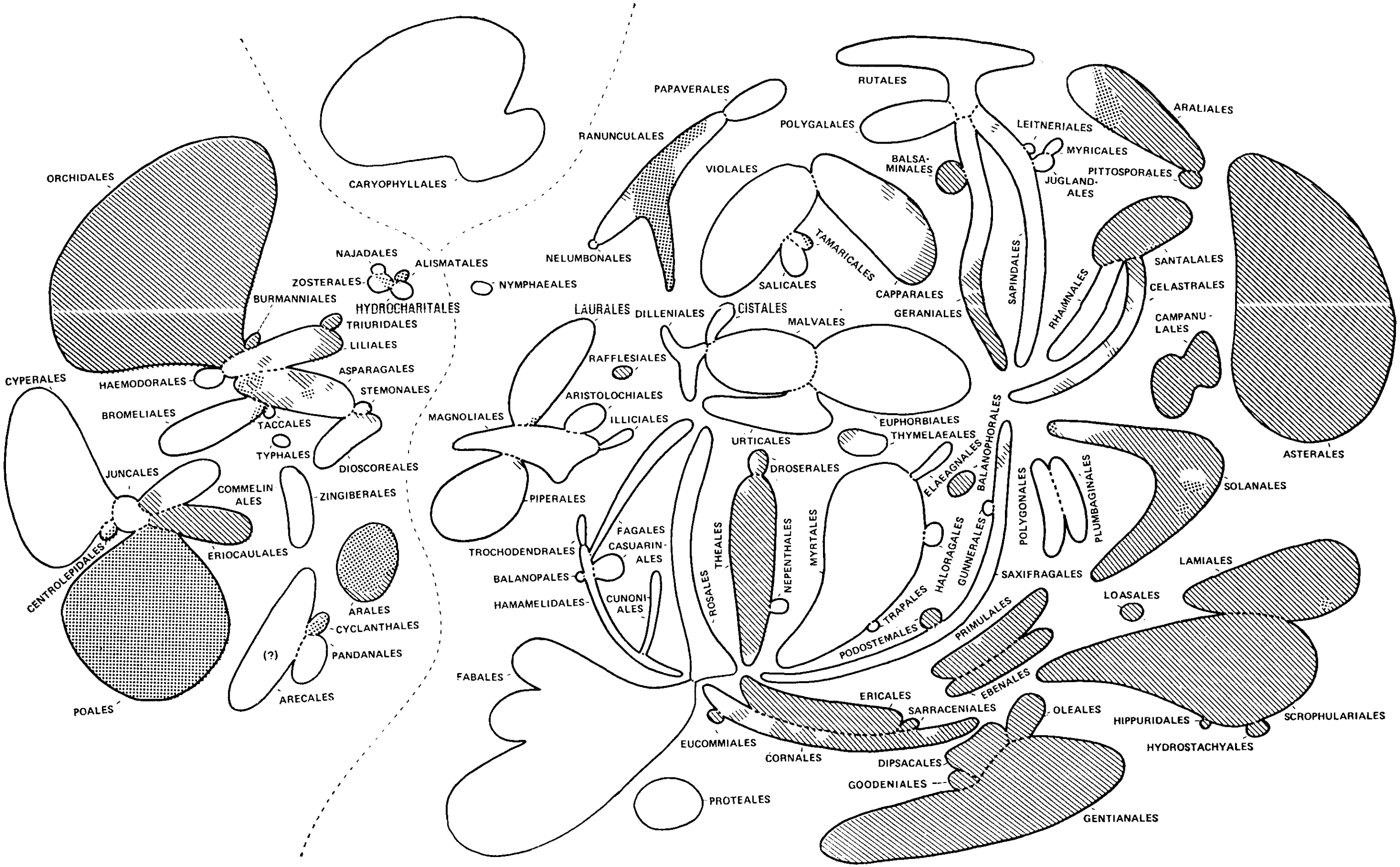

Fig. 2. Distribution of tenuinucellate (hatching), pseudocrassinucellate (shaded with dots) and crassinucellate ovules in orders of the angiosperm system.

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

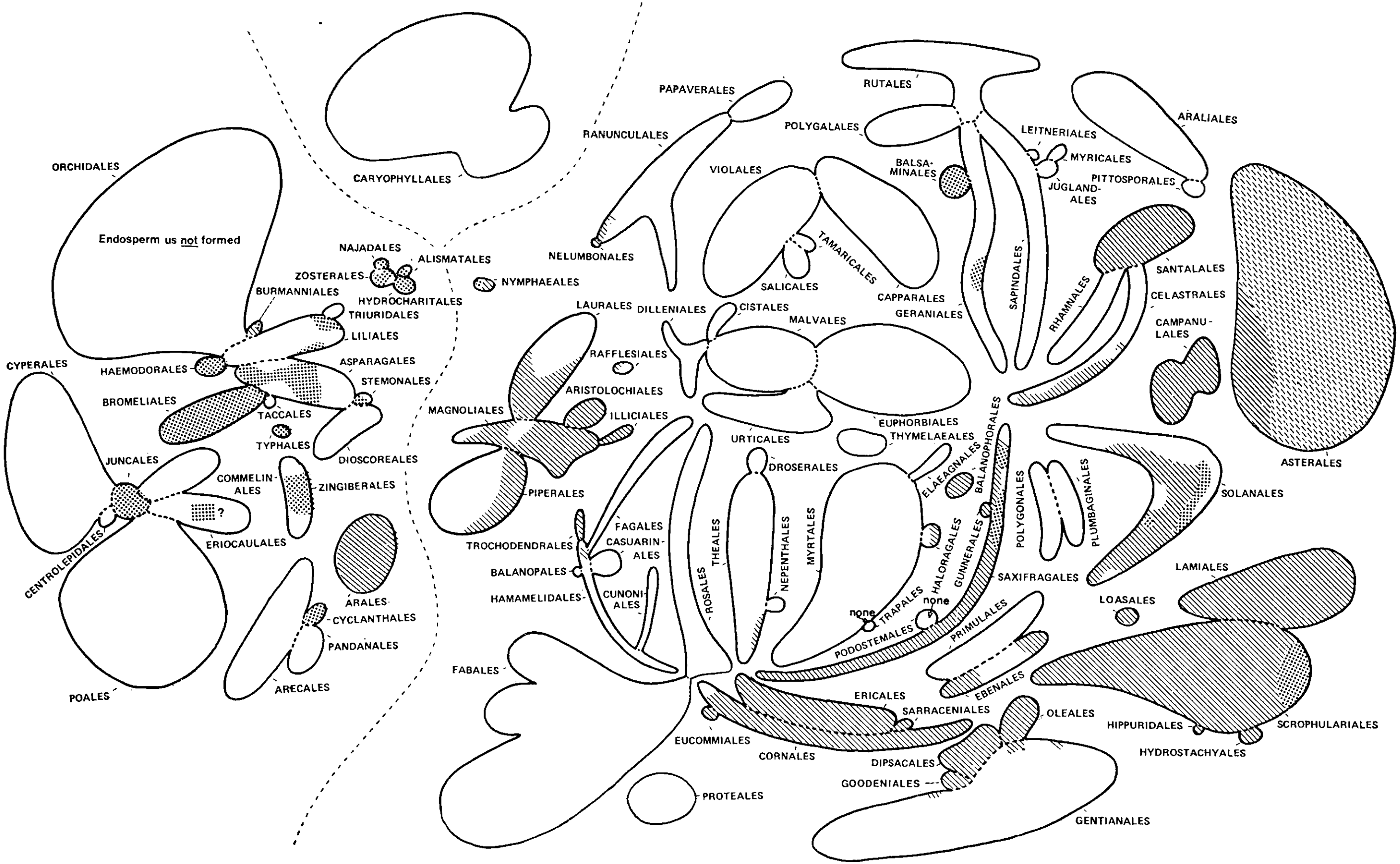

Fig. 3. Distribution of ab initio cellular (hatching), intermediate ("helobial" in a broad sense; shaded with dots) and nuclear endosperm. The great variation of endosperm in Asterales is indicated by hatching with broken lines. — Endosperm is not formed at all in Orchidales, Trapales and Podostemales.

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

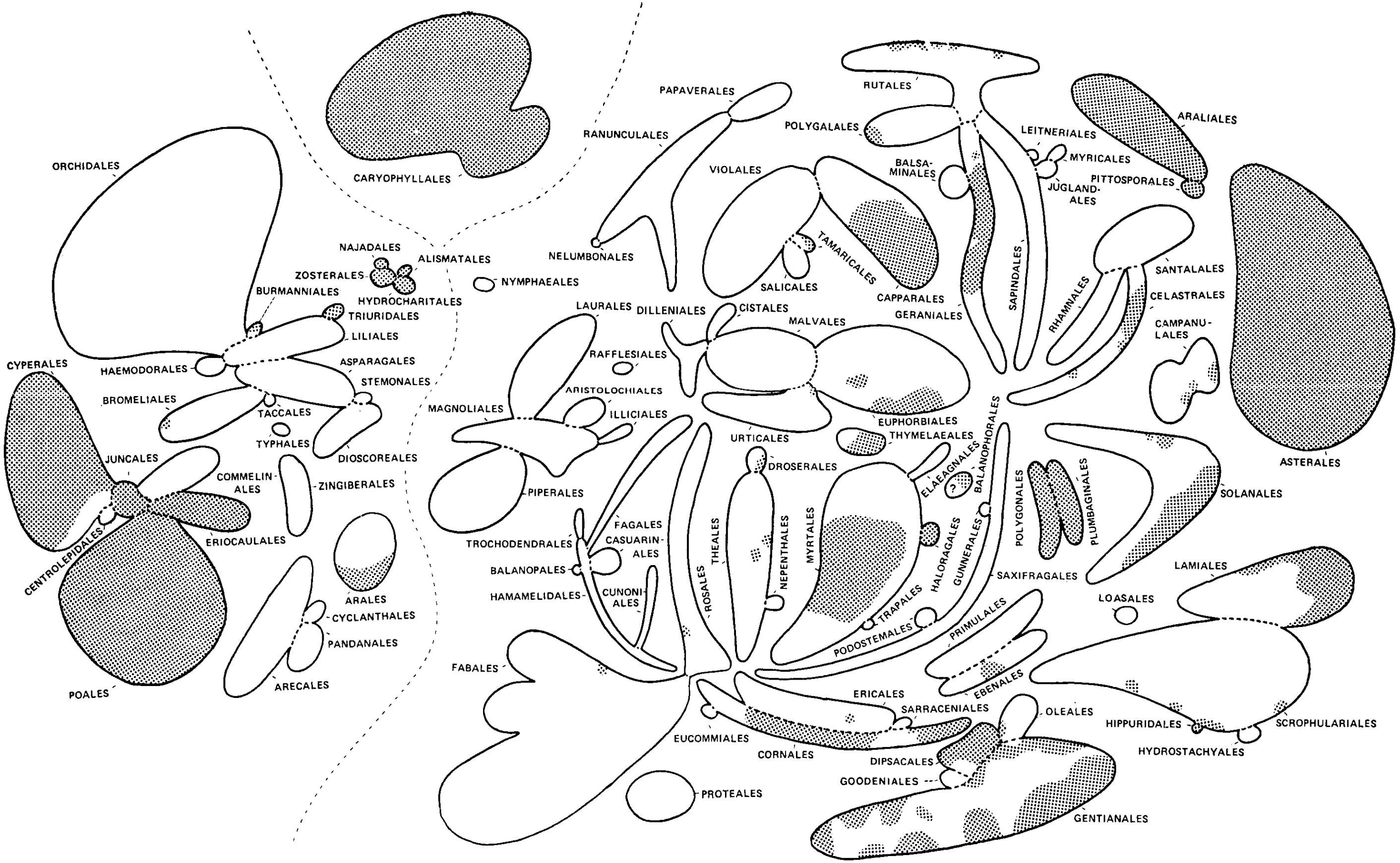

Fig. 4. Distribution of pollen grains released at the trinucleate stage (shaded) and in the binucleate stage in the orders of the angiosperm system.

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 macrolichens 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 worldwide coverage. It is the only international bibliography of distribution maps of vascular plants.

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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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