Drawings of Scandinavian Plants 109–110

Epilobium L. Sect. Epilobium

Alf Oredsson and Sven Snogerup

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Drawings and descriptions are given for *E. collinum* C. C. GMEL. and *E. montanum* L.

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The two species nos. 109 and 110 are closely related. Intermediates are few, but some of them, e.g. from southernmost Sweden, are apparently wholly fertile. Thus the genetic relationship of these species probably merits further investigation. They may be isolated by ecological differences and predominant autogamy rather than by barriers of intersterility.

109. **Epilobium collinum** C. C. GMELIN 1826

Perennial herb, (5—)15—35(—60) cm high. Stem often unbranched, but more or less stunted branches usually present in most leaf axils, sometimes prolonged and giving the plant a densely branched habit. Stem usually with 6—15 pairs of leaves below the inflorescence, leaves usually longer than the internodes, producing one or several (1—)3—6(—12)-flowered inflorescences. Stolons subterranean or occurring at the surface, very short and inconspicuous or up to 10 mm, reddish, with dense, scale-like leaves. Turions epigean, formed late in the autumn as dense rosettes of 10—20 fleshy, broadly obovate leaves 3—6 mm long, or rarely prolonged up to 20 mm with small and very thick leaves, reddish with green on the upper sides of the leaves.

Stem 0.5—2(—3) mm thick, quite terete, usually rather densely hairy, especially in the upper part and below the midribs of the leaves, hairs 0—0.25 mm, recurved to adpressed or some very short glands patent, mostly eglandular, only some of the shorter ones glandular.

Most leaves opposite, usually only the bracts alternate, all petiolate, petioles in middle and upper leaves 1—5 mm, in basal ones up to 10 mm, leaf bases usually not united, never decurrent. Basal leaves smaller, spathulate to obovate or elliptical. Middle cauline leaves 10—30 (—40) mm long, 5—12(—22) mm broad, ovate to narrowly ovate, obtuse to acute, regularly serrate with usually 6—12 up to 1 mm long, forwards-pointing teeth on each side. Upper leaves smaller, short-petiolate, usually narrowly to very narrowly ovate, sharply tapering to the acute or obtuse apex. Leaves sparsely hairy, denser on margins and both sides of the midrib, hairs like those of the stem.

Pedicels erect in all stages. Buds ellipsoidal to obovoidal, with a broad conical tip, not mucronate. Sepals (3—)3.5—6 mm, connate to 0.8—1.5 mm at base,

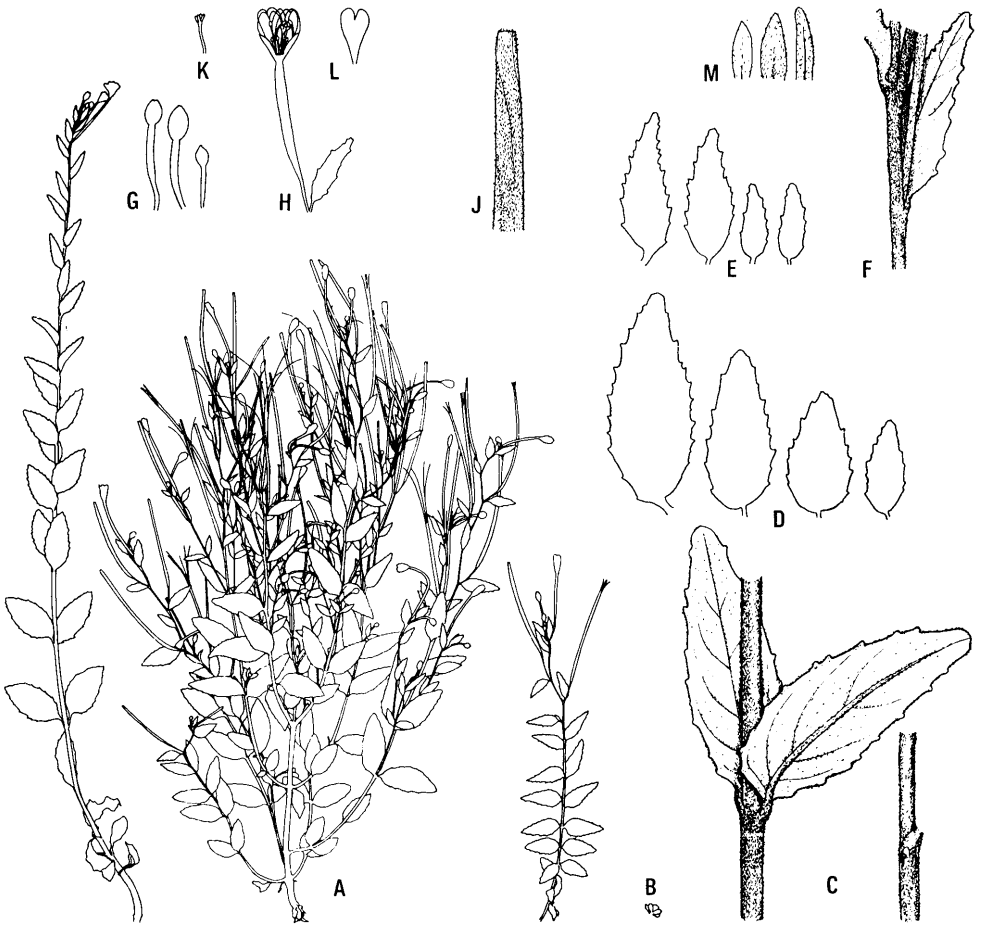
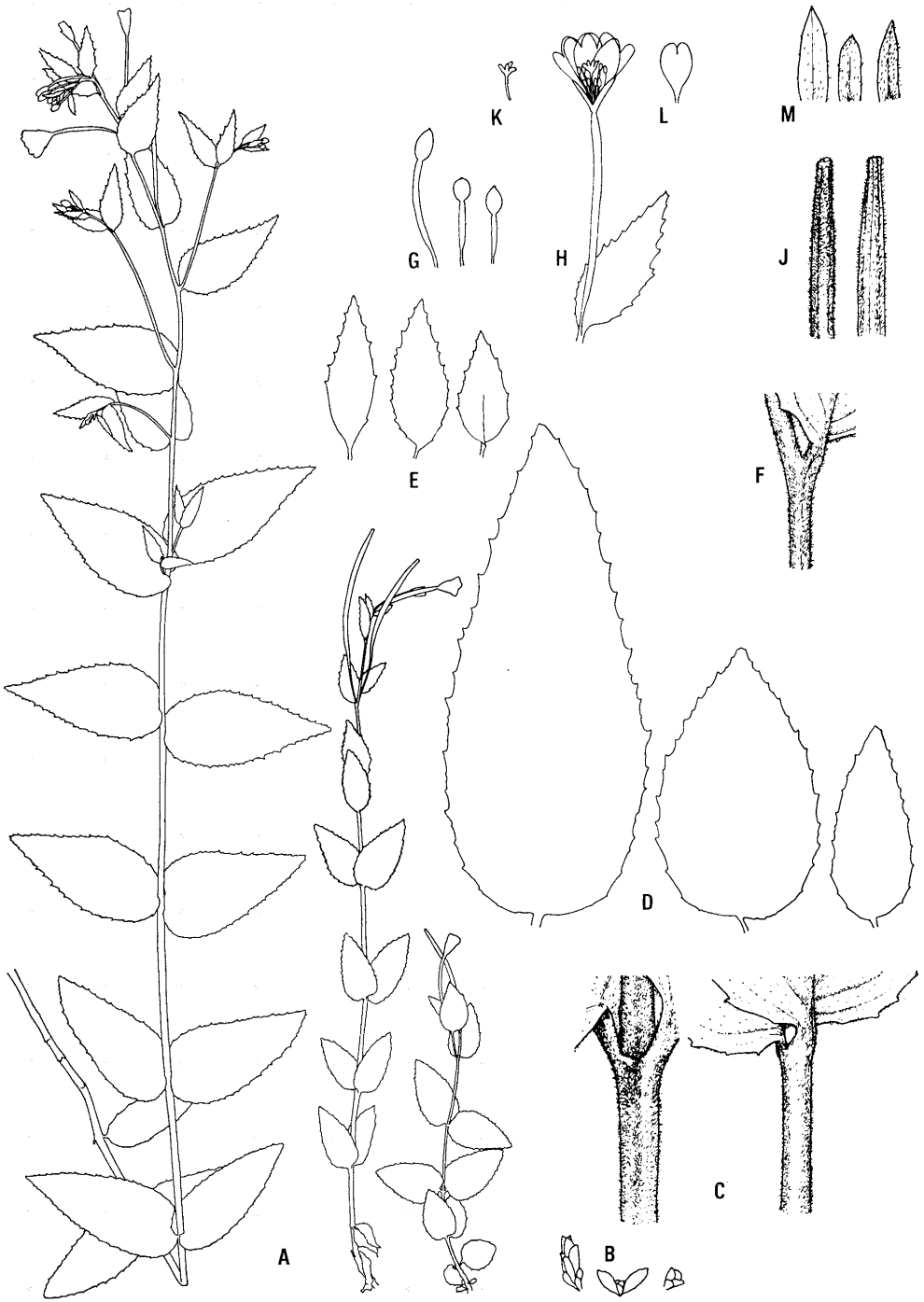


Fig. 109. *Epilobium collinum* C. C. Gmel. — A: Habit, ×1/3. — B: Winter bud, ×1/2. — C: Stem nodes, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem part with leaves, ×2.5. — G: Buds, ×1. — H: Flower, ×1. — J: Apical part of capsule, ×2.5. — K: Style, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.

narrowly ovate to lanceolate, reddish or pure green, moderately to densely hairy at base, sparsely above. Petals (5—)6—7.5(—9) mm, notched to 1—1.5 mm, reddish to purplish-pink, very rarely light pink or white. Anthers (0.5—)0.65—0.8 mm, long filaments 3.5—5(—6) mm, short filaments 3—3.5(—4) mm. Style usually shorter than the long stamens, stigma 4-lobed, lobes 1—2 mm.

Capsule stalk (3—)6—10(—20) mm. Capsule (30—)40—50(—60) mm, densely

Fig. 110. *Epilobium montanum* L. — A: Habit, ×1/3. — B: Winter buds, ×1/2. — C: Stem nodes, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem part with leaf, ×2.5. — G: Buds, ×1. — H: Flower, ×1. — J: Apical part of capsules, ×2.5. — K: Style, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.


A
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hairy, hairs like those of the stem, mostly eglandular, incurved to adpressed. Seeds 1—1.1(—1.2) mm long, 0.4—0.5 mm broad, narrowly obovoidal, obtuse at apex, tapering to an acute base, without a neck, flattened side with a marked obtuse ridge and two furrows, surface with many ± irregular rows of small but distinct papillae, chalazal hairs usually 40—45, 5.5—7.5 mm long. Flower homogamous.

E. collinum occurs mostly in rather dry habitats such as hillsides and rocks. It is rather common in Norway except for the arctic parts, in Sweden from Halland, Västergötland and Östergötland north to Medelpad and Jämtland, and in the southern coastal areas of Finland. In southernmost Sweden and in the more northeastern parts of Sweden and Finland it occurs only in more or less scattered localities. In the southern part of the mountain chain it grows up to at least 1250 m.

E. collinum is a European endemic, occurring in most parts of the continent but stated to be absent from the British Isles, the Netherlands and Denmark.

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

110. **Epilobium montanum** L. 1753

Perennial herb, 20—60(—90) cm high. Stem usually simple or branched in the upper part only, but more or less stunted branches present in most leaf axils, rarely prolonged and some specimens thus branched from the base. Stem producing one or several 4—10(—15)-flowered inflorescences, usually with 3—8 pairs of leaves below the inflorescence, leaves usually shorter than the internodes. Stolons formed at the surface or subterranean, very short and inconspicuous or up to 10 mm, reddish, with dense scale-like leaves. Turions epigean, formed late in the autumn as dense rosettes of 10—15 fleshy, broadly obovate leaves 4—10 mm long, reddish with green on the upper side of the leaves.

Stem (1—)2—3(—4) mm thick, quite terete, usually sparsely hairy below, moderately to densely above, hairs 0—0.3 mm, patent to incurved, mostly glandular, the eglandular ones long and incurved.

Most leaves opposite, only the bracts alternate, all petiolate, petioles in middle and upper ones 1—6 mm, in basal ones up to 10 mm, leaf bases usually not united, never decurrent. Basal leaves smaller, spathulate to lanceolate or elliptic. Middle cauline leaves (20—)35—60(—90) mm long, (10—) 20—30(—45) mm broad, ovate or rarely narrowly ovate, acute, serrate with usually 20—40, ± irregular teeth up to 1 mm long on each side. Upper leaves smaller, short-petiolate, ovate to narrowly ovate, acute. Basal leaves subglabrous, middle and upper ones gradually becoming more hairy especially on the margin and both sides of the veins, hairs like those of the stem.

Pedicels erect in all stages. Buds ellipsoidal, blunt with a small but usually distinct mucro. Sepals (5—)6—7.5 mm, connate to 1.5—2.5 mm at base, lanceolate, acute, pure green or more or less reddish, sparsely to moderately hairy. Petals (7—)9—12(—15) mm, notched to 1.5—2 mm, reddish to purplish pink, very rarely light pink or white. Anthers (0.7—)0.8—1.0 mm, long filaments 5.5—7.5(—8.5) mm, short filaments 3.5—5 mm. Style about equalling the long stamens, stigma 4-lobed, lobes c. 2 mm.

Capsule stalk (5—)10—15(—20) mm. Capsule (40—)60—70(—80) mm, densely or rarely sparsely hairy, hairs like those of the stem, mostly glandular, erect, eglandular ones only on the ridges. Seeds (1.15—)1.2—1.3 mm long, 0.4—0.5 mm broad, narrowly obovoidal, obtuse at apex, tapering to an acute base, without a neck, flattened side with a rather inconspicuous ridge and two shallow furrows, surface with many ± irregular rows of small but distinct papillae, chalazal hairs usually 45—55, 7.5—10 mm long. Flower homogamous.

E. montanum occurs in moist woods and similar shady habitats, sometimes also

in open, moist places, but also along small roads and in other disturbed habitats. It is common in the southern lowlands of Scandinavia up to c. 62°N and along the Norwegian west coast, with scattered occurrences further north and up to c. 600 m in the mountains. It is lacking in the northern part of Finland.

E. montanum occurs throughout Europe except in the southernmost parts, and through western and northern Asia to Japan.

Known hybrids: with *E. collinum, glandulosum, hirsutum, lactiflorum, obscurum, palustre, parviflorum, roseum* and *tetragonum.*

The Iris Subgenus Susiana in Lebanon and Syria

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Twenty-three taxa belonging to *Iris* subgenus *Susiana* SPACH (Oncocyclus irises) from Lebanon and Syria have been described, their limits established, and their inter-relationships discussed. Five of the taxa are new, two represent new combinations.

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The irises belonging to the subgenus *Susiana* SPACH are commonly treated as subgenus or section *Oncocyclus,* or simply referred to as oncocyclus irises, or sometimes as oncos only. *Iris susiana,* the type species for this subgenus was described by LINNAEUS in 1753 from material cultivated in Europe. During the latter part of the 19th century BOISSIER, BERBEY, BAKER and FOSTER described some *Oncocyclus* species from the region. The largest number of species, however, was described by DINSMORE from the region described as Syria, Palestine and Sinai (1933, 1934). DAVIS (1954) considered DINSMORE's species to be microspecies. The authors, on the other hand, have found DINSMORE's observations to be much more reliable in most cases compared with those of some of the later workers. WEST (1953) and later others following WEST have observed that *I. susiana* L. does not differ greatly from *I. basaltica* DINSM. and that *I. susiana* had therefore probably been introduced into Europe from the *I. basaltica* populations in Syria. Unfortunately the present authors are not very familiar with *I. susiana* but would like to point out that *I. kirkwoodi* (including its infraspecific taxa), *I. sofarana, I. sofarana* subsp. *kasruwana* and *I. westii* have often been confused even by professional taxonomists as have other taxa, too. One need only look in almost any herbarium to see the confusion in identification of the oncocyclus species from this region when pigmentation has been the major criterion used. We feel that it would require more intensive study to say with any degree of confidence whether *I. susiana* is the same as *I. basaltica.*

In the present work the authors have tried to make use of criteria such as the rhizome, the number of leaves, the number of nodes, the kind of beard, the kind of beard hair, the morphology of style branches, the kind of pollinator tunnels, to some extent the kind of pigments (Table 1), and the cytological evidence so far available. At the same time the undesirability of exaggerated lumping together or splitting up has been kept in mind.

MATERIAL

The oncocyclus irises are notoriously unsatisfactory for studying from herbarium material. As far as was possible, therefore, natural colonies of the different taxa were surveyed. This was generally re-located live material that was collected and directly studied, or planted at the farm of the American University of Beirut in the Beqa'a Valley of Lebanon for comparison and investigation during subsequent springs. Where colonies could not be relocated or reached

Table 1. Presence/absence of absorption peaks in different nM ranges in ethanol extracts from one fall + one standard of some *Iris* subgen. *Susiana* taxa. (+) denotes that peaks are present in some of the biotypes investigated. — Peak patterns could be used as an indicator of relationships. *Iris sofarana* f. *franjieh* is a mutant and has some peaks that differ from normal populations. All colour variations in normal *I. sofarana* subsp. *sofarana* were analysed to discount minor peak variations. — A Beckman DB-G self-recording spectrophotometer was used.

Taxon	nM ranges																
	750—740	670—660	655—645	620—615	572—567	560—550	537—527	525—465	450—445	400	395—337	325—322	320—315	300—290	285—275	272—257	230—210
kirkwoodii subsp. *calcarea*	+	+	−	+	+	+	−	+	+	+	−	−	+	−	−	−	+
kirkwoodii var. *kirkwoodii*	+	+	−	+	+	+	+	+	+	+	−	−	+	+	−	−	?
kirkwoodii var. *macrotepala*	+	+	−	+	+	+	+	+	+	−	−	−	+	+	−	−	?
basaltica	+	+	−	+	+	+	+	−	+	+	−	−	+	+	−	−	+
sofarana subsp. *kasruwana*	+	+	−	+	+	+	+	−	+	+	−	−	+	−	+	−	+
sofarana subsp. *sofarana*	+	+	−	+	+	+	+	+	+	+	−	−	+	−	+	−	+
yebrudii subsp. *yebrudii*	+	+	−	+	+	+	−	+	+	+	−	−	+	+	−	−	+
hermona	+	−	+	+	+	+	−	+	+	+	−	−	+	+	−	−	+
jordana	+	+	−	+	+	+	+	−	+	+	+	−	+	+	+	+	+
bostrensis	+	+	+	+	+	+	−	−	+	+	+	−	+	+	−	−	+
auranitica f. *auranitica*	+	+	−	+	+	+	−	−	+	+	+	−	+	+	−	+	+
auranitica f. *wilkiana*	+	+	−	+	+	+	−	−	+	+	+	−	+	−	−	+	+
swensoniana	+	+	−	+	+	+	−	−	+	+	−	−	+	−	−	−	+
assadiana	+	+	−	+	+	+	?	+	+	+	−	−	+	−	+	−	+
sofarana f. *franjieh*	+	−	+	−	(+)	(+)	−	−	+	+	−	+	−	−	(+)	+	+

live material was obtained, generally through the courtesy of the Aril Society International and its members — such material included taxa from localities which, because of the political situation, are inaccessable from Lebanon. The present studies are based upon observations on live material from natural populations, except for eight taxa in which case studies are based upon imported authentic material (from natural colonies) grown together with the other taxa under the same conditions, or only on herbarium material or literature as indicated under the respective taxa in the text. The herbarium material studied is from the collections in the Post Herbarium (BEI) at the American University of Beirut, the Royal Botanic Gardens, Kew (K), and the P. MOUTERDE Herbarium, part of which is at Geneva (G) part constituting the Herbarium of the Lebanese National Council for Scientific Research (LNRC).

MORPHOLOGY

The plants belonging to this subgenus are rhizomatous; the rhizomes, though sometimes stoloniferous, are generally short and compact, the plants forming clumps. The leaves are usually arcuately upright, sometimes very strongly recurved and even circinate, the degree of curvature often changing during cultivation. The number of leaves varies from 5 to 13 in the species in the region. The stem varies in length from about one decimeter to one metre. The general appearance of the plants is such that they can easily be identified as belonging to this subgenus on their vegetative parts alone, provided one is somewhat familiar with the group. The plants are uniflorous. The peduncle varies in length and may be completely covered by the leaves or exposed — the number of nodes visible above the basal leaves is very often a reliable character in the identification of some of the taxa. The flower has the characteristic iris morphology. It is enclosed by a pair of spathes or "valves" which may be inflated or not and then

tightly clasping the ovary. The outer perianth leaves are known as "falls" which in this subgenus are usually recurved and even folded back. The basal half of the fall has a patch of dense or sparse hairs on the dorsal face, the hairs constituting the beard. The beard hairs may be long (up to about 1 cm) or more often short (not exceeding 0.5 cm). When the beard is dense, the hairs may be longest in the middle gradually decreasing in length towards the sides, or the hairs may form a brush along the median region and the lateral piles may then be of very short hairs. Along the median region at the end of the beard a signal spot usually of a darker colour is present. In paler biotypes the signal spot can be paler or even indistinct. The inner perianth leaves, the standards, are erect and often laterally recurved. The petaloid style is trifurcate, the three branches superposed above the falls, each having a stamen tucked beneath it. At the tip each branch is divided into two lobes (the lobes have also been referred to as crests). These are upright, often recurved, and are usually the same colour as the falls.

The style branches are usually arched or keeled and laterally incurved. These branches, that by the degrees of their arching and lateral incurving form tubular, straight or oblique—horizontal or arched tunnels, are referred to here as pollinator tunnels, the floors of which are contributed by the respective fall. There are variations in the form and structure of the pollinator tunnels — in some the style branches and the falls contribute equally to the lateral walls of the tunnel, or the falls may contribute the floor only while the lateral walls are made by the proportionately wider style branches; or the style branches may be raised horizontally or obliquely upwards above the falls forming a sort of laterally open tunnel. Below the tip of each style branch is a pouch-like structure, the stigmatic pouch, facing outwards. The anthers lie almost parallel with and covered by the style branch, the tip of the anther hardly ever reaching beyond the base of the stigmatic pouch. Presumably, the floral pigmentation (together with the smell in certain cases) attracts the particular kind/s of pollinator/s to the flower. The wider the range of the pigments present the greater the number of different kinds of insects attracted may be. The size and the shape of the pollinator tunnel could possibly restrict the number of kinds of pollinators. The beard hairs are directed outwards and the pollinator, therefore, presumably riding the hairs reaches up first the stigmatic pouch (where any pollen that the pollinator may be carrying on its dorsal side would get deposited) and then the anthers.

The fruit is a 3-chambered capsule which is usually inflated, often appearing 6-lobed because of the two rows of seeds present in each chamber; in one species at least the pod is cylindrical and not lobed except when it begins to shrink during the process of drying up. The dehiscence of the capsule is longitudinal loculicidal. The seeds on drying up are usually dark, almost black in colour with a prominent white, circular, "sucker-mouth" aril. The term oncocyclus was probably derived from this "circular-callosity" by SIEMSSEN (1846) who first used it.

It could be of significance that in species inhabiting areas that are relatively more arid the style branches and their lobes are of a paler colour, contrasting with the falls. Moreover, the yellow pigment in these species is to some extent discernable, while the flower size and shape also differ to some extent from those of the species found growing in the western Lebanese ranges and the Anti-lebanon.

DELIMITATION, PHYLOGENY AND SUBDIVISION

Contrary to a number of treatments (e. g. LAWRENCE 1953, RODIONENKO 1961),

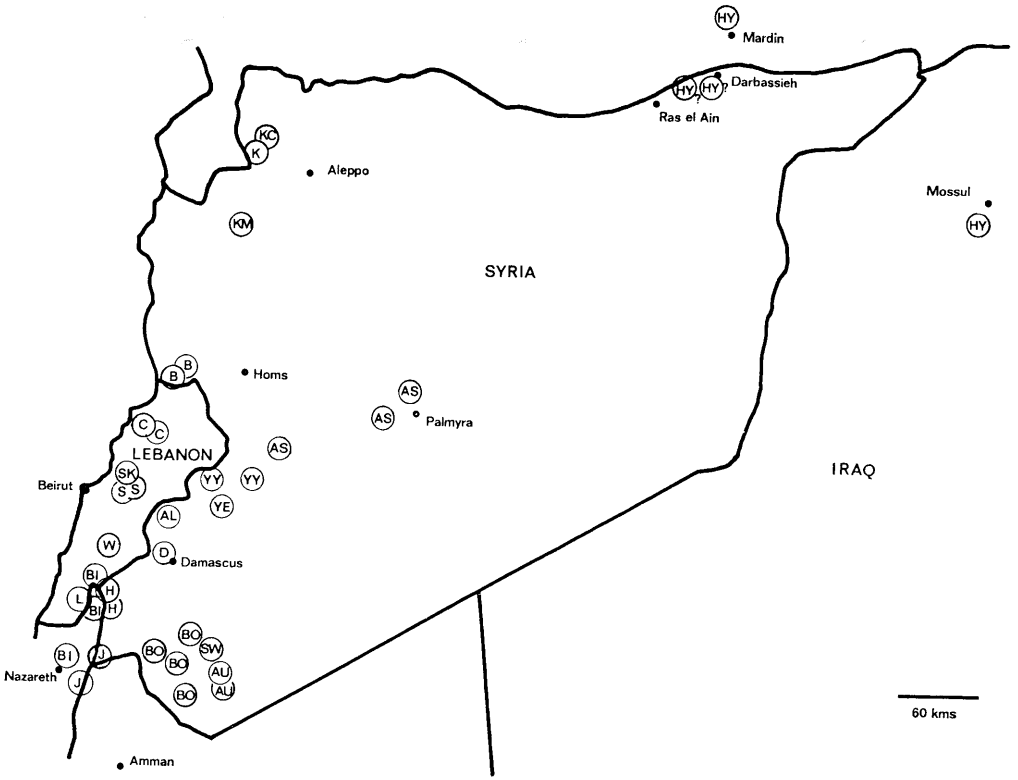


Fig. 1. Map of the region showing the distribution of the following *Iris* taxa: AL *antilibanotica*. — AS *assadiana*. — AU *auranitica*. — B *basaltica*. — BI *bismarckiana*. — BO *bostrensis*. — C *cedreti*. — D *damascena*. — H *hermona*. — HY, HY? *heylandiana*. — J *jordana*. — KC *kirkwoodii* subsp. *calcarea*. — K *kirkwoodii* subsp. *kirkwoodii* var. *kirkwoodii*. — KM *kirkwoodii* subsp. *kirkwoodii* var. *macrotepala*. — L *lortetii*. — SK *sofarana* subsp. *kasruwana*. — S *sofarana* subsp. *sofarana*. — SW *swensoniana*. — W *westii*. — YE *yebrudii* subsp. *edgecombii*. — YY *yebrudii* subsp. *yebrudii*.

the authors consider that the oncocyclus irises constitute a group sufficiently distinct both morphologically and cytologically to merit consideration at subgenus level — *Iris* subgenus *Susiana* SPACH. Morphologically, this group can be identified even on vegetative characters. Cytologically it is characterized by the basic chromosome number x=10, and in having probably the most asymmetrical karyotype in the genus *Iris*. The synonymy given below is reproduced chiefly from LAWRENCE (1953) and WERCKMEISTER (1967).

Iris L. subgenus **Susiana** SPACH

SPACH 1846 in Ann. Sc. Nat. Ser. 3, 5: 110; 1846 in Hist. Nat. Veg. 12: 70—71.

Genus *Oncocyclus* SIEMSS. 1846 in Bot. Zeit. 4: 706—707.

Subgenus *Oncocyclus* (SIEMSS.) ALEF. 1863 in Bot. Zeit. 21: 296; BAKER 1877 in J. Linn. Soc. Lond. (Bot). 16: 142.

Section *Oncocyclus* (SIEMSS.) BAK. 1876 in Gard. Chron. Ser. 3, 5: 788.

Subgenus *Pogoniris* RANDOLPH 1948 in Bull. Amer. Iris Soc. 109: 4; non SPACH 1846, nec BAK. 1876.

Subsection *Oncocyclus* (SIEMSS.) BENTH. as in LAWRENCE 1953 in Gentes Herb. 7, Fasc. 4: 346; as in RODIONENKO 1961, Genus Iris, Akad. Nauk. USSR.

On the basis of the present studies, the authors propose four definite groups of oncocyclus irises in the region (Fig. 1): (1) the species growing in the Lebanese western ranges and extending northwards into Syria; (2) the Antilebanon group of species; (3) the southern Syrian, Jordanian and partly Palestinian group of species; and (4) the eastern Syrian desert and northeastern Syrian group of species. The western Lebanese range and adjacent southwestern Syrian group includes *I. sofarana, I. cedreti, I. basaltica,* and *I. kirkwoodii.* The Antilebanon group includes species growing on this range and on the adjoining plateaux, viz. *I. bismarckiana, I. hermona, I. lortetii, I. antilibanotica, I. damascena,* and *I. yebrudii. I. westii* occupies a position midway between the above two groups. The Jabl-Druze, Hauran, northern Jordan and northeastern Palestine regions have species with clavate non-echinate beard hairs, and dense beards (except *I. jordana*). In most of these species the yellow pigment is discernable through the dense purple spotting, or the style branches are shades of yellow-orange. The eastern Syrian desert and its northeastern region have two reported species: *I. heylandiana,* and *I. assadiana.* Both of these have clavate-cylindrical, non-echinate beard hairs. *I. assadiana* is stoloniferous and, probably, so too is *I. heylandiana.* The latter has a linear beard of uniform-sized, relatively sparse hairs which spread out laterally near the base of the falls. *I. assadiana* has a linear median brush of long, dense hairs surrounded laterally by very short, dense, purple hairs. This beard character is intermediate between the northern Syrian—southern Turkish group of irises in the north and the Hauran—northern Palestine—Jordanian group in the south. Obviously, the northern Syrian—southern Turkish group of oncos needs to be studied in detail to establish the species limits in the complex. *I. jordana* is a taxon which shows similarities to the Hauran group of oncos though the beard and foliage characters are strikingly different and point to the possibility of another complex (or only a relict?) in the Palestinian region.

It has often been suggested (e.g. DAVIS 1954) that the oncocyclus group in the Levant has evolved from a southwestern expansion of the Irano-Turanian groups from the mountains south—west of the Caspian. Cytological evidence (WEYMOUTH & CHAUDHARY 1974) indicates that the species partly comprising the group *Sofaranae* of WEYMOUTH & CHAUDHARY and endemic to the western Lebanese ranges and to the adjoining Syria in the North are the most primitive of the species studied. The species endemic to Jabal-Druze, the Hauran, northern Jordan and the adjoining region are apparently the most advanced of the species investigated. Considering this evidence it could be suggested that the species endemic to the western Lebanese ranges and the adjoining Syrian territory in the north at least, have originated from a southerly expansion of the group from southern Turkey. Such a view would be supported by the karyotype of *I. kirkwoodii* subsp. *calcarea,* which could be regarded as the most primitive, a possibility suggested by WEYMOUTH and CHAUDHARY (1974).

In the present work we have followed WEYMOUTH and CHAUDHARY in dividing the subgenus *Susiana* into two groups — their "*Sofaranae*" and "*Purpuro-aurantae*". However, we feel that these groups should be treated as sections of the subgenus, and therefore, propose the sections as below. The species within a section have been arranged according to the sequence that we feel is the most natural in view of the information at present available. However, *I. jordana, I. heylandiana* and *I. assadiana* (*I.* sp. affin. *barnumae* in WEYMOUTH & CHAUDHARY 1974) have been placed under the section *Bostria* (group "*Purpuro-aurantae*" of WEYMOUTH & CHAUDHARY) only for the sake of convenience. They probably belong to other

complexes which may need to be separated as more information becomes available.

We do recognize section *Oncocyclus* (SIEMSS.) BAK. (with *I. paradoxa* STEVEN as the type species) as a section under the subgenus *Susiana,* which name has priority at the rank of section. This section is, apparently, quite distinct from those proposed below and is not represented in the region.

Section Sofaria

Group *Sofaranae* of WEYMOUTH & CHAUDHARY 1974.

Tepala externa fere numquam longiora quam 1 1/2 lata. Barba sparsa, capillis papillato-echinatis. In taxis a nos cognitis chromosomata quod longitudinem in series bene distinctas divisa.

Falls usually not more than 1.5 times as long as wide. Beard of sparse, papillate—echinate hairs. In the taxa for which the information is available (WEYMOUTH & CHAUDHARY 1974), the chromosomes fall into distinct length groups and do not intergrade from the longest to the shortest.

Type species: *I. sofarana* FOST.

Species included: *I. antilibanotica* DINSM., *I. basaltica* DINSM., *I. bismarckiana* DAMM. & SPRENG., *I. cedreti* DINSM. ex CHAUDHR., *I. damascena* MOUTRD., *I. hermona* DINSM., *I. kirkwoodii* CHAUDHR., *I. lortetii* BARB., *I. sofarana* FOST., *I. westii* DINSM., and *I. yebrudii* DINSM. ex CHAUDHR.

Section Bostria

Group *Purpuro-aurantae* of WEYMOUTH & CHAUDHARY 1974.

Tepala externa plerumque sescuplo longiora latiora. Barba densa, pulvino similis vel linearis (sparsa ut in *I. jordana*) vel capillis clavato-cylindratis, non echinatis. In taxis a nos cognitis longitudo chromosomatum variat sine limite distincto.

Falls usually more than 1 1/2 times as long as wide (except *I. jordana*). Beard hairs clavate—cylindrical, not echinate; beard dense and cushion-like or linear or both, or sparse (as in *I. jordana*). In the taxa for which information is available the chromosomes intergrade in length from the longest to the shortest without a sharp break into length groups.

Type species: *I. bostrensis* MOUTRD.

Species included: *I. assadiana* CHAUDHARY et al., sp. nov., *I. auranitica* DINSM., *I. bostrensis* MOUTRD., *I. heylandiana* BOISS. & REUT., *I. jordana* DINSM., *I. swensoniana* CHAUDHARY et al., sp. nov.

KEY TO THE TAXA IN LEBANON AND SYRIA

1. Falls usually not more than 1.5 times as long as wide; beard of sparse and/or papillate—echinate hairs 2
1. Falls usually more than 1.5 times as long as wide and/or the beard hairs clavate—cylindrical, not echinate 16
2. Rhizome stoloniferous ..... 10. *bismarckiana*
2. Rhizome not stoloniferous 3
3. Falls uniformly red-purple to dark purple or almost so, without any veins or spots ..... 16. *antilibanotica*
3. Falls obviously veined, dotted or spotted, not uniformly coloured 4
4. Width of a style branch equal to or greater than the combined width of its two lobes 5
4. Width of a style branch less than the combined width of its two lobes 8
5. Flower shades of pink—red; standards white with pink—violet veins; bases of standards tending to converge below style branches ..... 12. *lortetii*
5. Flowers not shades of pink—red, but shades of purple—dark purple 6
6. Venation of falls typically felty-thick, embossed on both surfaces; stem leaves 3—4 ..... 4. *basaltica*
6. Venation of falls not felty-thick, if embossed then only on upper surface; stem leaves less than 3 7
7. Venation of falls very dense (10—13 per cm); style branches less than 3 cm wide ..... 8. *cedreti*

7. Venation of falls less dense; style branches 3 cm wide or more ..... 7. *sofarana* subsp. *kasruwana*
8. Peduncle length usually more than 15 cm from the last node; stem leaves 2 or more 9
8. Peduncle length usually 15 cm or less from the last node; stem leaf 0—1 10
9. Leaves 5—7, about 1.5 cm wide; falls ovate—orbiculate, 8 cm long or less; signal spot nearer the distal end ..... 1. *kirkwoodii* var. *kirkwoodii*
9. Leaves 8—9, about 1 cm wide; falls ovate—oval, about 10 cm long; spot almost equidistant from the two ends ..... 2. *kirkwoodii* var. *macrotepala*
9. Leaves 7—9, about 1.5 cm wide; falls obovate—orbiculate, about 8 cm long or less; signal spot nearer the distal end ..... 3. *kirkwoodii* subsp. *calcarea*
10. Leaves more than 1 cm wide 11
10. Leaves 1 cm wide or less 13
11. Falls white or yellow, the yellowness due to dense spots of varying shades of yellow ..... 6. *sofarana* f. *franjieh*
11. Falls not white—yellow but shades of purple, maroon-purple or violet purple 12
12. Standards in striking contrast to the falls clear white with widely spaced very fine veins; leaves not widely divergent ..... 11. *hermona*
12. Standards without the clear white or dirty white colour dominating; the veins and dots thick and/or dense; leaves divergent, not closely appressed ..... 5. *sofarana* f. *sofarana*
13. Style branches more than 3 cm wide ..... 15. *yebrudii* subsp. *edgecombii*
13. Style branches 3 cm wide or less 14
14. Length of style branches including the lobes not more than 5 cm .... 13. *damascena*
14. Length of style branches including the lobes more than 5 cm 15
15. Style branches oblique—horizontal; plants rather tall (up to about 30 cm); leaves not strongly arched, usually exceeding 15 cm ..... 9. *westii*
15. Style branches arched downwards; plants usually not exceeding 20 cm; leaves strongly arched, hardly exceeding 15 cm ..... 14. *yebrudii* subsp. *yebrudii*
16. Beard linear or brush-like in the median region 17
16. Beard dense or cushion-like or of sparse hairs but not linear or brush-like 18
17. Plants small, hardly ever exceeding 20 cm; rhizome very small, stoloniferous; beard a median brush of yellow hairs more than 5 mm long and surrounded by lateral bands of very small, purple hairs ..... 18. *assadiana*
17. Plants taller; rhizome medium (stoloniferous?); beard linear, of white, uniform-sized, relatively sparse hairs spreading laterally in the basal region of the fall .... 17. *heylandiana*
18. Flowers yellow or bronze; flowering May—June 19
18. Flowers not yellow—bronze; flowering March—April 20
19. Falls and standards with fine, red—purple veins and very fine, dense dots ..... 21. *auranitica* f. *auranitica*
19. Falls and standards without fine, red—purple veins or dots .. 22. *auranitica* f. *wilkiana*
20. Leaves about 2 cm wide; beard of sparse hairs, not cushion-like ..... 19. *jordana*
20. Leaves usually 1 cm wide or less; beard of dense hairs, cushion-like 21
21. Falls and standards with the ground golden yellow, with dense spotting of purple (when apparently purple, the yellow ground still showing through it as dots or spots); beard hairs all yellow, minutely tipped with purple; style branches golden yellow with very minute dark brown—purple spots which become streaks towards the sides and the lobes ..... 20. *bostrensis*
21. Falls and standards uniformly purple; style branches orange, strongly streaked with purple; beard hairs in a golden yellow median band and purple lateral bands ..... 23. *swensoniana*

1. **Iris kirkwoodii** CHAUDHARY subsp. **kirkwoodii** var. **kirkwoodii** — Fig. 2

CHAUDHARY 1972 in Bot. Notiser 125: 499. — Orig. coll.: Syria, Bishmishly, April 1972, KIRKWOOD & CHAUDHARY 787 (holotype, BEI).

Plants up to 75 cm. Rhizome large, compact, yellowish-brown. Leaves 5—7 in number, rather grassy—droopy, up to 1.5 cm wide, 30 cm long, pale green. Stem leaves one or two with one or two internodes showing through or above the basal leaves; peduncle length usually 25 cm or more. Flowers about 15 cm tall, 8—10 cm wide; valves tightly clasping, not inflated, about 11 cm; ovary 3—3.5 cm, almost

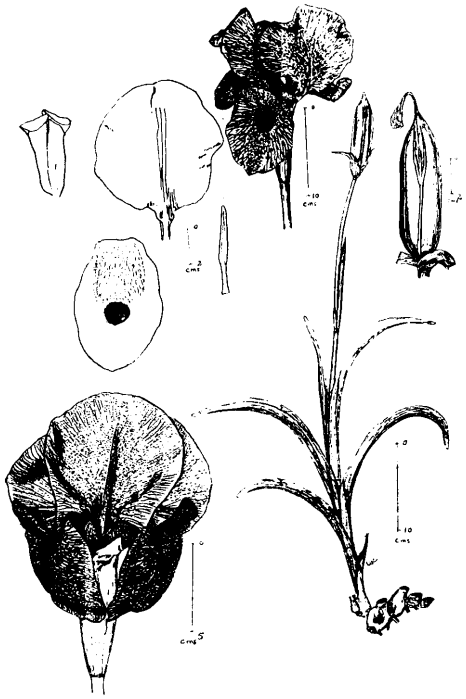


Fig. 2. *Iris kirkwoodii* subsp. *kirkwoodii* var. *kirkwoodii*.

terete or slightly trigonal with a stalk about 0.5 cm; perianth tube 2.5—3 cm. Falls 6—8 cm long, 4—5 cm wide, ovate—orbiculate, often strongly recurved, embossed with dark purple veins and fine dots densely scattered on a pale greenish or white, clear ground, the spots larger and denser below and to the sides of the signal spot; the signal spot orbicular, sometimes ovate, 1.5—2 cm long, about 1.5 cm wide; beard of long, maroon-purple or rusty-brown hairs. Standards about 8.5 cm long, 6—7.5 cm wide, orbicular—ovate, abruptly clawed with the claw channelled and about 1 cm; the standards with fine blue-purple veins and dots on a clear pale blue ground, the dots and veins embossed only near the base and along the midrib. Anthers 2—3.5 cm, purple-backed; filaments 1.2—2 cm, purple-dotted. Style branches about 7 cm long including the lobes, 3—4 cm wide, dark maroon in the middle, dark purple to the sides, ridge keeled, the ridge prominent; the lobes minutely serrate, turned upwards; the width of the two lobes greater than the width of the style branches; lobes with fine embossed veins and very fine dots like the falls; pollinator tunnel similar to that in *I. sofarana* subsp. *sofarana* (Fig. 4 C a). Pods about 9 cm long, cylindrical, not lobed, the veins thick, prominent, raised above the surface or level with it.

DISTRIBUTION: Endemic to the Bishmishly area in northern Syria.

MATERIAL: The natural population at the type locality and transplants from that locality.

2. **Iris kirkwoodii** CHAUDHARY subsp. **kirkwoodii** var. **macrotepala** CHAUDHARY et al., var. nov. — Fig. 3

Orig. coll.: Northern Syria, El-Bara, April 1974, KIRKWOOD 1403 (holotype, BEI).

Planta c. 1 m alta. Folia 8—10. Flores c.

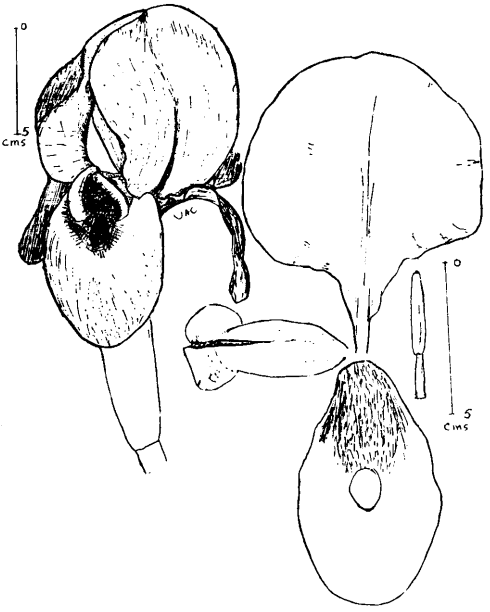


Fig. 3. *Iris kirkwoodii* subsp. *kirkwoodii* var. *macrotepala*.

17 cm longi a basi spatharum, 10—12 cm lati. Tepala externa ovato-elliptica, c. 10 cm longa, c. 6 cm lata, maculae et venae parum caelatae, maronino-purpureae ad violaceo-purpureae. Tepala interna orbiculata, abrupte unguiculata, c. 11.5 cm longa, c. 9.5 cm lata.

Plants about one metre. Rhizome large, compact, yellowish-brown. Leaves 8—10, about 1 cm wide, up to 50 cm long, grassy—droopy, pale green; stem leaves usually 3, with 2 or 3 nodes showing through or above the basal leaves. Peduncle about 20 cm. Flowers 15—17 cm tall from the base of the valves, 9—11 cm wide; valves 8—10 cm, purple-tinged, tightly clasping; ovary 3—3.5 cm; perianth tube about 2.5 cm. Falls about 10 cm long, 6 cm wide, ovate, ground creamy-white, the dots and veins slightly embossed, maroon-purple to violet-purple; signal spot oval or orbicular, enclosed in a dense band of strongly embossed maroon-purple dots; about 2 cm long and 1—1.5 cm wide; beard of violet-purple or golden hairs. Standards about 11.5 cm long, 9.5 cm wide, orbiculate, rather abruptly clawed, the claw about 1.5 cm, channelled; the ground pale blue with fine, violet-purple veins and dots, the latter denser and bigger towards the central and basal areas. Anthers about 3 cm, purple-backed; filaments about 2 cm. Style branches about 7 cm long including the lobes, 3.5 cm wide, ridge-keeled, the ridge very prominent; the width of the two lobes greater than the width of the style branch; pollinator tunnel similar to that in *I. sofarana* subsp. *sofarana*. Pod?

DISTRIBUTION: Endemic to the El-Bara area in northern Syria.

3. **Iris kirkwoodii** CHAUDHARY subsp. **calcarea** CHAUDHARY et al., subsp. nov. — Fig. 4 A

I. calcarea DINSMORE in sched. — Orig. coll.: Syria, Deir Semaan, April 1971, CHAUDHARY 785 (holotype, BEI).

Planta 30—80 cm alta. Rhizoma magnum, compactum. Folia 7—9, c. 25 cm longa, 1—1.5 cm lata, plus minusve firmiter recurva; folia caulina 2 vel 3. Flores 15—25 cm longi a basi spatharum, c. 8 cm lati; pedunculi 15—25 cm longi a nodo ultimo. Tepala externa obovato-orbiculata, c. 8 cm longa, 5—6 cm lata, maculis caelatis vel venis purpureis-atromaroninis; fundus leviter viridis: macula media 2—2.2 cm lata, 1.5—2 cm longa, atromaronina; barba capillis longis, non densis, atromaroninis. Tepala interna 8—11.5 cm longa, 5.5—8 cm lata, orbiculata, unguibus parvis; venis purpureis vel atropurpureis; maculae caelatae; fundus caeruleus, clarus. Antherae 2—2.2 cm longae; fila c. 1.5 cm, robusta. Rami styli c. 7 cm longi (lobis inclusis), 2.5—3 cm lati, cristati et carinati; maculae et venae loborum ut in tepalis externis; uterque lobus rami styli latior; canaliculus pollinicus fere ut in *I. sofarana* subsp. *sofarana*.

Plants 30—80 cm. Rhizome large, compact, light yellow to brownish-yellow. Leaves 7—9, 1—1.5 cm wide, up to 30 cm long, rather strongly recurved or droopy, pale green; stem leaves 2—3, the 2—3 nodes visible through or above the basal leaves. Peduncle 15—25 cm. Flowers about 15 cm tall from base of the valves, about 8 cm wide; valves rather leathery, tightly clasping, purple-tinged. Ovary 3—3.5 cm, almost terete; perianth tube about 4 cm. Falls about 8 cm long, 5—6 cm wide, obovate—orbiculate, embossed dotted and/or veined with dark purplish-red on a pale green ground: signal spot 2—2.2 cm wide, 1.5—2 cm long, velvety dark maroon; beard of long, dark maroon, rather sparse hairs; the signal spot and the peripheral part of the beard often surrounded by or heavily outlined with dark, dense, larger spots, the signal spot then appearing very large. Standards 8—11.5 cm long, 8 cm wide, the limb orbiculate, tapering to a thick claw about 1.5 cm; veined with purple or dark purple, the dots embossed, the veins not so, the ground light blue, clear, covered almost uniformly on and between the veins in the central area with blue-purple dots which become sparse towards the margin and denser and maroon towards the base. Anthers 2—2.2 cm; filaments about 1.5 cm, rather stout. Style branches about 7 cm long including the lobes, 2.5—3 cm wide, ridge-keeled,

the ridge more prominent near the lobes; the lobes upturned, slightly fringed at the margins, dotted and veined like the falls; the width of the two lobes greater than the width of the style branch; pollinator tunnel more or less like that in *I. sofarana* subsp. *sofarana* only flatter. Pod about 9 cm, cylindrical, not inflated, the veins thick, prominent, raised above the surface or level with it.

DISTRIBUTION: Endemic to the Deir Semaan area, Syria.

MATERIAL: Live culture. — Collections: April 1972, KIRKWOOD 790 (BEI); April 1938, DINSMORE 20393 (BEI).

NOTES: MOUTERDE (1969) considered this taxon was no different from *I. sofarana* subsp. *sofarana*. One of us (CHAUDHARY 1971) had also proposed the name *I. sofarana* var. *calcarea* (published only as an abstract of a paper read). However, a more careful study has shown that this taxon has its closest affinities with *I. kirkwoodii*, the affinities even with *I. basaltica* being closer than with *I. sofarana*.

4. **Iris basaltica** DINSMORE — Fig. 4 B

DINSMORE 1933, Pl. Post. Dinsm. 2: 9; 1934 in POST & DINSMORE, Fl. Syr. Pal. & Sin. 2: 597; MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 317. — Orig. coll.: Syria, Kalaat-ul Husn (Krak de Chevaliers) area, March—April 19--, WEST (DINSMORE Herbarium? not seen).

Plants up to 70 cm. Rhizome large, compact, dark brown. Leaves 9—12, thickish, slightly arched, 1.5—2 cm wide, about 24 cm long; stem leaves usually 3 or 4, the nodes bearing these visible through or above the basal leaves. Peduncle 15—25 cm. Flowers about 15 cm tall from the base of the valves, about 9 cm wide; valves about 11 cm, tightly clasping, distinctly keeled, purple-tinged in the top 1/4; ovary about 2.5 cm, trigonal; perianth tube about 2.8 cm. Falls about 9 cm long, about 5 cm broad, rather tightly clasping at the base, ovate or somewhat lanceolate, embossed with thick, almost felty, dark purple to almost black veins both on the upper and the lower faces, the dots restricted mostly to the middle region below the signal patch and laterally above the signal patch; the ground pale greenish, clear; signal patch usually truncate-triangular or orbiculate, about 1.5 cm long and 1.5 cm at its widest; beard of rather sparse, long, maroon-purple hairs tipped with rusty yellow. Standards 8.5—10.5 cm long, 7—7.5 cm wide, the limb almost orbicular, abruptly narrowed into a claw about 2 cm long and about 1 cm wide, with embossed (felty-thick) finer, dark purple veins and embossed dots on both surfaces, the dots restricted to the central area, the ground pale greenish, clear; more than 1/4 of the basal part with scattered long purple hairs, the hairs denser in the channel of the claw. Anthers creamy white, about 3 cm; filaments about 1.5 cm, stout. Style branches about 8 cm long including the lobes, about 3.5 cm wide, densely maroon-purple-spotted, the dots increasing in size towards the lobes; keel very prominently ridged; lobes with embossed dark spots and veins like the falls, irregularly serrate; the width of the lobes not more than the width of the style branch; pollinator tunnel rather flat and long, both the fall base and the style branch contributing to the walls of the tunnel. Pod inflated, 6-lobed, 6—11 cm, the veins lying in the furrows.

DISTRIBUTION: Endemic to the Tell Kalakh-Hadidia region, Syria. In danger of extinction.

MATERIAL: Tell Kalakh, Hadidia, and Kalaat-ul-Husn (type locality) populations, and cultivated material from the above areas. — Collections: Krak de Chevaliers, April 1943, DINSMORE 15956 (BEI, not in good condition); Hadidia, April 1972, CHAUDHARY 791 (lectotype, BEI).


A
B
C
D
a
a

5. **Iris sofarana** FOSTER subsp. **sofarana** f. **sofarana** — Fig. 4 C

FOSTER 1889 in Gard. Chron., iii. 26: 389; POST & DINSMORE 1933, Fl. Syr. Pal. & Sin. 2: 598; MOUTERDE 1966, Nouv. Fl. Lib. Syr. 2: 319. — Orig. coll.: Lebanon, Sofar (Ayen Sofar), April 18--, FOSTER (not seen).

Plants up to 40 cm. Rhizome rather large, compact, yellowish-brown. Leaves 8—9, 1.2—2.5 cm wide, up to 25 cm long, somewhat divergent, if falcate then not strongly so; the node bearing the single stem leaf only rarely visible above the basal leaves. Peduncle usually 11—14 cm (often longer under culture). Flowers 15—18 cm tall from base of valves, 10—12 cm wide: valves up to 11 cm, inflated, green; ovary about 3.5 cm, trigonal; perianth tube about 2.5 cm. Falls 8—8.5×5—6.5 cm, obovate, the limb orbiculate, rarely ovate, the base tightly clasping the style branches laterally; the ground creamy white, thickly covered with brown-purple to bluish-purple veins and spots, the colour range varying from bluish-purple to red-purple; beard hairs dark purple, rather scattered; signal spot orbiculate, wider than long, 1.2—1.5 cm long, 1.5—2 cm wide, dark purple, located more than halfway towards the apex. Standards about 9.5—10.5×7—8 cm, orbiculate, the limb abruptly narrowed into a short claw; the ground clear white to inky blue with the veins fine, blue-purple to dark purple or maroon-purple; the dots similar in colour to veins, very fine, rather dense in the central area making it look blue-purple or dark maroon-purple; the veins not dense (6—11 per cm). Stamens about 4 cm; anthers 2.5—3 cm, creamy yellow: filaments 1—1.5 cm, purplish. Style branches about 7 cm long including the lobes, 3 cm wide, the ridge of the keel very prominent; lobes of style branch upturned, crenate, veined and spotted like the falls; the total width of the two lobes more than the width of the style branch; pollinator tunnel formed by the fall and the style branch, the base of the fall tightly clasping the style branch (Fig. 4 C a). Pods about 10.5 cm long, 3 cm wide, inflated and 6-lobed, narrowed towards both ends.

DISTRIBUTION: Endemic to Lebanon in two known localities.

MATERIAL: The Falougha area (probably the type locality) and the Zehleh Pass population were investigated. — Collections: Falougha area: May 1963, EDGECOMBE A-1333, A-1189 (BEI); May 1964, EDGECOMBE B-295 (BEI); May 1972, CHAUDHARY 1215 (lectotype, BEI). Zahleh Pass area: May 1963, EDGECOMBE B-298 (BEI); May 1964, SLOANE (BEI). Between Beirut and Damascus (probably Falougha colony) May 1955, TROTT 3002 (K).

6. **Iris sofarana** FOSTER subsp. **sofarana** f. **franjieh** CHAUDHARY et al., f. nov.

Orig. coll.: Lebanon, Falougha area, April 1974, CHAUDHARY 1405 (holotype, BEI).

Haec forma differt a f. *sofarana* floribus flavis vel candidis pigmento purpureo carentibus.

This form differs from f. *sofarana* only in lacking blue-purple pigmentation in floral parts which may be pure silky white with yellow showing near the bases of floral parts, or the falls only are yellow on the basal half, or the falls look completely yellow and the standards lighter yellow or white. The yellowness of the floral parts is due to yellow, dense spots, the shades of yellow only varying.

DISTRIBUTION: So far these apparently mutant forms have been observed growing in the type locality only near Falougha in Lebanon.

NOTE: This form is named after Mrs IRIS FRANJIEH, patroness of the Horticultural Society of Lebanon.

Fig. 4. A: *Iris kirkwoodii* subsp. *calcarea*. — B: *Iris basaltica*. — C: *Iris sofarana* subsp. *sofarana* var. *sofarana*. — D: *Iris sofarana* subsp. *kasruwana*. — a: pollinator tunnel.

7. **Iris sofarana** FOSTER subsp. **kasruwana** (DINSMORE) CHAUDHARY et al., comb. nov. — Fig. 4 D

I. kasruwana DINSMORE 1933, Pl. Post. Dinsm. 2: 9; 1934 in POST & DINSMORE, Fl. Syr. Pal. & Sin. 2: 597. — *I. sofarana* f. *kasruwana* (DINSMORE) MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 319. — Orig. coll.: Lebanon, Naba-al-Asal, May 19--, WEST (DINSMORE Herbarium? not seen).

Plants about 50 cm. Rhizome rather large, compact, brown. Leaves up to 10, 1.2—1.7 cm wide, up to 20 cm long, not wide-spreading; stem leaves usually 2, often ending at about the same level. Peduncle about 22 cm, often the two nodes bearing the stem leaves visible above or through the basal leaves. Flowers about 18 cm tall from the base of the valves, about 10 cm wide; valves to about 9 cm, ventricose, pinkish-purple in the upper half; ovary 3—4.5 cm, broadly triangular; perianth tube 3.5—4 cm. Falls 8—10 cm long, 6—7.5 cm wide, ovate, the base rather flat, not tightly clasping; densely streaked and dotted with dark purple, the dots more prominent, smaller, and dense near the signal patch; the signal patch more or less tearshaped, longer than wide, 1.5—2.5×0.6—1.5 cm; the lower end of the signal spot more than halfway up the length of the fall towards the base; beard hairs sparse, purple, tipped with yellow or rusty brown. Standards 8—11 cm long, 6—8 cm wide, obovate, gradually tapering to a claw, the claw about 1 cm, channelled; the ground clear white to purplish-white to inky blue with dark purple veins and dots, the dots finer, elongating and anastomosing in the middle basal parts. Stamens up to 4 cm; anthers about 2.5 cm, creamy yellow or purple-backed; filaments about 1.5 cm, purple all over or towards the base only. Style branches 5.5—7.5 cm long including the lobes, 3—4 cm wide, maroon-purple in the middle, dark purple to the sides, ridge keeled, the ridge very prominent; the lobes of the style branches irregularly spotted and streaked like the falls; the width of the two lobes hardly if at all exceeding the width of the style branch; pollinator tunnel formed mainly by the style branch with the base of the fall contributing the floor of tunnel (Fig. 4 D a). Pods up to 10 cm long, up to about 4 cm wide, 6-lobed, narrowed towards both ends.

DISTRIBUTION: Endemic to Lebanon; in two known populations.

MATERIAL: The Naba-al-Asal (type locality) and the Laqlouq populations were investigated. — Collections: Naba-al-Asal April 1971, CHAUDHARY 790 (lectotype, BEI); May 1952, MOONEY 4383 (K).

8. **Iris cedreti** DINSMORE ex CHAUDHARY — Fig. 5 A

CHAUDHARY 1972 in Bot. Notiser 125: 497—499. — Orig. coll.: Lebanon, vicinity of Cedars of Lebanon, May 1972, CHAUDHARY, CHAUDHARY & WEYMOUTH 789 (holotype, BEI).

Plants rarely exceeding 40 cm. Rhizome medium, compact, light yellow. Leaves 8 or 9, 1—2 cm wide, up to 23 cm long, narrowed to the tip; stem leaf none or one. Peduncle 9—12 cm. Flowers about 18 cm tall from the base of the valves, up to 9 cm wide; valves about 10 cm, reaching to the level of the falls, inflated, green; ovary about 3.3 cm, triangular, 6-lobed, the ovary stalk 0.5 to 1 cm; perianth tube 2.5—3 cm. Falls 6.5—9.5 cm long, 4.5—5.5 cm wide, ovate, narrowed to the tip, finely crenate—irregularly serrate, the ground clear, white to lead-white; veins very fine, embossed, densely arranged (10—13 per cm), dark-maroon to maroon-purple; dots very fine, more embossed around the signal spot and the area above this level; in the darker biotypes the dots on the falls are larger, anastomosing so closely that the dots form the ground and the ground appears as irregular white spots; signal spot orbiculate, 1.7—2 cm long and about 1.5 cm wide, located almost in the middle of the fall, dark maroon-

purple; beard of sparse hairs, the hairs rusty brown, pink, purple or mottled on a pale green ground. Standards 8.5—11 cm long, 6—7.5 cm wide, obovate, clawed, the claw about 1.5 cm long, channelled; the ground characteristically white to lead-white; veins very fine purplish—dark maroon, rather embossed, parallelly densely arranged (13—20 per cm); dots very fine, very sparse near the margin, larger and sparse in the central area, finer and denser in the lateral zones; the inner and outer faces of the standard with distinctly different shades (a character very rarely to be seen in *I. sofarana* subsp. *sofarana* and often in *I. jordana*); on the inner face the white to lead-white ground dominates while on the outer face the purplish—dark maroon dominates. Stamens 3.5—4 cm, the anthers usually more than twice as long as the filaments, the anthers creamy white, sometimes purple-backed. Style branches 5.5—6 cm long including the lobes, about 2 cm wide, strongly arched along the arch of the fall (the latter contributing only the floor of the pollinator tunnel), strongly narrowly keeled, the keel with a small ridge, maroon-purple; the lobes about 1 cm long and wide, the total width of the two lobes not exceeding the width of the style branch; the lobes upturned, veined and spotted like the falls. Pod about 8 cm, inflated, lobed, narrowed towards both ends.

DISTRIBUTION: Endemic to the Cedars of Lebanon area. Also reported from Ehden and Hasrun areas of Lebanon but not seen recently.

MATERIAL: Vicinity of Cedars of Lebanon, 1940, DINSMORE 20513 (BEI); May 1880, BLANCHE 11095 (?); May 1966, ALBURY, CHEESE & WATSON 925 (K).

9. **Iris westii** DINSMORE — Fig. 5 B

DINSMORE 1933, Pl. Post. Dinsm. 2: 8; 1934 in POST & DINSMORE, Fl. Syr. Pal. & Sin. 2: 596. — *I. sofarana* FOSTER f. *westii* (DINSMORE) MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 319. — Orig. coll.: Lebanon, Tawmat-un-Niha, May 1930, WEST 1896 (holotype, DINSMORE Herbarium), not seen.

Plants up to about 30 cm. Rhizome medium, compact. Leaves 6—8, 1 cm wide or less, about 20 cm long, slightly falcate; stem leaf one or two. Peduncle 8—16 cm. Flowers 12.5—15 cm in diameter; valves about 11 cm, slightly inflated; ovary 3—4.5 cm, with a stalk about 1 cm; perianth tube 3—4 cm. Falls 5—8 cm long, 5—5.5 cm wide, elliptical—obovate, veins and spots prominently embossed, brown-purple to purple, the spots dense; signal spot about 1.5 cm long and wide, located in the middle of the fall; beard of long, rather sparse purple hairs, rather wide, extending almost to the edges of the fall and to almost the lower edge of the signal spot. Standards 6—9 cm long, 5—6 cm wide, obovate—cuneate, gradually narrowed into a claw about 1 cm long; the limb orbiculate; lilac-blue veins and minute dots on a pale lilac ground, the dots becoming bigger and embossed towards the base. Anthers about 2 cm; filaments about 1.7 cm. Style branches horizontal-oblique (apparently not arched downwards as seen in the herbarium material), 6—6.5 cm long, about 3 cm wide, thickly dotted-streaked with brown-purple on a "wine-coloured" ground; lobes upturned, dotted and veined like the falls; the width of the two lobes more than that of the style branch; pollinator tunnel is apparently mostly open, the fall and the style branch meeting only towards the basal area. Pod?

DISTRIBUTION: Endemic to heights in the Mashghara—Jezzine area, Lebanon.

MATERIAL: Heights between Jezzine and Mashghara, May 1965, EDGECOMBE B-571 (BEI).

NOTE: MOUTERDE (1966) included this taxon under *I. sofarana* as f. *westii*: indeed he included also *I. kirkwoodii* subsp. *calcarea* under f. *westii* (MOUTERDE 1969

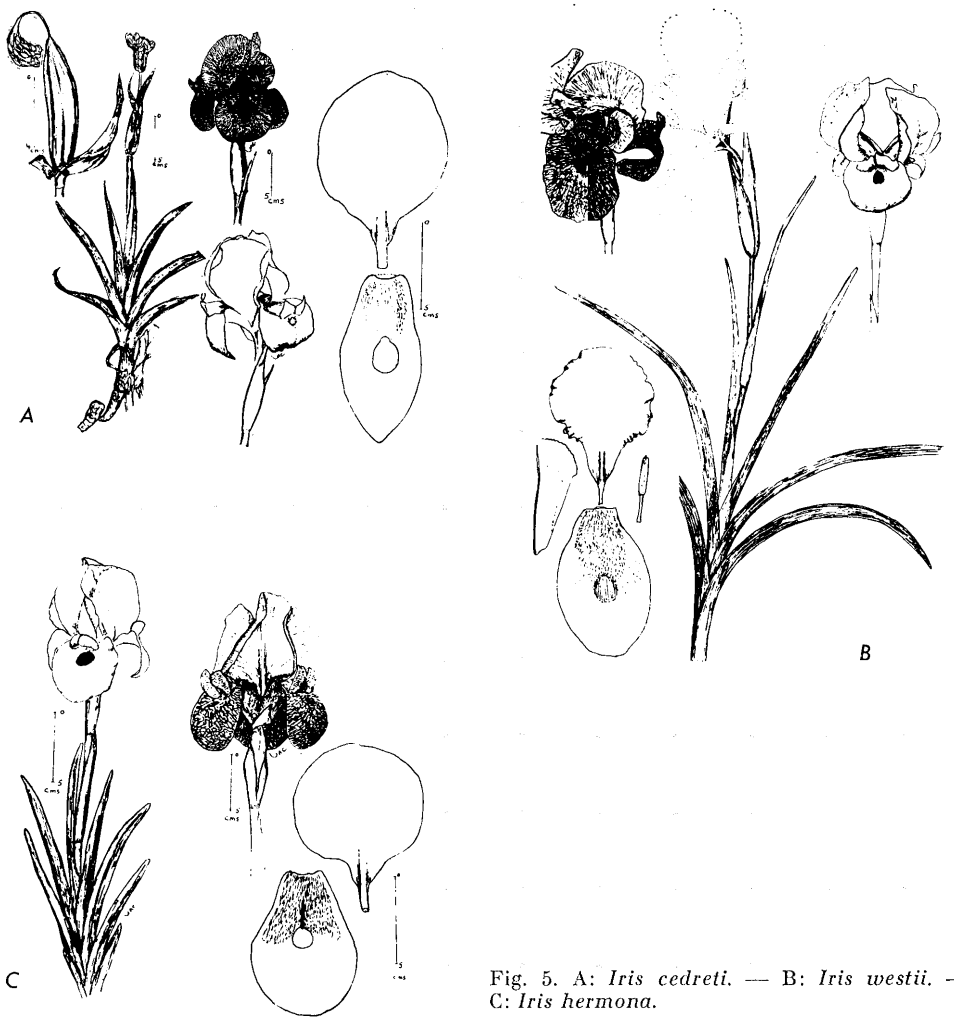


Fig. 5. A: *Iris cedreti.* — B: *Iris westii.* — C: *Iris hermona.*

p. 674). The authors consider that this taxon has the closest affinities with *I. hermona* and not with *I. sofarana;* the affinities with *I. kirkwoodii* subsp. *calcarea* being still remoter. In spite of all efforts the authors have not been able to rediscover any of the *I. westii* colonies during the past four years. It was possible to improve the original description by DINSMORE by studying the material collected by Mrs EDGECOMBE in 1965. From the characters of leaves, the flower and in particular the style branches combined with the general appearance of the plant, the authors feel that the taxon *I. westii* differs strikingly from any other taxon in the region and unless more evidence turns up from any future study of live material this taxon should retain is separate identity.

The sketches of flowers in Fig. 5 B are based upon photographs kindly supplied by Dr PETER WERCKMEISTER.

10. **Iris bismarckiana** E. DAMMAN & C. SPRENGER

E. DAMMAN & C. SPRENGER, May 1890 in Damman & Co. Catal. 51: 4, fig. 4; WEINER, Aug. 1890 in Illustr. Gartenzeitung 15: 352—353, fig. 72; BAKER 1892, Irid. 18. — Orig. coll.: Northern Palestine c. 1890, G. EGGERS (no record).

I. saarii SCHOTT var. *nazerena* (FOST. ex HERB), Herb and Wulle Catal. primo 1893, "sari"; HOGG (?) May 1893 in J. Hort. Ser. 3, 26: 373, "nazarensis". — *I. nazarena* (FOST. ex HERB) DINSM. 1934 in POST & DINSMORE Fl. Syr. Pal. & Sin. 2: 596.

Plants 30—50 cm. Rhizome medium—large, stoloniferous with long stolons. Leaves usually 8, spreading fan-like, rather obtuse, 2—3 cm wide, 25—40 cm long, oblique, closely sheathing. Flowers often 15 cm wide; perianth tube 7 cm. Falls 6—7 cm long, round—ovate; the ground creamy, thickly covered with oblong, embossed, red-brown spots, veined with maroon or purple, often with a few small crimson or red-brown spots; beard hairs dark purple; signal spot large, more or less orbicular, blackish red-purple. Standards 7—8 cm long, orbicular, with a white ground except at the yellowish base; veins blue, dots dense, prominent, purple. Style branches relatively long, marked with reddish-brown spots on a creamy ground. Pollinator tunnel apparently as in *I. sofarana* subsp. *sofarana,* only markedly longer.

DISTRIBUTION: Endemic to southern slopes of Mt Hermon and the areas to the south.

NOTE: MOUTERDE followed C. SPRENGER (Gard. Chron. 1904) and considered *I. saarii* SCHOTT var. *nazarena* FOST. ex HERB (*I. nazarena* (FOST. ex HERB) DINSM.) and *I. bismarckiana* "REGEL ex SPRENGER" to be one and the same taxon, as the collections on which the two taxa were based were made by the same person, G. EGGERS of Jaffa. Unfortunately, the authors are not very familiar with either of the above two taxa. Comparing the descriptions of rhizomes and leaves of *I. bismarckiana* (WEINER 1890, and in Gartenflora, 1893, both reproduced partly in WERCKMEISTER's Catal. Irid. p. 94) with those of *I. nazarena* (FOST. ex HERB) DINSM. we find that both have stoloniferous rhizomes ("like *I. iberica*", which is stoloniferous, in *I. bismarckiana*) and both have relatively very wide leaves. These characters were not mentioned by DINSMORE (1933, 1934) who, apparently, copied the description from BAKER (1892). The taxon *I. nazarena* (FOST. ex HERB) DINSM. is apparently the same as *I. bismarckiana* DAMMAN & SPRENGER (often quoted as *I. bismarckiana* REGEL ex SPRENGER). However, the inclusion of *I. hermona* under *I. bismarckiana* (as treated by MOUTERDE) is not justified. *I. hermona* has non-stoloniferous, compact rhizomes, narrower and almost erect leaves, and more orbiculate perianth leaves as compared with *I. bismarckiana.* Indeed, AWISHAI (1971) mentions seeing populations of *I. hermona* and "*I. nazarena*" as almost overlapping on the southern slopes of Mount Hermon. The synonymy of this taxon has very kindly been provided by Dr DAN NICOLSON.

11. **Iris hermona** DINSMORE — Fig. 5 C

DINSMORE 1933, Pl. Post. Dinsm. 2: 8; 1934, in POST & DINSMORE, Fl. Syr. Pal. & Sin. 2: 596; under *I. bismarckiana* REGEL in MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 320. — Orig. coll.: Syria, S of Qunaitra April—May 19--, DINSMORE 1895 (holotype, DINSMORE Herbarium? not seen).

Plants up to about 50 cm. Rhizome rather large, compact, yellowish-brown. Leaves usually 9, more or less erect, up to 1.8 cm wide and up to 30 cm long, very gradually narrowed to the apex; stem leaf usually one, the node bearing the stem leaf showing above or through the basal leaves. Peduncle up to 12 cm. Flowers about 18 cm tall from the base of the valves, about 10 cm wide; valves 8—10 cm, inflated; ovary 3.5—4 cm; perianth tube 2.5—3 cm. Falls about 8.5

cm long, 6 cm wide, obovate, gradually narrowed to the base, the limb appearing orbiculate, embossed dotted and embossed veined with brown-purple on a creamy yellow to creamy white ground, the ground showing prominently; the signal spot almost orbicular, about 1.2 cm long and 1.5 cm wide, darker brown-purple; beard of sparse, brown-purple hairs with the greenish-yellow ground showing through them. Standards about 9.5 cm long, about 8 cm wide, orbiculate, abruptly narrowed into a triangular basal area and then into a strongly channelled claw about 1 cm long; the limb wider than long, creamy white (dirty white in some biotypes), with widely spaced, very fine, purple and light purple veins, and very finely dotted with violet-purple, the dots and veins near the claw brown-purple, rather embossed. Anthers about 2.5 cm, yellowish white; the filaments about 1.7 cm, purple. Style branches about 6.5 cm long, about 4 cm wide, ridge-keeled with the ridge double and prominent, rather flattened out at the sides and then curving down to form a flattened pollinator tunnel with the base of the fall, red-purple and spotted in the middle, dark-purple to the sides; the lobes of the style branches creamy white, spotted with embossed, dark purple, irregularly crenate, overlapping. Pod?

DISTRIBUTION: Lebanon, Sarada area; Syria, near Qunaitra and southern slopes of Mt Hermon.

MATERIAL: Qunaitra, April 1943, DINSMORE 3895 (lectotype, BEI); live material from a population from the area of distribution (probably Qunaitra) April 1974 from culture, CHAUDHARY 1325 (BEI).

NOTE: The live material studied was obtained through the courtesy of Mr HERBERT MCKUSICK. It is presumed that the material was originally collected from near Qunaitra, Syria when the area was under Israeli control.

MOUTERDE treated this taxon under *I. bismarckiana* REGEL ex SPRENGER which does not appear justified. The rhizome and the leaf characters definitely show the two taxa to be different. Also see the note under *I. bismarckiana*.

12. **Iris lortetii** BARBEY — Fig. 6 A

BARBEY 1882, Herborization au Levant Pl. VII; in BOISSIER 1884, Fl. Orient. 5: 131; POST & DINSMORE 1934, Fl. Syr. Pal. & Sin. 2: 597; MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 319. — Orig. coll.: "Palestine", Mays to Hunin, May 1880, LORTET (holotype, G, not seen).

Plants about 40 cm. Rhizome short, compact, pinkish. Leaves usually about 8, 1—1.5 cm wide, characteristically obtuse and then abruptly narrowed into a tip; stem leaf usually one, erect. Peduncle about 8 cm. The flowers in general of pink-maroon shades, up to 13 cm long from base of valves, up to 8.5 cm wide. Falls about 5.5—6 cm long, 3—4 cm wide, obovate—oblong, densely spotted with maroon on a clear, lead-white ground; beard of small, yellowish-red, rather sparse hairs; signal spot dark maroon. Standards erect, about 7 cm long, 5 cm wide, limb orbicular, gradually narrowed into a claw, the claw about 0.5 cm; white with deep pink veins. Style branches about 5 cm long including the lobes, about 2.5 cm wide, horizontal—oblique, maroon, keeled; the lobes spotted with maroon like the falls, reflexed; the combined width of the two lobes less than the width of the style branch; pollinator tunnel mainly constituted by the style branch, the fall constituting the floor of the tunnel nearer the base. Like in *I. samariae* DINSM. the standards characteristically tend to converge below the style branches. Pod?

DISTRIBUTION: Southern Lebanon and "North Palestine". Endemic.

MATERIAL: Mays to Hunin May 1943, DINSMORE 15388 (BEI).

NOTE: The authors have not been able to study any live material because of the extreme hazard involved in collecting it from near the southern border of Lebanon with Israel. The sketch of the flower (Fig. 6 A) is based upon a photograph by Mr HERBERT MCKUSICK.

13. **Iris damascena** MOUTERDE — Fig. 6 F

MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 318—319. — Orig. coll.: Syria, Jabl Qasyoun 1951, PABOT P—5 (holotype, MOUTERDE Herbarium, now at G).

I. sofarana FOST. f. *quassiomensis* WERCKMEISTER 1957 in (Brit.) Iris Soc. Yearbook, nomen nudum.

Plants rarely more than 30 cm. Rhizome short, compact. Leaves 5—8, usually 7, arched—strongly recurved, 1 cm wide or less, up to 27 cm long; stem leaf one. Peduncle up to 15 cm. Flowers up to 15 cm long from base of the valves, about 9 cm wide; the base of the valves often partly enclosed by the upper one or two leaves; valves up to 10 cm, inflated, a little coloured with pale violet-purple. Falls obovate—elliptical, up to 8 cm long, about 5 cm wide, rather flat in the basal area, droopy from immediately beyond the beard area; ground creamy white, densely dotted and veined with dark brown-purple like *I. sofarana* subsp. *sofarana*; the dots and veins slightly embossed; signal spot small, elliptical, about 1.5 cm long, about 1 cm wide, dark purple; beard of sparse, purple hairs. Standards oval, about 9 cm long, about 6 cm wide, ground creamy white, densely fine-dotted and fine-veined with purple, the veins denser and embossed in the basal area; narrowed into a triangular area and then abruptly clawed, the claw about 1 cm long and with long, purple hairs; the veins denser and embossed in the basal area. Anthers about 2.5 cm; filaments about 1.5 cm. Style branches short, 4—5 cm long including the lobes, narrowly ridge-keeled, strongly arched, hardly produced beyond the spread of the standards; the lobes rather short, the combined width of the two lobes not more than the width of a style branch; pollinator tunnel rather short as compared with other taxa, like that in *I. sofarana* subsp. *kasruwana*. Pods?

DISTRIBUTION: Endemic to Jabl Qassoun near Damascus, Syria. In danger of extinction.

MATERIAL: Jabl Qasyoun, Syria, March 1952, HIGHWOOD (K); March 1975, KHATEEB (BEI).

NOTE: Figure 6 F is a pen and ink resketch of a plate of this taxon in the Kew Herbarium of the Royal Botanic Gardens, permitted to be published in the present form by courtesy of the Director of the Herbarium. The sketches of the flower parts are from fresh material collected from the type locality.

14. **Iris yebrudii** CHAUDHARY subsp. **yebrudii** — Fig. 6 C

CHAUDHARY 1972 in Bot. Notiser 125: 259—60. — Orig. coll.: Syria, Yebrud, May 1971, CHAUDHARY 786 (holotype, BEI).

Plants usually 15—18 cm, up to 30 cm under cultivation. Rhizome small, compact, pale yellow. Leaves 5—8, covering the whole of the stem or the stem leaf reaching beyond middle of the valves, usually less than 1 cm wide, up to 21 cm long, dark green to bluish-green with a white bloom, strongly recurved to slightly so; stem leaf one. Peduncle up to 11 cm. Flowers about 13 cm long from base of the valves, 8—9.5 cm wide; valves 7—9 cm, reaching above the level of the falls, keeled, purplish-pink in the upper half, inflated; ovary about 3 cm, broadly trigonal; perianth tube about 2.0 cm. Falls about 7 cm long, 5 cm wide, oval to obovate, the ground pale yellow with dark brown-purple, embossed veins prominent all around except in the area below the signal patch to the margin which has only fine spots, the spots

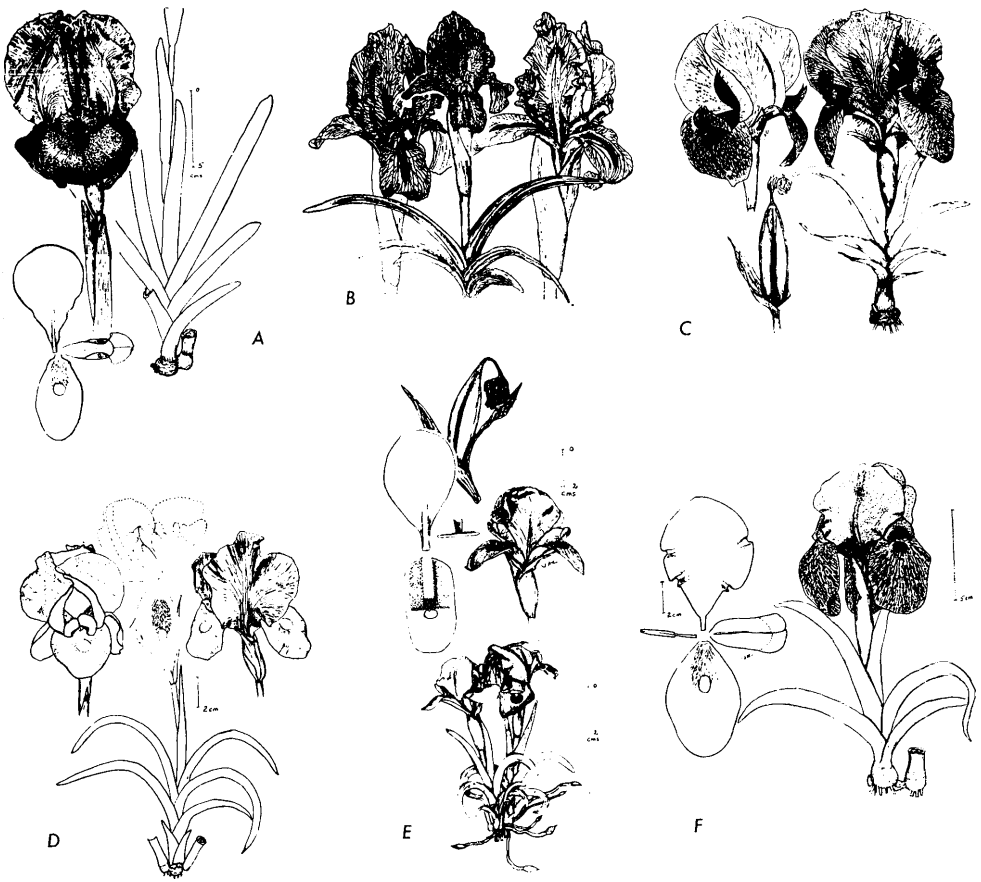


Fig. 6. A: *Iris lortetii*. — B: *Iris ? heylandiana*. — C: *Iris yebrudii* subsp. *yebrudii*. — D: *Iris antilibanotica*. — E: *Iris assadiana*. — F: *Iris damascena*.

denser and anastomosing immediately below the signal spot; signal spot dark purple, about 1×1 cm, rhomboid to transversely ovate; beard of long, purple hairs, the hairs reaching below the signal spot on either side. Standards about 7.5 cm long, about 6.5 cm wide, with the claw about 1 cm, orbicular, reflexed at sides, pale yellow with prominent but fine, purple veins and dots; the dots very fine, sparse in the middle region, denser towards the margin; the major veins and those in the central top end usually distinctly yellow; a few long hairs usually present on the inner basal area. Anthers about 3 cm, tapering, yellow on the back; filaments about 1.5 cm. Style branches 5.5—6.5 cm long, 2—3 cm wide, rather narrowly (transversely) curved, dark-purple to maroon-purple towards the base, speckled with dark purple in the outer half, the keel with a double prominent crest is also speckled; the width of the two lobes more than the width of the style branch; pollinator tunnel as in *I. sofarana* subsp. *sofarana*. Pods about 7 cm long, about 2 cm wide, usually with the 3 major lobes more prominent.

Variant biotypes with purplish slaty-grey ground both in the falls and the standards with only fine, darker dots, densely and uniformly distributed.

DISTRIBUTION: Endemic to the Yebrud area in Syria.

MATERIAL: Yebrud, Syria, May 1935, DINSMORE 25515 (BEI); May 1974, CHAUDHARY & RASHID SHAD 1310 (BEI); Deir Atiyeh, May 1879, POST (K).

15. **Iris yebrudii** DINSMORE ex CHAUDHARY subsp. **edgecombii** CHAUDHARY

CHAUDHARY 1972 in Bot. Notiser 125: 499—500. — Orig. coll.: Syria, Kastel, April 1972, KIRKWOOD 788 (holotype, BEI).

Plants 25—40 cm. Rhizome small, compact, light yellow-brown. Leaves 6—7, greyish-green, about 8 mm wide, about 11 cm long, strongly recurved; stem leaf one, erect, reaching or surpassing the valves. Peduncle c. 11 cm. Flowers about 15 cm (often more) tall from base of the valves, c. 12 cm wide; valves 7—9 cm, inflated keeled, pink-tinged; ovary about 5 cm, broadly trigonal; perianth tube about 3.5 cm. Falls about 9 cm long, about 7 cm wide, ovate to orbiculate, covered with red-purple embossed dots and fine, dark purple veins, the latter perceptible only at or above the level of the signal spot (in pale biotypes the red-purple dots much smaller and the red-purple veins visible all along the margin); the ground pale yellow or pale greenish, clear; signal spot ovate, about 1.5 cm long, 1 cm wide, maroon-purple with darker veins perceptible through it; beard of dark purple hairs tipped with yellow, the hairs covering part of the signal spot and coming down its side to about 1/4 the length. Standards about 10 cm long, 8.5 cm wide, the limb orbiculate and gradually tapering to a small claw, uniformly covered with maroon-purple veins more distinct near the margin and small densely arranged dots on a white, clear ground; the margin slightly crenulate, the inner basal area with a few long yellow hairs (pale biotypes with the standard uniformly pale yellow, clear with very fine purple veins and sparsely scattered, fine purple dots or the standard with uniformly densely scattered fine purple dots only, or with larger, sparse dots only). Anthers about 3 cm, with minute red-purple dots on the back; filaments about 1.5 cm. Style branches flattish, about 7 cm long including the lobes, 4 cm wide, with minute dark purple dots on the maroon, median and pale greenish lateral bands; lobes upturned, continuing as a prominent double crest over the keel, sometimes the crest folded over near the lobes, the double crest dotted and streaked with red-purple like the lobes; pollinator tunnel more or less as in *I. sofarana* subsp. *sofarana*, only flatter. Pod about 11 cm long, 2.7 cm wide, inflated-lobed, gradually tapering to the top.

DISTRIBUTION: Endemic to Kastel area in Syria. In danger of extinction.

MATERIAL: Transplants from this population.

16. **Iris antilibanotica** DINSMORE — Fig. 6 D

DINSMORE 1933, Pl. Post. Dinsm. 2: 10; 1934 in POST & DINSMORE, Fl. Syr. Pal. & Sin. 2: 599; MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 316. — Orig. coll.: Syria, above Bludan, May 19--. WEST (holotype, DINSMORE Herbarium?).

Plants up to 40 cm. Rhizome small, compact. Leaves 7—8, usually 1 cm wide or less, up to 20 cm long, falcate, sheathing 2/3 or more of the stem; stem leaf one. Peduncle up to 10 cm. Flowers about 13 cm tall from base of valves, about 10 cm wide; valves relatively large, about 7—9 cm, slightly inflated; ovary about 2 cm; perianth tube about 3.5 cm. Falls 6—8 cm long, up to 5 cm wide, oblong, darker than the standards, maroon or

reddish-brown with a purple cast, varying in depth of colour, without veins or dots; signal spot small; beard of usually pure yellow, sometimes purple-tipped or of reddish-purple hairs on a creamy—bright yellow ground; beard hairs only slightly papillate-echinate, especially near the tip. Standards up to 10 cm long, up to 8 cm wide, ground intense purple without any dots and with veins of a darker colour or the veins sometimes not discernable. Anthers about 2.5 cm; filaments about 1.5 cm. Style branches light brown, about 5.5 cm including the lobes, about 2.5 cm wide, strongly keeled; lobes coloured like the falls; pollinator tunnel apparently oblique. Pods?

DISTRIBUTION: Endemic to heights above Bludan, Syria.

MATERIAL: Above Bludan, May 1953, KHATEEB 24 (lectotype, BEI and Damascus Univ. Herbarium).

NOTES: The above description has been adopted from those of DINSMORE (1933), MOUTERDE (1966), WERCKMEISTER (1957), WEST (1935), and modified in places from the study of herbarium material.

Sketches of flowers in Fig. 6 D are based upon photographs by PETER WERCKMEISTER.

17. **Iris ? heylandiana** BOISSIER & REUTER — Fig. 6 B

BOISSIER & REUTER 1877 in BAKER in J. Linn. Soc. 16: 142; BOISSIER 1884, Fl. Orient. 5: 130—131; POST & DINSMORE 1934, Fl. Syr. Pal. & Sin. 2: 596; MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 317. — Orig. coll.: Turkey, between Diarbekir and Mardin, 18--, KOTSCHY 307 (syntype); Iraq, between Mossul and Baghdad, 18--. OLIVER (syntype, not seen).

Plants up to 35 cm. Rhizome medium—small, shortly creeping (apparently stoloniferous). Leaves up to 9, less than 1 cm wide, about 20 cm long, strongly arched; stem leaf 0—1. Peduncle about 9 cm. Flowers about 15 cm tall from base of the valves, about 7 cm wide; valves about 7 cm, more or less inflated, with a brownish-pink tinge. Falls obovate—cuneate, veined and spotted with brown-violet forming an open pattern on a whitish, clear ground, dark brown at the throat (?); signal spot dark, narrow, elongate with the distal edge irregular in outline; beard linear but spreading out laterally near the base; beard hairs white, relatively sparse (like *I. barnumae*), of almost uniform length, less than 5 mm in length. Standards broader than the falls, orbiculate—unguiculate, white with fine purplish-brown veins and sparse dotting. Style branches horizontal—oblique, rahter wide, orange (?); the lobes short, crenate, the width of the two lobes less than the width of the style branch; pollinator tunnel constituted mainly of the style branch, the fall contributing the floor near the base only, otherwise the tunnel open on the lower side and the linear beard laterally visible. Pod?

DISTRIBUTION: Reported from north-eastern Syria, southern Turkey, and from between Mosul and Baghdad in Iraq.

MATERIAL: Syria, Derbassieh, April 1940, DINSMORE 21512 (BEI); between Derbassieh and Ras-el-Ayen, April 1934, GOMBAULT 5769 (LNRC)?

NOTES: The authors have not seen any live material. The above description has been adopted from the original and modified in places based upon study of herbarium material from the Darbassieh area and descriptions and pictures kindly supplied by Mr CLAY H. OSBORNE and Mr HERBERT MCKUSICK. Sketch of this taxon based upon pictures provided by Mr OSBORNE.

I. heylandiana is apparently a component of the complex of species in southern Turkey and north-eastern Syria. GOMBAULT 5769 bears the name *I. gombaultii* DINSMORE but MOUTERDE cited this sheet as *I. heylandiana*. The rhizome in

this plant is long stoloniferous, the leaves arcuate making a complete circle and covering the stem to a little below the valves. Is this a normal variation within the species *I. heylandiana*? Or is it a separate taxon as considered by DINSMORE? The syntypes for *I. heylandiana* are material collected from two relatively widely separated localities. BRIAN MATHEW of Kew Herbarium states (pers. comm.) that *I. heylandiana* material is "large-flowered" while the Derbassieh material is "small-flowered" and presents aspects of *I. meda* STAPF from Iran. Only further studies of live material from the two syntype localities can prove whether the two syntypes truly represents one taxon or two separate taxa or that the Derbassieh material represents an entirely different taxon. The Derbassieh region complex is characterized by the linear beard as too is the *I. barnumae* complex. However, in *I. heylandiana* (photographs seen by the authors) the linear beard appears to spread out transversely near the base. Another taxon which has an apparent linear beard is *I. assadiana*; but in this species the median brush of longer hairs (more than 5 mm) is more densely arranged and is surrounded on either side by a dense band of very short hairs — in other words, this taxon has the median brush of longer hairs as in *I. heylandiana* and *I. barnumae* complexes and a denser beard with the lateral bands of dense (though very short) hairs as in the Hauran group of oncocycli.

The beard and beard-hair characters used in the key and given in the text are from material collected from the Derbassieh area and pictures provided by Mr CLAY OSBORNE.

18. **Iris assadiana** CHAUDHARY et al., sp. nov. — Fig. 6 E

Orig. coll.: Syria, Sadad area, April 1974, KIRKWOOD 1312 (holotype, BEI).

I. barnumae FOSTER & BAKER var. *zenobiae* MOUTERDE (in part) 1966, Nouv. Fl. Lib. Syr. 1: 315—316.

Planta c. 15 cm alta. Rhizoma parvum, stoloniferum. Folia 6—8, firmiter arcuata, 4—12 cm longa, 1 cm vel infra lata. Flores odoriferi, 9.5—13 cm longi a basi spatharum. Tepala externa 5—6.5 cm longa, 2.5—3.5 cm lata, uniformiter purpurea, venis paucis fuscioribus instructa; macula media fuscior, latior quam longior; barba in medio capillis longis (supra 5 mm), flavis, ad margines brevissimis lineis purpurascentibus. Tepala interna 6—8 cm longa, 4—5 cm lata, obovata, unguiculis parvis. Antherae 1.3—1.8 cm longae; fila 1.8—2 cm longa. Rami styli obliqui—aequi arcuati, non-carinati, 4—5.5 cm longi (lobis inclusis), amborum loborum latiores, lutei: canaliculus pollinicus apertus, tepalis externis basi tantum convenientibus. Capsula c. 4 cm longa, 1.25 cm lata.

Plants up to 15 cm. Rhizomes at base of individual shoots very small, the buds at the base only a few and forming small clumps; several long, spindly or stout stolons (of several nodes each) coming from the base of each shoot constitute the main rhizome; stolons up to 12 cm long, becoming conical at the base of the single plantlet that develops from the apical bud on each stolon. Leaves 6—8, usually falcate, strongly reflexed, 1 cm wide or less, 4—12 cm long, usually the single stem leaf or the uppermost leaf longer than the stem. Peduncle about 4 cm. Flowers odorous, about 9.5—13 cm long from base of the valves, 6—7.8 cm wide; valves about 5.5—7 cm, rather inflated, keeled, pale green to yellowish-pink on drying; ovary about 2 cm; perianth tube about 2 cm. Falls 5—6.6 cm long, 2.5—3.5 cm wide, uniformly dark-maroon to dark-purple to almost black with a few darker veins; signal spot velvety, darker, transversely oval, wider than long, notched, less than 1 cm long, about 1 cm wide or slightly more; beard of a median band (about 0.5 cm wide) of long (about 1 cm) hairs; the hairs on either side of the median band very short; the long hairs bright yellow, either without purple tips or some with very small purple tips or the bright yellow masking the purple tips; the short hairs purple; the ground below the long hairs bright yellow, in some biotypes the

beard hairs completely lacking and only a yellow band on the falls present. Standards 6—8 cm long, 4—5 cm wide, obovate, gradually narrowed to the base into the claw; the claw 1—1.5 cm long, channelled, the channel with a few yellow hairs, maroon-purple with darker veins, some biotypes dark purple. Anthers creamy white, 1.3—1.8 cm; filaments 1.8—2 cm. Style branches 4—5.5 cm long including the lobes, strongly arched, not keeled, if keeled then not ridged, pale orange (not purple as described by MOUTERDE 1966), streaked with purple, becoming darker towards the centre, with a purple median streak; width of the two lobes less than the width of the style branch; pollinator tunnel constituted mainly by the style branch, the fall forming only a part of the tunnel floor near the very base; the style branches often raised relatively high above the falls and the long beard hairs then laterally visible. Pods about 4 cm long, about 1.25 cm wide, tapering.

DISTRIBUTION: Apparently endemic to the Syrian desert.

MATERIAL: Ain-al-Baida, Syrian desert, April 1944, MOUTERDE 8159 (now at G); Chalky hills, Palmyra Road, April 1943, DAVIS 5769 (K); Qaryatein, April 1943, DAVIS 5721, 5668 (K); Hafar, April 1935 (?), DINSMORE 24313 (K); loc. ? (probably Syrian desert) April 1913, EGGERS (K).

NOTES: W. R. HIGHWOOD reports having seen white, yellow, and lighter-colored forms, apparently around the Qaryatein area.

MOUTERDE described this taxon as *I. barnumae* var. *zenobiae* and included the Tell Chehan material (*I. swensoniana* sp. nov.) under this taxon. The stoloniferous habit of the desert material was apparently overlooked by him because the type specimens that he used for description are without rhizomes while the Tell Chehan material that he probably used in his description (MOUTERDE 7558) does have the non-stoloniferous rhizomes. Also, the type of beard in the two taxa was confused by him. *I. assadiana* apparently shows close affinities to *I. barnumae*, but is probably even closer to *I. heylandiana* found in the extreme north of the Syrian desert on the southern Turkish border. Also, *I. barnumae* and all of its infra-specific taxa have a distribution in mountainous, non-desert habitats. The stoloniferous habit, the median band of long hairs amidst lateral piles of very short hairs, the non-echinate beard hairs, the presence of darker veins in the perianth and its distribution justifies, we feel, treating the desert material as a separate species, *I. assadiana* sp. nov.

This species is named after Mr H. ASSAD, Patron of the Horticultural Society of Syria.

19. **Iris jordana** DINSMORE — Fig. 7 A

DINSMORE 1933, Pl. Post. Dinsm. 2: 9; 1934 in POST & DINSMORE, Fl. Syr. Pal. & Sin. 2: 598; MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 316. — Orig. coll.: Jordan Valley, near Baysan, April 1921, DINSMORE 1893 (holotype, DINSMORE Herbarium), not seen.

Plants up to 40 cm. Rhizome rather large, compact. Leaves usually 9, slightly falcate, erect, about 2 cm wide, up to 30 cm long, the two uppermost sometimes ending at the same level, sheathing the stem completely. Peduncle about 12 cm. Flowers 13—18 cm long, from base of the valves; valves 10—12 cm, light green, often streaked with purple; ovary about 4 cm; perianth tube about 3 cm. Falls about 9×5 cm, rather leathery, obovate—elliptical, slightly irregularly crenate, densely red-purple spotted and with dark purple veins, the spotting so dense that the ground appears as lead-white spots through the dense spots and veins; signal spot orbicular, about 2 cm in diameter, velvety, very dark purple, almost black, wider and diffusing towards the tip end; beard of relatively sparse hairs, the hairs

creamy white, tipped with very small, purple dots. Standards 10.5—13 cm long, 7.5—9.5 cm wide, orbicular, abruptly narrowed into a triangular area and then into a channelled claw, the claw about 2 cm; densely spotted with fine red-purple dots and dark purple veins, the dots very dense and the veins very thick in the central area on a lead-white ground; the dots sparser on the inner face and the lead-white ground much more prominent. Anthers about 4 cm, creamy white; filaments about 1 cm. Style branches about 6 cm long, about 4 cm wide, greenish-yellow, densely finely spotted with dark purple, with the greenish-yellow colour showing through, ridge-keeled, the ridge prominent; lobes of the style branches turned upwards, darker, the width of the two lobes more than the width of style branches; pollinator tunnel rather similar to that in *I. sofarana* subsp. *kasruwana* (Fig. 4 D a). Pods?

DISTRIBUTION: Endemic to the Jordan River Valley.

MATERIAL: Live material in culture apparently from around the type locality. — Collections: Near Yarmouk river, April 1943, DINSMORE 5893 (BEI); Baysan area (?), from culture, April 1974, CHAUDHARY 1403 (BEI).

NOTE: The live material studied was obtained through the courtesy of the Aril Society International, but is definitely from the Jordan valley under Israeli administration at present. The original supplier identified it as *I. jordana* DINSM. which indicated that it had come from area around Baysan, the type locality for *I. jordana*. The type localities for *I. jordana* and *I. hauranensis* DINSM. lie on opposite banks of the river Jordan about 30 kms apart. However, DINSMORE also labelled his no. 5893 (BEI) *I. jordana,* collected near the Yarmouk river (April 1943), apparently from the East bank of the Jordan river. The two taxa were published by DINSMORE at the same time in the same publication. MOUTERDE (1966) considered the two taxa to be identical. From the study of limited material, while we tend to support MOUTERDE's treatment of the two taxa, we cannot with confidence say that they should be united. A thorough study of material from both localities is needed to clear up this point.

20. **Iris bostrensis** MOUTERDE — Fig. 7 B

MOUTERDE 1954 in Bull. Soc. Bot. France 101: 420—421; based on *I. atropurpurea* BAKER var. *purpurea* DINSMORE 1933 in POST & DINSMORE, Fl. Syr. Pal. & Sin. 2: 600; MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 317. — Orig. coll.: Syria, 10 km N of Draa, March 1952, HIGHWOOD HG 6 (holotype, Herb. MOUTERDE, now at G).

Plants up to 40 cm. Rhizome short, compact, brown. Leaves usually 8, less than 1 cm wide, up to 20 cm long, weakly or strongly recurved or erect; stem leaf one. Peduncle about 12 cm. Flowers about 14—17 cm tall from base of the valves, about 8 cm wide; valves pale green to yellowish-green, slightly inflated, about 9 cm; ovary about 3.5 cm; perianth tube about 3 cm. Falls 6.5—7.5 cm long, 3—4.5 cm wide, reflexed, often folded back; the limb ovate, abruptly narrowed into the haft, the latter rather tightly clasping the style branch; densely spotted and veined with dark brown-purple so that the yellow ground appears spotted through the dark brown-purple; signal spot semi-circular, usually truncate, often notched or with two shallow notches, wider than long, 1.5—2 cm wide, about 1.5—1.6 cm long, velvety dark maroon-purple; beard dense, beard hairs all bright yellow, minutely purple-tipped, about 0.5 cm long in the middle, gradually reduced in length towards the sides; the bright or pale yellow ground visible throughout the beard. Standards about 8—10 cm long, about 5—7 cm wide, limb orbiculate, rather abruptly narrowed into the claw, the claw channelled, about 1.5 cm long with fine yellow hairs, densely finely streaked with dark

brown-purple, the spotting density variable, giving rise to different shades; the ground brownish-yellow to greenish-yellow. Stamens creamy white; anthers about 2 cm; filaments about 1 cm. Style branches 5.5—6.5 cm long including the lobes, about 2.5 cm wide, ridge-keeled, golden yellow with dense, very minute, dark brown-purple spots, the spots becoming bigger or streaks towards the sides and the lobes; the two lobes as wide as or wider than the style branch; pollinator tunnel almost like that in *I. sofarana* subsp. *sofarana,* but the style branches rather obliquely raised above the falls away from the immediate basal areas. Pods about 8 cm long, about 1.25 cm wide, 6-lobed, slightly inflated.

DISTRIBUTION: The Hauran, Syria. The commonest of the "black irises", often a weed in grain-fields.

MATERIAL: Live culture. — Collections: Salkhad to Bosra, April 1964, WEGMANN B-157 (BEI); Shehba Road, April 1972, CHAUDHARY & KIRKWOOD 795 (BEI); Jabl Druze region, April 1973, WEYMOUTH 1298 (BEI); in fields around Damascus-Jordan road, April 1952, HIGHWOOD (K).

21. **Iris auranitica** DINSMORE f. **auranitica** — Fig. 7 C

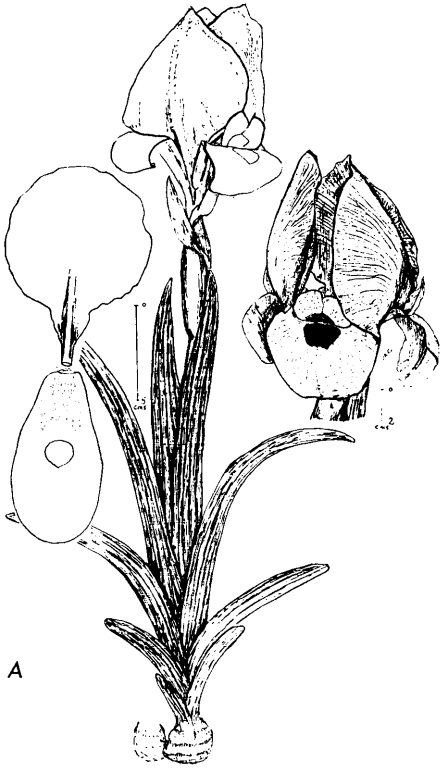
I. auranitica DINSMORE 1933, Pl. Post. Dinsm. 2: 11; 1934 in POST & DINSMORE, Fl. Syr. Pal. & Sin. 2: 601; MOUTERDE 1966, Nouv. Fl. Lib. Syr. 1: 315. — Orig. coll.: Syria, Jabl Kulayb, May 1933, DINSMORE 13045 (DINSMORE Herbarium), not seen.

Plants up to 50 cm. Rhizome medium, compact, yellow. Leaves up to 9, about 1 cm wide or rarely more, about 25 cm long, erect or slightly arched, sheathing the stem almost to the top; stem leaves one or two. Peduncle up to 15 cm. Flowers odorous, about 15 cm tall from base of the valves, valves rather tightly clasping, 8—9.5 cm long, greenish-yellow; ovary about 4 cm long, 1 cm broad with a stalk about 5 mm; perianth tube about 2 cm. Falls about 7×4 cm, obovate, bronze, with very minute, uniformly and rather densely distributed purplish-red spots and very fine reddish-purple veins or without spots and with only faint venation; signal spot about 1.5×1.5 cm, orbiculate to pendulum-shaped, dark maroon or reddish-yellow; beard dense, the hairs bright yellow with very minute purple-red tips; the hairs longest in the middle (about 0.5 cm) and gradually becoming shorter towards the sides. Standards about 8.5×5.5 cm, obovate, golden-yellow to bronze, with very fine purplish-red veins or without dots and with only faint veins; claw about 1 cm long, channelled, with golden yellow, dull brown-tipped, dense hairs. Anthers about 2.2—3 cm, tailed, creamy white to light yellow; filaments about 1—2 cm, light yellow. Style branches 4.7—5.5 cm long including the lobes, about 3 cm wide, golden yellow with very fine purple to brownish-purple dots, rather oblique and arched, ridge-keeled, the ridge more prominent near the lobes; the lobes not wider than the width of the style branches, upturned, spotted and veined like the falls; the style branches forming a rather short pollinator tunnel with the falls near their bases, the tunnel open away from base. Pods about 8 cm, rather narrow.

DISTRIBUTION: Endemic to the Jabl Druze area in Syria.

MATERIAL: Jabl Kulayb, May 1943, DINSMORE 15095 (damaged, BEI); Mayamas near Tell Jaffna, April 1973, CHAUDHARY & KIRKWOOD 800 (BEI) (collected in bud and brought to Beirut where it flowered and fruited).

Fig. 7. A: *Iris jordana.* — B: *Iris bostrensis.* — C: *Iris auranitica* f. *auranitica.* — D: *Iris swensoniana.*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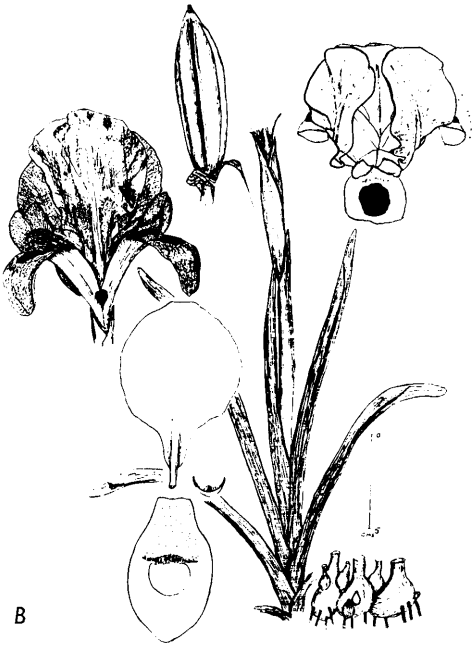
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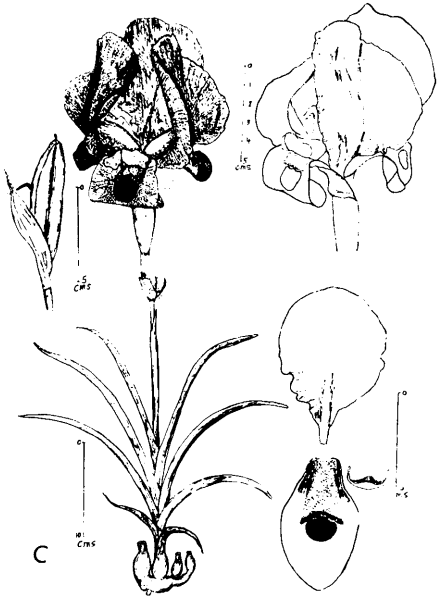
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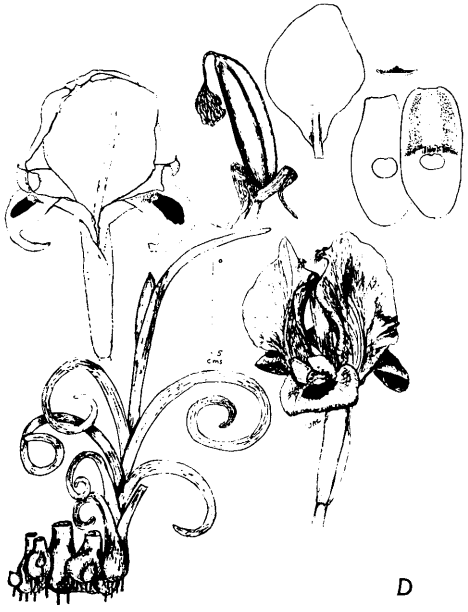
D

22. **Iris auranitica** DINSMORE f. **wilkiana** CHAUDHARY et. al., stat. et nom. nov.

Base: *I. auranitica* DINSMORE var. *unicolor* MOUTERDE 1953, Fl. Djebel Druze, p. 82; 1966, Nouv. Fl. Lib. Syr. 1: 315. — Orig. coll.: Syria, Tell Jaffna (type not indicated); Mayamas near Tell Jaffna, April 1973, CHAUDHARY & KIRKWOOD 800-A (neotype, BEI).

This form differs from f. *auranitica* in having bright yellow flowers without red-purple dots or veins. The falls and standards often tend to be wavy. MOUTERDE considered this to be a variety (*unicolor*) which is inappropriate as both the forms are found growing together — the differences are apparently minor genetic variations and the biotypes best merit recognition as forms. The name "unicolor" could be misleading and be contrued as implying that the biotypes were completely lacking in any other pigment except yellow which is not so, or that the falls and standards were like-coloured (as in f. *auranitica*).

NOTE: This form is named after Mr THOMAS WILKES of the Aril Society International, USA.

23. **Iris swensoniana** CHAUDHARY et al., sp. nov. — Fig. 7 D

Orig. coll.: Syria, Tell Chehan, April 1972, CHAUDHARY & KIRKWOOD 796 (holotype, BEI).

I. barnumae FOSTER & BAKER var. *zenobiae* MOUTERDE (in part) 1966, Nouv. Fl. Lib. Syr. 1: 315—316.

Planta c. 40 cm alta. Rhizoma parvum, compactum. Folia c. 8, infra 1 cm lata, c. 20 cm longa, infirmiter recurva, etiam circinata. Flores odoriferi, c. 15 cm longi a basi spatharum. Tepala externa 6—7 cm longa, 3—3.5 cm lata, ovato-spathulata, saepe retroflexa, uniformiter atropurpurea, venis fuscioribus; macula media orbicularis—reniformis; barba sicut pulvinus, capillis densis, marginem versus gradatim brevioribus, infra 5 mm longis, in medio flavis, ad marginem purpurascentibus. Tepala interna 6—8.5 cm longa, 3.5—5 cm lata, uniformiter purpurea vel maronina, unguiculata. Antherae 2—3.5 cm longae; fila 1—1.5 cm. Rami styli 4—6 cm longi (lobis inclusis), 2.5—3 cm lati, lineis interruptis, cristati et carinati; canaliculus pollinicus praecipue e ramo styli formatus. Capsula 8—10 cm longa, c. 2.5 cm lata.

Plants about 40 cm. Rhizomes small, compact, yellowish-brown. Leaves up to 8, less than 1 cm wide, about 20 cm long, strongly recurved, even circinate; stem leaf one. Peduncle about 15 cm. Flowers odorous, about 12—19 cm long from base of the valves, 7—8 cm wide; valves more or less inflated, keeled, pale green to green, ovary 2.5—4 cm, terete—broadly trigonal; perianth tube 2—4 cm. Falls 6—7 cm long, 3—3.5 cm wide, ovate—spathulate, narrowed or not into a haft, strongly recurved, often folded back; uniformly dark purple, almost black, with darker veins; signal spot orbiculate-reniform, notched, wider than long, 1—1.5 cm long, 1.5—2 cm wide, velvety dark maroon—dark purple (almost black); beard of purple-tipped bright yellow hairs (less than 0.5 cm long) in the median region on yellow ground, the hairs gradually becoming shorter towards the sides where they are purple on a purple ground. Standards 6—8.5 cm long, 3.5—5 cm wide, oblong, gradually or abruptly narrowed into the claw; claw 1—1.5 cm, channelled, the channel with a few purple and yellow hairs; limb uniformly purple or dark maroon, slightly lighter than the falls. Stamens creamy white; anthers about 2—3.5 cm; filaments 1—1.5 cm. Style branches 4—6 cm long including the lobes, 2.5—3 cm wide, orange, strongly streaked with purple, becoming darker towards the tip, ridge-keeled; lobes coloured and veined like the falls, triangular, crenate, recurved; lobes narrower than the style branch; pollinator tunnel formed mainly by the style branch, the fall contributing only part of the tunnel floor. Pod 8—10 cm long, about 2.5 cm wide.

DISTRIBUTION: Endemic to Tell Chehan area, Syria.

MATERIAL: Live culture. — Collections: Tell Chehan, April 1943, MOUTERDE 7558 (LNRC); April 1973, WEYMOUTH 1299 (BEI).

NOTES: PETER WERCKMEISTER (pers. comm.) has made a very interesting comment: "The Chehan (Tell Chehan) iris has close clumps. There is an interesting equilibrium between the luxurient growth of its rhizomes with an astonishing multiplication of its sprout buds and the existence of the larvae of a lepidoptera (a kind of iris-borer): the plants would die out without the borer, as the plants would be unable to get enough nutrition for so many sprouts" (from the poor soil? auths.).

This species is named after the late Dr. S. P. SWENSON, former Dean of the Faculty of Agriculture at the American University of Beirut, Lebanon and at the University of Agriculture, Lyallpur, Pakistan.

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Peroxydase Isozymes in Quercus petraea and Quercus robur

Ulf Olsson

OLSSON, U. 1976 05 06. Peroxydase isozymes in Quercus petraea and Quercus robur. — Bot. Notiser 128: 408—411. Lund. ISSN 0006-8195.

An investigation of the occurrence of multiple molecular forms of peroxydases in the leaf tissues of *Q. petraea* and *Q. robur* has been carried out. In all, eleven different isozymes have been found. These are classified into four groups, one of which is only found in *Q. petraea* and introgressive populations. However, one of the *petraea* populations examined also lacks this group of peroxydases. The possibility of the occurrence of introgressive individuals not revealed by morphological analysis is discussed. The intraspecific variation of the zymograms is great, indicating the genetic heterogeneity of oak populations.

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It has been found that a number of different enzymes exist in multiple molecular forms (isozymes), within a species, or within the tissues of a single plant or animal and even within a single cell. A well-known example of this is lactate dehydrogenase (LDH). This enzyme exists in five different forms, each of which has been found to consist of four polypeptide chains of two different types only. These are coded by two different genes. The discovery of this molecular heterogeneity among enzymes has led to such applications as the analysis of genetic variation in plant populations (SCOGIN 1968, CONKLIN & SMITH 1971, JUO & STOTZKY 1973, RUDIN & RASMUSON 1973).

The aim of this investigation is to evaluate interspecific differences and, in some cases to find out the degree of introgression, or the occurrence of hybrid trees, in sympatric populations of *Q. robur* and *Q. petraea*.

Extractions of proteins from green oak-leaf tissues were separated by anodic disc electrophoresis and the polypeptides stained for the presence of peroxydases.

MATERIAL AND METHODS

Collections and Growth Conditions

The material used was in the main obtained from mature trees of *Q. petraea* (MATTUSCHKA) LIEBL. and *Q. robur* L. and their intermediates growing in natural stands in southern Sweden as in the population investigation (OLSSON 1975), viz. two *petraea,* three *robur,* three intermediate or mixed oak populations and one progeny sample of *Q. robur* (Fig. 1). Twigs taken from the south sides of the trees were brought to the laboratory in plastic buckets filled with tap water. They were exposed to daylight at room temperature (20° C). In addition, leaves were taken from seedlings grown from acorns of a single individual of *Q. robur*. The seedlings were grown under greenhouse conditions with a combination of daylight and artificial fluorescent light, and a minimum temperature of 20° C and transferred to the laboratory. Fresh, well-developed leaves of medium size were removed not more than two days after twigs and seedlings had been moved to the laboratory, and the enzymes immediately extracted.

Extraction and Electrophoresis

To extract peroxydase, oak-leaf tissue with the thickest veins removed was homogenized with a pestle and mortar in a buffer con-

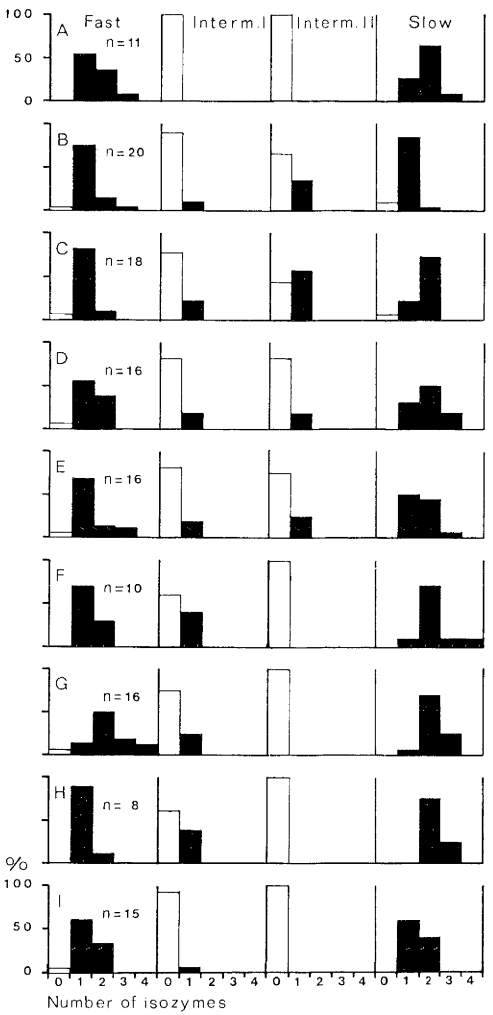

Fig. 1. *Quercus robur* and *Q. petraea*. The results of an analysis of isoperoxydases in leaves from mature trees and from the progeny of a given oak. Histograms show the frequency distribution of individuals with 0 (unfilled colums) or 1, 2, 3, 4 (filled columns) isozymes within each of four groups of peroxydases with different relative mobilities. — A, B: Populations of *Q. petraea*. — C, D, E: Introgressive populations. — F, G, I: Populations of *Q. robur*. — H: Progeny of *Q. robur*.

taining 0.02 M 2-amino-2-hydroxymethyl-1, 3-propanediol (TRIS) and 0.19 M glycine (the same as was used in the electrode

Table 1. A comparison of isoperoxydase activity in fresh and frozen oak leaf material. QA refers to a population of *Q. petraea*, QO to *Q. robur*. The relative degree of activity as seen in the densitometer traces of the bands is indicated by +, ++ and +++. The change in relative mobility is noted for each sample.

Oak no.	RELATIVE MOBILITIES		
	Fresh	Frozen	Absolute difference
QA 06	0.60 ++	0.64 ++	0.04
	0.27 ++	0.26 ++	0.01
	0.23 ++	0.19 +	0.04
QA 07	0.58 ++	—	—
	0.23 +++	0.24 ++	0.01
	0.17 +	—	—
QA 08	0.66 ++	0.66 ++	0.00
	0.59 +	0.59 +	0.00
	0.54 +	—	—
	0.25 +++	0.25 +++	0.00
	0.19 ++	—	—
QA 09	0.64 ++	0.68 ++	0.04
	0.61 ++	0.65 ++	0.04
	0.24 +++	0.26 +++	0.02
	0.18 ++	—	—
	Fresh 26/7 (1973)	Fresh 20/8 (1973)	
QO 04	0.62 +++	0.59 ++	0.03
	0.60 +++	0.56 ++	0.04
	0.22 +++	0.22 ++	0.00
	—	0.12 +	—
QO 05	0.58 +++	0.59 +++	0.01
	0.22 +++	0.23 +++	0.01
	0.17 +	—	—

assembly) supplemented with 12 % sucrose and 1 % unsoluable Polyclar AT. (A similar substance often used is unsoluable polyvinylpyrrolidon, PVP.) The buffer was combined with tissue in the ratio of 10:1. After homogenization the preparations were centrifuged at 3650 g for 5 minutes. 20 µl from each supernatant sample was used for disc electrophoresis with the Shandon kit. Buffers and gels were prepared according to the Canalco system (Canalco Instructions 1965) with the following modifications. First the stacking solution (pH 8.8—9.0) was polymerized by means of UV-light (360 nm) and then the separating solution by means of D-riboflavin. The sample was layered over the stacking gel and anionic enzymes and other proteins were separated out at 2 mA per sample tube for 60 minutes. There was sufficient pigment in the oak leaves to make the

use of a tracking dye unnecessary. After electrophoresis the gels were stained for isoperoxydases with 3,3′-dimethoxybenzidine by means of the H_2O_2-o-dianisidine method (WORTHINGTON 1969). The banding patterns of the gels were scanned for absorbancy by using a densitometer (580—650 nm). The distance from the stacking-separating gel interphase reached by each enzyme was measured and the relative mobility (RM) calculated as percentage of the run of the pigment.

Introductory Trials

To test the presence of isozymes in oak leaves six extracts samples from *Q. robur* L. (3), *Q. robur* L. f. *pendula* (1), *Q. robur* L. f. *pyramidalis* (1) and *Q. hungarica* KIT. (1) were prepared and analysed according to the Canalco system. The material (except for *Q. robur* L.) was taken from the garden of The Svalöf Seed Association, Svalöv, Sweden, and the preliminary analysis carried out at the laboratory there.

Two tests on each oak sample gave identical results as follows: peroxydases (4—5 bands) in all samples; phosphatases and esterases no bands at all. (Note: corresponding analyses of hybrids of *Linaria repens* × *vulgaris* in the same electrophoresis indicated the presence of three isoesterases.)

A comparison of enzyme activity (here only used in the sense of degree of quantity as seen in the zymograms) in fresh and frozen plant material, together with a test to show possible changes in peroxydase activity on two occasions about one month apart, gave some information about the reproducibility of the experiments. Frozen oak leaves seem to lose some isozymes. In one case the remaining bands displayed a lower activity (in Table 1 indicated by +, ++ or +++ according to the value of relative mobility, RM). Repeated analyses of fresh leaves at different times showed a similar decrease of activity later in the growing season. The isozymes present on both occasions showed a difference in RM not exceeding 0.04.

RESULTS

A maximum number of seven different isoperoxydases was found in individual trees of *Q. robur* and in leaves from putative hybrids. A total of eleven different peroxydases have been found. With this method it is not possible to make an analysis of the segregation of genes for the different polypeptide chains that combine to form the isozymes (here seen as narrow bands), owing to the very slight differences in migration rates. Although the same type of pattern is obtained repeatedly for a given individual, a given peak of the zymogram obtained in two succeeding analyses of the same extract may differ. The difference may be equal to the differences in migration rate between the same isozyme and an adjacent one or it may be greater than this. Therefore from the calculations of relative migration rates the enzymes are divided into four groups, viz. fast, intermediate (I), intermediate (II), and slow (Fig. 1). Within each of these four groups of peroxydases the frequency distribution of individuals with 0, 1, 2, 3 or 4 isozymes is noted. All populations of *Q. robur* including the progeny sample lack isozymes belonging to the second intermediate group. However, one of the *Q. petraea* populations (A) also lacks the same isozymes.

A comparison of zymograms discloses the diverse profiles of enzymes of different trees in a natural stand of oaks of either species. The enzyme patterns or phenotypes of the seedlings grown from a single tree of *Q. robur* may also indicate heterozygosity. This is shown in Fig. 2 (A—E, *Q. robur*; F—J, progeny of *Q. robur*). In addition the zymograms show that the peroxydase activity in full-grown seedling leaves is a rule quantitatively somewhat greater than that of full-grown leaves from mature trees picked at the same time of the year.

As pointed out elsewhere (OLSSON 1975) the indigenous oak species in Sweden hybridize spontaneously forming introgressive populations so that it is very difficult to find isolated stands of *Q. petraea*. The biotopes considered to be preferred by *Q. petraea* are relatively small in Sweden. Adjacent sites of both species and sites that are within potential crossing distance may be occupied by *Q. robur* as

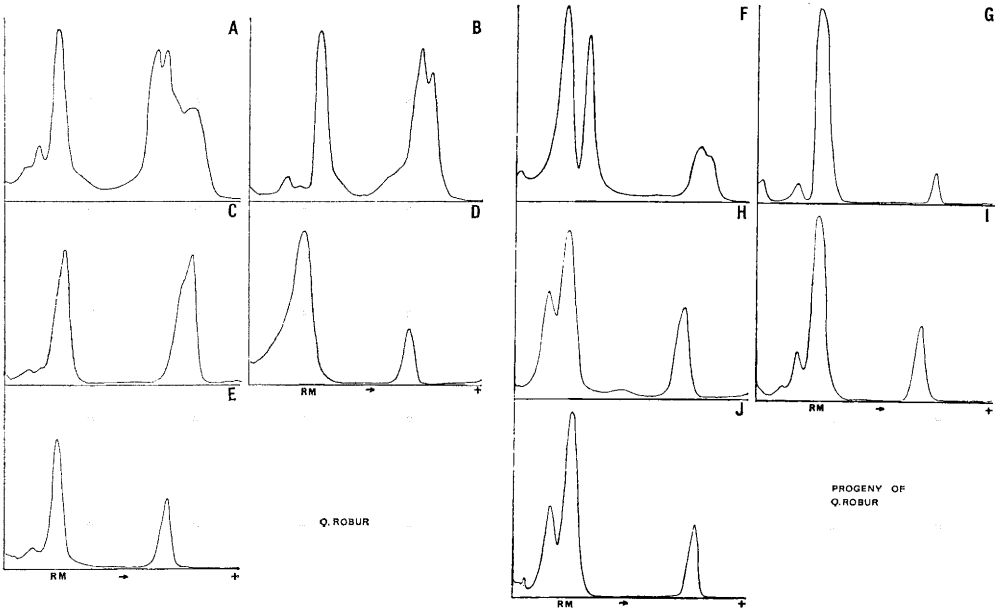

Fig. 2. *Quercus robur*. — Densitometer traces of anionic isoperoxydase banding patterns from adult trees (A—E) and seedlings (F—J) of leaf enzyme extracts. The zymograms show the heterozygosity in the controlled progeny of a mother tree as well as the diverse phenotypes (chemotypes) of mature trees in natural biotopes. Material was taken from five mature trees and five seedlings. — RM: relative mobility. The gels are scanned for absorbancy or optical density in the absorption interval 580—650 nanometers.

a result of spontaneous migration or of having been planted.

The species populations used in this investigation are the most representative judged by the results of analyses of the morphological structure. However, there may be reason to suspect gene flow between the species. Where introgression is concealed or displayed in minor morphological differences only it may be disclosed by the isozyme profile. Thus the unexpected lack of isoperoxydases in the group Intermediate II of the *Q. petraea* population (A) may be due to the presence of introgressive individuals (Fig. 1).

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The Structure of Stellate Trichomes and Their Taxonomic Implication in Some Quercus Species (Fagaceae)

Ulf Olsson

OLSSON, U. 1976 05 06. The structure of stellate trichomes and their taxonomic implication in some Quercus species (Fagaceae). — Bot. Notiser 128: 412—424. Lund. ISSN 0006-8195.

An indumentum analysis of leaf material from populations of oak in regions of sessile oak (*Quercus petraea* (MATTUSCHKA) LIEBL.) in southern Sweden and from herbarium specimens (LD) from the same area has been performed. The combined results of this study and other morphological observations are reported. About 40 % of the pedunculate oaks have the same kinds of stellate trichomes as *Q. petraea* and may constitute introgressive intermediates of *Q. robur* and *Q. petraea*. In the glabrous individuals of the *Q. robur* material pollen stainability is on the average higher than in the pubescent ones. According to the criteria in the subspecies concept given there is no reason to subdivide *Q. robur* into pubescent and glabrous subspecies. It would be more reasonable to treat *Q. robur* and *Q. petraea* as subspecies.

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SCHWARZ (1964) treats twenty-four oak species in Europe. The indumentum characteristics of the leaves are of great diagnostic value, but there are still many questions about the frequency and the type of hairs in some species. SCHWARZ (1936) has a detailed description of all hair types observed. The present study is limited to *Q. petraea* (MATTUSCHKA) LIEBL. and *Q. robur* L. in southern Sweden with the aim of analysing and discussing the presence of stellate trichomes on the abaxial side of the leaves in relation to other characteristics. These species have in past times probably been mutually influenced in morphological characters including pubescence by spontaneous intercrossing and introgression. The resulting great variation of oak types has led many authors of *Quercus* taxonomy to describe a number of taxa within each species.

An extreme point of view is represented by FRIES (1865) and DE CANDOLLE (1864) who join *Q. robur* and *Q. petraea* in one species, whereas later botanists have shown that the apparently fertile intermediate forms have meiotic disturbances pointing to a hybrid origin (HOEG 1929). This suggests that *Q. petraea* and *Q. robur* are to some extent reproductively isolated species. SALISBURY (1940) and WEIMARCK (1947 c) described the somewhat different ecological claims of the two species. The author (OLSSON 1975) has shown, as did COUSENS (1963), that the species intercross to a rather high extent in natural populations.

SCHWARZ (1937) and WEIMARCK (1947 a) have noted the presence or absence of stellate trichomes on the abaxial side of the leaves of *Q. robur*. SCHWARZ designates the pubescent kind of pedunculate oak *Q. robur* ssp. *pedunculata* var. *puberula* and the glabrous one, ssp. *pedunculata* var. *glabra*. WEIMARCK raises the pubescent variety to the rank of subspecies naming it *Q. robur* L. ssp. *puberula* (LASCH) WEIM. According to WEIMARCK, *Q. robur*

L. ssp. *pedunculata* DC. may have "very thin, simple winding hairs" but lacks stellate trichomes of any kind. The naming of the subspecies (WEIMARCK 1947 b) is not in accordance with the now-existing international code of botanical nomenclature. If the two subspecies are maintained the proper name of the taxon which lacks stellate trichomes would be *Q. robur* L. ssp. *robur*. The name of the subspecies with stellate trichomes would be *Q. robur* L. ssp. *puberula* (SCHWARZ) WEIM. (see Taxonomy below).

In this paper some of the oaks examined are grouped according to WEIMARCK (1947 a, b; 1963). However, the author has not unreservedly accepted the taxa. The evidence of the present material does not support maintaining the two subspecies under *Q. robur*. The taxa are used here as samples or statistical groups which are compared.

MATERIAL AND METHODS

Three categories of oak have been investigated. (A list of localities is given in Appendix 1.)

(1) Herbarium Specimens

In the Scandinavian Herbarium of the Botanical Museum in Lund (LD) specimens of the following taxa were borrowed for a preliminary examination of the morphological variation in the most important kinds of Swedish oaks:

(A) *Q. robur* L. ssp. *puberula* (SCHWARZ) WEIM.
(B) *Q. robur* L. ssp. *robur* (*Q. robur* L. ssp. *pedunculata* DC.)
(C) *Q. petraea* (MATTUSCHA) LIEBL.
(D) *Q. petraea*×*robur*

The classification is confirmed by the author by a comparison with the results of the population investigation (OLSSON 1975). Thus B corresponds to the *robur* phenotype and C to the *petraea* phenotype and A and D to the intermediate or interspecific phenotypes.

(2) Pedunculate Oaks from Skåne

The oak material was taken from throughout the woodlands of Skåne and is considered as being representative. Planted oak forests of uncertain origin or of foreign provenance were avoided. In the area concerned *Q. petraea* is rare or absent.

(3) Populations in Regions of Sessile Oaks

The population structure of oak woods within the distribution range of sessile oak in Sweden has previously been reported on (OLSSON 1975). The results of an indumentum analysis of different phenotypes of that plant material are given in the present study.

A disadvantage of the investigation may be the grouping of the material in three "samples" investigated separately. Owing to differences in sampling technique and in time of collecting, and varying possibilities of obtaining suitable material to demonstrate all characters, new methods of analysis were subsequently adapted and introduced. The combined results are discussed. Indeed the three different oak samples used may better represent the variation in these taxa than one type of sample alone would have done. The first sample of herbarium specimens was used to obtain a general idea of some of the diagnostic characters hitherto applied in *Quercus* taxonomy. My own taxonomic views are grounded primarily on the results of the population studies (3) (cf. OLSSON 1975).

Biometry

Measurements were made chiefly for leaf characters. At least five samples of leaves were examined from each oak collection (A—D). The measurements used are illustrated in Fig. 1. Samples collected by the author are more representative of an oak individual than the corresponding herbarium material owing to the sampling technique used. A minimum of ten leaves was used for each character examined. In addition to the study of various characters of leaves as well as flowers and fruits, the percentage of pollen stainable in cotton blue in my own material has also been calculated. Maximum and minimum values with standard errors are given for some characters (Table 1). In the population analysis (OLSSON 1975) the variation in pubescence and other characters were shown in scatter diagrams.

Some Definitions and Methods Applied to Biometry

Leaf shape: The ratio of the length of the apical part above widest point to the total leaf length is used as a numerical value of the leaf outline. From Fig. 1 it can be

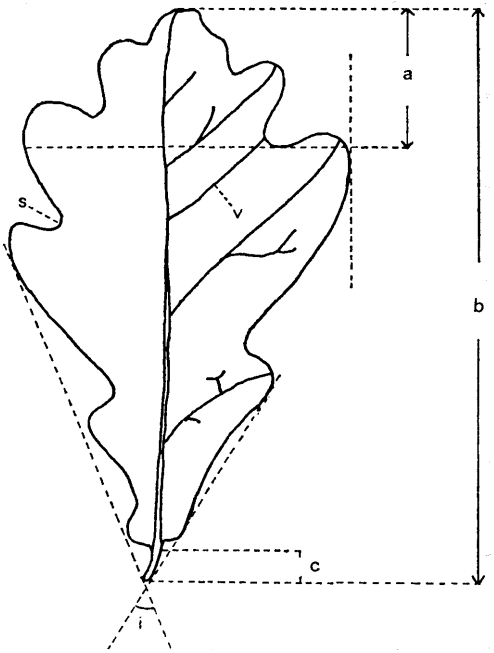

Fig. 1. General view of an oak leaf. Code to the measurements. — a. Length of apical part of leaf above widest point (mm). — b. Total length of leaf (mm). — c. Length of petiole (mm). — i. Angle of leaf base (degrees). — v. Sinus vein. — s. Sinus.

seen that the inequality $1 > a/b > 0.50$ represents an ovate leaf and $0 > a/b > 0.50$, an obovate leaf. The leaf shape value of about 0.50 characterizes the elliptical leaf.

Leaf veins (Coefficient of venation): A numerical value for the absence or presence of sinus veins is the ratio of the number of sinus veins to the number of sinuses of one side of a leaf. This coefficient varies between 0 and 1.

Peduncle "length": The distance between the base and the first flower bract or scar of bract.

RESULTS

Habit

Q. petraea and *Q. robur*: Deciduous trees with a decurrent habit forming wide crowns and with short trunks when growing in open fields. In closed stands the habit is modified with tall trunks and rather narrow crowns.

Q. robur: Angles between stem and branches rather wide; leaves clustered forming an open crown.

Q. petraea: Narrower angles between branches; foliage uniformly distributed, forming a more or less dense crown.

The modification of these gross morphological characters is marked and can lead to difficulties in identification when the trees have dropped their leaves.

Oaks have a certain tendency to form epicormic shoots. This capability is heritable and varies with the provenance.

Table 1. Biometric data of *Quercus*. — A: *Q. robur* ssp. *puberula*. — B: *Q. robur* ssp. *robur*. — C: *Q. petraea*. — D: *Q. petraea*× *robur*. — E: Pedunculate oak (Skåne). — MM: Average mean value. — m: Standard error. — n: Number of mean values (trees). — I: Angle of leaf base (degrees). — II: Leaf shape. — III: Length of petiole (mm). — IV: Coefficient of venation. — V: Peduncle length (mm).

		Min. value	MM ± m	Max. value	n
I	A	45	58.1 ±1.2	77	20
	B	40	60.7 ±1.6	82	20
	C	48	70.1 ±1.4	102	20
	D	20	64.0 ±2.1	110	20
	E	43	59.8 ±1.1	80	57
II	A	0.28	0.40 ± 0.01	0.61	20
	B	0.25	0.40 ± 0.01	0.54	20
	C	0.23	0.41 ± 0.01	0.58	20
	D	0.24	0.41 ± 0.01	0.59	20
III	A	2	5.7 ±0.4	10	20
	B	3	6.0 ±0.4	14	20
	C	5	12.8 ±0.6	23	20
	D	3	9.9 ±0.6	17	20
	E	4	6.3 ±0.2	12	57
IV	A	0	0.66 ± 0.03	1	20
	B	0	0.63 ± 0.05	1	20
	C	0	0.19 ± 0.03	1	20
	D	0	0.37 ± 0.03	1	20
	E	0	0.61 ± 0.02	1	55
V	E	6	31.1 ±1.4	59	53

An increase in light condition initiates the formation of the epicormics. Another type of branch, the so-called Lammas shoots can also affect the form of the crown. This second type of shoot is developed from a new terminal bud of the annual shoot.

Morphology — Herbarium Specimens

The following summary of the results of the analysis of the artificial aggregates of herbarium specimens should first be used as a provisional assessment of the amplitudes of certain characters. The same number of specimens has been used within each taxon, which of course does not correspond to the natural distribution.

Leaf shape (outline): All oak leaves examined are on the average obovate and the shape of the leaf is in practice unreliable as a discriminating character.

Leaf base: Nearly all *Q. robur* leaves have cordate bases with inflexed margins (ears). In *Q. petraea* the leaf base is obtuse or cuneate. Aberrant forms occur, often with an oblique base, sometimes more truncate than obtuse, especially in the putative hybrid material.

Venation: (Figs. 1, 2, Table 1: IV). The average MM-values lie closer to 0 for *Q. petraea* and closer to 1 for the *Q. robur* subspecies. The value for *Q. petraea*× *robur* (D) is intermediate.

The length of the petiole: On the average the length of the petiole of *Q. petraea* is twice that of *Q. robur*, the hybrid material being intermediate. Observe the small differences between the *Q. robur* subspecies (Table 1: III).

Leaf base angle: (Table 1: I). The differences between the oak taxa are rather marked, but there is a certain tendency towards higher values, i.e. wider angle, in *Q. petraea.*

Buds: All buds of *Q. robur* are more or less obtuse. About two thirds of the *Q. petraea* buds examined are more or less acute. Most of the hybrids resemble *Q. robur* in this character.

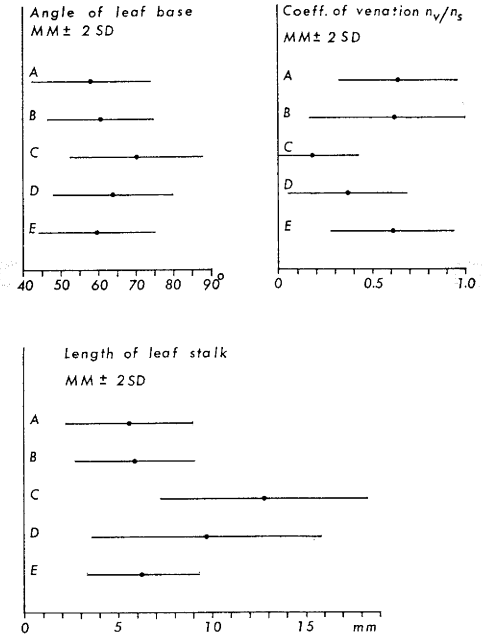

Fig. 2. Average means and doubled standard deviations (MM± 2 SD) of three characters examined.

Observe that *Q. robur* ssp. *puberula* (A) is nearly identical with *Q. robur* ssp. *robur* (B) in all morphological characters except pubescence.

Indumentum

The frequencies of different types of trichomes were determined under the microscope (×125). Five fields distributed over the abaxial surface of the leaf make up to a total area of about 5 mm².

Two kinds of simple hairs are recognized. First, thin multicellular hairs of a glandular nature with bulbous bases are found in all oak taxa in this study. The majority of these small hairs often have a withered appearance (Figs. 7 A, 3). Secondly, one can find a type of simple hair which retains its form when dried as do the bifurcate and stellate trichomes. The "simple hair" in Table 2 belongs to

Table 2. Density of hairs on abaxial surface of leaf in *Quercus*. Mean number of trichomes per mm² and percentage (within brackets) of total number of trichomes observed within each taxon. — A: *Q. robur* ssp. *puberula*. — B: *Q. robur* ssp. *robur*. — C: *Q. petraea*. — D: *Q. petraea*×*robur*.

Type of hair	Taxa							
	A		B		C		D	
Simple	1	(12.4)	0	(—)	1	(4.7)	1	(15.7)
Bifurcate	2	(33.6)	0	(—)	6	(38.1)	3	(43.3)
3-branched	1	(7.5)	0	(—)	2	(11.6)	1	(8.0)
4-branched	3	(45.5)	0	(—)	6	(45.3)	2	(31.7)
5-branched	< 1	(0.8)	0	(—)	< 1	(0.2)	< 1	(0.7)
6-branched	< 1	(0.1)	0	(—)	0	(—)	< 1	(0.1)
7-branched	< 1	(0.1)	0	(—)	< 1	(0.1)	0	(—)
8-branched	0	(—)	0	(—)	0	(—)	< 1	(0.4)
Total	7	(100.0)	0	(—)	c. 15	(100.0)	c. 7	(100.0)

the second type. The first type of trichome will be termed "glandular hairs" and the second type "simple hairs" or "simple trichomes".

Stellate trichomes: Each branch of a stellate trichome is unicellular. Under the SEM the stellate trichomes are often seen to be a combination of simpler units forming multibranched hairs joined at the base (Fig. 3 C, D). The characteristics of the constituent elements (1—4-branched trichomes) are maintained. No attempt is made to describe the distribution of the different combination types of multibranched trichomes.

The author has confirmed that the "glabrous" *Quercus* material is *Q. robur* ssp. *robur*. In addition to the "glandular hairs" found on all oak leaves, if more than five areas/leaf are examined a few isolated trichomes may be revealed. ("Glabrous" is used below in the meaning of "no one simple trichome or branched trichome observed".)

Bifurcate and four-branched stellate trichomes dominate the indumentum of the pubescent specimens (Fig. 7 B). The percentages are 79, 83.4 and 75, respectively, for taxa A, C, and D (Table 2). However, trichomes with up to eight branches have also been found. Note the density of trichomes in *Q. petraea* (C), on an average c. 15 per mm², compared with 6—7 trichomes per square unit in *Q. robur* ssp. *puberula* (A) and the putative hybrid material (D).

Tufts of hairs in the vein axils on the abaxial side of the leaf have been regarded as a rather good character for distinguishing sessile oaks. The tufts consist of especially long simple and stellate trichomes (Fig. 7 C). *Q. robur* ssp. *puberula* usually lacks these tufts of hairs. In this subspecies one can see conspicuously long trichomes along the midribs.

Pedunculate Oaks (Skåne)

The oak material (Table 1 E, Fig. 2) was analysed as one (statistical) sample. No preliminary subdivision into pubescent and glabrous material was made. The oaks may include the subspecies *puberula* and *robur* (A, B resp.) and the putative hybrid intermediates (cf. D) of *Q. robur* and *Q. petraea*. Morphological data (except for pubescence) are presented in brief as follows.

The average mean values (MM) in Table 1 for the *Quercus* group E agree well with the MM values of the subspecies of *Q. robur* (A, B) previously described. The length of the petiole (III) and the venation (IV) are two characters of pro-

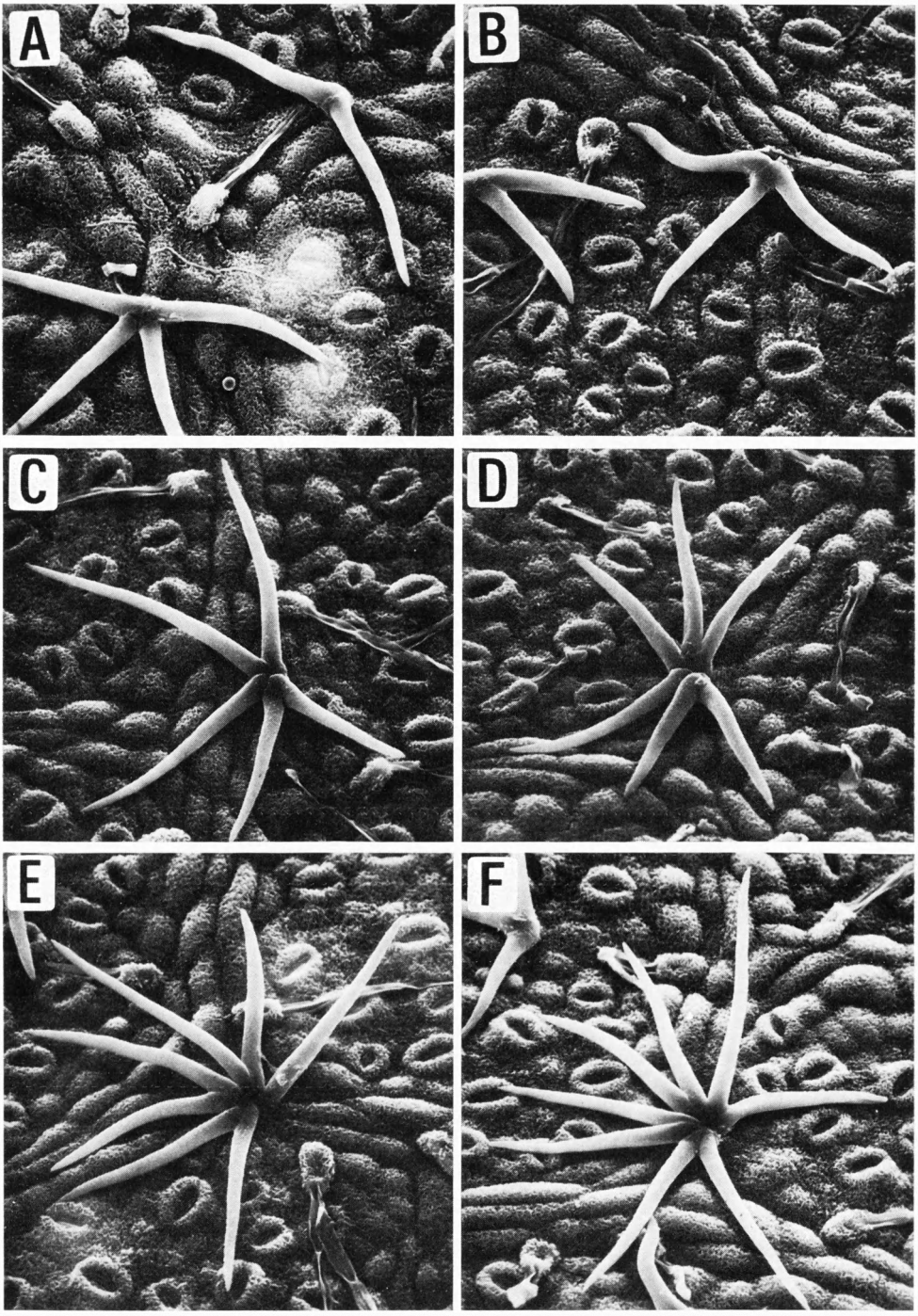

Fig. 3. Types of stellate trichomes (A—F) with 2—8 branches; SE micrographs ×600.

Table 3. Pedunculate oak (Skåne). Correlation between percentage stainable pollen and morphological variation. — a: Leaf base angle (degrees). — b: Petiole length (mm). — c: Peduncle length (mm). — d: Ratio, length/width of acorn. — e: Density of trichomes. "Glabrous" oaks excluded. — f: Coefficient of venation.

Character	t^2	Degrees of freedom	Limits of signif. (P %)	Correlation (r)
a	14.60	1/48	$P < 0.1$	+0.48
b	109.07	1/48	$P < 0.1$	+0.83
c	8.89	1/45	$1 > P > 0.1$	+0.41
d	0.26	1/45	$P > 5$	—0.08
e	132.00	1/18	$P < 0.1$	+0.94
f	456.00	1/47	$P < 0.1$	—0.003

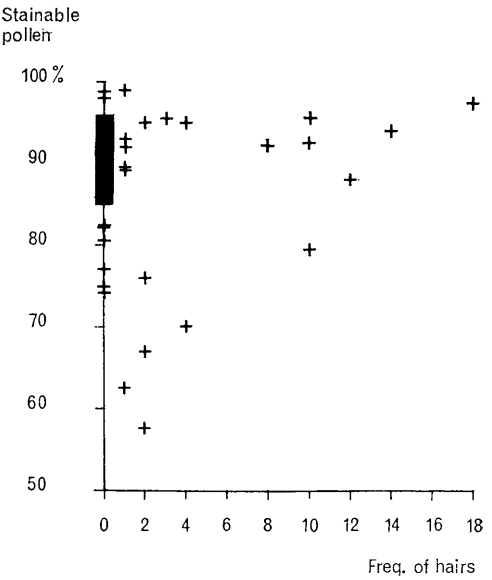

Fig. 4. Pedunculate oak (E). Correlation between pollen stainability and density of trichomes. Each + sign represents one individual. The dark field indicates a sample of twenty-two glabrous oaks.

nounced diagnostic value. Observe the slight displacement of the MM-values of the E oaks towards the hybrid group (D) indicating that some of the material from Skåne (E) is of hybrid origin. Another possible indication of this is revealed in the comparison of morphology and percentage stainable pollen (below).

The average mean for peduncle length as defined above is 31.1 ± 1.4 mm (53 trees).

Two types of female catkins with reduced fruits occur. The commonest fructification has many undeveloped acorns at the top of the peduncle. One can also find catkins with acorn rudiments along the entire axis or on both sides of one or two normal acorns. This second type of catkin discloses reduced female fertility. A corresponding reduction in percentage of stainable pollen in the same individual has in some cases been observed.

The shape of the acorn and its cupule varies. The involucre can be shallowly cupular or relatively deep and funnel-shaped. The commonest type of acorn has a length/width quotient of 1.5.

Indumentum

43.9 per cent of the *robur* oaks collected in Skåne were pubescent. Four types of trichomes are found on the abaxial surfaces of the leaves: simple, bifurcate and 3- and 4-branched. As a rule bifurcate and 4-branched trichomes dominate. The density ranges from 1 to 18 per mm^2. In this oak material (E) no trichomes were found with more than four branches (Table 2).

Pollen Stainability and Morphological Variation

The percentage of pollen grains stainable in cotton blue is often used as a measure of pollen fertility. The correlation between pollen stainability and distribution of morphological characters is shown in Table 3. The length/width of the acorn and the venation coefficient seem to be entirely unrelated to pollen stainability.

The distribution of the individuals with low and high degrees of pollen stainability in relation to different degrees of pubescence is seen in Fig. 4 (cf. Table 3 e).

Fifty oaks were examined, thirty of which are glabrous. Note that the pubescent oaks have a tendency to display higher stainability with increasing density of trichomes ($r = +0.94$; $P < 0.1$). The oaks with a very low degree of pollen stainability (< 70 per cent) have a trichome density of less than five per mm^2.

The histograms in Fig. 5 illustrate the distribution of pollen stainability in glabrous and pubescent oaks of the material from Skåne in a different way, the frequency of trichomes not being taken into consideration.

In glabrous oaks there is a relatively high degree of stainability. In 78.6 per cent of them pollen stainability is more than 85 per cent. The corresponding value for the pubescent oaks is 72.7 per cent. However, one can find a group (18 per cent) with a low stainability, falling below the minimum value for the glabrous oaks. This indicates to some degree that the glabrous oaks are closer to the species state (*robur*).

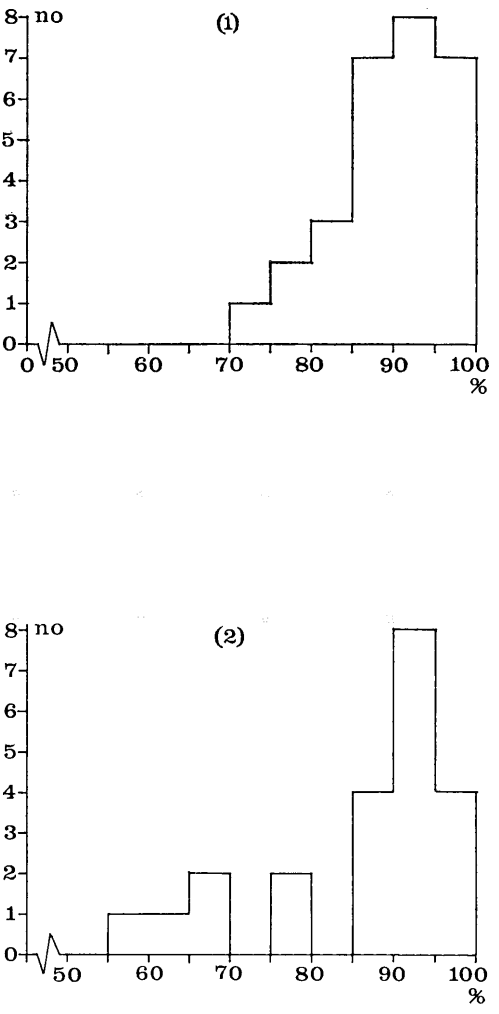

Fig. 5. Pedunculate oak (E). Frequency distribution of glabrous (1) and pubescent (2) individuals in different classes of pollen stainability.

The Distribution of Pubescent Phenotypes within Natural Populations of Oak

In view of the preceding observations it would be of great interest to study the distribution of the indumentum characters, in particular of the representatives of spontaneously introgressive oakwoods. In the following report, where not otherwise stated, the results refer to a previous examination of oak stands (Olsson 1975) where the population structure as regards nine different phenotypes (*a*—*i*) was demonstrated by the use of pictorial scatter diagrams. Six of the nine types of combined characters include pubescence. In the study referred to the pubescent phenotypes were designated *a*, *b*, *c*, *d*, *e*, and *g* respectively (Olsson 1975 Fig. 4). Divided into classes according to distance from either species type, pubescent individuals are to be found in the classes I—IV. Taken in this order the classes of phenotypes (as means of combined coordinates in the scatter diagram) constitute a line introgression with a gene flow from the pubescent species (*Q. petraea*) to the glabrous species (*Q. robur*).

Of especial interest is the distribution of *d* (ssp. *puberula*). It is noteworthy that this phenotype has approximately the same centre of distribution as the *robur* type (*i*), (Olsson 1975 Fig. 3 A, C, E).

This agrees well with the result of the comparison of the *robur* subspecies in the herbarium material (1). In twenty per cent of the "*puberula*-phenotypes" pollen stainability lies below 70 per cent, wich may indicate that they are to some extent hybrids or introgressives.

Multibranched trichomes: Stellate trichomes with more than four branches are unusual. They are found in 7 per cent of the oaks examined, mainly among the sessile oaks (fourteen trees of phenotype *a*.) But two other oak types were also represented, viz. four oaks of phenotype *b* which is rather closely affined to *a*, and finally one individual only of the intermediate type *d*.

There is a remarkable degree of correlation between low pollen stainability and occurrence of multibranched trichomes. Thus the distribution of pollen stainability in the sessile group (*a*) of fourteen oaks with multibranched trichomes is as follows, 2 (21—30 %), 1 (61—70), 5 (71—80), 3 (81—90), 3 (91—100). The stainability in all oaks of type *b* with multistellate trichomes is above 85 per cent.

CONCLUSIONS AND DISCUSSION

Controversial Aspects of Hybridity

In Skåne and many other parts of southern Sweden the climatic, topographic and edaphic conditions are very varied within a relatively small area, so that the different *Quercus* species can grow together in the same area. Thus gene exchange is possible. Ecological conditions for the establishment of new hybrids are also good.

Phenological factors, such as different times of flowering in *Q. robur* and *Q. petraea*, may prevent the formation of hybrids. However, KRAHL-URBAN (1957), who studied leaf-shedding and flowering found that any extreme difference between provenances of a single species far exceeds the difference between the average characteristics of the two species.

A few crossing experiments have been carried out to determine the presence or absence of incompatibility factors. PYATNITSKII (1939) crossed species within the subgenus *Quercus* (syn. *Lepidobalanus* (ENDL.) ÖRSTED) as well as from different subgenera. He records a very low percentage successful crosses. DENGLER (1941) confirms this result and reports two per cent fertile seeds from the cross *Q. robur* (♂) × *Q. petraea* (♀). He also made successful reciprocal crosses, unlike PYATNITSKII who failed to cross *robur* (♀) and *petraea* (♂).

The results of the investigation of artificial and spontaneous hybrids noted above demonstrate that many of the intermediate forms in actual fact constitute hybrid offspring of *Q. robur* and *Q. petraea*.

DENGLER (1941) and JONES (1959) believe that spontaneous hybrids in nature do not exist to the extent often stated. This is grounded on the difficulty in obtaining a high percentage of fertile acorns with artificial cross-pollination. This theory has not been verified and may be wrong. Better methods of pollination may raise the yield of hybrid acorns. DENGLER discloses the fact that a change in the method of pollination increased the crop of acorns from 29 to 61 per cent in intraspecific (*Q. robur*) cross-pollination. Even a frequency of less than one to two per cent in natural intercrossing might be sufficient for the formation of introgressive populations.

Given that the prevailing view regarding species interpretation (SCHWARZ 1964, KOMAROV 1970) holds, the occurrence of introgressive intermediates of *Q. robur* and *Q. petraea* must be very high. In fact, c. 40 per cent of the pedunculate oaks (Skåne) have the same kinds of stellate trichomes as *Q. petraea*. This view is confirmed by the results of the population study (3). 45 per cent of all oaks examined are interspecific. If the two phenotypes

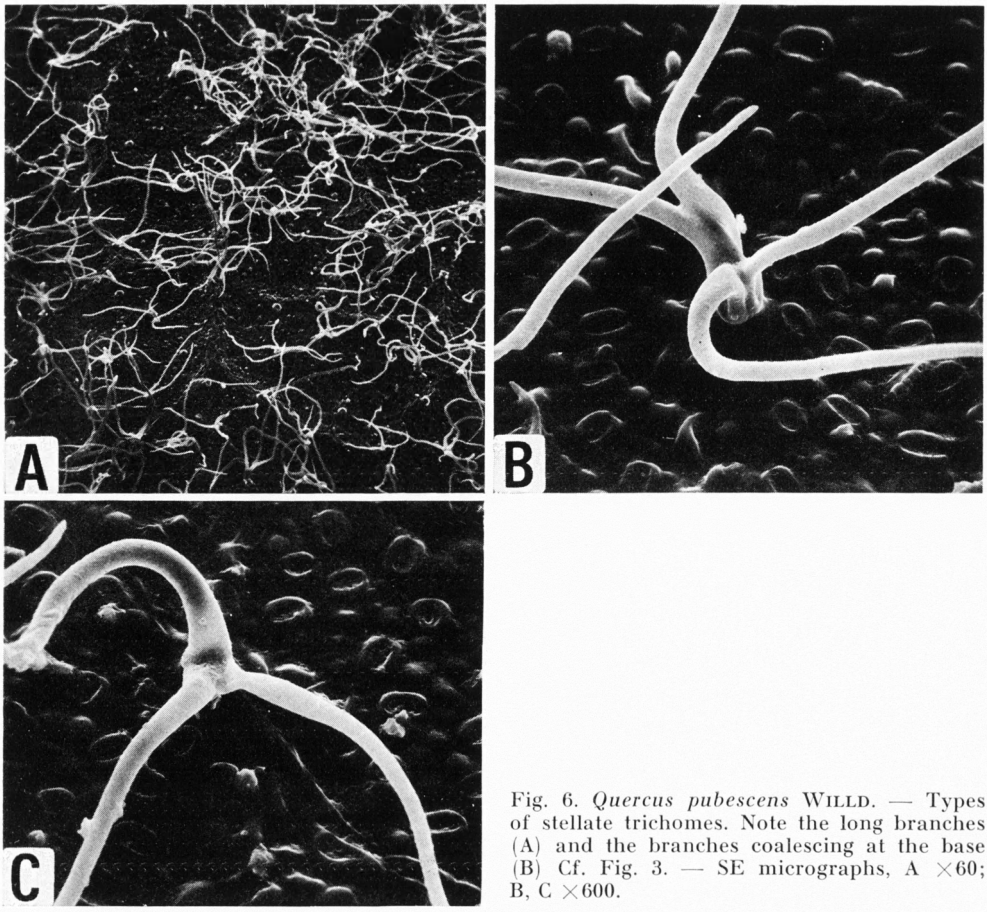

Fig. 6. *Quercus pubescens* WILLD. — Types of stellate trichomes. Note the long branches (A) and the branches coalescing at the base (B) Cf. Fig. 3. — SE micrographs, A ×60; B, C ×600.

b and *h* (OLSSON 1975 Table 2) are excluded, the phenotypes *c*—*g*, which are presumably introgressives, still constitute about 17 per cent of the material.

The morphological observations presented in this investigation also suggest that hybridization occurs between the species. As *Q. robur* is the commonest oak in Sweden a displacement of the gene pool of *Q. petraea* in the direction of *Q. robur* has probably occured. Due to introgressive hybridization the evolution of *Q. robur* from glabrous to pubescent forms has probably taken place. This statement is also supported by the fact that in the glabrous individuals of the *Q. robur* material pollen stainability is on the average higher than in the pubescent ones.

Some authors have expressed the possibility of including a third oak species in the intercrossing system of *Q. petraea* and *Q. robur*. WEIMARCK (1947 a) argues that *Q. pubescens* WILLD. may be a possible parent. A comparison of trichome types and the epidermal structure of the species concerned indicates that no crossing has taken place between *Q. pubescens* and either sessile or pedunculate oak as regards these characteristics (Figs. 3 and 6).

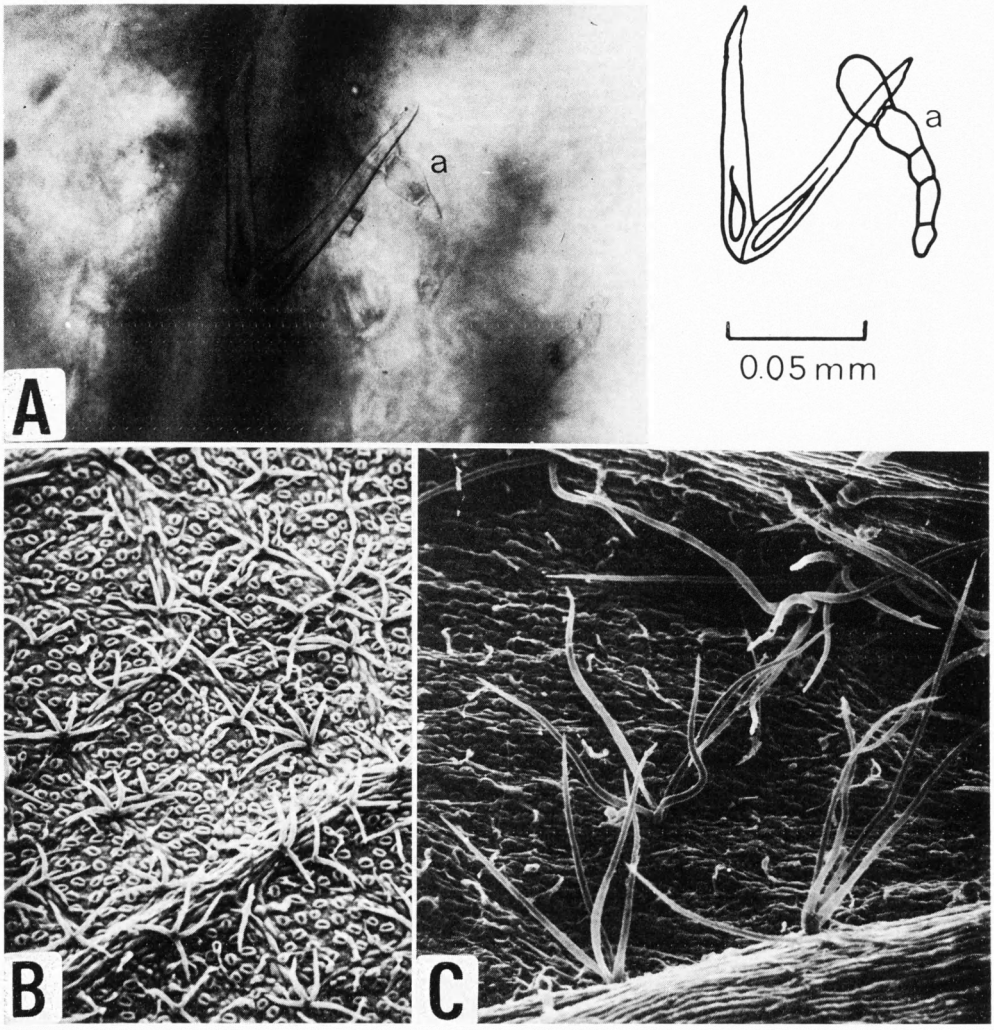

Fig. 7. Light and SE micrographs of hairs on the abaxial side of *Quercus* leaves. — A: Bifurcate trichome with unicellular branches and multicellular glandular hair (a) (see drawing on right). — B: General view of pubescent side of a leaf of sessile oak. — C: Tufts of stellate and simple hairs in the vein axils of sessile oak.

TAXONOMY

Pubescent and glabrous types of *Q. robur* considered above belong to different subspecies according to WEIMARCK (1947 a) and other authors. In my opinion the glabrous state represents the "pure species" state of *Q. robur*. Part of the material of *puberula* probably represents the hybrid *Q. petraea*×*robur* or the derivatives thereof. As regards the remainder of the material evidence of hybridity other than pubescence is lacking. However, it is possible that also this material represents introgressives.

The author follows the subspecies concept given by RUNEMARK (1961), "that two populations are referred to different subspecies if (1) the gene exchanges between them is restricted on genetic grounds or is limited or made impossible by external means and if (2) they are separated by a more or less strong hereditary discontinuity in one or several basic morphological characters or a combination of such characters". According to these criteria there is no reason to subdivide *Q. robur* into pubescent and glabrous subspecies, but it would be more reasonable to treat *Q. robur* and *Q. petraea* as subspecies.

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APPENDIX 1. Localities of Oaks Examined

A. Quercus robur ssp. puberula

SKÅNE. Brönnestad, Harröd, 300 m NW Lillsjödal (H. WEIMARCK): 450201 — Lund (T. HÅKANSSON): 450301 — Löderup (T. HÅKANSSON): 450401 — Riseberga (T. HÅKANSSON): 450501 — Löderup, Sandhammaren, close to the lighthouse (H. WEIMARCK): 450601 — N Mellby, W Furutorp, pine forest (H. WEIMARCK): 450701 — Genarp, Skoggård (H. WEIMARCK): 450801 — Gladsax, sand meadow (H. WEIMARCK): 450901 — Höör, hill NNE Fogdaröd (G. OLSSON): 451001 — Rörum (H. WEIMARCK): 451101 — Torna Hällestad, Boreslund, sand hills (H. WEIMARCK): 451701 — southern lake shore of Vomb (J. LINDERS): 451801 — Torna Hällestad, beech-hill, sand (H. WEIMARCK): 451901 — S Mellby, hill slope ENE Gladelund — SMÅLAND. Färgaryd, Ulfshult (H. WEIMARCK): 450101 — V Torsås, Nybygden (H. WEIMARCK): 451601 — VÄSTERGÖTLAND. Borås, Hultberg (A. HOLMERZ): 451501 — Göteborg, Liseberg (H. C. KINDBERG: 451401 — ÖSTERGÖTLAND. Fjärstad, Boda (H. WEIMARCK): 451301 — UPPLAND. Roslagen, Gregersboda (H. & A. FRIES): 451201.

B. Quercus robur ssp. robur

SKÅNE. Bosjökloster. (T. HÅKANSSON): 453401 — Löderup, Sandhammaren, close to the lighthouse (H. WEIMARCK): 453501 — Visseltofta, 1 km W Boalt (H. WEIMARCK): 453601 — Brösarp, pine forest at the railway station (H. WEIMARCK): 453701 — S Mellby, 1 km NE Svinaberga (Stenshuvud)

(T. HÅKANSSON): 453801 — Riseberga, 400 m SSE Skäralid (T. HÅKANSSON): 453901 — Riseberga, 300 m S Skäralid (T. HÅKANSSON): 454001 — SMÅLAND. Jät, Lindeberg (H. WEIMARCK): 452301 — Väckelsång, Esbjörnamåla (H. WEIMARCK): 452401 — Värnamo, Hjulshammar—Funtabo (H. WEIMARCK): 452501 — Bolmsö, close to the church (H. WEIMARCK): 452601 — Långaryd, Yttersjöholm (H. WEIMARCK): 452701 — Öjaby (G. BJÖRNSTRÖM): 452801 — Bosebo, Bolbynäs (H. WEIMARCK): 452901 — Nydala, Moboda (H. WEIMARCK): 453001 — Villstad, Sännås (H. WEIMARCK): 453101 — V Torsås, Piparelid (H. WEIMARCK): 453201 — Virestad, Högelid (H. WEIMARCK): 453301 — HALLAND. Gunnarp, Strättebo (H. WEIMARCK): 452101 — Gunnarp, Joarsbo (H. WEIMARCK): 452201.

C. Quercus petraea

SKÅNE. Osby, Skansen (H. WEIMARCK): 460101 — V Sönnarslöv, NW Kroken (T. DONNÉR & H. WEIMARCK): 460201 — Konga (T. HÅKANSSON): 460301 — Riseberga (T. HÅKANSSON): 461101 — Röke, 1 km E Slättsjö, rubble gravel (H. WEIMARCK): 461201 — Klöva Hallar, V Sönnarslöv (T. HÅKANSSON): 461301 — Osby, 600 m S. Sibbarp, morain (H. WEIMARCK): 461901 — Riseberga, 1 km WNW Slåaröd, rubble gravel (H. WEIMARCK): 462001 — SMÅLAND. Ryd (O. TEDIN): 460601 — Hovmantorp (T. HÅKANSSON): 460701 — Bolmsö close to the ferry-station (G. OLSSON): 460801 — Möckelsnäs (N. JOHANSSON): 460901 — HALLAND. Askome, Fyllekleva (H. WEIMARCK): 461401 — Ljungby, Gislestad (H. WEIMARCK): 461501 — Askome, Hansabo (H. WEIMARCK): 461601 — Ränneslöv, Perstorp (G. OLSSON): 461701 — Fjärås (H. C. KINDBERG): 461801 — VÄSTERGÖTLAND. Närryda, Rävelås (H. FRIES): 460401 — Göteborg, Slättskogen (J. H. KYLIN): 460501.

D. Quercus petraea × robur

SKÅNE. S Mellby, hill slope ESE Gladelund (H. WEIMARCK): 471301 — Osby, Hönjarum (F. LUNDBERG): 471401 — S Mellby, Stenshuvud (E. ASPLUND): 471501 — Hanaskog (TH. LANGE): 471601 — Örkelljunga, 1 km ENE Havabygget (H. WEIMARCK): 471701 — Ässjö, close to Storegård farm (H. NILSSON): 471801 — N Sandby (A. OREDSSON): 471901 — BLEKINGE. Nättraby, Skärva Korpanabben (B. HOLMGREN): 472001 — Karlshamn, Bellevue (I. LINDERHOLM): 470401 — SMÅLAND. Gullabo, Lönbomåla (H. WEIMARCK): 470501 — Färgaryd, Ekenäs-Skoga (H. WEIMARCK): 470601 — Burseryd, 2 km S church (H. WEIMARCK): 470701 — Villstad, Markås (H. WEIMARCK): 470801 — Gnosjö, Bottningabo (H. WEIMARCK): 470901 — HALLAND: Ysby, Skogaby (T. PERSSON): 471201 — VÄSTERGÖTLAND. Ljushult, Hallaved (O. OLSSON): 471001 — Borås, Ryås (C. SANDBERG): 471101 — ÖSTERGÖTLAND. Oppeby, 1 km ESE Björkfors (H. WEIMARCK): 470101 — VÄRMLAND. Visnumskil, Dyrön (H. WEIMARCK): 470201 — Millesvik, Staglerud (H. WEIMARCK): 470301.

E. Pedunculate Oaks Collected by the Author

SKÅNE. Frueräften, 3 km NW S Sandby: 462101 — Måryd, 100 m N Måryd farm: 462201 — 2 km NNE Torna Hällestad church: 462301 — Tryggaröd (by the road Broby—Hässleholm): 462701 — 2 km N Bosjökloster: 462801 — Långstorp, 5 km NNW Höör: 462901 & 463001 — Höör, 2 km N Sjunnerup: 463101 — Höör, 2.5 km N Sjunnerup: 463201 — Höör, Misseröd (Höör—S Rörum): 463301 — Kvesarum, E the castle: 463401 — S Rörum, 1 km W church (S side of the road): 463501 — S Rörum, 1 km W church (N side of the road): 463601 — S Rörum, Bjävröd: 463701 — Sösdala, Oskarsfarm: 463801 — Silvåkra, NE Skrivaremöllan: 463901 — Silvåkra farm, SW Krankesjön: 464001 — Hasslemöllan, 2 km E Veberöd: 464101, 464201 — 3 km E Anklam: 464301, 464401 — 1.5 km NE Lövestad (Lövestad—Andrarum): 464501 — Ry, at the "county" boundary SSW Andrarum church: 464601 — 5.2 km NE Lövestad: 464701 — SW Molleröd (Sillaröd—Vallarum): 464801 — 3 km E Eslöv, Skoghuset: 464901 — Fairyhill (W lake of V Ringsjön): 465001 — Stehag, Värlinge farm: 465301 — Stockamöllan, Hasslebro 465401 — Stockamöllan, Mickelborg: 465501 — ENE Billinge (close to Rönne river): 465601 — ENE Billinge, Hultseröd: 465701 — NW Hallaröd, N Hultarp: 465801 — Hallaröd—Färingtofta at the "county" boundary: 465901 — Rögnaröd, 3 km S Färingtofta: 466101 — Forestad, SW Färingtofta: 466201 — Perstorp, Hunseröd farm: 466301 — Perstorp, Gustavsberg: 466401 — Perstorp, Bosarp: 466501 — 2 km E Tyringe: 466601 — Finja, 0.5 km N Mölleröd farm: 466701 — N Stoby church: 466801 — Hästveda, Amundtorp: 466901 — Veberöd, Grönland: 467001 — Everlöv, Kumlatofta: 467101 — Sövdeborg: 467301 — NW lake Snogeholm, shore: 467401, 467501 — between the lakes of Ellestad and Snogeholm: 467601 — NE lake Snogeholm, Eriksdal at the cross-roads: 467701 — 0.5 km NW S Åsum church: 467801 — Övedskloster: 467901, 468001 — Gammalstorp, NE Äspinge: 468101 — N Vismosse, E Äspinge: 468201 — Påbro, E Tormestorp: 468301.

Contribution à l'étude du genre Cololejeunea

V. Quelques espèces de la région indo-pacifique

P. Tixier

TIXIER, P. 1976 05 06. Contribution à l'étude du genre Cololejeunea. V. Quelques espèces de la région indo-pacifique. — Bot. Notiser 128: 425—431. Lund. ISSN 0006-8195.

Five new species of the genus *Cololejeunea* (SPRUCE) STEPHANI are described and illustrated, viz. *C. hebridensis, C. mackeeana, C. plagiochiliana, C. sophiana* and *C. stoniana.*

P. Tixier, I.N.A. d'El Harrach, Alger Xème, Algérie.

Nous définirons la région indo-pacifique, sur le plan bryologique, comme un vaste courant allant à l'ouest de l'Afrique Orientale, a l'est de la Nouvelle Zélande et remontant vers le nord jusqu'au Japon et aux îles Hawaii.

Ici nous n'insisterons pas sur la systématique du genre *Cololejeunea.* Ce grand genre, qui représente à peu près 50 % des espèces dans les florules épiphylles d'Hépatiques, peut être, chez les Orchidées, au point de vue complexité, comparé par exemple au genre *Dendrobium.* Cela nous évite des développements même brefs sur ce point.

Rappelons seulement que M. MIZUTANI (1961), PAN CHIEH CHEN et PAN CHENG WU (1964) ont fourni des monographies pour le genre au Japon et en Chine, en ce qui concerne les flores tropicales représentant les franges extérieures des flores indo-malaises.

E. H. BENEDIX (1953) n'a envisagé qu'un certain nombre du sous-genres du genre *Cololejeunea* en Indo-Malaisie. Le travail demeura incomplet. R. M. SCHUSTER (1963) a fourni dans son synopsis des genres appartenant aux Lejeuneacées, une revue des différents sous-genres de *Cololejeunea.* Cela n'est qu'un premier aperçu qui demanderait à être complété. Aussi, donnons-nous ici cinq nouvelles espèces: une originaire de Madagascar, une de Malaisie et trois de Mélanésie.

Cololejeunea hebridensis P. TIXIER sp. nov. — Fig. 1

Planta modica, albo viridis, foliicola, substrato appressa. Caules usque ad 1 cm longi, pauciter ramosi, 0,05 mm crassi, cum foliis 1,4 mm lati. Folia sub angulo 90° inserta, interseque 0,4 mm distantia. Cellulae cum trigonibus incrassionibus intermediis in cellulis basalibus. Margo sine cellulis hyalinis. Cellulae marginales 8×10 μ; cellulae partis mediae 15×15 μ; cellulae basales 30—50× ×15—20 μ. Lobus reniformis cum sinu inter lobum carenamque, caulem tegens 0,9 mm longus, 0,6 mm latus. Lobulus saccatus, leviter inflatus 0,3 mm longus, 0,2 mm latus. Apex lobuli laxe truncatus cum 3 dentibus, dente subapiculi, dente apicali, dente media. Papilla hyalina haud visa. Propagulis discoideis, 70 μ in diametro, cum 28 cellulis. Planta monoica. Flos femineus lateralis. Perianthia sub foliis floralibus. Folia floralia cum lobo 0,9 mm, 0,6 mm lato, lobuloque elongato 0,04 mm longo, 0,15 mm lato. Perianthia cum rostro notato, cum alis parvis sinibuque ventralibus, 0,7 mm alta, 0,6 mm lata. Flos masculus lateralis, sessilis, 0,4 mm altus, cum bracteis 3 jugis.

ECHANTILLON EXAMINÉ. Nouvelles Hébrides: Vaté, en forêt dense, 200—300 m, 1973, M. SCHMID s.n. (holotype PC).

Plante moyenne, blanc verdâtre, épiphylle, appliquée au support. Tiges longues

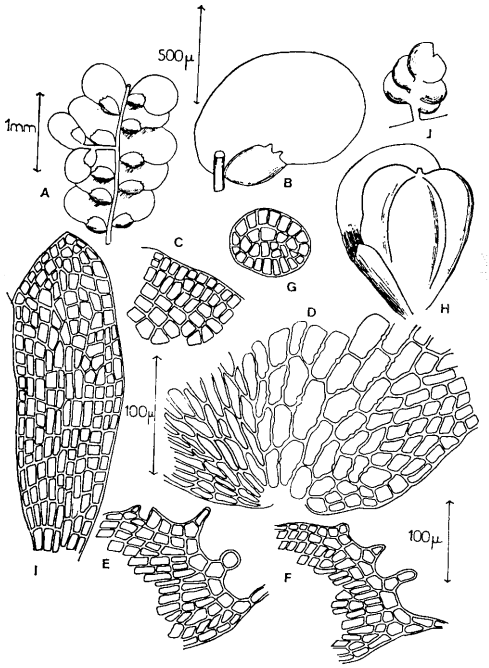

Fig. 1. *Cololejeunea hebridensis*. — A: Tige. — B: Feuille. — C: Apex du lobe. — D: Base du lobe. — E, F: Apex du lobule. — G: Propagule (p=28). — H: Périanthe. — I: Lobule de la bractée périanthaire. — J: Inflorescence mâle.

atteignant jusqu'à 1 cm; peu divisées, épaisses de 0,05 mm, larges avec les feuilles de 1,4 mm. Feuilles insérées sous un angle de 90° et distantes entre elles de 0,04 mm. Cellules présentant des trigones et des épaississements intermédiaires dans les cellules basales. Pas de marge hyaline. Cellules marginales 8×10 µ; cellules de la partie moyenne 15×15 µ; cellules basales 30—50×15—20 µ. Lobe réniforme avec un sinus entre le lobe et la carène recouvrant la tige long de 0,9 mm, large de 0,6 mm. Lobule en sac, moyennement gonflé, long de 0,3 mm, large de 0,2 mm. Sommet largement ouvert, à trois dents avec la présence d'une petite dent surapicale. Papille hyaline non observée. Propagules discoïdes, de 70 µ et avec 28 cellules. Plante monoïque. Inflorescence femelle latérale. Périanthe inclus dans les bractées périanthaires. Bractées périanthaires avec un lobe long de 0,9 mm et large de 0,6 mm, lobule allongé, long de 0,4 mm, large de 0,15 mm. Périanthe à bec bien marqué, à oreillettes et avec deux plis ventraux, haut de 0,7 mm, large de 0,6 mm. Inflorescence mâle latérale courte, implantée directement sur la tige, de 0,4 mm de haut avec 3 étages de bractées fertiles.

Nous classons cette espèce au sous-genre *Pedinolejeunea* (BENEDIX) MIZUTANI dû à son aspect macroscopique (plante très appliquée au support avec un aspect glauque brillant) et à un certain nombre de caractères microscopiques (cellules sans ornements, lobule à trois dents, etc.).

Cololejeunea mackeeana P. TIXIER sp. nov. — Fig. 2

Planta parva, foliicola, substrato appressa. Caulis longus usque ad 5 mm, pauciter ramosus, 40 µ crassus, cum foliis 1 mm latus, in sectione, 5 cellulis visis. Folia sub angulo 40° inserta interseque 0,3 mm distantia. Folia lingulata, lobo 0,4 mm longo, 0,3 mm lato. Margo irregulariter denticulatus. Cellulis cum parietibus plus aut minus tenuibus, incrassionibusque intermediis. Cellulae marginales 30—20×20—15 µ; cellulae basales 40—20× ×20—15 µ. Lobulus usque tertiam partem folii, saccatus, inflatus, cum apice late truncato, duae dentes, apicalis brevis, media plus aut minus hamata. Papilla hyalina ovalis, 20 µ longa, sub angulo. Stylus hyalinus unicellularis, 20 µ altus. Flos femineus lateralis. Folia floralia cum lobo crenulato, 0,5 mm longo, 0,17 mm lato, lobuloque 0,3 mm longo, 0,10 mm lato. Perianthia 4-plicata, denticulata, 0,6 mm alta, 0,3 mm lata. Flos masculus lateralis, 0,6—0,3 mm altus, cum bracteis 3—4 jugis.

ECHANTILLONS EXAMINÉS. Nouvelle Calédonie: Forêt de montagne sur terrain serpentineux, épiphylle sur *Rapanea*, 900 m, 15.V. 1975, MC KEE 30117 (holotype PC). — 24.IV. 1975, MC KEE 30082. — Pic du Rocher, Montagne des Sources, pente ombragée d'un entonnoir, sur feuilles de fougère, 960 m, 8.III. 1951, H. HÜRLIMANN 2394, 2395. — Montée de la "route de Gomen", vers le sommet de l'Ignambi, en forêt de montagne sur Rubiacée, 1200 m, 17.VIII. 1951, H. HÜRLIMANN 2851. — Dumbéa, vallée de la Sunshine, côté du Mont Do, sur Hymenophyllacées, 700 m, 28.VII. 1951, H. HÜRLIMANN 2748.

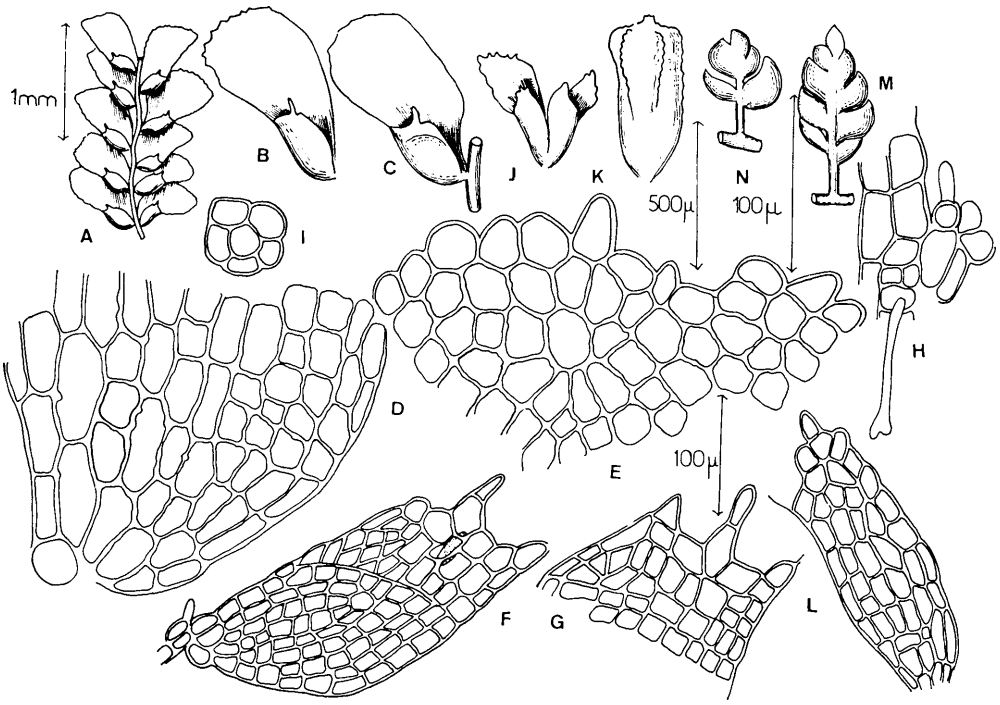

Fig. 2. *Cololejeunea mackeeana*. — A: Tige. — B, C: Feuilles. — D: Base du lobe. — E: Apex du lobe. — F, G: Lobule. — H: Base du lobule. — I: Coupe de la tige. — J: Bractées périanthaires. — K: Périanthe. — L: Lobule de la bractée. — M, N: Inflorescences mâles. — A, B, D—F, H—J, L: MAC KEE 30082. — C, G: MAC KEE 30117. — K, M, N: HÜRLIMANN 2394.

Plante petite, vert pâle, épiphylle, appliquée au support. Tige longue atteignant jusqu'à 0,5 mm, peu ramifiée, épaisse de 40 µ, large avec des feuilles de 1,4 mm, à 5 cellules en section. Feuilles insérées sous un angle de 40° et distantes entre elles de 0,3 mm. Feuille spatulée, à lobe long de 0,5 mm, large de 0,3 mm. Marge irrégulièrement dentelée, rappelant la marge de *Diplasiolejeunea cornuta* STEPHANI. Cellules à parois moyennement minces avec épaississements intermédiaires. Cellules marginales 30—20×20—15 µ; cellules basales 40—20×20—15 µ. Lobule long, dépassant le tiers de la longueur de la feuille, en sac, gonflé, largement ouvert au sommet. Deux dents au sommet, dent apicale courte, dent médiane de deux cellules plus ou moins en crochet. Papille hyaline ovale, allongée, longue de 20 µ, sous le lobule. Style hyalin unicellulaire, haut de 20 µ. Inflorescence femelle latérale. Bractées périanthaires à lobe crénelé, long de 0,5 mm, large de 0,17 mm, lobule long de 0,3 mm, large de 0,10 mm. Périanthe à quatre plis dont deux ventraux, à bords denticulés, haut de 0,6 mm, large de 0,3 mm. Inflorescence mâle latérale de 0,3 à 0,6 mm de haut et avec 3—6 paires de bractées fertiles.

Cette espèce appartient au sous-genre *Lasiolejeunea* BENEDIX, elle diffère de toutes les espèces du sous-genre du Pacifique Sud tropical.

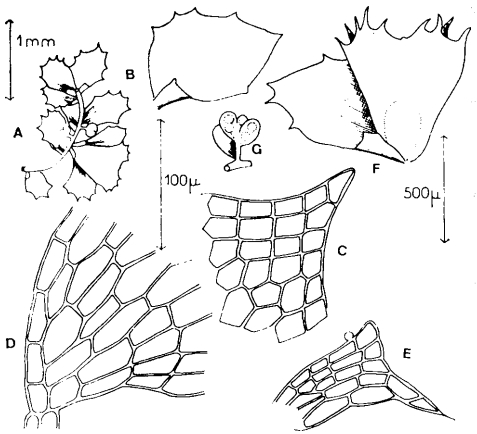

Fig. 3. *Cololejeunea plagiochiliana*. — A: Tige. — B: Feuille. — C: Apex du lobe. — D: Base du lobe. — E: Lobule. — F: Périanthe. — G: Inflorescence mâle.

Cololejeunea plagiochiliana P. TIXIER sp. nov. — Fig. 3

Planta fragilis, viridis, foliicola ad substratum appressa. Caules usque ad 1 cm longi, 0,04 mm crassi, cum foliis 0,6 mm lati, folia sub angulo 90° inserta interseque 0,4 mm distantia. Cellulae magnae, parietibus tenuibus. Cellulae marginales 20×40 µ, basalesque 60—40×20 µ. Folia scutulata, ad marginem denticulata. Lobus 0,7 mm longus, 0,4 mm latus. Lobulus reductus, circum 15 cellulis. Dens media sola visa. Papilla hyalina ad marginem lobuli, sphaerica, 10 µ in diametro. Perianthia lateralia, folia floralia, tam longiora quam perianthia, similia foliis caulis. Perianthia complanata, sine sinibus ventralibus, apice cum alis notatis, ciliatis, 0,6 mm alta, 0,4 mm lata, rostrum parvum. Flos masculus, parvus, lateralis, cum bracteis 2—3 jugis fertilibus cuique cum 2 antheridibus.

ECHANTILLON EXAMINÉ. Madagascar: Périnet, épiphylle en forêt, 3.IX. 1951, R. BENOIST s.n. (holotype PC).

Plante fragile, verte, épiphylle, appliquée au support. Tige atteignant jusqu'à 1 cm de long, épaisse de 0,04 mm, large avec les feuilles de 0,8 mm, feuilles insérées sous un angle de 90° et distantes entre elles de 0,4 mm. Cellules grandes à parois minces, cellules marginales de 20×40 µ, cellules basales 60—40×20 µ. Feuilles rhomboïdales à bords denticulés. Lobe long de 0,7 mm, large de 0,4 mm, lobule réduit à une quinzaine de cellules. Dent médiane seule marquée, papille hyaline sur le bord du lobule de moins de 10 µ de diamètre. Style non-observé. Périanthes latéraux, bractées égales au périanthe, de même forme et de même taille que les feuilles caulinaires. Périanthe aplati, sans plis ventraux, sommet à oreillettes marquées, munies de cils, plus ou moins longs, haut de 0,6 mm, large de 0,4 mm, bec peu visible. Inflorescence mâle, petite, latérale de 2—3 étages de bractées fertiles comportant 2 anthéridies.

Espèce proche de *Cololejeunea apiculata* (E. W. JONES) SCHUSTER, espèce unique, supposons nous, de la section *Apiculatae* de SCHUSTER.

Cololejeunea sophiana P. TIXIER sp. nov. — Fig. 4

Planta parva, foliicola, albo-viridis, substrato appressa. Caules usque 0,9—1 cm longi, 0,1 mm crassi cum foliis 2 mm lati, folia sub angulo 60° inserta interseque 0,4 mm distantia, parietibus cellularum tenuibus cum trigonibus incrassionibusque intermediis, margo semihyalina, cellulis exterioribus lobi hexagonalibus, 30 µ in diametro, cellulis basalibus, elongatis, 40 µ longis, 20 µ latis. Folia rotundata, lobus 0,8 mm longus, 0,5 mm latus. Lobulus rotundatus, adplanatus, saccatus 0,15 mm longus, 0,15 mm latus. Apex laxe truncatus cum duobus dentibus, apicali mediaque parvis. Papilla hyalina ovalis, ad basin proximam dentis mediae, 20 µ longa. Propaguli discoidei ovales 90 µ longi, in statu, 28 cellularis. Species monoica. Perianthia lateralia majora quam folia floralia, flora floralia cum lobo 0,8 mm longo, 0,5 mm lato, lobuloque 0,3 mm longo, 0,1 mm lato. Perianthia cordiformia complanata cum duobus sinibus ventralibus, rostro minus notato. Flos masculus lateralis, 0,5 mm altus, bracteis 4 jugis.

ECHANTILLONS EXAMINÉS. Nouvelle Calédonie: Mont Panié, forêt de pente à palmiers, épiphylle, 800 m, I.XII. 1972, M. SCHMID 248 (holotype PC), 260, 261. — Monts Dzumac, forêt basse sur péridotites, épiphylles sur *Cupaniopsis*, 15.II. 1973, J. VEILLON s.n.

Espèce dédiée à Mme SCHMID.

Plante petite, blanc verdâtre, épiphylle, appliquée au support. Tige d'environ 0,5 à 1 cm de long, épaisse de 0,1 mm, large avec des feuilles de 2 mm, feuilles insérées

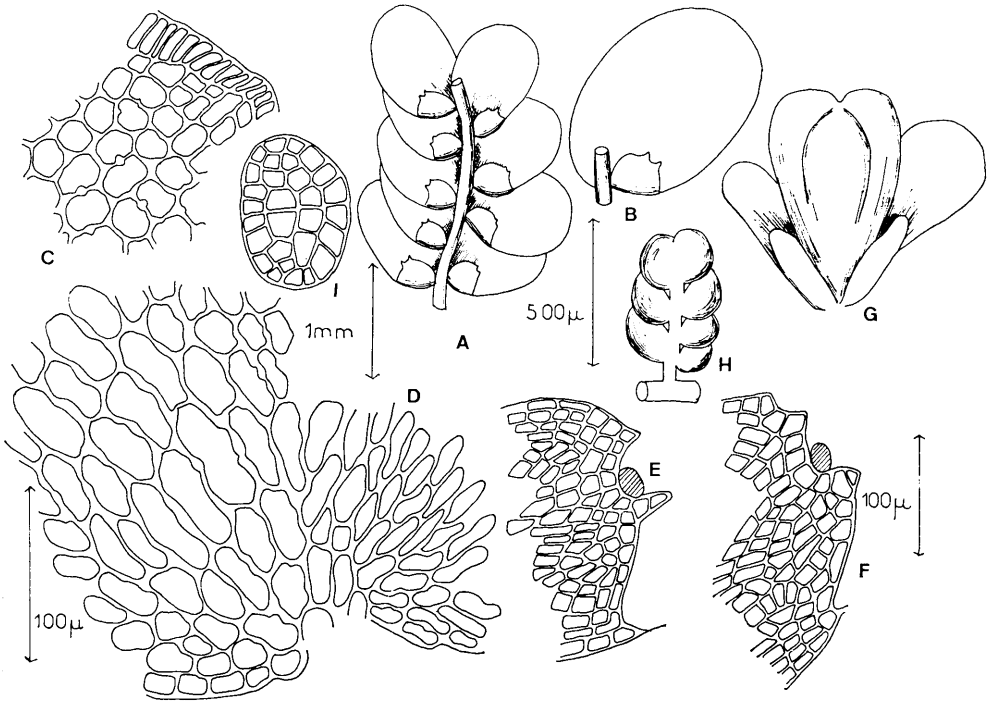

Fig. 4. *Cololejeunea sophiana*. — A: Tige. — B: Feuille. — C: Apex du lobe. — D: Base du lobe. — E, F: Apex du lobule. — G: Périanthe. — H: Inflorescence mâle. — I: Propagule (p=28).

sous un angle de 60° et distantes entre elles de 0,4 mm. Cellules à parois minces, à trigones et épaississements intermédiaires. Marge semi-hyaline constituée de cellules allongées, arrondies de 20 µ de long et de 7—8 µ de large. Cellules périphériques du lobe hexagonales de 30 µ de diamètre, cellules de la base allongées de 40 µ de long et de 20 µ de large. Lobe arrondi, recouvrant largement la tige, long de 0,8 mm, large de 0,5 mm. Apex largement tronqué avec deux dents, apicale et médiane à faible développement. Propagules en forme de disque, ovales, longues de 90 µ et avec 28 cellules. Espèce monoïque. Périanthe latéral dépassant les bractées périanthaires, bractées périanthaires à lobe long de 0,8 mm, large de 0,5 mm, lobule long de 0,3 mm et large de 0,1 mm. Périanthe cordiforme aplati avec deux plis ventraux peu marqués, haut de 0,6 mm, large de 0,4 mm. Inflorescence mâle latérale, haut de 0,5 mm, avec 4 étages de bractées fertiles.

Espèce assez difficile à classer à un des sous-genres classiques, se rapprochant du sous-genre *Pedinolejeunea* (marge et agencement de la feuille). On peut rapprocher cette espèce de *C. caledonica* STEPHANI, de *C. pulchella* (MITT.) SCHUSTER et de *C. virotiana* P. TIXIER nom.sol.

Cololejeunea stoniana P. TIXIER sp. nov. — Fig. 5

Planta parva, viridis, foliicola, substrato appressa. Caules usque ad 1 cm longi, 0,09 mm crassi, cum foliis 1,2 mm lati. Folia sub angulo 60° inserta interseque 0,4 mm distantia. Cellulis cum trigonibus incrassionibusque intermediis praecipue visis in vicinate marginis,

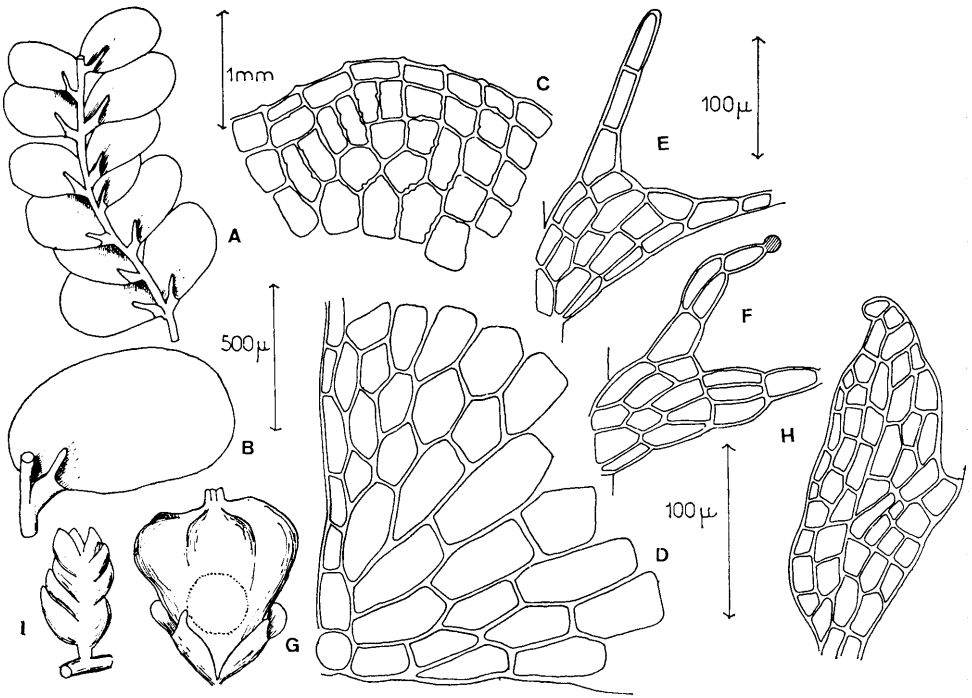

Fig. 5. *Cololejeunea stoniana*. — A: Tige. — B: Feuille. — C: Apex du lobe. — D: Base du lobe. — E, F: Lobule. — G: Périanthe. — H: Lobule de la bractée périanthaire. — I: Inflorescence mâle.

cellulis marginalibus rectangularibus 20×10 µ metientibus, cellulis basalibus majoribus 60—30×20—15 µ. Lobus obovatus fere caulem tegens 0,6 mm longus, 0,4 mm latus. Lobulus minutus, ciliatus, plus aut minus decurrens sub caule, 0,2 mm altus, 0,2 mm latus. Papilla hyalina, sphaerica, 10 µ in diametro. Planta monoica. Flores feminei laterales, foliis floralibus brevibus, cum lobo 0,3 mm longo, 0,15 mm lato, lobuloque 0,2 mm longo, 0,1 mm lato. Perianthia complanata, 4-plicata, duobus sinibus ventralibus fortiter notatis, cordiformia, 0,45 mm alta, 0,45 mm lata. Rostrum magnum. Flores masculi parvi, 0,4 mm alti, laterales, cum 3—5 jugis bractearum fertilium.

ECHANTILLON EXAMINÉ. Malaisie: Johore, Mont Ophir, brousse secondaire auprès du réservoir, 300 m, épiphylle, 20.IV. 1972, P. TIXIER 6248 (holotype PC).

Plante petite, verte, épiphylle, appliquée au support. Tige atteignant jusqu'à 1 cm, épaisse de 0,09 mm, large avec des feuilles de 1,2 mm. Feuilles insérées sous un angle de 60° et distantes entre elles de 0,4 mm. Cellules à trigones et épaississements intermédiaires surtout marqués vers la marge. Cellules marginales rectangulaires de 20×10 µ, cellules sous-adjacentes des 20×20 µ. Cellules à la base de la feuille, plus grandes, de 60—30×20—15 µ. Lobe obovale couvrant à peine la tige, 0,6 mm de long sur 0,4 mm de large. Lobule réduit, cilié plus ou moins décurrent sur la tige; haut de 0,2 mm, large de 0,2 mm. Papille hyaline sphérique de 10 µ diamètre. Inflorescences femelles latérales, bractées périanthaires courtes, lobe long de 0,3 mm, large de 0,15 mm et lobule long de 0,2 mm, large de 0,1 mm. Périanthe aplati avec 4 plis, dont deux ventraux peu marqués, cordiforme de 0,45 mm de large et de 0,45 mm de haut, bec bien visible. Inflorescence

mâle petite, de 0,4 mm de haut, latérale, avec 3—5 paires de bractées fertiles très imbriquées.

Espèce difficile à classer parmi les sous-genres *Pedinolejeunea* (BENEDIX) MIZUTANI et *Lasiolejeunea* BENEDIX. On peut rapprocher cette espèce de *C. plagiochiliana* décrite plus haut, à cause du tissu foliaire, l'agencement du lobule et des petites inflorescences mâles.

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Studies in the Lentibulariaceae

7. The Development of Endosperm and Embryo in Utricularia coerulea var. filicaulis Clarke

Saeed A. Siddiqui

SIDDIQUI, S. A. 1976 05 06. Studies in the Lentibulariaceae. 7. The development of endosperm and embryo in Utricularia coerulea var. filicaulis Clarke. — Bot. Notiser 128: 432—437. Lund. ISSN 0006-8195.

The development of endosperm conforms essentially to the Scutellaria type of SCHNARF (1917). The first division in the primary endosperm cell is transverse. The division in both primary endosperm chambers is longitudinal and the walls laid down are complete. Thus four completely partitioned cells are produced. The micropylar endosperm haustorium differentiates at the 8-celled stage of the endosperm. However, a typical chalazal endosperm haustorium does not differentiate. The mature endosperm is strongly curved. Considerable variations in the plane and in early cell divisions in the development of endosperm have been observed. Free nuclear divisions frequently occur in the cells of the young endosperm. Occasionally the endosperm develops by repeated transverse divisions.

Three types of embryogeny have been observed. Usually the embryo development conforms to the Capsella variation and occasionally to the Ruta variation of the Onagrad Type. Sometimes the proembryonic tetrad may be linear and the embryogeny appears to conform to the Chenopodiad or Solanad Type. The mature embryo does not differentiate into the usual embryonal parts. The only differentiation is the epidermis of the embryo and its meristematic apical region.

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The life history of *Utricularia coerulea* L. has been described by KAUSIK (1935, 1938) and KAUSIK and RAJU (1956). The present investigation was undertaken to compare the embryological features of the main species with that of its variety *Utricularia coerulea* var. *filicaulis* CLARKE.

The material of *U. coerulea* var. *filicaulis* was collected from Manbhum, (Bihar) India. The conventional method of embedding in paraffin wax was adopted. The sections were cut at 8—10 μ. The preparations were stained with safranin and fast green combination.

OBSERVATIONS

Endosperm

The development of the endosperm is cellular and conforms to the Scutellaria type of SCHNARF (1917). The first division in the primary endosperm cell is transverse, dividing the embryo sac into micropylar and chalazal endosperm chambers (Fig. 1 A, B). The division in the micropylar chamber precedes that in chalazal (Fig. 1 C, D). The division in both primary chambers is longitudinal and the walls laid down are complete. Thus four completely partitioned cells are produced (Fig. 1 C—E). The cells of the micropylar chamber divide earlier than the chalazal cells (Fig. 1 F). The second division in both the endosperm chambers is transverse. Thus at the 8-celled stage the endosperm cells are arranged in plate-like form (Fig. 1 G). The four cells of the middle two tiers give rise to the endosperm proper while the two micropylar cells differentiate as a 2-celled micropylar haus-

torium. The two chalazal cells are considerably elongated. However, a typical chalazal endosperm haustorium does not differentiate. The partition walls of these haustoria disappear soon and both of them become 2-nucleate.

Variations in the plane and sequence of cell divisions occur during the early stages of endosperm development. In one case the primary chalazal endosperm chamber is dividing transversely (Fig. 1 H) and after wall formation the arrangement of the four cells would have been T-shaped. In another case the primary micropylar endosperm chamber is dividing transversely, while the chalazal chamber is still undivided (Fig. 1 I). In still another case it appears that the primary micropylar endosperm chamber has divided transversely and the chalazal chamber longitudinally. There are three free nuclei in the upper daughter cell of the micropylar chamber, whereas the lower one is 1-nucleate (Fig. 1 J). Rarely is the second division in the micropylar chamber vertical instead of transverse (Fig. 1 K). In an 8-nucleate endosperm the micropylar endosperm chamber is 2-celled, the middle tier having two cells with two nuclei each. The nuclei of the two cells of the chalazal chamber are dividing (Fig. 1 L). In a 10-nucleate endosperm, one of the two cells of the micropylar tier contains three free nuclei, while the other has only one; the two cells of the middle tier have two free nuclei each and there are two 1-nucleate cells in the chalazal chamber (Fig. 1 M). Still in another case the endosperm cells are disposed in three tiers, the micropylar tier consists of two longitudinally partitioned cells with two nuclei each. In the middle tier one of the two cells has two nuclei. The nuclei in the two cells of the third tier are undergoing division (Fig. 1 N).

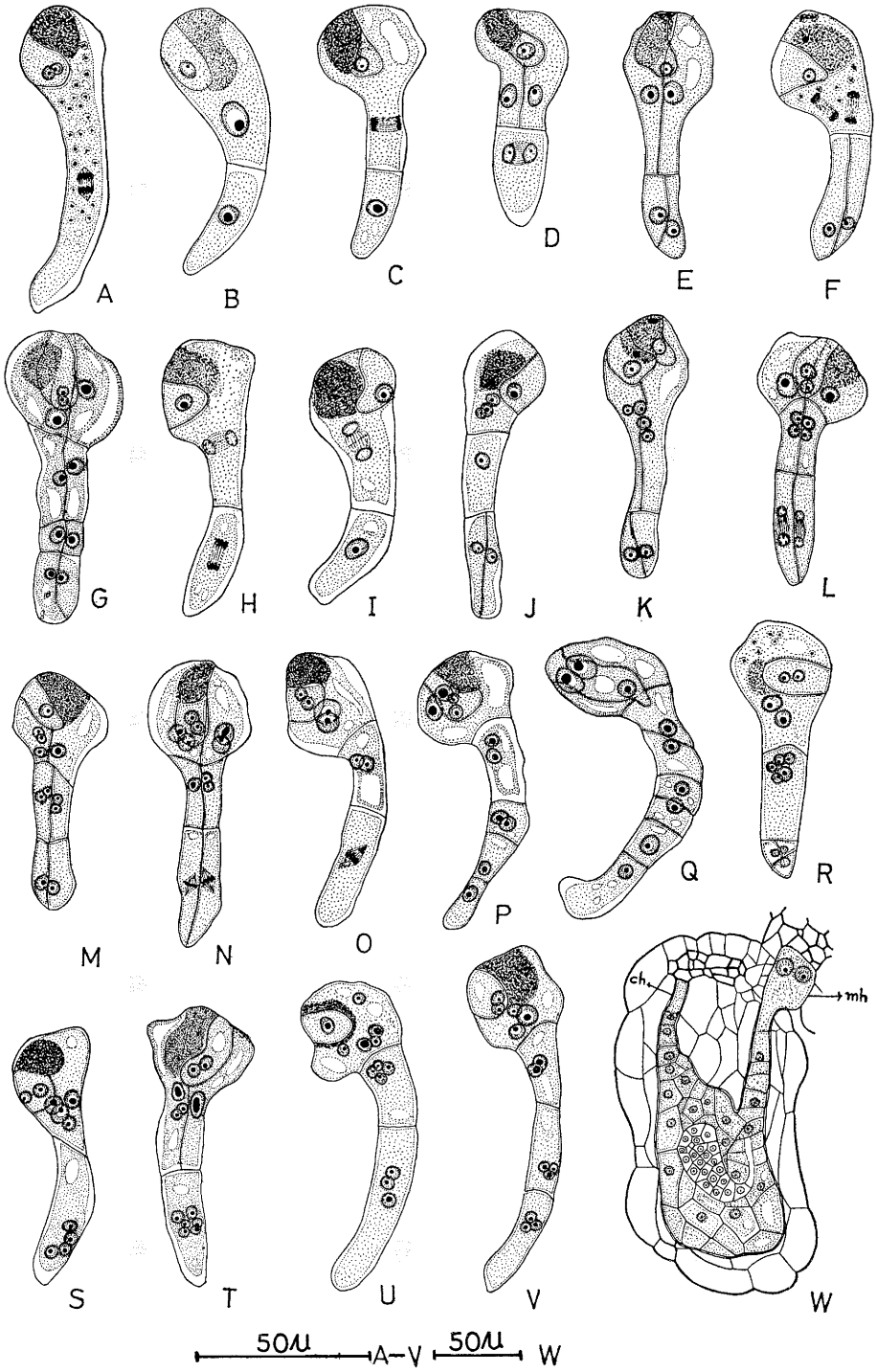
In some cases the divisions are transverse in the early stages of the endosperm development, particularly so in the chalazal chamber (Fig. 1 O—Q). In one case the chalazal endosperm chamber is dividing transversely, while two divisions have already been completed in the micropylar chamber (Fig. 1 O). In an 8-nucleate endosperm, the four cells of the chalazal chamber have a T-shaped arrangement (Fig. 1 P). In another 8-nucleate endosperm the micropylar haustorium is 2-nucleate, below which six endosperm cells are arranged in a linear fashion. The basal cell of the row is elongated and could have differentiated as a 1-nucleate chalazal haustorium (Fig. 1 Q).

An interesting phenomenon of free nuclear division has been observed in the cells of the young endosperm (Fig. 1 R—V). This is a novel feature and cannot be assigned to any principal type of endosperm development.

The micropylar haustorium is very aggressive and all the cells of placental "nutritive tissue" are consumed in the older stages of seed development. The haustorium remains 2-nucleate throughout. The so-called chalazal haustorium consists of two juxtaposed cells. It does not cause any damage to the chalazal "nutritive tissue" at any stage (Fig. 1 W). The chalazal end of the endosperm is directed towards the funicle from the very beginning. The curvature of the ovule, and consequently of the endosperm, becomes more pronounced in the advanced stages. Ultimately the endosperm assumes a U-shape (Fig. 1 W).

Embryogeny

The tubular zygotic tube contains the nucleus in its dilated apex (Fig. 2 A). The nucleus divides transversely producing a small apical cell (ca) and a long basal cell (cb; Fig. 2 B). cb divides transversely to produce the cells m and ci (Fig. 2 C), while ca divides vertically producing two juxtaposed cells, q (Fig. 2 D). Now ci divides transversely giving rise to the cells n and n' (Fig. 2 E) followed by a vertical division in m (Fig. 2 F). Later the cells of the tier q undergo vertical divisions and the quadrant stage is reached (Fig. 2 F, G).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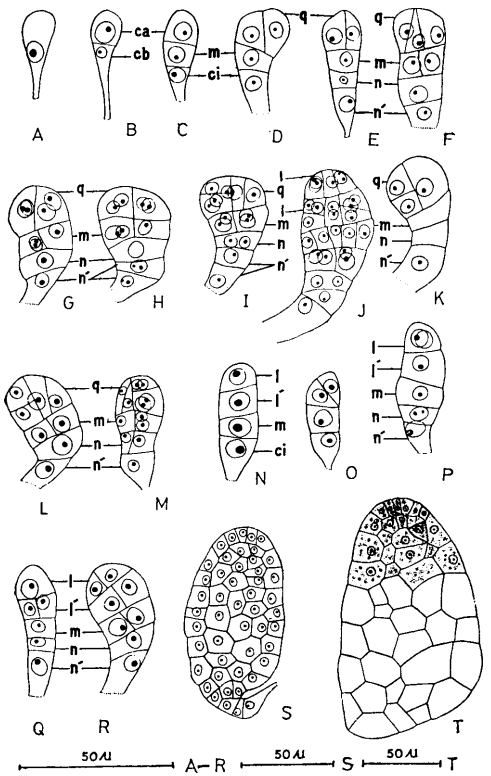

Fig. 2. Embryo development (see text).

n' divides transversely (Fig. 2 H). Meanwhile the quadrant cells segment transversely (Fig. 2 I), consequently at the octant and post octant stages the derivatives of the apical cell are disposed in two tiers, l and l' (Fig. 2 I, J). Vertical divisions in m produce four or more daughter cells (Fig. 2 I) and n undergoes two vertical divisions (Fig. 2 J). The development of the embryo could not be followed closely because further divisions in the proembryo become irregular. Presumably the daughter cells of m and ci take part in the construction of the embryonal body and a part of ci gives rise to the uniseriate suspensor (Fig. 2 J). Thus the embryogeny conforms to the Capsella variation of the Onagrad Type.

Occasionally the T-shaped proembryonic tetrad may develop in conformity to the Ruta variation of the Onagrad Type. Here one of the two juxtaposed cells of q is segmented transversely and the other one longitudinally (Fig. 2 K, L). m divides vertically and ci transversely (Fig. 2 L). In Fig. 2 M the two superposed quadrant cells divide vertically producing four cells, whereas the two cells placed side by side have not entered upon division. One of the daughter cells of m has divided vertically and the division in n has produced two juxtaposed cells (Fig. 2 M). Further stages of this type of embryo development could not be followed. However, the disposition of the proembryonic cells suggests that it had developed according to the Ruta variation of the Onagrad Type.

Sometimes a linear proembryonic tetrad develops by two transverse divisions in the zygote (Fig. 2 N). Rarely the apical cell will divide by producing an oblique wall which results in a condition intermediate between T-shaped and linear proembryonic tetrads (Fig. 2 O). The sequence of division in the tiers l and l' is variable (Fig. 2 P, Q). The tiers l and l' divide vertically giving rise to quadrants (Fig. 2 R). m divides vertically and ci transversely (Fig. 2 R). Further stages of the proembryo could not be observed. The proembryo could have belonged to the Chenopodiad or to the Solanad Type.

The embryo elongates along its axis. In a longitudinal section it appears to be elliptical and the suspensor is clearly seen (Fig. 2 S). The mature embryo rounds off at both ends and the suspensor ultimately disappears (Fig. 2 T). The embryo narrows at its apical end. There is a well-marked apical growing region represented by small

Fig. 1. Endosperm development (see text). — A—G: Normal development. — H—V: Abnormal development. — W: L. S. old ovule showing older endosperm and the embryo. — mh = micropylar haustorium; ch = chalazal haustorium.

Table 1. The present investigation reveals that *U. coerulea* var. *filicaulis* differs from *U. coerulea* in the following embryological features.

U. coerulea var. *coerulea*	*U. coerulea* var. *filicaulis*
The walls laid down in the two primary endosperm chambers are incomplete, thus four incompletely partitioned cells are produced.	The walls laid down are complete and result in four completely partitioned cells.
A 2-nucleate chalazal endosperm haustorium differentiates.	A typical chalazal endosperm haustorium does not differentiate.
The wall of the micropylar haustorium dissolves. The cells of the placental nutritive tissue break down and their contents are incorporated into the cytoplasm of the haustorium.	The haustorium is quite aggressive. The wall of the micropylar haustorium persists. The contents of the cells of the placental nutritive tissue are not incorporated into the haustorium.
Repeated transverse divisions do not occur during endosperm development.	Repeated transverse divisions occur during early stages of the endosperm development.
Free nuclear divisions do not occur.	Free nuclear divisions frequently occur in the cells of the young endosperm.
The embryogeny conforms to the Ruta variation of the Onagrad Type.	The embryogeny conforms to the Capsella variation of the Onagrad Type.

meristematic cells (Fig. 2 T). The remaining part of the embryo consists of large and polygonal cells which are rich in starch grains and some food material of unknown chemical nature. The usual embryonal parts are not differentiated in the mature embryo.

Irregularities during the early developmental stages of the proembryo and the lack of differentiation of the usual embryonal parts in the mature embryo does not allow a precise classification of embryogeny in the species. However, on the basis of early cell divisions in the development of the proembryo it appears that the embryogeny in the species generally conforms to the Capsella, occasionally to the Ruta variation of the Onagrad Type and sometimes to the Chenopodiad Type or Solanad Type.

DISCUSSION

The development of endosperm conforms to the Scutellaria type of SCHNARF (1917) in the investigated species of *Utricularia*. In *U. flexuosa* (KHAN 1954), *U. reticulata* (KAUSIK & RAJU 1955), *U. stellaris* var. *inflexa*, *U. arcuata* and *U. uliginosa* (FAROOQ 1964, 1965 a, 1965 b) and *U. stellaris* (FAROOQ & SIDDIQUI 1967) the partition walls laid down at the time of first division in the primary endosperm chambers are incomplete towards their micropylar and chalazal ends respectively, whereas in *U. coerulea* var. *filicaulis* these walls are complete, thus four completely partitioned cells are produced. In *U. striatula* (FAROOQ 1966) the two cells at the chalazal end of the endosperm are completely partitioned, while those in the micropylar chamber are incompletely partitioned.

The occasional occurrence of repeated transverse divisions during the early stage of endosperm development as described here has been reported in *U. flexuosa* (KHAN 1954) and *U. vulgaris americana* (FAROOQ & SIDDIQUI 1966). From outside the family, *Villarsia reinformis* (STOLT 1921) and *Phacelia congesta* (SVENSSON 1925) may be cited as examples in which this type of endosperm development occurs normally.

Frequent free nuclear divisions at different stages of endosperm development as

described here rarely occur in *U. scandens* (FAROOQ & BILQUIS 1966 b) and *U. arcuata* (FAROOQ 1965 a). This type of endosperm development resembles that of *Hyoscyamus niger* (SVENSSON 1926).

The Capsella variation of the Onagrad Type of embryogeny as described in *U. coerulea* var. *filicaulis* has been reported earlier in *U. uliginosa* and *U. striatula* (FAROOQ 1965 b, 1966), while in *U. coerulea* (KAUSIK & RAJU 1956) and *U. scandens* (FAROOQ & BILQUIS 1966 a) the embryogeny conforms to the Ruta variation of the Onagrad Type. The Chenopodiad Type of embryogeny usually occurs in *U. stellaris* var. *inflexa* (FAROOQ 1958), whereas its occasional occurrence has been reported in *U. coerulea* (KAUSIK & RAJU 1956) and *U. scandens* (FAROOQ & BILQUIS 1966 a) and rarely in *U. coerulea* var. *filicaulis*. Thus it is concluded that the embryogeny in the genus *Utricularia* is variable.

ACKNOWLEDGEMENT

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Contribution To the Embryology of Celsia coromandeliana Vahl. With a Discussion On Its Affinities With Verbascum thapsus L.

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The development of the endosperm, embryo and testa of *Celsia coromandeliana* VAHL. is described. A single hypodermal archesporial initial functions as the megaspore mother cell. The tetrad is linear, and the chalazal megaspore develops into an 8-nucleate embryo sac of the Polygonum type. The endosperm is cellular with 4-celled micropylar and chalazal haustoria. The endosperm is ruminate due to unequal elongation of a few endothelial cells. The embryogeny conforms to the Onagrad type. The testa of the mature seed consists of epidermis, compressed middle layers and an endothelium with thickened inner tangential and radial walls.

The morphology and embryology of *Celsia coromandeliana* indicates that it is distinct from *Verbascum thapsus* L.

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Celsia coromandeliana occurs in India throughout the plains and also in the Himalayan regions upto 1525 metres extending to Afghanistan, Burma and China (DUTHIE 1960). SANTAPAU (1950) considered *Celsia coromandeliana* and *Verbascum thapsus* to be cogeneric and suggested that the former is a synonym for the latter. FERGUSON (1971) also merged *Celsia* with *Verbascum* because according to him the presence of four or five stamens is not always constant and some species of both *Celsia* and *Verbascum* have four stamens with a staminode. The present investigation was undertaken to study the embryology of *C. coromandeliana* and to resolve on comparative exomorphic and embryological features whether this taxon is *pro parte V. thapsus.*

MATERIAL AND METHODS

Buds, flowers and fruits of *Celsia coromandeliana* were collected from Yamuna Banks, Delhi, India and fixed in Formalin-acetic-alcohol or Carnoy's fluid and subsequently stored in 70 per cent ethanol. The material was dehydrated and cleared by conventional methods and embedded in paraffin wax. Seeds were immersed for a week in a mixture of 10 per cent glycerine and 70 per cent ethyl alcohol (1:1 v/v) before dehydration which rendered the seeds quite soft, suitable for sectioning. Serial sections were cut between 5 and 12 microns thick and stained with either Safranin-fast green or Heidenhain's iron alum haematoxylin with a counterstain of fast green.

OBSERVATIONS

External Morphology

Celsia coromandeliana grows in moist shady places. The inflorescence is a panicle bearing numerous small, yellow, bisexual flowers. Calyx and corolla are pentamerous (Fig. 1 A, B). The androecium consists of four epipetalous stamens (Fig. 1 B). Each stamen has a dorsifixed, reniform and bilobed anther (Fig. 1 C),

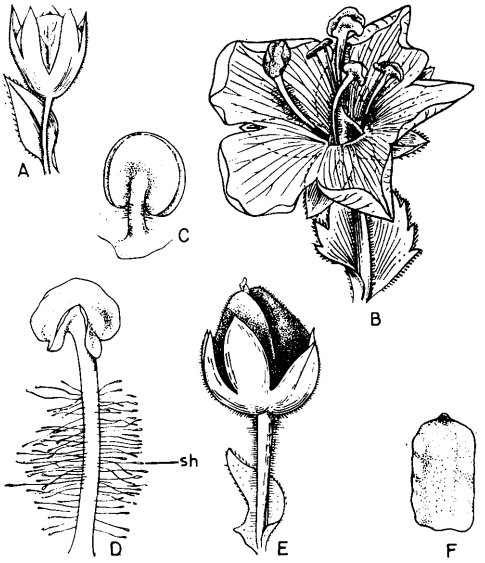


Fig. 1. *Celsia coromandeliana* (sh, staminal hairs). — A: Young bud. — B: Flower. — C: Young stamen. — D: Dehisced stamen. Unicellular hairs are present on the filaments. — E: Fruit with persistent calyx. — F: Mature seed. — A—B, E ×3, C—D ×6, F ×20.

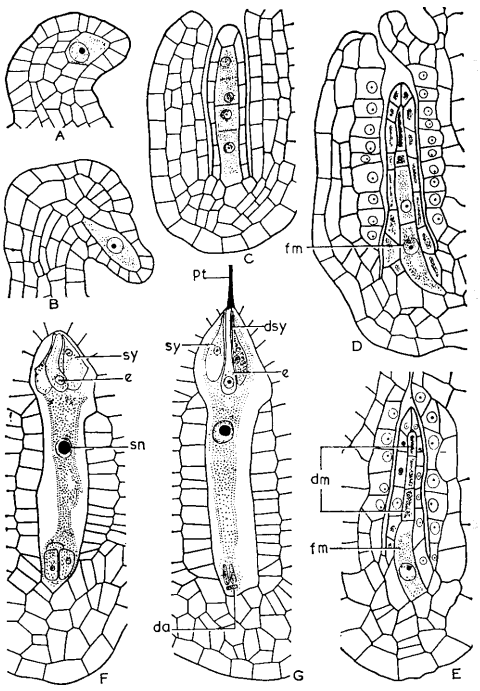


Fig. 2. *Celsia coromandeliana* (dm, degenerating megaspore; fm, functional megaspore; da, degenerating antipodal cells; dsy, degenerating synergids; e, egg; pt, pollen tube; sn, secondary nucleus; sy, synergid). — A: Archesporial initial. — B: Megaspore mother cell. — C: Dyad in division. — D—E: Megaspore tetrads; note degeneration of non-functional megaspores from the micropylar end and curvature of the functional megaspore. — F—G: Embryo sacs at maturity. In G, the pollen tube enters through the micropyle and discharges its contents into the degenerating synergid. A—E ×340, F—G ×550.

the filaments of the mature anthers are densely covered with hairs (Fig. 1 D). The gynoecium is bicarpellary and syncarpous with numerous ovules. The style is long and ends in a simple bilobed stigma (Fig. 1 B). The ovary is bilocular with axile placentation at the base but becomes unilocular with parietal placentation at the apex. The fruit is a septicidal capsule with a persistent, hairy calyx (Fig. 1 E), while the seeds are oblong and contain ruminate endosperm (Fig. 1 F).

Megasporangium and Megasporogenesis

The ovular primordia arise as small protuberances on the massive placentae. Differential rates of growth of each primordium makes the developing ovule curve towards the direction of the placenta. Usually a single hypodermal archesporial cell with prominent nucleus and dense cytoplasm differentiates (Fig. 2 A). It does not cut off a parietal cell but functions directly as the megaspore mother cell (Fig. 2 B). Occasionally two archesporial initials are observed. The megaspore mother cell elongates considerably and then undergoes meiosis resulting in a dyad. Meiosis II in both these cells is simultaneous (Fig. 2 C) forming a linear tetrad of megaspores (Fig. 2 D, E). The non-functional micropylar megaspores degenerate (Fig. 2 D, E) and only the chalazal member functions (Fig. 2 E).

Female Gametophyte

The functional megaspore elongates and becomes slightly curved (Fig. 2 D, E). Many tiny vacuoles appear in the cytoplasm, the megaspore nucleus then undergoes three mitotic divisions and produces the 8-nucleate embryo sac. The mature embryo sac comprises an egg apparatus, a secondary nucleus and three antipodal cells (Fig. 2 F). The egg is pyriform, the synergids have prominent hooks, two polar nuclei fuse to form the secondary nucleus and the antipodal cells are uninucleate. The development of the embryo sac conforms to the Polygonum type. Pollen tubes are frequently seen in the micropyle (Fig. 2 G) and although the actual process of double fertilization has not been observed, the pollen tube entry into the embryo sac destroys one of the synergids. The antipodal cells degenerate.

Endosperm

The primary endosperm nucleus lies in the centre of the embryo sac (Fig. 3 A, B) and divides prior to the division of the zygote. The division is followed by a transverse wall, resulting in micropylar and chalazal chambers (Fig. 3 C). The development of the endosperm is cellular. The first two divisions in the micropylar and chalazal chambers are longitudinal (Fig. 3 D), the four cells of the chalazal chamber form the chalazal haustorium directly, whereas the four elongated micropylar cells divide transversely (Fig. 3 E). The derivatives of the upper tier form the four-celled micropylar haustorium while the lower four cells divide in longitudinal and transverse planes to form the endosperm proper (Fig. 3 F, I).

The four-celled chalazal haustorium is short and non-aggressive. It has one nucleus in each cell (Fig. 3 F, J) and is early to organize and early to degenerate. The four-celled micropylar haustorium is also non-aggressive with uninucleate cells (Fig. 3 F, H). The remnants of the micropylar and chalazal haustoria persist in the mature seed (Fig. 5 G).

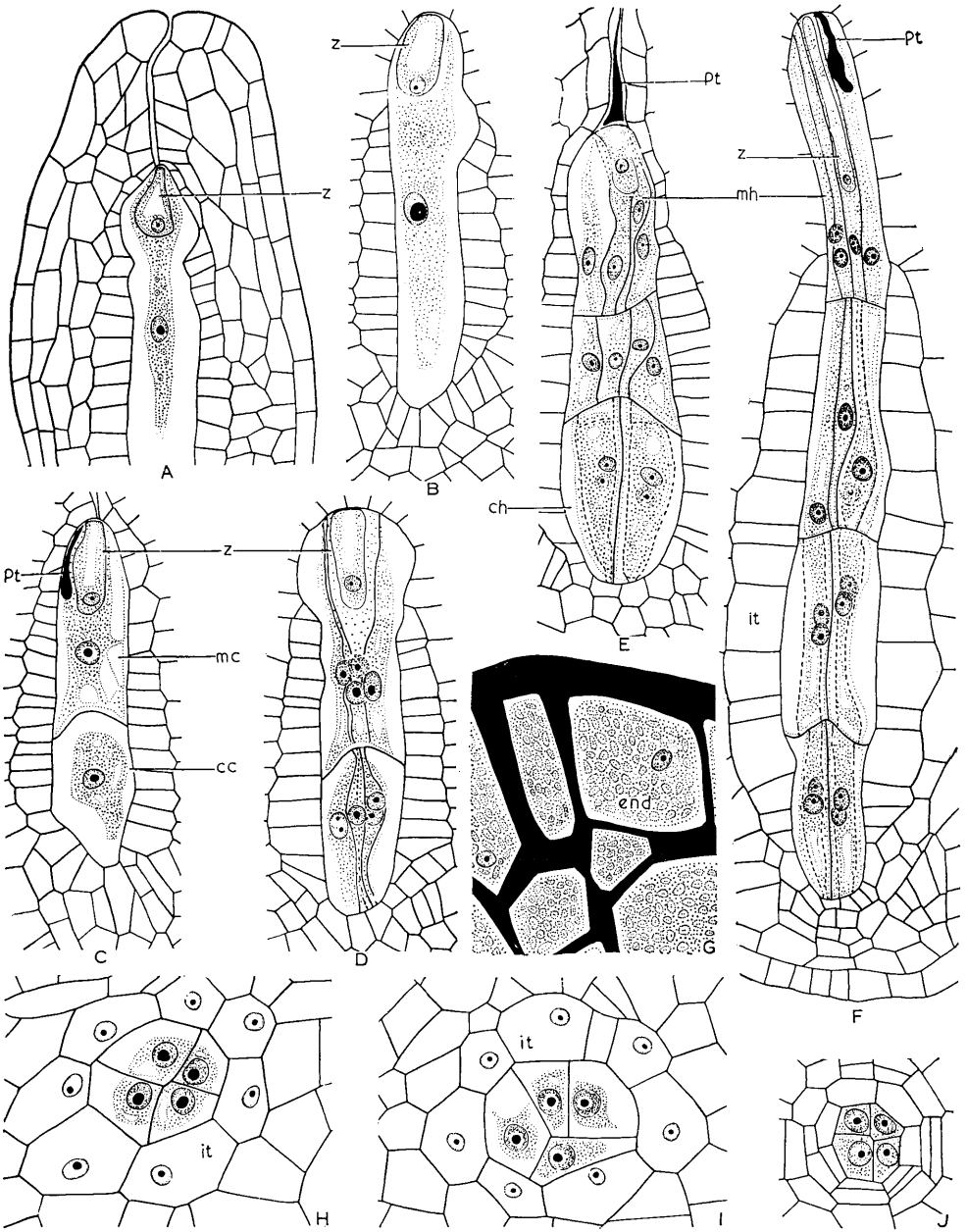
The endothelium is a prominent layer and increases in size after fertilization (Fig. 5 F). Some endothelial cells elongate both in radial and tangential directions causing the surface of the endosperm to become wavy and irregular (Fig. 5 H). The endosperm is thus at maturity, ruminate (unpublished observation) and its cells are full of reserve food materials (Fig. 3 G).

Embryogenesis

The zygote elongates considerably (Fig. 4 A), becomes tubular, enters the central mass of endosperm and remains quiescent for a long time. The nucleus migrates and occupies the distal end of the zygote. A transverse division produces the terminal cell ca and basal cell cb (Fig. 4 B). The next vertical division occurs in the terminal cell resulting in two juxtaposed cells (Fig. 4 C, D). The basal cell cb segments transversely to form two superposed cells m and ci, resulting in a proembryonal tetrad arranged in an ⊥-shaped manner (Fig. 4 D).

Each of the two derivatives of the terminal cell ca, divides vertically at right angles to the previous plane giving rise to the quadrant q (Fig. 4 E, F). The four cells of the quadrant engender the octant by transverse divisions (Fig. 4 G, H). The cells of the octant are thus disposed in two tiers of four cells each, designated as l and l' (Fig. 4 H). Division in the tier l occasionally lags behind that of l' during

Fig. 3. *Celsia coromandeliana* (cc, chalazal chamber; ch, chalazal haustorium; end endosperm; it, integumentary tapetum; mc, micropylar chamber; mh, micropylar haustorium; pt, pollen tube; z, zygote). — A: Longitudinal section of seed showing zygote, primary endosperm nucleus and seed coat. — B—D: Longitudinal sections of seeds to show central cell, two- and eight-celled endosperm respectively. The chalazal chamber forms the



4-celled chalazal haustorium directly in D. — E—F: Same as above. The micropylar chamber segments transversely and the upper tier forms the micropylar haustorium in E. The middle tier forms the endosperm proper by further transverse and longitudinal divisions, in F. — G: A few cells of the mature endosperm enlarged to show thickenings and reserve food materials. — H—J: Transections of endosperm at the levels of micropylar haustorium (H), middle region (I) and chalazal haustorium (J). — A—J ×560.

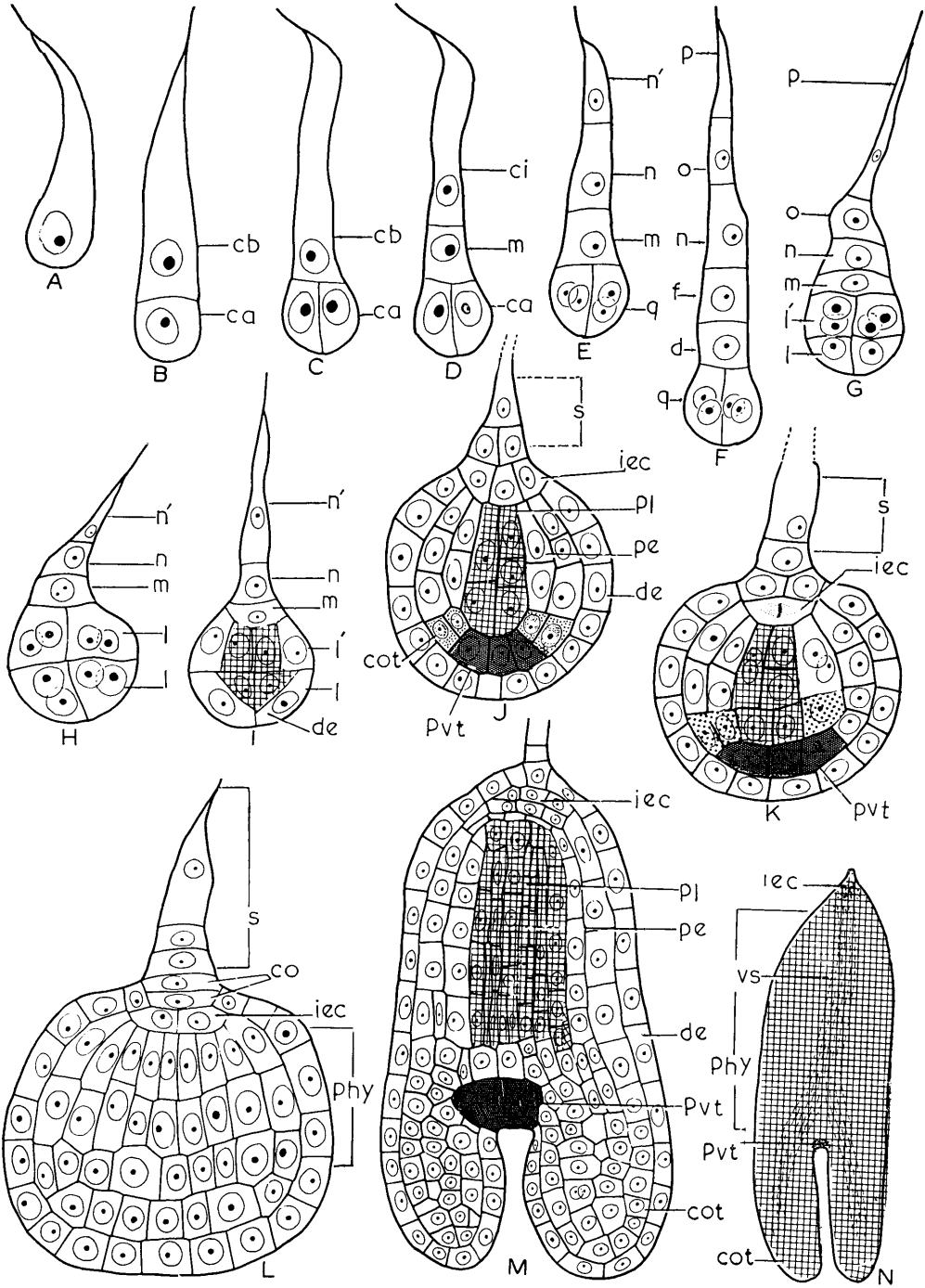
the formation of the octant (Fig. 4 G). Periclinal divisions occur simultaneously in both the tiers 1 and 1' demarcating dermatogen (de) from the inner group of cells (Fig. 4 I, J). The inner group of cells of tier 1' gives rise, by vertical divisions to periblem and plerome (pe, pl Fig. 4 J). Longitudinal and transverse divisions in the inner group of cells of tier 1 yield two cotyledonary initials (cot) and an embryo apex (epicotyl, pvt), while those of 1' form the hypocotyledonary region of the proembryo (phy, Fig. 4 J—L).

Meanwhile the uppermost cell ci of the proembryonal tetrad undergoes a transverse division resulting in cell n and n' (Fig. 4 E). The division in the cell ci is not constant and produces either a long or a short suspensor (Fig. 4 F—I, L). The middle cell m sometimes divides to form d and f (Fig. 4 F) but it usually undergoes a few vertical divisions forming 2 or 3 juxtaposed cells, and contributes to the root cortex and root cap (iec, co) (Fig. 4 J—L). The globular proembryo (Fig. 4 L) differentiates into the heart-shaped and dicotyledonous embryo (Fig. 4 M, N). The mature embryo comprises two prominent cotyledons, epicotyl, hypocotyl and root apex. The embryogeny corresponds to the Onagrad type (MAHESHWARI 1950).

Seed Coat

In the young ovule, initiation of integument occurs at the archesporial cell stage (Fig. 5 A). At megaspore mother cell stage (Fig. 5 B), the integument comprises three layers of parenchymatous cells at the top, and four layers below. The outer epidermis at this stage is well differentiated and divides periclinally. The number of layers comprising the testa remain unchanged at dyad stage. Cells of the inner epidermis however, show pronounced radial elongation, with uniform, dense cytoplasm and prominent nuclei (Fig. 5 C). The seed coat consists of five layers of cells during the functional megaspore stage and the cells of the outer epidermis undergo expansion (Fig. 5 D). The seed coat is six or seven layers thick at mature embryo sac stage (Fig. 5 E, F). Cells between the two epidermes show scanty cytoplasm and are highly vacuolated. Development of the endothelium does not keep pace with the expansion of the embryo sac and hence does not fully cover the micropylar and the chalazal ends. At about the two-cell stage of the proembryo, cells comprising testa remain unchanged but the endothelial cells undergo unequal expansion forming larger and smaller cells causing thus rumination of the endosperm (Fig. 5 G, H). Subsequently the cell layers between the inner and outer epidermes degenerate. The outer tangential wall of the endothelial cells is devoid of thickenings whereas the inner tangential wall shows thickenings which almost occupy two-thirds of the cell space. The endosperm cells bordering the endothelium also develop thickenings (Fig. 5 H). Histochemical studies are necessary to ascertain the nature of the thickenings in the endothelium and endosperm. The cells of the outer epidermis show degenerating nuclei. In the mature seed the testa is represented

Fig. 4. *Celsia coromandeliana* (co, initials of root cap; cot, cotyledon; de, dermatogen; iec, initials of root cortex; pe, periblem; pl, plerome; phy, hypocotyledonary region; pvt, epicotyledonary region; s, suspensor; vs, vascular strand). — A: Zygote. — B: Two-celled proembryo. — C—D: Three- and four-celled proembryos; terminal cell (ca) segments with a vertical wall whereas the basal cell (cb) divides transversely. — E—F: Quadrant stages of proembryos. — G—H: Octant stages of proembryos. Note the precocious division in the tier 1' in G. — I: Proembryo showing demarcation of dermatogen (de) with the onset of periclinal divisions in tiers 1 and 1'. — J—L: Stages leading to the formation of globular embryos. The periblem and plerome are demarcated. Note the initiation of epicotyl (pvt) and cotyledonary loci (cot) in J and K. — M—N: Dicotyledonous embryos. The procambium is well developed in N. — A—L ×680, M ×415, N ×170.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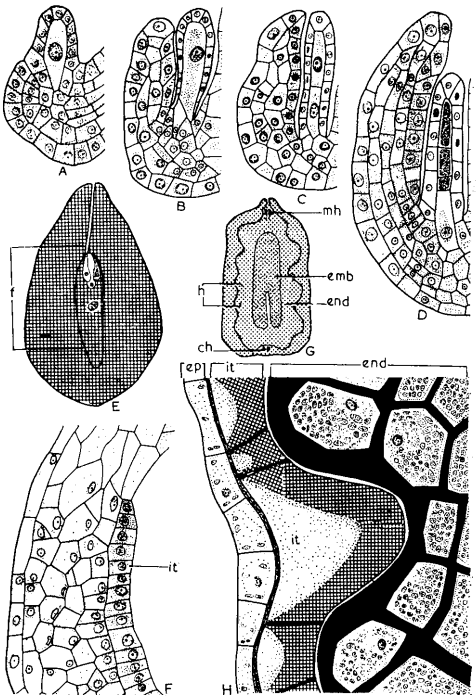

Fig. 5. *Celsia coromandeliana* (ch, chalazal haustorium; ep, epidermis; emb, embryo; end, endosperm; it, integumentary tapetum; mh, micropylar haustorium). — A: Longitudinal section of ovule showing the initiation of integument at the archesporial cell stage. — B—C: Longitudinal sections of ovules at megaspore mother cell and dyad stages; integument is 3- or 4-layered. The endothelium is well differentiated at dyad stage. — D: Five-layered testa at functional megaspore stage. The outer epidermis shows cell expansion. — E—G: Median longitudinal sections of ovules at embryo sac and dicotyledonous embryo stages. — F: Magnified view of portion marked f in E showing epidermis with elongated cells containing meagre cytoplasm. Cells of middle layers also present poor cytoplasm whereas the cells of endothelium reveal dense cytoplasm with prominent nuclei. — H: Magnified view of the region marked h in G showing tenuous epidermis, crushed middle layers, thickened and prominent integumentary tapetum. The inner tangential and radial walls of endothelium show thickenings. Note that endosperm cells (end) bordering the endothelium also show prominent thickenings. — A—D, F, H, ×350, E ×140, G ×35.

by a tenuous epidermis, degenerated middle layers and a well developed but irregular endothelium (Fig. 5 H).

DISCUSSION

Megasporangium and Megasporogenesis

The ovule in *Celsia coromandeliana* is unitegmic, anatropous and tenuinucellate as in many genera of the Scrophulariaceae. This is in contrast to the hemianatropous condition met with in *Euphrasia arctica* (Arekal 1963 a), *Melampyrum arvense* and *M. nemorosum* (Tiagi 1965); campylotropous in *Torenia fournieri* (Guilford & Fisk 1952), *Pedicularis sylvatica* (Berg 1954), *Orthocarpus luteus* (Arekal 1963 a), *Rhinanthus major* and *R. serotinus* (Tiagi 1966). Arekal (1963 a) states that in *Melampyrum lineare* the inner epidermis of integument around the micropylar part of the embryo sac breaks down and the hypodermis takes over the function of integumentary tapetum. In *Celsia coromandeliana* however, the innermost layer of the integument functions as endothelium and does not entirely surround the micropylar and chalazal parts of the embryo sac.

In *Celsia coromandeliana*, the mode of female gametophyte development is monosporic, Polygonum type. This holds true for *Alectorolophus hirsutus, A. minor, Lathraea squamaria,* and *Tozzia alpina* (Schmid 1906), *Centranthera hispida* and *Rhamphicarpa longiflora* (Krishna Iyengar 1942 b), *Pedicularis sylvatica* (Berg 1954), *Euphrasia arctica* and *Orthocarpus luteus* (Arekal 1963 a). In *Linaria ramosissima* occurrence of bisporic Allium type (Arekal & Raju 1964), in *Alectra thomsoni* coexistence of both monosporic, Polygonum and bisporic Allium types of embryo sacs (Vijayaraghavan & Ratnaparkhi 1972) are reported. Schmid (1906) reported monosporic Polygonum type in *Melampyrum pratense* and *M. silvaticum* but Arekal (1963 a) observed tetrasporic 7-nucleate embryo sac in *M. lineare.*

Interestingly in *M. pratense, M. silvaticum* (SCHMID 1906) and *M. lineare* (AREKAL 1963 a), fusion of polar nuclei does not occur. The antipodal cells in *C. coromandeliana* degenerate before fertilization. This is in contrast to *Pedicularis palustris* (BALICKA-IWANOWSKA 1899), where they persist even after fertilization. SCHMID (1906) observed two antipodal cells in *Pedicularis caespitosa* one of which is larger and binucleate. In *Lathraea squamaria* (GLIŠIĆ 1932) and *Orthocarpus luteus* (AREKAL 1963 a), the antipodal cells are large and persist even during seed development whereas in *Melampyrum lineare*, degenerated nuclei constitute the antipodals (AREKAL 1963 a).

The embryo sac extends towards the micropyle in *Alectorolophus minor, Lathraea squamaria* (SCHMID 1906), *Pedicularis zeylanica* (KRISHNA IYENGAR 1942 b), *P. sylvatica* (BERG 1954) and *Euphrasia arctica* and *Orthocarpus luteus* (AREKAL 1963 a) while it becomes extra-micropylar in *Vandellia hirsuta, Torenia cordifolia* and *T. hirsuta* (KRISHNA IYENGAR 1940 a, 1941). *Celsia coromandeliana* presents no tendencies of an extra-micropylar development of female gametophyte.

Endosperm and Haustoria

The endosperm in the Scrophulariaceae is cellular resulting in two superposed chambers — micropylar and chalazal. The sequence of the further divisions however, varies in different genera of this family. The next division in the micropylar chamber is transverse in *Anticharis linearis* (JOSHI & VARGHESE 1963), but vertical in *C. coromandeliana* as in *Pedicularis sylvatica* (BERG 1954) and *Alectra thomsoni* (VIJAYARAGHAVAN & RATNAPARKHI 1972). Another vertical division occurs in the micropylar chamber in *C. coromandeliana*. Such a condition is reported in *Isoplexis canariensis, Verbascum thapsus* (KRISHNA IYENGAR 1939, 1942 a), *Lindernia hyssopioides* and *Scoparia dulcis* (AREKAL et al. 1970, 1971).

The micropylar chamber then undergoes transverse division in *C. coromandeliana* and four cells of the upper tier develop into the 4-celled micropylar haustorium. The micropylar haustorium is, however, two-celled but each cell is binucleate in *Striga orobanchoides* and *S. euphrasioides* (TIAGI 1956) and *Alectra thomsoni* (VIJAYARAGHAVAN & RATNAPARKHI 1972). In *Euphrasia arctica, Orthocarpus luteus* and *Melampyrum lineare* (AREKAL 1963 a), division in the micropylar chamber is by an incomplete vertical wall. The micropylar haustorium in *Melampyrum arvense* and *M. nemorosum* (TIAGI 1965) and *M. lineare* (AREKAL 1963 a) produces many tubular extensions which pass through the micropyle whereas in *Alectorolophus hirsutus* (SCHMID 1906) and *Orthocarpus luteus* (AREKAL 1963 a) the micropylar haustorium extends in the direction of the funiculus. The micropylar haustorium usually exhibits elaborate features as compared to the chalazal haustorium. It is highly branched in *Alonsoa* sp., bulbous in *Isoplexis canariensis,* club-shaped in *Bonnaya tenuifolia* (KRISHNA IYENGAR 1937, 1939, 1940 b), tubular and filiform in *Melampyrum silvaticum* (SCHMID 1906) and U-shaped in *Orthocarpus luteus* (AREKAL 1963 a), but simple and non-aggressive in *Celsia coromandeliana* (present work).

The chalazal chamber develops directly into the chalazal haustorium. Variations are reported regarding the number of cells and nuclei taking part in the formation of chalazal haustorium. Uninucleate, single-celled haustorium is recorded in *Chaenorrhinum minus* (AREKAL 1963 c), binucleate, single-celled in *Orthocarpus luteus, Gerardia pedicularia, Veronica serpyllifolia* (AREKAL 1963 a, 1964, 1966), *Melampyrum arvense, M. nemorosum, Rhinanthus major, R. serotinus* (TIAGI 1965, 1966), two-celled in *Vandellia hirsuta* (KRISHNA IYENGAR 1940 a), *Calceolaria mexicana* (AREKAL & RAJU 1971), incompletely two-celled in *Chelone glabra* (AREKAL 1963 b) but four-celled, each cell

being uninucleate in *Verbascum thapsus* (KRISHNA IYENGAR 1942 a), *Microcarpaea* (AREKAL & SWAMY 1974) and *Celsia coromandeliana* (present work).

Occurrence of secondary haustoria is an important feature met with in some members of the family. The haustoria arise from the micropylar end in *Centranthera hispida* (KRISHNA IYENGAR 1942 b) and *Alectra thomsoni* (VIJAYARAGHAVAN & RATNAPARKHI 1972) but no such secondary haustoria develop in *Celsia coromandeliana*. COOK (1924), PERSIDSKY (1934) and AREKAL (1963 c), have reported absence of micropylar haustorium in *Linaria vulgaris, L. genistaefolia* and *Chaenorrhinum minus* respectively, whereas CRÉTÉ (1950 a, b), reported that the chalazal chamber never develops into the chalazal haustorium in *Nemesia floribunda* and *N. melissaefolia*.

The endosperm cells in *C. coromandeliana* adjacent to the haustoria are small when compared to those in the middle region, but in *Verbascum thapsus* the endosperm cells adjacent to the micropylar and chalazal haustoria are larger and exhibit rich protoplasm (unpublished observations).

Embryogenesis and Testa

The present investigation on *Celsia coromandeliana* is the first report on embryogeny in this plant. The development follows the Crucifer type (MAHESHWARI 1950) as in *Euphrasia arctica* (AREKAL 1963 a), *Pedicularis sylvatica* (BERG 1954), *Striga orobanchoides* (TIAGI 1956), *Mimulus ringens* (AREKAL 1965) and *Scoparia dulcis* (AREKAL et al. 1971). In *Ellisiophyllum pinnatum* it follows the Solanad type (YAMAZAKI 1957).

In *Anticharis linearis* (JOSHI & VARGHESE 1963), hypodermal integumentary cells undergo periclinal divisions and all layers of the integument except the endothelium form the testa. In *Pedicularis sylvatica* (BERG 1954), the seed has in its micropylar end a white spongy 'elaiosome' derived from the micropylar haustorium and a dark warty outgrowth at the chalazal end. The testa in *Melampyrum arvense* (TIAGI 1965) is made up of the thickened epidermis and a few degenerated hypodermal layers, whereas in *Euphrasia arctica* and *Orthocarpus luteus* (AREKAL 1963 a) it comprises cuticularized epidermis and thickened endothelium. In *Celsia coromandeliana* (present work), the epidermal cells undergo elongation, the middle layers are crushed and thickened endothelial cells elongate radially and tangentially at many places causing unevenness in the testa.

RELATIONSHIP OF CELSIA COROMANDELIANA WITH VERBASCUM THAPSUS

The morphological, anatomical and embryological features of *Celsia coromandeliana* are compared with the available data on *Verbascum thapsus* in Table 1 (for literature see FERGUSON 1971, HÅKANSSON 1926, KAPOOR 1975, KRISHNA IYENGAR 1939, 1942 a, METCALFE & CHALK 1957, SANTAPAU 1950, VISHNU-MITTRE & ROBERT 1969 and present work).

Table 1 indicates that *Celsia coromandeliana* differs from *Verbascum thapsus* especially in: (1) trichomes on bract and calyx being peltate and uniseriate; (2) absence of trichomes on the carpel; (3) presence of crystal idioblasts in the mesophyll; (4) absence of uniseriate medullary rays; (5) presence of four stamens; (6) the functional megaspore forming an L-shaped contour; (7) endosperm cells abutting the chalazal and micropylar haustoria are smaller in size and (8) unequal random expansion of the integumentary cells.

The morphological and embryological data on *Verbascum thapsus* are meagre. The data on development of wall layers, anther tapetum, tapetal dimorphism, anther dehiscence, embryogenesis, testa and pericarp of this taxon are totally lacking.

Table 1. A comparison of *Celsia coromandeliana* and *Verbascum thapsus*. * points of difference; ** unpublished observations.

Features	*Celsia coromandeliana*	*Verbascum thapsus*
Habit	Erect, pubescent, short herb	Erect, woolly, usually tall herb
Trichomes on:		
*Bract	Peltate, uniseriate	**Branched
*Calyx	Peltate, uniseriate	**Branched
Corolla	Nil	Nil
Stamens	Unicellular	**Unicellular
*Carpel	Nil, or a few	**Numerous, heavily clothed with branched hairs
*Crystals	Crystals occur in the mesophyll and the vascular bundles of the veins	Absent
*Pericyclic fibres	Arranged in a loose ring	Arranged in isolated strands
*Uniseriate medullary rays	Absent	Present
*Stamens	Four	Five
Anther development	**Dicotyledonous type	Data not available
Wall layers	**Four, including epidermis	Data not available
Endothecial thickenings	**Present in endothecium and connective region	Data not available
Anther tapetum	**Dual origin, being derived partly from the parietal layer and partly from the cells of the connective	Data not available
Tapetal dimorphism	**Present, the tapetal cells are radially elongated towards the connective, and small towards the outside	Data not available
Stomium	Present	Data not available
*Gynoecium	Bicarpellary, bilocular at the base and unilocular at the top	Bicarpellary, bilocular
*Placentation	Axile at the base and parietal at the summit	Axile
Ovule	Anatropous, unitegminal, tenuinucellate	Anatropous, unitegminal, tenuinucellate
*Megaspore tetrads	The functional megaspore undergoes curvature to form an L-shaped contour	**Straight
Embryo sac	Polygonum type	Polygonum type
Endosperm	Cellular, ruminated	Cellular, ruminated
*Micropylar haustorium	Four-celled, endosperm cells** next to the haustorial cells are smaller in size than other cells of endosperm	Four-celled, endosperm cells** next to the haustorial cells are larger than other cells of endosperm
Chalazal haustorium	Four-celled; endosperm cells** abutting the haustorium are small and rich in protoplasm	Four-celled; endosperm cells** abutting the haustorium are large and radially elongated
Embryogeny	Onagrad type; cells of mature embryo are full of reserve food materials	Data not available
Seed coat	Initially 6- or 7-layered but only epidermis and the endothelium persist	Data not available
	Endothelium is the prominent layer and its cells elongate at random and have thickenings on inner tangential and radial walls	Endothelial cells** show a row of alternating larger and smaller cells
Pericarp	Sub-epidermal cavities present	Data not available

The available information indicates that *Celsia coromandeliana* is not *pro parte Verbascum thapsus* and maintenance of these two taxa as independent genera is justified on morphological and embryological grounds.

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Syngenesious Anthers of Helianthus annuus – a Histochemical Study

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In *Helianthus annuus* L. the outer epidermes of the two adjacent anther lobes secrete a cementing substance in the form of a hyaline membrane, prior to the microspore mother cells entering meiosis. Gradually, the neighbouring anthers become bound together by the hyaline membrane. They remain in this stage only for a short period (up to meiosis I). The membrane then disorganises and at dehiscence the five anthers are almost free again. The histochemical studies have shown that the hyaline cementing membrane is PAS-negative and does not seem to contain cellulose or pectin. Tests for lignin, cutin, suberin and lipids are also negative. Furthermore it is not resistant to acetolysis which suggests that sporopollenin is absent.

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The occurrence of syngenesious anthers in the Compositae has been known for nearly a century. As early as 1917, SMALL wrote "... the stamens are five in number, and usually have the anthers syngenesious". As described by CASSINI (1826, cited in SMALL 1917), the stamen is composed of a filament, anther, connective, apical and basal appendages, pollen and a prolongation of the connective below the anther to form the 'article anthérifère'. Though this structure is an additional one, but its exact nature is not clear from the description. SAUNDERS (1931) writes that "... anthers as they develop become loosely coherent (syngenesious)". LAWRENCE (1951) thinks that the stamens are connate by their anthers to form a cylinder around the style in the Compositae. According to PORTER (1959), the syngenesious condition refers to stamens or anthers united by the anthers in a ring. WILLIS (1960) defines the syngenesious condition as united anthers.

Syngenesious anthers are found in most of the genera of the Compositae and forms a unique characteristic feature of the family. Though the anthers have been invariably referred to as syngenesious, only a few have been investigated from this point of view. While studying the life-history of *Podolepis jaceoides* DAVIS (1961) mentioned that "the young anthers are free from each other and their apparent fusion at maturity results from the adhesion of epidermal cuticle on adjacent anthers. There is never an organic fusion between the five anthers as, it appears, they remain distinct entities throughout their life-cycle" (see also DAVIS 1962 a, b, 1966).

The present investigation was undertaken to elucidate the ontogeny with special emphasis on the histochemical nature of the membrane which brings about this temporary cohesion of the anthers.

MATERIAL AND METHODS

Young capitula as well as individual disc florets of *Helianthus annuus* L. were fixed in formalin-acetic-alcohol for 24 hours at 30—31° C during July 1970 and later stored in 70 % ethanol. The voucher specimens KANAN 22—24 are deposited in the Delhi University Herbarium.

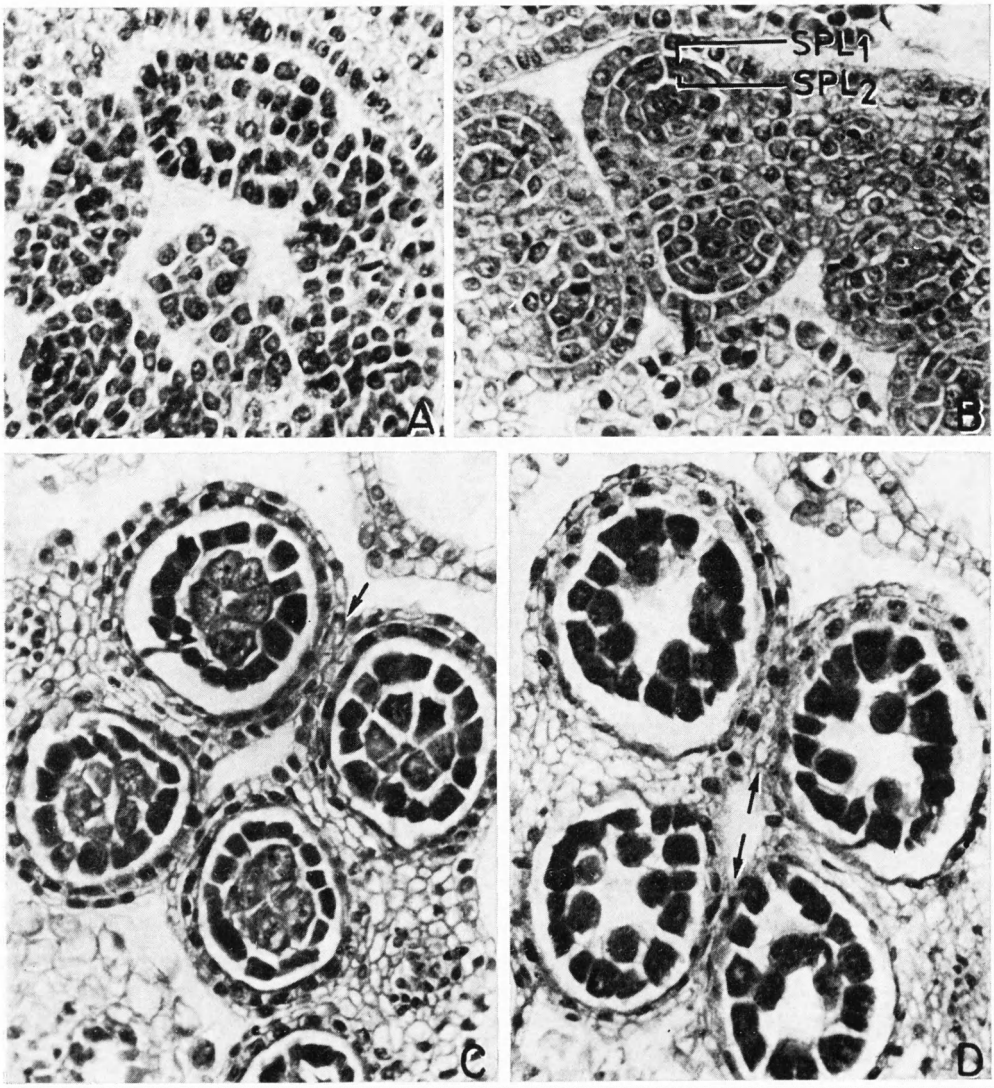

Fig. 1. *Helianthus annuus.* — A: T.s. disc floret, showing undifferentiated but free anthers. — B: Same, secondary parietal layers (SPL 1, 2) differentiated on the epidermal side; note that the anthers are still free. — C: Same, showing anthers at premeiosis, and the two adjacent microsporangia adpressed on lateral sides. — D: Same, at meiosis II. — All ×200.

After dehydration in alcohol-xylene series, the material was embedded in paraffin. Sections were cut at 3—10 microns and stained with safranin-fast green for ontogenetic studies, and for histochemical investigations they were put to various tests as detailed in Table 1.

RESULTS AND DISCUSSION

Ontogeny

The disc florets of *Helianthus annuus* have five stamens alternating with the

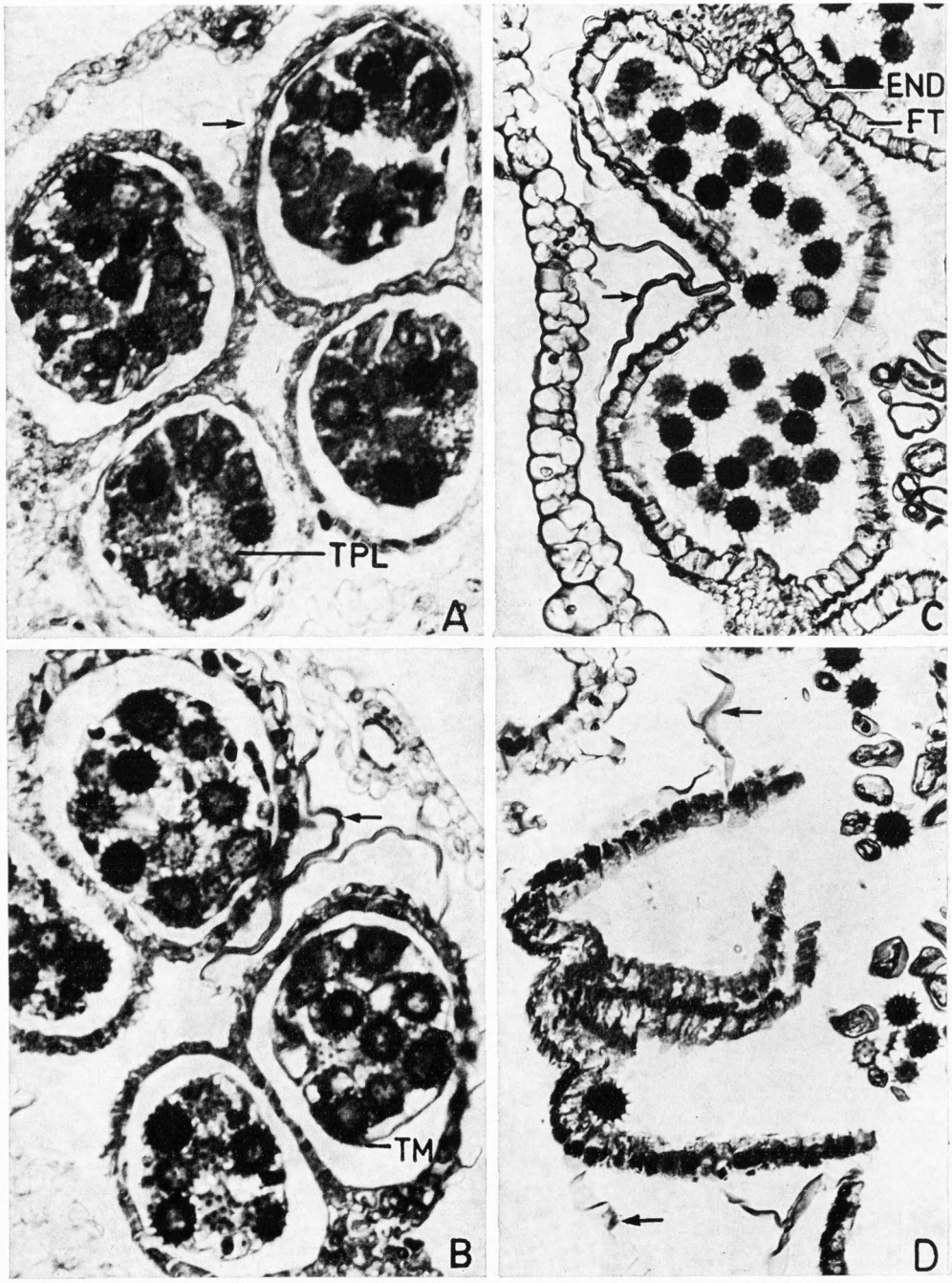

Fig. 2. *Helianthus annuus.* — A: T.s. disc floret at uni-nucleate pollen stage with tapetal periplasmodium (TPL); the membrane ruptured at places (marked by arrow) to separate the anthers. — B: Same, at 2-celled pollen stage (the cells are not clear due to highly

Table 1. Histochemical techniques.

Metabolite	Technique employed	Control	Reference
Total carbohydrates of insoluble polysaccharides	(a) PAS reaction	Acetylation	JENSEN 1962
Cellulose	(a) Zinc-chlor-iodide test	Cellulase treatment	JENSEN 1962, MEPHAM & LANE 1969
	(b) IKI-H_2SO_4	Cellulase treatment	JENSEN 1962, MEPHAM & LANE 1969
Pectin	(a) Ruthenium red technique	Pectinase treatment	JENSEN 1962, MEPHAM & LANE 1969
Lignin	(a) Maule's test	—	FOSSARD 1969
	(b) Phloroglucinol test	—	JENSEN 1962, FOSSARD 1969
Cutin	(a) KOH-chlorzinc-iodide test	—	JOHANSEN 1940
Suberin	(a) KOH-chlorzinc-iodide test	—	JOHANSEN 1940
Total lipids	(a) Sudan dyes	—	JENSEN 1962

petals and are said to be syngenesious. Anthers are dithecous and terminally appendiculate. The anther wall development in *Helianthus* (Fig. 1 A—C) follows the Dicot type of ontogeny and its details are being published elsewhere. It has been observed that initially the anthers are free and they remain so until the differentiation of the various wall layers occurs (Fig. 1 A, B). Subsequently, the two adjacent anthers gradually become adpressed (Fig. 1 C). During meiosis the epidermes of the two adpressed adjacent anther lobes secrete a hyaline cementing substance which leads to apparent fusion of the five anthers.

The two thecae of the adjacent anthers become adpressed along their entire length during meiosis I. Then they start stretching away from the central part at the septum region (Fig. 1 D). As the anthers mature, the separation continues, both towards the lateral and the dorsal sides (Fig. 2 A) until the anthers have completely separated from each other (Fig. 2 B—D). Thus, it is observed that the cementing substance is secreted by the epidermal cells of anthers on the lateral as well as dorsal sides. As the anthers mature (2-celled stage), this substance forms a hyaline membrane which later starts peeling off from the epidermal cells (Fig. 2 A, B). In this process, the otherwise free anthers remain coherent for only a very short period during ontogeny. At maturity anthers have been described as syngenesious, but histologically speaking they are completely free from each other (Fig. 2 C, D). At times, however, they might appear united at places if the cementing membrane has not completely separated from the epidermal cells.

Histochemistry

When tested histochemically, the cementing membrane has been found to be PAS-negative. It does not stain with aqueous ruthenium red for pectin. With zinc-chloriodide, it takes a brown colour similar to that of pollen exine but not the characteristic blue of cellulose. Further with IKI-H_2SO_4 test a negative reaction for

ornamented thich exine). The tapetal membrane (TM) and the periplasmodium in free anthers (arrow marked). — C: Same, at dehisced anther stage showing the degenerated epidermis and endothecial cells (END) with thickenings (FT). The membrane has almost peeled off from the epidermis (marked by arrow). — D: Same, after pollen shedding with remnants of the membrane seen at places (marked by arrow). — All ×200.

cellulose is obtained. Thus, the membrane does not contain any insoluble polysaccharide, pectin or cellulose. When tested for cutin and suberin by JOHANSEN'S (1940) method, using concentrated potassium hydroxide, it gives a very feeble reaction (indicated by a very pale yellow colour) for suberin. Therefore, the presence of suberin is possible although the results of more specific tests are required before a definitive statement is possible. The membrane gives a negative result for cutin on interaction with KOH-chlorzinciodide. The Maule's and phloroglucinol tests for lignin are negative. The membrane is non-resistant to boiling acetolysis mixture (9 parts acetic anhydride: 1 part conc. H_2SO_4), indicating that its composition does not include sporopollenin.

When the fresh membrane is stained with Sudan Black B (in 70 % ethanol) for total lipids, it gives a light pink colouration indicating absence of lipids. DAVIS (1961, 1962 b) has suggested that in *Podolepis jaceoides* and *Ammobium alatum* the membrane is cuticular in nature, however, our histochemical investigations do not confirm her remarks. The present studies, however, do not indicate the nature of the membrane although many of the typical components of plant cell walls appear not to be present, with the possible exception of suberin. Further investigation is in progress. On the basis of present ontogenic investigations, it is suggested that the earlier concept of "syngenesious" anthers, characteristic of the Compositae, should be modified.

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Isoenzyme Studies in Members of the Genus Brassica

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DENFORD, K. E. 1976 05 06. Isoenzyme studies in members of the genus Brassica. — Bot. Notiser 128: 455—462. Lund. ISSN 0006-8195.

A gel electrophoretic study has been carried out on the seed isoenzymes of 10 members of the genus *Brassica*. Eleven isoenzyme systems have been studied and the distribution of the isoenzymes used to indicate a possible historical relationship between the major recognized taxa. Three basic centres of the complex have been indicated; Indo-European, China and Mediterranean as exemplified by *B. rapa* (turnip, turnip-rape), *B. chinensis* (Pak Choi), and *B. tournefortii* (wild turnip) respectively.

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In recent years much work has been carried out in biochemical relationships with respect to plant, animal and bacterial taxonomy. The usefulness of such studies has been discussed by several workers including ALSTON and TURNER (1963), SWAIN (1963) and HAWKES (1968). Volatile oil investigations have been made by ETTLINGER and KJAER (1969) on some *Brassica* species, using seeds, roots and shoots, whilst other naturally occurring compounds, such as phenols have been investigated by DASS and NYBOM (1967) and DURKEE and HARBORNE (1973). Investigations of the genus have been carried out with respect to the use of seed proteins as taxonomic characters (VAUGHAN et al. 1966, VAUGHAN & DENFORD 1968, VAUGHAN et al. 1970), with results supporting the previous morphological studies of SCHULZ (1919). Further work has been carried out on certain enzymes in the seeds (VAUGHAN and WAITE 1967 a, b, VAUGHAN et al. 1968) such as, β-galactosidases, β-glucosidases, esterases and myrosinase.

The genus includes certain polymorphic species, and this tends to complicate the taxonomy of its members (BAILEY 1930, 1940). Such an example is found in the ten chromosome complex comprising *B. rapa* L., its allies, and *B. tournefortii* GOUAN (Table 1). This group of plants shows a wide range of polymorphy and hence rather special problems concerning the establishment of specific characters relating to its taxonomy. The members of the ten chromosome complex do have characters distinguishing them from other taxa present in the genus, and hence are essentially as follows:

Annual or biennial plants possessing tap roots; stems erect, branching; basal leaves petiolate; stem leaves sessile, lyrate and pinnatipartite with lateral alternate lobes, the terminal lobe being obovate or ovate.

The stem leaves are also deeply caudate and clasp the stem at their bases, distinguishing the species from *B. oleracea*, generally accepted as its nearest taxonomic relative, whose stem leaves are only slightly clasping. The lowest leaves of *B. rapa* L. are always more or less bristly, and the open flowers of the raceme overtop the unopened flower buds. The filaments of the outer stamens are distinctly curved at their base (cf. the straight stamens of *B. oleracea*), and the petals are bright yellow. It is interesting to note that a combination of characters, rather than absolutely specific ones, separate close relatives from one

Table 1. *Brassica rapa* and its allies investigated.

Taxon	Trivial name
B. rapa L. ssp. *rapa*	Turnip
B. rapa L. ssp. *sylvestris* (L.) JANCHEN	Wild turnip-rape
B. rapa L. ssp. *oleifera* DC.	Cultivated turnip-rape
B. rapa L. ssp. *sarson* (PRAIN) DENFORD comb. nov. Basionym *B. campestris* L. var. *sarson* PRAIN, Agr. Ledger 5: 27—28 (1898)	Sarson
B. rapa L. ssp. *toria* (PRAIN) DENFORD comb. nov. Basionym *B. campestris* L. var. *toria* PRAIN, Agr. Ledger 5: 23—25 (1898)	Toria
B. chinensis L.	Pak Choi
B. pekinensis RUPR.	Petsai
B. perviridis BAILEY	Tendergreen
B. tournefortii GOUAN	Wild turnip, Jangli-rai

another, an example of this can be found in *B. napus* which has characters in common with both *B. rapa* L. (with respect to clasping stem leaves) and *B. oleracea* (glaucous nature of the leaves, and an inflorescence similar to *B. oleracea*).

To avoid making too many new combinations in this preliminary paper, *B. chinensis*, *B. pekinensis* and *B. perviridis* are treated as species, although they should better be reduced to some lower rank.

Within the complex, work has been carried out on the seed coat, and its surface features (MUSIL 1948), however because of variability in seed size and surface markings very little has been accomplished in distinguishing between the races present, except in the case of *B. rapa* ssp. *sarson* which produces mucilage when placed in water (ALAM 1936). Seed coat pigmentation appears to be variable and of no real use in distinguishing between varieties as PRAIN (1898) has noted varying coloured seeds on the same plants of *sarson*. The genetic control of colour was investigated by SUN (1945) who found that a homozygous dominant gene gave rise to purple seeds; homozygous recessive produced yellow seeds, and the heterozygous state gave rise to intermediate forms. The histology of the testa has also been investigated by VAUGHAN et al. (1963) on certain ten chromosome taxa, for example, *B. rapa* L. and *B. chinensis*, with little distinction between them being found.

ALAM (1936) studied meiotic chromosome associations in certain races of *B. rapa* (*sarson* and *toria*) concluding that the basic chromosome number to have been 5. Various crosses were carried out by MOHAMMAD et al. (1931) between *sarson*, *toria* and turnip giving fertile offspring, indicating close relationship. SIKKA (1940) indicated that segmental interchanges and inversions may well have played an important part in separating *B. tournefortii* from the other ten chromosome members of the complex as crosses produced by him, using *sarson*, gave hybrids which at meiosis showed rings of 4 chromosomes. Further attempts to repeat this line of investigation by MOHAMMAD and SIKKA (1940) did not succeed. OLSSON (1954) also attempted to cross *B. tournefortii* with *B. rapa* subspecies (*sarson*, *toria*, *oleifera*), *B. chinensis* and *B. pekinensis*, but was not successful. The work indicated a discontinuity between *B. tournefortii* and the remaining members of the complex.

Studies of the volatile oils and glucosides present in the seeds of the *B. rapa* complex have been carried out by DELAVEAU (1959), and VAUGHAN et al. (1963). The glucosides

of certain members of the complex were examined using paper chromatography to identify the isothiocyanates produced. DELAVEAU (1959), using turnip-rape showed that the glucosides present produced butanyl, pentenyl and phenylethyl isothiocyanates. VAUGHAN (1963) and co-workers examined a larger selection of ten chromosome species including varieties of *B. rapa, B. chinensis* and *B. pekinensis*, showing the glucosides present produced 3-butanyl isothiocyanates in varying quantities. No distinction between these taxa was made in this investigation.

In all classifications the most important factor involved is the use of stable and non-trivial characters. As has previously been mentioned, the characters used in the ten chromosome *Brassica* species: leaf shape, growth habit, hairiness, glaucous nature of leaf, and root shape, are all subject to environmental alteration (BAILEY 1940, SUN 1946) and hence are of questionable value in classification.

Previous preliminary work on *Brassica* species has been carried out with the aid of serological and electrophoretic techniques by VAUGHAN et al. (1966), VAUGHAN and WAITE (1967 a, b) and VAUGHAN and DENFORD (1968).

The present investigation is a continuation of this work to evaluate the seed isoenzyme profiles of the major taxa recognized as allies of *B. rapa* and to determine the possible phylogenetic relationships, such a study might indicate.

MATERIAL AND METHODS

Wherever possible, seeds were obtained from research stations using authenticated seed from their crop breeding programme, as most of the varieties used were of commercial use. The wild species were collected by the author and authenticated accordingly. Unless all other seed samples were accompanied by an acceptable certificate of authentication, they were grown at the University of London Botanical Supply Unit (Egham., England).

Voucher specimens of all material are lodged at the Atkins Laboratories, Queen Elizabeth College, University of London, England.

Table 2. Enzyme systems studied using gel electrophoresis.

Enzyme	Method
Acid phosphatase	HALL et al. 1969
Alkaline phosphatase	EVERSON-PEARSE 1960
α-amylase	OLERED & JÖNSSON 1970
Catalase	THORUP et al. 1961
Esterase	HALL et al. 1969
β-galactosidase	VAUGHAN & WAITE 1967 a
β-glucosidase	COHEN 1952
Glutamic dehydrogenase	LAYCOCK et al. 1965
Leucine aminopeptidase	NACHLAS et al. 1957
Myrosinase	VAUGHAN et al. 1968
Peroxidase	HALL et al. 1969

Protein extracts, purification and electrophoresis were carried out as in previous studies using acrylamide gel electrophoresis (ORNSTEIN & DAVIS 1961, VAUGHAN & DENFORD 1968). Enzyme staining techniques were carried out using specific methods as in Table 2. All tests were carried out at 30° C and pH 7.0 using a tris-glycine buffered medium.

Rp (×100) were calculated from fresh gels and given to the centre of each band. No distinction was made as to intensity or rate of reaction. All estimations were made on a presence or absence basis.

ENZYME DISTRIBUTION AND TAXONOMIC RELATIONSHIPS

The presence of all the enzymes to be investigated was first of all established using agarose gel before a detailed investi-

Table 3. Enzymes occurring in all the ten chromosome *Brassica* species examined.

Enzyme	Rp
β-galactosidase	34
acid phosphatase	17
Leucine aminopeptidase	55
Peroxidase	52
Glutamic dehydrogenase	43
Glutamic dehydrogenase	60
Esterase	17
Esterase	83
Esterase	87

Table 4. Isoenzymes only found in one of the two ten chromosome "groups" of *Brassica*.

Group (1) Turnip/turnip-rape complex		Group (2) *B. chinensis* complex	
Enzyme	Rp	Enzyme	Rp
β-galactosidase	11	β-galactosidase	17
	73		63
Acid phosphatase	47		87
Leucine aminopeptidase	15	Alkaline phosphatase	67
	47	Leucine aminopeptidase	20
Peroxidase	15	Peroxidase	27
β-glucosidase	47	β-glucosidase	43
	63		67
Glutamic dehydrogenase	70	Catalase	15
Catalase	11		34
	30		43
	52		57
Esterase	93	Esterase	77

gation on acrylamide gel was carried out (VAUGHAN et al. 1970). The results of the enzyme analysis were tabulated according to Rp (Tables 3—6), each pattern being the result of ten different seed samples of each taxon (ten gels for each variety used). It was found that within each variety investigated, the enzyme pattern was constant with respect to Rp value, even though intensity of staining varied. Between varieties there appeared to be distinct differences in the patterns of certain enzymes, but within each variety the enzyme patterns were constant. It was also found that certain Rps were constantly shared between two varieties. Turnip and turnip-rape always shared the following Rps between themselves and only rarely with other taxa: Rp 15, β-glucosidase; Rp 52, β-glucosidase, also shared with *B. perviridis*; Rps 27 and 70, β-galactosidase, the former being found in *B. perviridis*; Rp 38, catalase; Rp 20, esterase; Rp 50, esterase, also found in *B. chinensis*.

Sarson and *toria* appeared to have a much smaller number of bands unique to themselves, only the catalase enzyme was found to be unique, giving bands as follows: Rps 17, 40 and 50, also found in *B. perviridis*.

The largest group of shared enzyme bands appeared to fall in the *B. perviridis*, *B. pekinensis* and *B. chinensis* complex. These bands were as follows: Rp 70, β-glucosidase shared between *B. chinensis* and *B. pekinensis* (also found in *toria*); Rp 50, acid phosphatase. All the following were found shared between *B. perviridis*, *B. pekinensis* and *B. chinensis*: Rps 15, 34, 45 and 57, catalase; Rps 38 and 77, esterase.

B. tournefortii shares one enzyme band Rp 25, catalase, with turnip, and Rp 15, ß-glucosidase, with turnip-rape. All other enzyme bands present in *B. tournefortii* are found to some extent in all the other taxa investigated, or they are only found in *B. tournefortii* (see Tables 3 and 6).

The relationships between the various

Table 5. Isoenzymes unique to *Brassica tournefortii* GOUAN.

Enzyme	Rp
β-galactosidase	60
Leucine aminopeptidase	77
Glutamic dehydrogenase	87
Catalase	50
	60
α-amylase	70
	77

Table 6. "Unique" isoenzymes.

Enzyme	Rp	Taxon
β-galactosidase	60	*B. tournefortii*
α-amylase	70	*B. tournefortii*
	77	
Leucine aminopeptidase	30	*Sarson*
	38	*B. pekinensis*
	57	*B. perviridis*
	77	*B. tournefortii*
Peroxidase	60	*Sarson*
Glutamic dehydrogenase	63	Turnip
	73	Turnip
	87	*B. tournefortii*
Catalase	08	*B. perviridis*
	50	*B. tournefortii*
	60	*B. tournefortii*
	63	Turnip-rape
Esterase	30	*B. chinensis*
	60	*B. pekinensis*

taxa based on enzyme Rps were tabulated as percentage similarities (Table 7) and a three-dimensional model was constructed using this information (Fig. 1). It was found that the similarity coefficients between turnip and turnip-rape; *sarson* and *toria*; *B. chinensis* and *B. pekinensis*, were very high (75 %). Also there appeared to be two distinct groups within the complex, the first containing turnip, turnip-rape, *sarson* and *toria*, and the other containing *B. perviridis*, *B. pekinensis* and *B. chinensis*. The other taxon investigated, *B. tournefortii*, seemed to fall somewhere between these two groups (see Fig. 1) nearer to *sarson* and *toria* than the other taxa.

Isoenzyme distributions in this complex were of four types: (1) Those occurring throughout all the taxa investigated; (2) Those occurring in one of the two groups mentioned; (3) Those found in one taxon alone, and never in any of the other taxa; and (4) Those distributed in a "random" manner.

It is interesting to note that *B. tournefortii*, a 'weed' has the greatest number of specific enzyme bands.

Within each taxon investigated the isoenzyme pattern remained constant and hence at the varietal level the taxa were indistinguishable (on the basis of presence or absence). This situation is shown in a three-dimensional manner indicating the presence of three basic 'groups' of ten chromosome taxa. One 'group' is made up of *B. chinensis*, *B. pekinensis* and *B. perviridis*, the second group is formed by the *B. rapa* complex (*sarson*, *toria*, turnip and turnip-rape) and the third 'group' is formed by the species *B. tournefortii*. Morphologically this latter separation is in agreement with all the major classifications of the *Brassica* species (SCHULZ 1919, MUSIL 1948). The grouping of garden turnip, turnip-rape, *sarson* and *toria* is in agreement with PRAIN (1898), SCHULZ (1919) and MUSIL (1948), but not with LINNAEUS (1753) and DE CANDOLLE (1821, 1824). The former workers placed all the turnips and turnip-rapes under the one species, *campestris*, whereas the latter described a separate species for the garden turnip. The other 'group' incorporates the oriental ten chromosome species described by BAILEY

Table 7. Percentage similarity between the ten chromosome *Brassica* species, using isoenzyme data.

	Tr	S	To	Pv	Ch	Pk	Tf
T	75	60	60	22	22	20	30
	Tr	60	60	21	20	20	30
		S	75	21	24	23	42
			To	28	25	24	44
				Pv	60	60	31
					Ch	75	35
						Pk	30

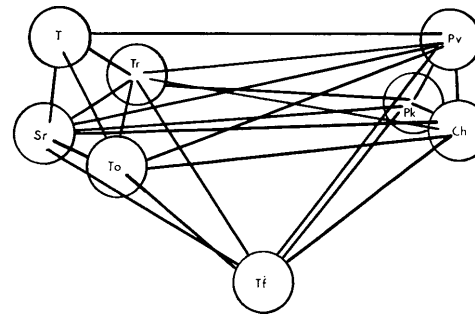

Fig. 1. Spatial taxonomic relationships between 10 taxa of *Brassica* based on isoenzyme data.

(1930), KRAUS (1940), SUN (1946) and MUSIL (1948). However, this work indicates the presence of only one species, and not three, which contradicts these workers. Such a conclusion is arrived at very readily on the grouping of the taxa in the three-dimensional model with the enzyme data (Fig. 1).

From these studies it is postulated that in my material there are three basic ten chromosome species in the genus *Brassica*:

(1) *B. rapa* which includes turnip, turnip-rape, *sarson* and *toria.*

(2) *B. chinensis* which includes *chinensis*, *pekinensis* and *perviridis.* The inclusion of *perviridis* under the species *B. chinensis* opposes the classification of BAILEY (1940) who originally gave it varietal status under *B. rapa* L., and later gave it species status as *B. perviridis.*

(3) *B. tournefortii*, a wild ten chromosome *Brassica* species.

Support for this hypothesis is found in the distribution of enzymes. There would appear to be several categories:

(i) Those only present in the turnip-turnip-rape complex (Table 4).

(ii) Those found in the *B. chinensis* complex (Table 4).

(iii) Those unique to *B. tournefortii* (Table 5).

Two other categories are present incorporating those enzymes present in all the taxa (Table 3), and those which are unique to a particular taxon (Table 6).

It is of interest to note that each of the three complexes postulated are found in three distinct geographical areas. *B. tournefortii* grows wild in the Mediterranean (endemic to this area, SCHULZ 1919). *B. rapa* and its races are found distributed throughout the Indo-European regions, and *B. chinensis* and its relatives are found in China.

It has been suggested (SUN 1946) that there are two races of *B. rapa*, an eastern and a western race. From this present study it is concluded that there are two distinct Eastern and Western species (Fig. 1). Furthermore, it would be of interest to know how these two species arose and from where they originated, with special reference to their relationship to *B. tournefortii*. One explanation for this three species situation could be that one of the species (*B. tournefortii*) gave rise to the other two. As *B. tournefortii* (of Mediterranean origin) is a weedy ten chromosome species it could be the nearest species to the original archetype suggested by SIKKA (1940) with a basic chromosome number of five. If this were true then the ten chromosome polyploid may have arisen in the Mediterranean region and spread to India/Europe and then China.

Another explanation for this situation is that there were three centres of origin for

the five chromosome archetype which eventually died out after the polyploid was formed. Possibly at each centre of origin the plants developed along their own lines, as in the case of *B. tournefortii*, or came under different selection pressures by man, as in the case of *B. rapa* and its varieties, and *B. chinensis* and its varieties. Ultimately such a process would give rise to three different groups of plants.

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Scandinavian Species of the Genus Brachythecium (Bryophyta)

I. Modification and Biometric Studies in the B. rutabulum — B. rivulare Complex

Kai Wigh

WIGH, K. 1976 05 06. Scandinavian species of the genus Brachythecium (Bryophyta). I. Modification and biometric studies in the B. rutabulum — B. rivulare complex. — Bot. Notiser 128: 463—475. Lund. ISSN 0006-8195.

Brachythecium rutabulum and *B. rivulare* have been experimentally cultivated in controlled environments to study the constancy of morphological characters. The humidity, temperature and light factors have been varied.

The variations of quantitative characters have been biometrically analysed in the cultivated mosses as well as in samples from spontaneous populations. The diagnostic value of the characters studied have been estimated for taxonomic purposes.

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Many species of mosses are extremely variable. The purpose of this investigation is to study which characters become modified thus being of little taxonomic value, and which characters are relatively constant. The morphology, taxonomy and cytology of the polymorphic complex including the two species *Brachythecium rutabulum* and *B. rivulare* will be discussed in a forthcoming paper (WIGH 1976).

The two species have been taxonomically delimited in different ways, and several varieties have been described. Some of these subspecific taxa are presumed to be modifications only. In order to assess their taxonomic value modification experiments have been carried out.

Biometric analysis revealed that certain quantitative characters are useful in distinguishing between *Brachythecium rutabulum* and *B. rivulare*.

METHODS

The modification experiments have been carried out in 9 different environments (Table 1) where the material was grown for some months. Samples grown under dry conditions grew rather slowly and were therefore kept in culture for a longer period than the others.

No nutritive was added during the experiments as it has previously been observed that these mosses can go on growing for at least two years without any additional nutritive. After the period of cultivation the plants were dried and used for the modification studies.

Measurements of leaves, nerves, cells and spores have been made under a light microscope. The magnitudes used were ×30 for the leaves and nerves, ×400 for the cells and ×1,000 for the spores. The accuracy of the measurements was 40 μ, 3 μ and 1.2 μ respectively.

The length of the leaves was measured from the insertion of the nerve on the stem to the tip of the leaves, and the length of the nerves from the insertion to the tip of the nerves. The length of the cells was measured from cells near the middle of the leaves, apart from the nerves. From each sample 30 leaves and cells were measured, and 20 spores.

MATERIAL

The investigations are based on the material previously analysed cytologically and on herbarium material. The live material of *B. ruta-*

Table 1. Climatic conditions for cultivated material.

Environment	Light		Temperature		Humidity	
	Lux	Hours	°C	Hours	%	Hours
I a	5,000	15.5	14	15	40	15
	0	8.5	14→11	2	40→60	2
			11	5	60	5
			11→14	2	60→40	2
I b	as I a	as I a	as I a	as I a	100	24
I c	2,000	15.5	as I a	as I a	as I a	as I a
	0	8.5				
I d	as I c	as I c	as I a	as I a	100	24
II	4,600	12	14	10	100	24
	0	12	14→12	2		
			12	10		
			12→14	2		
III a	9,200	15	19	12	60	12
	0	9	19→10	2	60→90	2
			10	8	90	8
			10→19	2	90→60	2
III b	7,200	15	as III a	as III a	as III a	as III a
	0	9				
III c	as III a	as III a	as III a	as III a	100	24
III d	as III b	as III a	as III a	as III a	100	24

bulum is represented by the n=12 cytotype and *B. rivulare* by the n=6 cytotype. The reference numbers are listed in WIGH (1976).

Voucher specimens are deposited at the Botanical Museum of Göteborg (GB), Sweden.

MODIFICATION EXPERIMENTS

Many intraspecific taxa in the *Brachythecium rutabulum* — *B. rivulare* complex have been described on such characters as the size and colour of the plant, length of seta, shape of lid, etc. These taxa are often modifications only. If corresponding studies were to be carried out in other species complexes also, many taxa would probably prove to be modifications only.

It seems likely that a given character can display a high degree of modifiability in one species, whereas in another species the same character is more constant, an example being the shape of the lid in the family Brachytheciaceae. This character is variable in certain species such as *Brachythecium rutabulum*, but in other genera it is probably more constant.

Some populations of *Brachythecium rutabulum* and *B. rivulare* have been cultivated in 9 different environments in climate chambers. The climatic conditions are given in Table 1. The environments have been called I a—d, II and III a—d, three climate chambers having been used.

The modification experiments have been divided into two separate investigations, one biometric, discussed on p. 469 and one in the main qualitative. In the latter some characters have also been measured but the results have not been analysed statistically.

Modificative Characters

GAMETOPHYTIC CHARACTERS

Both species become extensively modified. This was anticipated as they are also highly variable under natural conditions.

PLICATION OF LEAVES. Plication is highly modificative in both species which may give rise to problems of identification, as in several keys species with plicated leaves have been separated from species without plications. The reduced plications in *B. rutabulum* may cause trouble when distinguishing between this species and, for instance, *B. mildeanum* and *B. curtum* (WIGH 1976).

COLOUR OF PLANT. There is an obvious difference in the colour of plants cultivated in light with an intensity of 2,000 lux and those cultivated in 5,000 lux. Those grown in less light are a darker green than those cultivated in 5,000 lux. This is true of both species.

BRANCHING. The number of branches per cm of the shoot stands in direct relation to the humidity. Under conditions of saturated humidity both species produce only a few branches.

ANGULAR CELLS. In all 9 environments *B. rivulare* produces large and well-developed angular cells (Fig. 1 E, F), the size of these cells being somewhat variable, but they are always fairly large and well-delimited.

B. rutabulum displays greater variation in the development of angular cells when cultivated. Under dry conditions the angular cells do not become enlarged or more clearly delimited (Fig. 1 B). Under conditions of saturated humidity the variation, both within a sample and between samples from different populations, is more extensive, plants in some samples then producing large and well-delimited angular cells as in *B. rivulare*. Plants in other samples only produce somewhat larger angular cells. In Fig. 1 C the angular cells are somewhat enlarged.

The structure of the angular cells has been regarded by several authors as the most important diagnostic character for separating *B. rutabulum* and *B. rivulare*. This investigation shows that this character is highly modifiable in *B. rutabulum*. Natural populations of this species with large and well-delimited angular cells are also found, such forms being extremely difficult to distinguish from *B. rivulare*.

DECURRENCY OF LEAVES. The decurrent part of the leaves in cultivated samples is shown in Fig. 2. In *B. rivulare* the leaves are always longly and broadly decurrent. In *B. rutabulum* the decurrency increases with humidity, both with regard to length and breadth. This character has been accorded the same taxonomic importance as the angular cells, and it must be observed that the decurrency is extremely modifiable in *B. rutabulum*.

LENGTH OF INTERNODES. In both species the internodes attain a greater length in 2,000 lux than in 5,000 lux both where humidity is saturated and under drier conditions. The differences are marked. In 2,000 lux there are about 25 leaves per cm of the shoot and in 5,000 lux about 33. When grown in 7,200 lux or 9,000 lux there are no differences, either where the humidity is saturated or under drier conditions.

There are quite obvious differences between samples cultivated when the humidity is saturated and under drier conditions as regards length of internodes, the internodes being shorter under drier conditions. This is true of both species and with all light intensities.

NUMBER OF RHIZOIDS. The number of rhizoids is related to light intensity and to humidity, but also to the degree of contact the shoots have with the substratum. When grown in contact with the substratum the shoots produce far more rhizoids than when growing erect with no contact.

If the influence of light and of humidity are compared as regards number of rhizoids, it seems that humidity has the greater effect. Under conditions of lower humidity the number of rhizoids increases.

SPOROPHYTIC CHARACTERS

Brachythecium rutabulum only has been investigated.

LENGTH OF SETA. The length of the seta is highly modifiable and varies with hu-

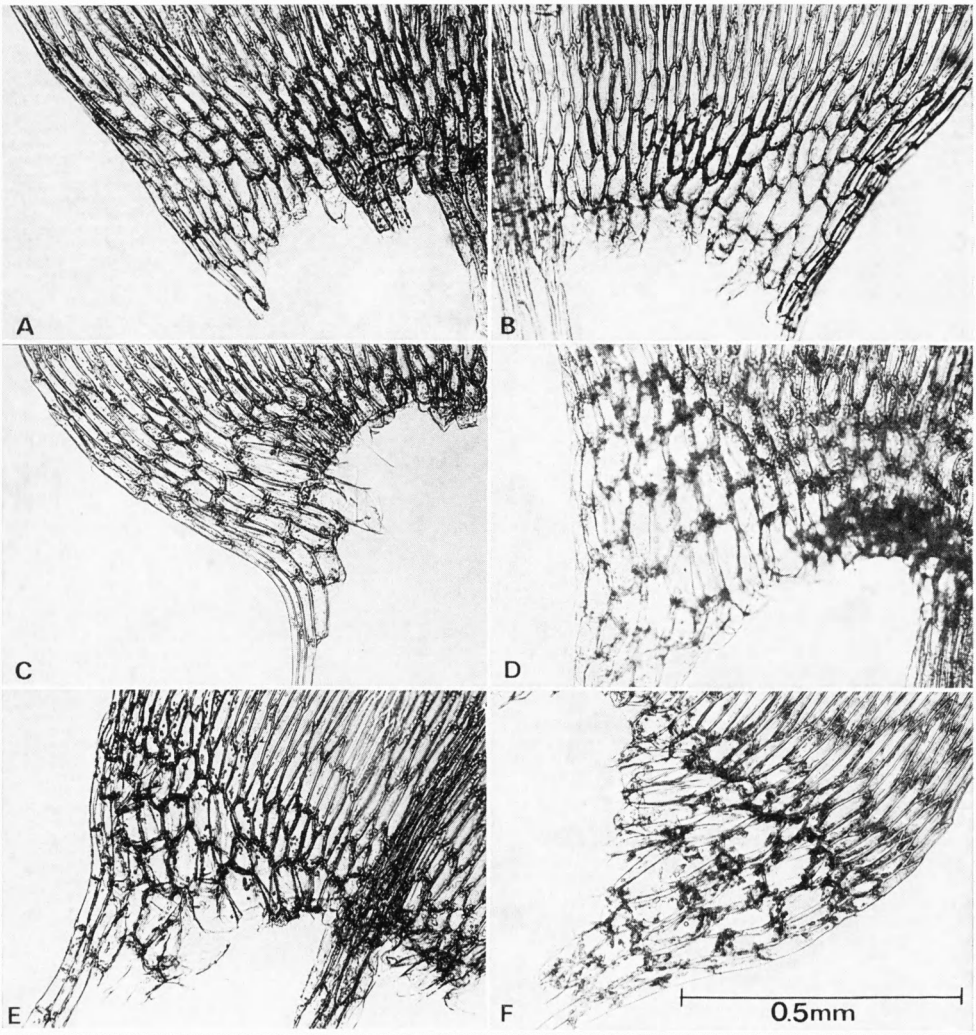

Fig. 1. Photographs of angular cells. — A—C: *Brachythecium rutabulum*. — D—F: *B. rivulare*. — A: 71-90 (spontaneous population). — B: 71-90 (environment IIIb). — C: 71-90 (environment IIId). — D: 71-169 (spontaneous population). — E: 71—127 (environment Ib). — F: 71-127 (environment Id). — The climatic conditions are given in Table 1.

midity. The differences between spontaneous material and samples cultivated under conditions of saturated humidity are marked. The length of the seta in cultivated samples is often more than twice or three times that found in spontaneous material. In one population the mean of the length of the seta in spontaneous samples was 1.5 cm and the new sporophytes produced when humidity was saturated was 4.5 cm. This observation is important since there are varieties of *B. rutabulum* described which differ from the nomenclatural type material in having longer seta.

LENGTH AND SHAPE OF LID. Under conditions of saturated humidity some

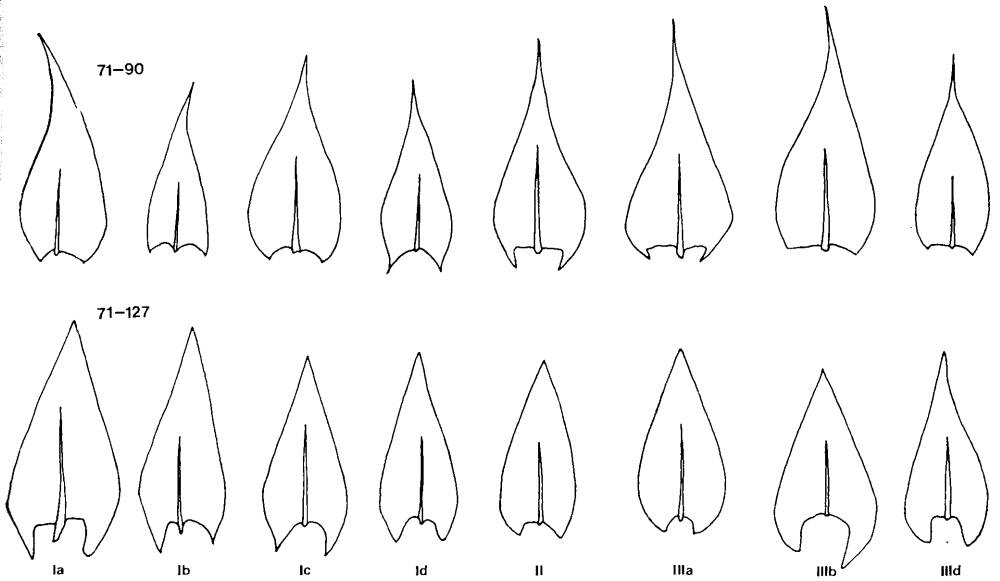

Fig. 2. Leaves of cultivated samples of *Brachythecium rutabulum* (71-90) and *B. rivulare* (71-127). The climatic conditions are given in Table 1.

populations of *B. rutabulum* produce longer lids than those found in the corresponding spontaneous material. The lid is not conical, but more or less oblique. Plants displaying this modification have been described as a variety and have also been treated as a good species.

LAZARENKO et al. (1971) investigated the chromosomes in *B. eurhynchioides* (LIMPR.) LOESKE, a taxon diverging from *B. rutabulum* in the long oblique lid only. They reported two chromosome numbers, n=6 and n=12. The chromosome complement of the n=6 and n=12 cytotypes agreed with that of the corresponding cytotypes of *B. rutabulum* which supports the statement that *B. eurhynchioides* is only a modification of *B. rutabulum*.

The long oblique lid is a character found in some genera in the family Brachytheciaceae, e.g. *Rhynchostegiella, Rhynchostegium, Cirriphyllum* and *Eurhynchium*, whereas *Brachythecium* has a short conical lid. The lid in the first-mentioned genera is probably less modifiable than in *Brachythecium rutabulum*.

Difference in shape of lid has often been the only character given in keys in separating *Brachythecium* from other genera. It must be noted that *B. rutabulum* at least could key out wrongly using such keys.

Not Modificative Characters

GAMETOPHYTIC CHARACTERS

SHAPE OF LEAVES. Neither in *B. rutabulum* nor in *B. rivulare* is the shape of the leaves modifiable (Fig. 2). This character is one of the most useful for separating the two species. In all 9 environments the leaves of *B. rutabulum* are long and pointed in contrast with the acute leaves of *B. rivulare*. Fig. 2 also gives an indication of the size of the leaves in the different environments. Leaves from 8 environments only are illustrated as no material of population 71—90 cultivated in III c was available.

DENTICULATION OF LEAVES. Neither in *B. rutabulum* nor in *B. rivulare* does the denticulation of the leaves vary

Table 2. Modificative and non-modificative characters in *Brachythecium rutabulum* and *B. rivulare*. Gametophytic characters have been studied in both species and sporophytic characters in *B. rutabulum* only. — Modificative characters: +, non-modificative characters: —. — Modification depends on humidity: H, on light: L.

Gametophytic characters		
Growth	+	H
Plication	+	H
Colour	+	L
Branching	+	H
Angular cells	+	H
Decurrency of leaves	+	H
Internodes	+	H, L
Rhizoids	+	H, L
Shape of leaves	—	
Denticulation of leaves	—	
Length of leaves	+	H, L
Length of nerves	+	H, L
Length of cells	+	H, L
Sporophytic characters		
Length of seta	+	H
Lid	+	H
Size of spores	—	
Papillae on seta	—	
Form of capsule	—	
Size of capsule	—	
Exothecial cells	—	
Peristome	—	
Stomata	—	

in any of the environments. This character is of no value for separating these two species, but is of importance in distinguishing *B. rutabulum* from *B. mildeanum* (WIGH 1976).

SPOROPHYTIC CHARACTERS

Brachythecium rutabulum only has been investigated.

PAPILLATION OF SETA. When cultivated samples were compared with spontaneous populations no differences in the papillae of the seta were observed. This is important since the papillae is one of the most widely used diagnostic characters in the genus *Brachythecium*. Whether or not these papillae are modifiable in other species has not yet been investigated.

SHAPE AND SIZE OF CAPSULE. There are no obvious differences in the shape and size of capsules of cultivated and spontaneous specimens except for the lid as stated above.

EXOTHECIAL CELLS. If natural and cultivated material are compared as regards size and arrangement of exothecial cells no differences are observed. In cultivated samples the exothecial cells are arranged in rows and have longitudinal walls that are more incrassate than the transverse walls.

PERISTOME. In cultivated samples there are no observable modifications in either the outer or inner peristome. The cilia of the inner peristome are papillose and nodose precisely as in natural populations.

STOMATA. As there are only a few stomata on each capsule no extensive biometric investigation has been undertaken. There were no differences in the shape and size of stomata in natural and cultivated material.

Summary of the Modification Experiments

The modification experiments can be summarized as follows (Table 2):

(1) Gametophytic characters display a higher degree of modification than sporophytic characters.

(2) Variations in humidity give rise to more extensive modification than do variations in light intensity. Temperature probably has little influence on the plants, at least within the range of temperatures used in this experiment.

(3) Some morphological characters are modified by humidity, others by light, whereas still others are modified by both humidity and light.

(4) In most cases the gametophytic characters of *B. rutabulum* and *B. rivulare* modify in the same way, but there are some exceptions, such as length of cells, p. 471.

(5) The most important modificative characters of taxonomic value are: size of

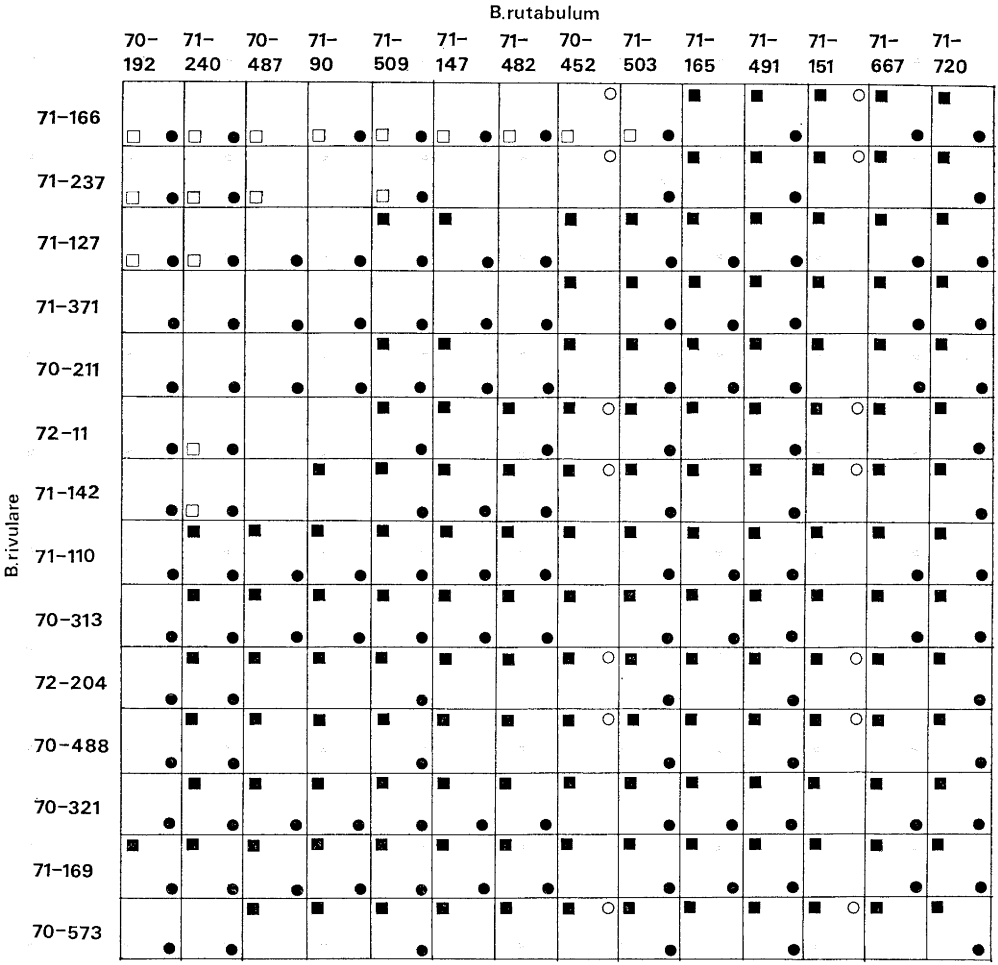

Fig. 3. Statistical analysis of biometric characters in spontaneous samples of *Brachythecium rutabulum* and *B. rivulare*. — Squares show that the leaves are longer in *B. rutabulum*, open squares that the leaves are longer in *B. rivulare*, dots that the relative length of the nerves is greater in *B. rivulare* and rings that relative length of the nerves is greater in *B. rutabulum*.

plants, length of internodes, angular cells, decurrency of leaves, colour of plant, plication of leaves, length of seta and length and shape of lid.

(6) The most important non-modificative characters are: shape of leaves, denticulation of leaves, papillation of seta, size and shape of capsules and peristome.

BIOMETRIC STUDIES

Spontaneous Populations

The length and shape of the leaves, two of the most important morphological characters for separating *Brachythecium rutabulum* from *B. rivulare* have been studied biometrically as well as other characters of possible diagnostic value.

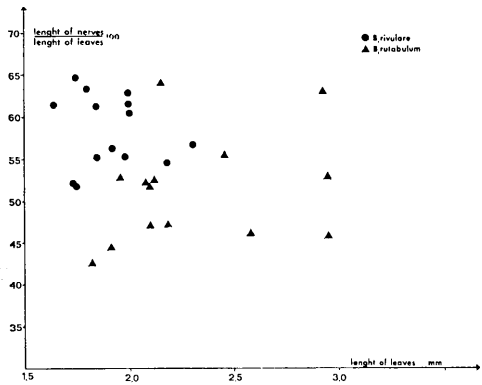

Fig. 4. Variations in length of leaves and relative length of nerves in spontaneous samples of *B. rutabulum* (triangles) and *B. rivulare* (dots).

SIZE OF SPORES

There is no statistically significant difference between the size of the spores in *B. rutabulum* and *B. rivulare*. The mean value in the populations studied is 17—21 ±1—2 μ in both species.

LENGTH OF LEAVES, NERVES AND CELLS

In both species 14 populations have been selected at random (Figs. 3, 4). The length of the leaves, nerves and cells has been measured. *B. rutabulum* and *B. rivulare* do not differ with regard to length of cells.

The shortly pointed leaves in *B. rivulare* can be expressed biometrically as the ratio of the length of the nerves to the length of the leaves. The length of the leaves and the relative length of the nerves are very useful distinguishing characters. There is, however, great variation between populations within both species. In most populations of *B. rivulare* the leaves are shorter and the nerves relatively longer than in the populations of *B. rutabulum*. The variations in these characters are shown in Fig. 4. The differences have been estimated by means of a t-test significant at the 5 % level.

Table 3. Differences significant at the 5 % level between spontaneous populations of *B. rutabulum* and *B. rivulare* with reference to length of leaves and relative length of nerves. For explanation see text and Fig. 3.

Characters	Number of combinations	%
Leaves longer in *B. rutabulum* (+character)	147	75.0
Leaves longer in *B. rivulare* (— character)	20	10.2
No differences	29	14.8
Rel. length of nerves greater in *B. rivulare* (+character)	133	67.9
Rel. length of nerves greater in *B. rutabulum* (— character)	14	7.1
No differences	49	25.0
2+characters	94	48.0
1+character	63	32.1
2 — characters	1	0.5
1 — character	3	1.5
1+ and 1 — character	29	14.8
No differences	6	3.1

In Fig. 3 the squares show that the leaves are significantly longer in *B. rutabulum* (a + character) and the dots that the relative length of the nerves is significantly greater in *B. rivulare* (a + character). The open squares show that the leaves are significantly longer in *B. rivulare* (a — character) and the rings that the relative length of the nerves is significantly greater in *B. rutabulum* (a — character).

In Table 3 the results for the population studied are summarized. In 75.0 % of the combinations the leaves of *B. rutabulum* are longer than those of *B. rivulare* (a + character). In only 10.2 % of the combinations are the leaves of *B. rivulare* longer (a — character). In 67.9 % of the combinations the relative length of the nerves is greater in *B. rivulare* (a + character) and in only 7.1 % of the combinations is the relative length of the nerves greater in *B. rutabulum* (a — character).

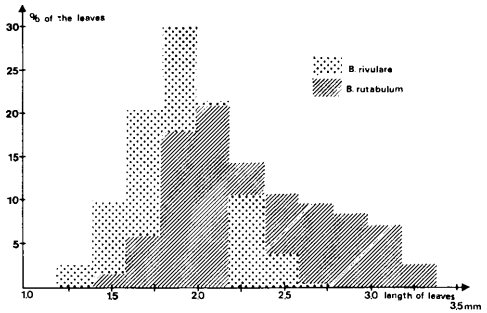

Fig. 5. Length of leaves in spontaneous samples of *Brachythecium rutabulum* and *B. rivulare*.

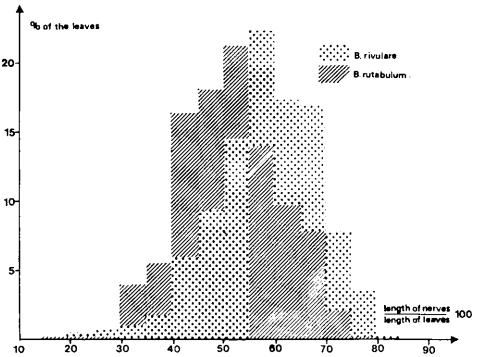

Fig. 6. Relative length of nerves in spontaneous samples of *Brachythecium rutabulum* and *B. rivulare*.

The lower half of Table 3 shows that in 48.0 % of the combinations there are two + characters and that in 0.5 % only are there two — characters. One + character occurs in 32.1 % of the combinations and one — character in 1.5 %.

Thus in 80.1 % of the combinations there are either one or two + characters (in such cases the biometric information will be helpful in identifying the species). In 14.8 % of the combinations there is one + character and one — character (the one character indicates *B. rutabulum* and the other *B. rivulare*). In 3.1 % of the combinations no differences are found and in only 2 % are one or two — characters found (here the biometric information will lead to an erroneous identification of the species).

It should be noted that these populations have been selected at random from the populations studied cytologically and that *B. rutabulum* is represented by the n=12 cytotype and *B. rivulare* by the n=6 cytotype.

The 14 populations of each species cannot cover the whole morphological variation of the species. This is the case in the length of the leaves at least.

Variation in length of leaves is shown in Fig. 5 and the relative length of the nerves in Fig. 6. These figures are very useful for separating the two species. This biometrical test should always be correlated with qualitative characters.

Cultivated Material

The same characters that were measured in natural samples have been studied in the cultivated samples. Only a limited amount of cultivated material has been available for this investigation so that the statistical analyses are based on a smaller number of samples than in the natural populations.

SIZE OF SPORES

When natural and cultivated material of *Brachythecium rutabulum* is compared no differences in size of spores is observed. *B. rutabulum* is an autoecious species often producing sporophytes when cultivated, in contrast with *B. rivulare* which is dioecious and of which no sporophytes have been available for study.

LENGTH OF LEAF CELLS

The length of the cells in cultivated material in relation to spontaneous populations is given in Table 4.

In *B. rutabulum* the cells in cultivated material are always longer than in spontaneous material. When cultivated in drier habitats the cells are longer, except in environments I c and I d.

In cultivated material of *B. rivulare* the cells are longer in the environments I a—d

Table 4. Comparison between length of cells in spontaneous and cultivated material of *Brachythecium rutabulum* and *B. rivulare*. Length of cells in cultivated samples is calculated as percentage of length of cells in the corresponding natural populations. The environmental conditions are given in Table 1.

Lux	Humidity	Environment	*B. rutabulum*	*B. rivulare*
2,000	<100 %	I c	105.7	104.4
2,000	100 %	I d	107.4	104.2
5,000	<100 %	I a	113.5	100.4
5,000	100 %	I b	108.7	107.5
7,200	<100 %	III b	114.0	93.4
7,200	100 %	III d	108.1	95.3
9,200	<100 %	III a	111.1	92.6
9,200	100 %	III c	102.7	96.5

than in the corresponding spontaneous populations. In environments III a—d the reverse is true. This difference is probably due to intensity of light. In environments III a—d light intensity is 7,200 lux or 9,200 lux and in I a—d 2,000 lux or 5,000 lux.

In drier environments there is a tendency for the cells to be somewhat smaller than where humidity is saturated. The opposite holds for *B. rutabulum*. This difference can probably be explained by the fact that *B. rivulare* is a hydrophilous species and *B. rutabulum* mesophilous.

LENGTH OF NERVES AND LEAVES

In Table 5 the mean values of absolute and relative lengths of the nerves in cultivated samples and the corresponding natural material is given.

In cultivated samples of *Brachythecium rutabulum* and *B. rivulare* both the absolute and relative length of the nerves is less than in the corresponding spontaneous material.

The relative length of the nerves has decreased more in *B. rivulare* than in *B. rutabulum*, but is greater in *B. rivulare* just as in the natural populations. The mean value of all relative lengths in cultivated samples is 47.7 % in *B. rivulare* and 44.9 % in *B. rutabulum*. In the corresponding spontaneous material the relative length of the nerves is 58.7 % in *B. rivulare* and 53.1 % in *B. rutabulum* (see also Table 7).

Table 5. Length of nerves in cultivated material (Mod.) of *Brachythecium rutabulum* and *B. rivulare* and length of nerves in corresponding spontaneous material (Spon.).

Environment	Humidity	*B. rutabulum*				*B. rivulare*			
		Absolute length mm		in % of leaf length		Absolute length mm		in % of leaf length	
		Mod.	Spon.	Mod.	Spon.	Mod.	Spon.	Mod.	Spon.
I a	<100 %	0.78	1.19	42.0	53.0	0.68	1.17	43.7	59.4
I b	100 %	0.67	1.22	42.4	53.7	0.69	1.10	48.8	59.2
I c	<100 %	0.88	1.09	46.8	51.6	0.74	1.20	48.8	60.8
I d	100 %	0.71	1.09	47.6	51.9	0.67	1.10	51.5	59.2
III a	<100 %	1.05	1.26	46.3	52.7	0.76	1.15	46.8	57.3
III c	100 %	0.81	1.38	44.3	55.7	0.70	1.21	48.4	58.0
III b	<100 %	0.92	1.25	43.3	53.2	0.88	1.11	48.2	58.3
III d	100 %	0.85	1.25	46.2	52.8	0.74	1.15	45.3	57.3

Table 6. Length of leaves in cultivated material of *Brachythecium rutabulum* and *B. rivulare* calculated as percentage of length in corresponding spontaneous populations. — In the upper half of the table the lengths are arranged according to variation in humidity. In the lower half the lengths are arranged according to variation in light intensity.

Lux	Humidity	Environment	*B. rutabulum*	*B. rivulare*
2,000	<100 %	I c	89.2	78.4
2,000	100 %	I d	70.7	71.2
5,000	<100 %	I a	80.5	79.5
5,000	100 %	I b	70.2	75.7
7,200	<100 %	III b	87.1	85.3
7,200	100 %	III d	80.7	75.9
9,200	<100 %	III a	95.2	81.1
9,200	100 %	III c	79.5	75.6
2,000	<100 %	I c	89.2	78.4
5,000	<100 %	I a	80.5	79.5
2,000	100 %	I d	70.7	71.2
5,000	100 %	I b	70.2	75.7
7,200	<100 %	III b	87.1	85.3
9,200	<100 %	III a	95.2	81.1
7,200	100 %	III d	80.7	75.9
9,200	100 %	III c	79.5	75.6

The absolute length of the nerves is greater in drier environments than where humidity is saturated. This holds for both species but the difference is more pronounced in *B. rutabulum*.

In both species the nerves are longer in environments III a—d than in I a—d. In *B. rutabulum* the mean values are 0.91 mm and 0.76 mm respectively, and in *B. rivulare* the corresponding values are 0.77 mm and 0.70 mm.

The length of the nerves is thus modified both by degree of humidity and light intensity.

Table 7. Differences significant at the 5 % level in biometric characters in cultivated samples of *B. rutabulum* and *B. rivulare*. — The climatic conditions are given in Table 1. For explanation see text.

Samples	Number of combinations	Leaves longer in *B. rutabulum*		Nerves relatively longer in *B. rivulare*	
		Number of combinations	%	Number of combinations	%
I c	25	22	88.0	11	44.0
Spon.	25	14	56.0	21	84.0
II	45	35	77.8	7	15.6
Spon.	45	22	48.9	24	53.3
III a	25	25	100.0	8	32.0
Spon.	25	21	84.0	11	44.0
III b	20	18	90.0	11	55.0
Spon.	20	15	75.0	8	40.0
III c	25	23	92.0	16	69.6
Spon.	25	13	52.0	20	80.0
III d	20	17	85.0	6	30.0
Spon.	20	13	65.0	11	55.0

In most cases the leaves are shorter in cultivated material than in spontaneous populations. In Table 6 the length of the leaves in cultivated material is calculated as percentage of the length in spontaneous populations.

In both *B. rutabulum* and *B. rivulare* the leaves are shorter in saturated humidity than in drier environments (Table 6, upper half).

If the length of the leaves is related to intensity of light, (Table 6, lower half) there are almost no differences between samples cultivated in environments I d and I b, and in III d and III c. This demonstrates that humidity modifies the length of the leaves to a greater extent than intensity of light does.

In drier habitats intensity of light has little or no influence on length of leaves in *B. rivulare* (compare I c with I a, and III b with III a). In *B. rutabulum* intensity of light modifies the length of the leaves to a greater extent.

The length of the leaves is thus modified by both humidity and intensity of light.

The statistical analysis of biometric characters in cultivated samples has been carried out in the same way as in the spontaneous material, p. 470.

In the corresponding study of spontaneous populations 14 populations of each species were used, the number of combinations thus being 196. Unfortunately much fewer cultivated samples were available but the tendency is quite clear.

The procedure followed for statistical analysis was such that the biometric results for cultivated material have been compared with the results for the corresponding spontaneous samples. The results are summarized in Table 7. For conditions of saturated humidity environments II, III c and III d have been used, and for drier habitats I c, III a and III b. These environments were chosen as the number of samples available was greater in them than in the other environments.

As regards length of leaves there is always a greater number of combinations in cultivated material than in spontaneous material which show statistically significant differences. The opposite is true of the relative length of the nerves except in environment III b.

These investigations show that biometric methods are diagnostically useful in separating *Brachythecium rutabulum* from *B. rivulare*.

Summary of the Biometric Investigations

SPONTANEOUS SAMPLES

(1) *Brachythecium rutabulum* and *B. rivulare* do not differ in size of spores and length of cells in the leaves.

(2) The leaves are significantly longer in *B. rutabulum*.

(3) The relative length of the nerves is significantly greater in *B. rivulare*.

(4) These last two characters are useful in separating the species.

CULTIVATED MATERIAL

(1) The cells in cultivated material of *B. rutabulum* are longer than in spontaneous populations. When *B. rivulare* is cultivated in lower intensities of light the cells are longer than in spontaneous populations, in lighter environments the cells are shorter.

(2) In *B. rutabulum* the cells are shorter under conditions of saturated humidity than in drier environments but longer in *B. rivulare*.

(3) Both the absolute and relative length of nerves is less in cultivated samples of both species.

(4) In lower intensities of light the nerves are shorter in both species.

(5) In drier environments the nerves are longer in both species.

(6) In both species the leaves are shorter in cultivated samples.

(7) In both species the leaves are shorter under conditions of saturated humidity than in drier habitats.

(8) Under conditions of saturated humidity the length of the leaves of both species is little influenced by light intensity or not at all.

(9) Humidity modifies the quantitative characters more than light intensity does.

ACKNOWLEDGEMENTS

The climate chambers of the Department of Physiological Botany, the University of Göteborg, have kindly been put at my disposal for which I am most obliged to Professor HEMMING VIRGIN and Dr STIG FALK.

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Scandinavian Species of the Genus Brachythecium (Bryophyta)

II. Morphology, Taxonomy and Cytology in the B. rutabulum — B. rivulare Complex

Kai Wigh

WIGH, K. 1976 05 06. Scandinavian species of the genus Brachythecium (Bryophyta). II. Morphology, taxonomy and cytology in the B. rutabulum — B. rivulare complex. — Bot. Notiser 128: 476—496. Lund. ISSN 0006-8195.

Chromosome numbers in 264 gatherings of *B. rutabulum* and 42 gatherings of *B. rivulare* have been established. The cytological information obtained has formed the basis for the taxonomic treatment of the complex. In *B. rutabulum* the only chromosome number observed was n=12 and in *B. rivulare* n=6.

Some taxa in the complex have been typified and some new synonyms are given. The distribution and habitats of the species in Scandinavia are commented on.

Kai Wigh, Department of Physics and Measurement Technology, University of Linköping, S-581 83 Linköping, Sweden.

The section *Rutabula* of the genus *Brachythecium* has been delimited in different ways by different authors. The two species *Brachythecium rutabulum* (HEDW.) B.S.G. and *B. rivulare* B.S.G. can be said to constitute the centre of this section. Other species presumed to be related to these two species have been grouped in the section *Rutabula* (WIGH 1974). The taxonomic treatment of these latter species in the section has, however, been discussed and the delimitation of the section varies between different bryologists. Only a few controversial species will be mentioned here, e.g. *Brachythecium latifolium* KINDB., *B. ryanii* KAUR. and *B. mildeanum* (SCHIMP.) SCHIMP.

In Scandinavia the *Brachythecium rutabulum — B. rivulare* complex is relatively well delimited comprising only these two species. They are characterized by the chromosome number n=12 and n=6 respectively in contrast with the species mentioned above, *B. latifolium* and *B. ryanii* having the chromosome number n=11 and *B. mildeanum* n=13.

MATERIAL

This study is based on live material and herbarium material. The gatherings that have been studied cytologically were collected between 1970 and 1973. The localities are given in the appendix. The names of some collaborators who have contributed with some of the gatherings are shown in parentheses after the gatherings concerned. 264 gatherings of *B. rutabulum* and 42 of *B. rivulare* have been studied cytologically and voucher specimens have been deposited at the Botanical Museum of Göteborg (GB), Sweden. Reference numbers are given in the appendix.

About 2,000 herbarium specimens of each species have been studied from the following herbaria: AAU, B, BG, C, G, GB, H, LD, O, OULU, S, TRH, TROM, TUR and UPS. The abbreviations used are as in LANJOUW and STAFLEU (1964).

METHODS

The cultivation techniques used for the populations that have been studied cytologically are as in WIGH & STRANDHEDE (1971).

Two different cytological methods have been used: The Feulgen method used by WIGH & STRANDHEDE (1971) and the aceto-orcein methods used by WIGH (1972 a). Both methods

give equally good staining results. The first method is to be recommended for permanent preparations but is more difficult to standardize. The importance of pretreatments is stressed. Only with suitable pretreatment is it possible to count mitotic chromosomes in a great number of populations. Cold treatment has been used in this study (WIGH & STRANDHEDE 1971, WIGH 1972 a).

The chromosomes have been photographed as in WIGH (1973 a).

The drawings of morphological details have been made with the aid of a camera lucida.

DELIMITATION OF THE BRACHYTHECIUM RUTABULUM — B. RIVULARE COMPLEX

Brachythecium rutabulum and *B. rivulare* can be distinguished from the other Scandinavian species of the genus with the aid of the following simplified key. The key comprises all species recognized by NYHOLM (1954—1969) except for *B. geheebii* which has been transferred to the genus *Homalothecium* (WIGH 1973 b).

1. Seta ± smooth. (*B. collinum, B. curtum, B. populeum, B. plumosum, B. erythrorrhizon, B. albicans, B. groenlandicum, B. mildeanum, B. campestre, B. salebrosum, B. glareosum, B. turgidum*).
1. Seta rough throughout the whole length 2
2. Cilia of the inner peristome appendiculate, leaves often plane, as a rule not plicate. (*B. glaciale, B. velutinum, B. trachypodium, B. reflexum, B. starkei, B. latifolium*).
2. Cilia of the inner peristome nodose, leaves concave, plicate 3
3. Autoecious species ..... *B. rutabulum*
3. Dioecious species 4
4. Angular cells inflated ..... *B. rivulare*
4. Angular cells not inflated. (*B. ryanii*).

Brachythecium rutabulum (HEDW.) B.S.G.

BRUCH, SCHIMPER & GÜMBEL, Bryol. Eur. 6: 15 543 (1853) (fasc. 52—54 Mon. 11: 9). — *Hypnum rutabulum* HEDWIG, Spec. Musc. 276 (1801). Lectotype: sheet 3106/87 in the HEDWIG—SCHWAEGRICHEN herbarium (G). Coll. no. 12.

Brachythecium rutabulum var. *aureo-virens* BRID.) BROCKMÜLLER, Arch. Ver. Freund. Naturg. Mecklenburg 23: 122 (1870). — *Hypnum rutabulum* var. *aureo-virens* BRIDEL, Spec. Musc. 2: 184 (1812). Lectotype: sheet 3001/94 in the BRIDEL herbarium (B). The specimen in the lower right corner. Coll. no. 21. Collected by DEJEAN.

Brachythecium rutabulum var. *brevisetum* (FIEDL.) BROCKMÜLLER, Arch. Ver. Freund. Naturg. Mecklenburg 23: 122 (1870). — *Hypnum rutabulum* var. *brevisetum* FIEDLER, Syn. Laubm. Mecklenburg 111 (1844).

Brachythecium rutabulum var. *crassum* LANGE, Bot. Tidsskr. 2: 248 (1868) nom. nud.

Brachythecium rivulare var. *cuspidatum* JENSEN, Danm. Moss. 2: 141 (1923). Lectotype: (C). Collected by C. JENSEN in Denmark, Zealand, Allindelille Fredskov in 1882.

Brachythecium rutabulum var. *dumetorum* JENSEN, in BAUER Musci Eur. Exs. ser 14 nr. 693 (1910). Lectotype: (C). Collected by C. JENSEN in Denmark, Zealand, Hvalsö in 1904.

Brachythecium rutabulum var. *eurhynchioides* LIMPRICHT, Laubm. Deutschl. 3: 109 (1896). — *B. eurhynchioides* (LIMPR.) LOESKE, Moosfl. Harz. 273. (1903) nom. inval. prov.

Brachythecium rutabulum var. *explanatum* (BRID.) BROCKMÜLLER, Arch. Ver. Freund. Naturg. Mecklenburg 23: 122 (1870). — *Hypnum rutabulum* var. *explanatum* BRIDEL, Spec. Musc. 2: 184 (1812). — *B. starkei* (BRID.) B.S.G. var. *explanatum* (BRID.) MÖNKEMEYER, Laubm. Eur. 819 (1927). Lectotype: Sheet 3001/97 in the BRIDEL herbarium (B). The specimen in the upper left corner. Collected by BLANDOW in 1803 in Neubrandenburg. Coll. no. 25.

Hypnum rutabulum var. *flaccidum* BRIDEL, Spec. Musc. 2: 184 (1812). Lectotype: sheet 3001/4 in the BRIDEL herbarium (B). The specimen on the lower half of the sheet. Collected in 1797.

Brachythecium rutabulum var. *flavescens* (BRID.) BRUCH, SCHIMPER & GÜMBEL, Bryol. Eur. 6: 16 544 (1853) (fasc. 52—54 Mon. 12: 10). — *Hypnum rutabulum* var. *flavescens* BRIDEL, Bryol. Univ. 2: 488 (1827). — *Hypnum flavescens* BRIDEL, Spec. Musc. 2: 185 (1812) nom. illeg. — *Brachythecium rivulare* ssp. *flavescens* (BRID.) KINDB. Canad. Rec. Sc. 6(2): 73 (1894). Lectotype: sheet 3001/2 in the BRIDEL herbarium (B). The specimen in the upper left corner. Coll. no. 5.

Hypnum rutabulum var. *laxifolium* BRIDEL, Bryol. Univ. 2: 488 (1827). — *Brachythecium plumosum* (HEDW.) B.S.G. cf. LIMPRICHT, Laubm. Deutschl. 3: 87 (1896). Lectotype: sheet 3001/6 in the BRIDEL herbarium (B). Collected in 1825 by PYLAIE.

Brachythecium rutabulum var. *laxum* ROTH, Eur. Laubm. 2: 244 (1904).

Brachythecium rutabulum var. *longisetum* (BRID.) BRUCH, SCHIMPER & GÜMBEL, Bryol. Eur. 6: 16 544 (1853) (fasc. 52—54 Mon. 12: 10). — *Hypnum rutabulum* var. *longisetum* BRIDEL, Musc. Rec. 2(2): 161 (1801). Lectotype: sheet 3001/15 in the BRIDEL herbarium (B). The specimen in the upper right corner. Collected in 1798.

Brachythecium rutabulum var. *lutescens* WARNSTORF, Verh. Bot. Ver. Brandenburg 41: 73 (1899).

Brachythecium rutabulum var. *plumulosum* BRUCH, SCHIMPER & GÜMBEL, Bryol. Eur. 6: 16 544 (1853) (fasc. 52—54 Mon. 12: 10).

Brachythecium rutabulum var. *robustum* BRUCH, SCHIMPER & GÜMBEL, Bryol. Eur. 6: 16 544 (1853) (fasc. 52—54 Mon. 11: 10). — *B. robustum* (B.S.G.) LOESKE, Moosfl. Harz 273 (1903).

Hypnum uliginosum DEJEAN in BRIDEL, Bryol. Univ. 2: 487 (1827). nom. nud. Orig. coll.: sheet 3001/15 in the BRIDEL herbarium (B). The specimen in the lower left corner. Coll. no. 45. Collected by DEJEAN.

Robust plants with creeping stems and ± erect branches (Fig. 2 E), often growing in extensive green or yellowish mats. *Autoecious. Leaves* 1.8—3.0 mm, erect—spreading, more or less decurrent in a ± narrow band, slightly or strongly plicated, gradually narrowing to an acuminate point (Fig. 1 B). *Margin* denticulate, as a rule slightly recurved at base of leaf. *Nerve* reaching to about middle of leaf. *Cells* in middle of leaf 70 to more than 100 µ, towards the base near the nerve porose. *Angular cells* rectangular, ± well delimited and occasionally inflated. *Seta* as a rule 1.5—3 cm, rough throughout (Fig. 1 G). *Capsule* ± horizontal (Fig. 1 F). *Exothecial cells* in middle and upper part of capsule in rows, ± rectangular with longitudinal walls thicker than transverse walls (Fig. 1 D) at the base of capsule exothecial cells more irregular, not in rows and more incrassate (Fig. 1 E). *Stomata* large, 31—39×28—35 µ. *Inner peristome* with nodose and strongly papillose cilia (Fig. 1 A). *Lid* short and conical (Fig. 1 F). *Spores* papillose, about 17—21 µ.

VARIATION. The plants show considerable variation in size and colour. Sometimes the stems are ± ascending in a way characteristic of *Brachythecium rivulare*. When growing in wet habitats the angular cells are more clearly defined and longly and broadly decurrent. These forms are very similar to *B. rivulare*. The leaves are always acuminate but the degree of plication and the denticulation is variable. In small forms of the species the leaves are often without any plication, but there are also forms with strongly plicated leaves resembling *B. salebrosum* (WEB. & MOHR) B.S.G. (Table 3). The leaves are often denticulate along the whole margin, but the denticulation is sometimes restricted to the upper part of the leaves, and there are also forms with no denticulation at all, resembling *B. mildeanum* (SCHIMP.) SCHIMP. (Table 3). The length of the seta varies. Shape and length of lid also vary. These last two characters are considered to be of great importance for separating the genera in the family Brachytheciaceae.

EXCLUDED NAMES

Specimens of a number of varieties of *Brachythecium rutabulum* have been studied. The following varieties cannot be maintained as taxa and are regarded by the author as synonyms of *B. rutabulum*: var. *aureo-virens*, var. *brevisetum*, var. *crassum*, var. *dumetorum*, var. *eurhynchioides*, var. *explanatum*, var. *flaccidum*, var. *flavescens*, var. *laxifolium*, var. *laxum*, var. *longisetum*, var. *lutescens*, var. *plumosum* and var. *robustum* (cf. list of synonyms).

B. rivulare var. *cuspidatum* is also regarded as a synonym of *B. rutabulum*. The longly pointed leaves clearly show that it is a form of *B. rutabulum*. This statement is also supported by the fact that the specimens are autoecious.

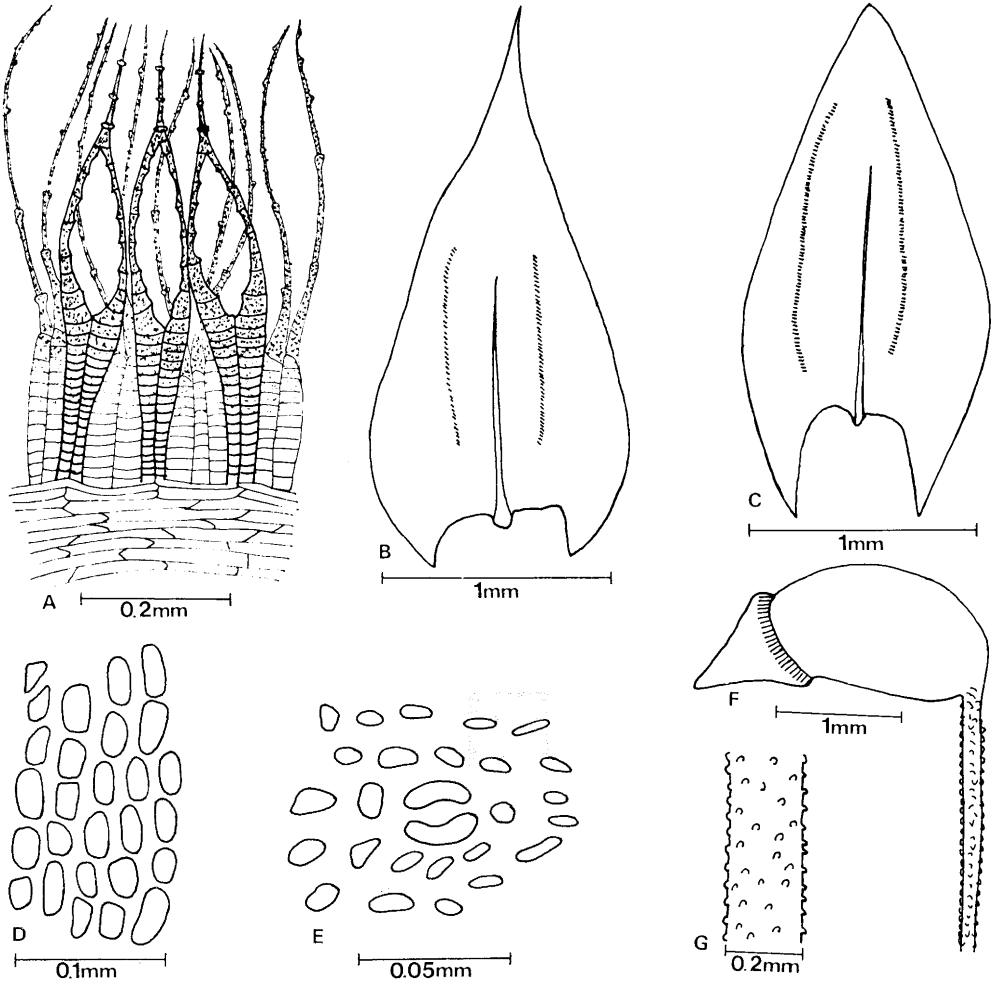

Fig. 1. A, B, D—G: *Brachythecium rutabulum*. — C: *B. rivulare*. — A: Inner peristome. — B, C: Leaves. — D: Exothecial cells from the middle of the capsule. — E: Exothecial cells from the base of the capsule. — F: Sporophyte. — G: Part of seta.

B. rutabulum var. *cavifolium* LINDB. belongs to the *B. turgidum* complex as has been pointed out by ARNELL & MÅRTENSSON (1959).

The specimens of *B. rutabulum* var. *rivulare* LANGE belong to *B. rivulare* (cf. list of synonyms under this species).

Material of *B. rutabulum* var. *viviparum* BRYHN from the type locality has been studied. According to the author this taxon does not belong to the genus *Brachythecium* but to the genus *Drepanocladus* in the family Amblystegiaceae. The differences between this taxon and *B. rutabulum* can be summarized as follows: it grows submerged (not common in *B. rutabulum*), it seems to be dioecious, the angular cells are inflated and almost reaching the nerve

Table 1. Varieties of *Brachythecium rutabulum* regarded as synonyms of *B. rutabulum* s. str. The characters listed are those diverging from the taxonomic type of *B. rutabulum*. — Characters modificative +, non-modificative —.

Taxon	Characters	
var. *aureo-virens*	± yellowish	+
	abundant rhizoids	+
	abundantly branched	+
	seta long	+
var. *brevisetum*	internodes short	+
	seta short	+
var. *crassum*	leaves long	+
	leaves strongly plicate	+
var. *dumetorum*	few branches	+
	branches elongated	+
	internodes long	+
	leaves longly decurrent	+
var. *eurhynchioides*	lid long, oblique	+
var. *explanatum*	leaves ± arranged in 2 rows	?
var. *flaccidum*	± yellowish	+
	branches elongated	+
	abundantly branched	+
var. *flavescens*	stem elongated	+
	± yellowish	+
	robust	+
var. *laxifolium*	internodes long	+
	seta long	+
	seta ± smooth	—
var. *laxum*	branches elongated	+
	internodes long	+
	lid ± long	+
var. *longisetum*	seta long	+
	stem elongated	+
var. *lutescens*	slightly plicate	+
	± yellowish	+
	nerve thin	+
var. *plumulosum*	small	+
var. *robustum*	dark green—green	+
	robust	+
	internodes short	+

(inflated angular cells are uncommon in the autoecious species *B. rutabulum*), in habit it agrees much more with species in the genus *Drepanocladus* than with species of *Brachythecium*, leaves not denticulate (this is uncommon in *B. rutabulum*), leaves not plicate (in most cases the leaves in *B. rutabulum* are more or less plicate). The author regards *B. rutabulum* var. *viviparum* as being conspecific with *Drepanocladus pseudostramineus* (C. MÜLL.) ROTH. Characters supporting this statement are: probably dioecious, leaves not plicate or denticulate, angular cells inflated, almost reaching the nerve, leaves rather shortly pointed with a recurved point, nerve rather thin.

In Table 1 taxa regarded by the author as synonyms of *Brachythecium rutabulum* s. str. are listed. The most important characters diverging from the taxonomic type specimen of *B. rutabulum* are shown in

the table. The diverging characters are denoted modificative (+), not modificative (—), and (?) (WIGH 1976).

DISTRIBUTION IN SCANDINAVIA

B. rutabulum is common in Denmark and in the southern and central parts of Sweden. It is also reported from a few localities in the northernmost parts of the country, where reports have been controlled they have proved to be incorrect, *B. rutabulum* having been confused with *B. rivulare* or species in the *B. salebrosum* complex. In a broad sense this complex can be said to comprise the following taxa: *B. salebrosum* (WEB. & MOHR) B.S.G., *B. turgidum* (HARTM.) KINDB., *B. groenlandicum* (C. JENS.) SCHLJAK and *B. mildeanum* (SCHIMP.) SCHIMP. var. *udum* (HAG.) MÖNK.

In Norway *B. rutabulum* is a common coastal species to about the province of Sör-Tröndelag. It is rather uncommon inland and does not occur in the high mountains.

In the southernmost parts of Finland it is common, rapidly decreasing in frequency towards the north.

As in Sweden *B. rutabulum* has been reported from the northern parts of Norway and Finland. Along the coast of Norway it is found in the far north, but in Finland it is uncommon in the north and in the northernmost parts of the country probably absent. Reports of *B. rutabulum* from these districts are erroneous, due to confusion with the above-mentioned species.

HABITATS

B. rutabulum grows on different kinds of substrata, for example calcareous and siliceous stones, bare soil, logs, etc. It is an apophytic species and often grows along roads, in ditches, in gardens, etc.

In ditches it sometimes grows together with *B. mildeanum* and on logs together with *B. salebrosum*. Occasionally in wet habitats it can grow together with *B. rivulare*.

Brachythecium rivulare B.S.G.

BRUCH, SCHIMPER & GÜMBEL, Bryol. Eur. 6: 17 546 (1853) (fasc. 52—54 Mon. 13: 12). Type material not seen.

Brachythecium rivulare var. *cataractarum* SAUTER, Fl. Herzogth. Salzburg 3: 60 (1870).

Brachythecium rivulare var. *gracile* JENSEN, Danm. Moss. 2: 141 (1923). Lectotype: (C). Collected by C. JENSEN in Denmark, Juteland, Norring Uhre in 1894.

Brachythecium rivulare var. *nitidum* SAUTER, Fl. Herzogth. Salzburg 3: 60 (1870).

Brachythecium rivulare var. *umbrosum* LIMPRICHT, Laubm. Deutschl. 3: 130 (1896).

Brachythecium rutabulum var. *rivulare* (B.S.G.) LANGE, Bot. Tidsskr. 3: 30 (1869).

Robust plants with creeping stem and ascending secondary stems which are more or less branched (Figs. 2 B, F). *Dioecious. Leaves* 1.6—2.3 mm, erect—spreading, longly and broadly decurrent, usually plicate, with an acute point (Fig. 1 C). *Margin* ± recurved at the base of the leaf, ± denticulate. *Nerve* reaching beyond the middle of the leaf. *Cells* in the middle of the leaf 70 to more than 100 µ, towards the base near the nerve porose. *Angular cells* rectangular, large, well-delimited, ± inflated. *Sporophyte* similar to that of *B. rutabulum*.

VARIATION. The most obvious variation is in habit. There are sometimes no secondary stems, but the stem is regularly branched (Figs. 2 A, C). When growing submerged in streams it has an elongated stem with secondary stems, differentiated or not, and without leaves at the base of the main stem (Fig. 2 D). The degree of plication and denticulation varies as in *B. rutabulum*. The size of the plants ranges from a few cm to more than 20 cm.

Some varieties of *B. rivulare* have been investigated. The following are regarded as synonyms of *B. rivulare* s. str.: var. *cataractarum*, var. *gracile*, var. *nitidum* and var. *umbrosum* (cf. list of synonyms).

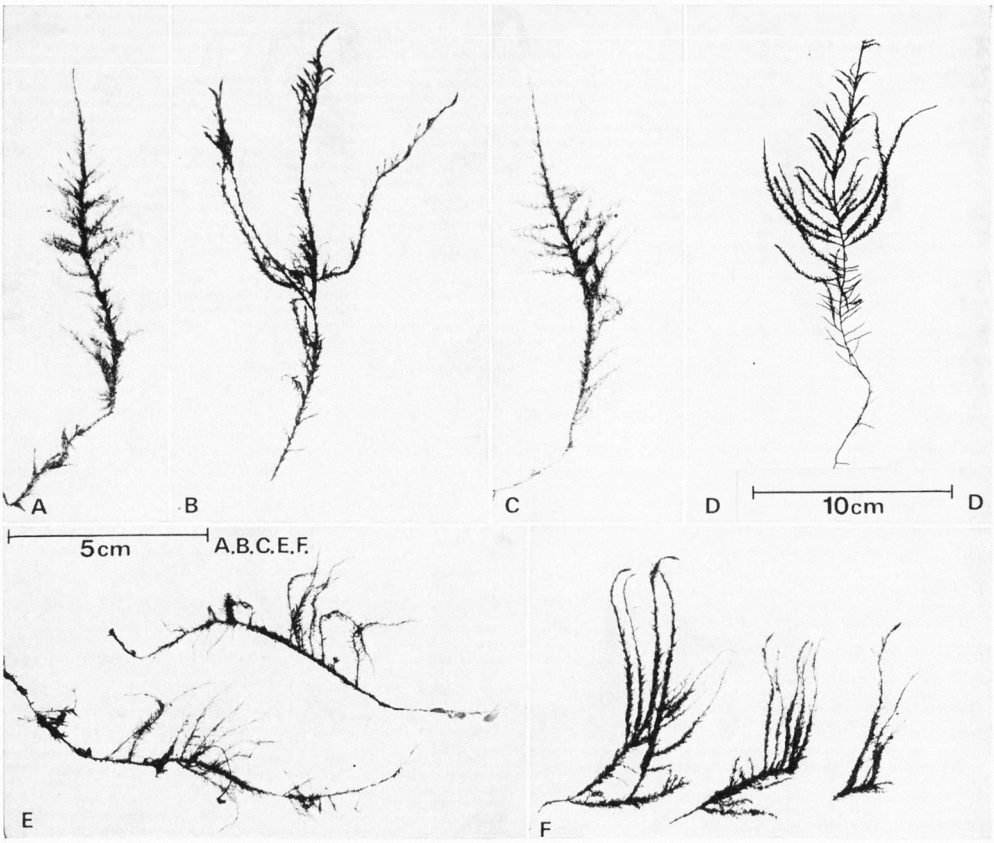

Fig. 2. A—D, F: *Brachythecium rivulare*. — E: *B. rutabulum*. — A, C: Regularly branched, secondary stems not differentiated. — B: Secondary stems differentiated. — D: Regularly branched, secondary stems poorly differentiated. Without leaves at the base of the primary stem. — E: Creeping stem with ± erect branches. — F: Creeping primary stem and erect secondary stems.

As has already been pointed out under *B. rutabulum*, *B. rivulare* var. *cuspidatum* is a synonym of *B. rutabulum*.

B. rivulare var. *longifolium* does not belong to the *B. rutabulum—B. rivulare* complex but to the *B. salebrosum* complex, which has already been pointed out by WARNSTORF (1906) who treated it as a form of *B. mildeanum* (SCHIMP.) SCHIMP. This form will be discussed in a forthcoming paper.

Brachythecium rivulare can easily be confused with *B. rutabulum*.

B. rivulare has also often been confused with *Rhynchostegium riparioides* (HEDW.) CARD. This confusion is probably largely of ecological origin as the two species often grow together in streams. They are not morphologically alike and *B. rivulare* is readily distinguished from *R. riparioides* on the inflated, longly and broadly decurrent angular cells. Another distinguishing character is the shape of the leaves. In the latter species they are ± rounded and in the former somewhat elongated. *R. riparioides* is an autoecious species often producing sporophytes, in contrast with *B. rivulare* which is dioecious and rarely

Table 2. Differences between *Brachythecium rutabulum* and *B. rivulare*.

Characters	*B. rutabulum*	*B. rivulare*	Characters modificative (+) or not (—)
Leaves	± longly pointed, Fig. 1 B.	± acute, Fig. 1 C.	—
Angular cells	rectangular, rather small, usually not well delimited or inflated	rectangular, large, ± inflated, always well delimited	+
Decurrent part of leaf	as a rule narrow and not longly decurrent	broadly and longly decurrent	+
Length of nerve	to middle of leaf	somewhat beyond middle of leaf	+
Sex condition	autoecious	dioecious	
Sporophytes	common	rare	
Habitats	often in dry habitats, but also in wet	always in wet habitats	
Type of branching	as a rule strongly branched	often poorly branched	+
Secondary stems	not often differentiated	often differentiated	+
Rhizoid bundles	often produced	not often produced	+
Chromosome number	n=12, Figs. 3, 4	n=6, Fig. 3.	
Number of large heteropycnotic bodies	2, Fig. 5	1, Fig. 5	

produces sporophytes. The seta is smooth in the former and rough in the latter.

DISTRIBUTION IN SCANDINAVIA

B. rivulare is widely distributed in the whole of Scandinavia but it is not common except in a few districts, e.g. the west coast of Norway.

HABITATS

B. rivulare always grows in wet habitats, often on stones in or beside streams. It often grows together with *Rhynchostegium riparioides* and *B. plumosum*.

Differences Between B. rutabulum and B. rivulare

The differences between the two species are given in Table 2. The most useful characters are the shape of the leaves, the angular cells and the decurrent part of the leaf. The first character is not modifiable whereas the development of the angular cells and the decurrent part of the leaves in *B. rutabulum* are characters highly dependent of humidity (WIGH 1976). The type of branching can sometimes be of diagnostic value (Fig. 2), but in some forms of *B. rutabulum* the habit is that otherwise characteristic of *B. rivulare*, just as there are forms of *B. rivulare* which have the type of branching characteristic of *B. rutabulum*.

In *B. rivulare* sporophytes if present are few, whereas *B. rutabulum* often produces abundant sporophytes. A character also of some diagnostic value is the number of rhizoids produced by the plant. *B. rutabulum* often produces bundles of rhizoids, in contrast to *B. rivulare*. This very modifiable character is dependent on humidity, light intensity and whether the shoot has grown in contact with the substratum (WIGH 1976).

If the above-mentioned characters cannot be used for diagnosis it is sometimes necessary to determine whether the plant is autoecious or dioecious. Some authors hold that *B. rivulare* can be both autoecious and

Table 3. Differences between *Brachythecium rutabulum* and other species in the genus.

Characters	Characters in *B. rutabulum*	Characters in the other species
		B. salebrosum
Seta	rough throughout	smooth
Plication	as a rule not strongly plicated, plications ± restricted to middle of leaf	strongly and regularly plicate with plications beginning from the base of the leaf
Apex of leaf	acuminate	more longly pointed
Chromosome number	n=12	n=13
		B. mildeanum
Denticulation	usually ± denticulate	not denticulate
Angular cells	mostly ± well developed	not well developed
Shape of leaf	rounded—ovate	regularly triangular
Seta	rough throughout	± smooth
Plication	± plicate	often without plication
Chromosome number	n=12	n=13
		B. curtum
Leaf	concave, exceptionally plane	plane
Nerve of branch leaf	not ending in a spine-like projection	often ending in a spine-like projection at back of leaf
Branch leaf	denticulate	dentate
Size of plant	robust—medium	medium—small
End of branches	without bundles of rhizoids	often with bundles of rhizoids
Habitat	usually not in pine forests	often in pine forests
Seta	rough throughout	often partly less papillose
Cilia of inner peristome	nodose	appendiculate
Capsule	often more than 2 mm	usually smaller
Chromosome number	n=12	n=22
		B. plumosum
Seta	rough	± smooth
Length of cells in middle of leaf	70—100 μ	often shorter than 70 μ
Leaf	erect—spreading	often secund
Nerve of branch leaf	not ending in a spine-like projection	often ending in a spine-like projection
Angular cells	rectangular, not incrassate, ± well developed	incrassate, not well developed, rectangular or quadrate
Habitat	usually not submerged in streams	often submerged in streams
Chromosome number	n=12	n=10

dioecious, but autoecious plants have not been observed by the author.

The leaves are longer in *B. rutabulum* and the relative length of the nerves longer in *B. rivulare* (WIGH 1976).

Differences Between B. rutabulum and Some Other Brachythecium Species

Brachythecium rutabulum has often been confused with other species in the genus, e.g. *B. salebrosum* (WEB. & MOHR) B.S.G., *B. mildeanum* (SCHIMP.) SCHIMP., *B. curtum* (LINDB.) LIMPR. and *B. plumosum* (HEDW.) B.S.G. The differences between *B. rutabulum* and these species are given in Table 3.

The most obvious difference between *B. rutabulum* and *B. salebrosum* is the seta. Where no sporophytes are available the plication of the leaves is a useful diagnostic character.

B. mildeanum and *B. rutabulum* sometimes grow together on clayey soil in ditches etc. These two species are similar in habit, but under the microscope there is usually no difficulty in separating the two species. The denticulation and the shape of the leaves are the two most useful distinguishing characters.

Apart from *B. rivulare*, *B. curtum* can sometimes be the most difficult species to distinguish from *B. rutabulum*, small forms of which have often been confused with *B. curtum*. These forms often have more or less plane leaves so that this character is of less value. In such cases all the other characters listed must be taken into consideration. The best distinguishing characters are the end of the nerve in the branch-leaves and the presence or absence of rhizoid bundles at the tip of the branches. Too much reliance must, however, not be placed on the latter character.

B. plumosum has also often been confused with *B. rutabulum* but it is generally easy to distinguish between the two species. As a rule it is sufficient to note whether the leaves are secund or not, but in some forms of *B. plumosum* the leaves are more or less erect and in such cases the other distinguishing characters must be used.

CYTOLOGY OF BRACHYTHECIUM RUTABULUM

Chromosome Complement

In all the gatherings studied the chromosome number was found to be identical, viz. n=12 which is remarkable since several other chromosome numbers have been reported for this species (Fig. 6).

In a few gatherings one of the chromosomes has a negatively heteropycnotic end segment (Fig. 3 E, H). This segment appears to vary in size in different populations and even within a population. In a few cases it is quite conspicuous, whereas in others it is very small and in most populations no end segment is observed at all. This indicates that the size is partly due to the degree of contraction caused by the pretreatment. The same phenomenon has been observed by the author in *Mnium undulatum* HEDW. (WIGH 1972 b).

Several hundreds of metaphases have been studied, but in none have the centromeres in all the chromosomes been observed in one single metaphase plate. This makes it difficult to construct an idiogram for the species.

It was sometimes observed that the chromosomes were built up of lightly and darkly staining blocks (Figs. 3 A—C, E, G, I, 4 A, B). The lightly staining segments are presumed to be built up of heterochromatin and are the possible sites of kinetic activity, perhaps in the same way as reported by VAARAMA (1954) for *Pleurozium schreberi*.

If different populations are compared as to the distribution of eu- and heterochromatic segments in the chromosomes, it is sometimes possible to find the same pattern of eu- and heterochromatic blocks in the presumably corresponding chromosomes from different populations. In other cases, however, the chromatic patterns were observed to differ. Such comparisons are rendered difficult as in no cases do all the chromosomes of a metaphase plate show this differentiation. This may, of course, be due to the fact that some chromosomes are wholly built up of euchromatin or almost so. Such a chromosome is observed to be darkly staining in its whole length. Thus it cannot yet be proved whether corresponding chromosomes always have identical chromatic patterns, but this investigation indicates the possibility that chromosomes often have the same chromatic pattern, but in other cases they may have different patterns, possibly due to structural changes such as translocations or inversions.

Heteropycnosis

In the resting nuclei of this species the number of positively heteropycnotic bodies

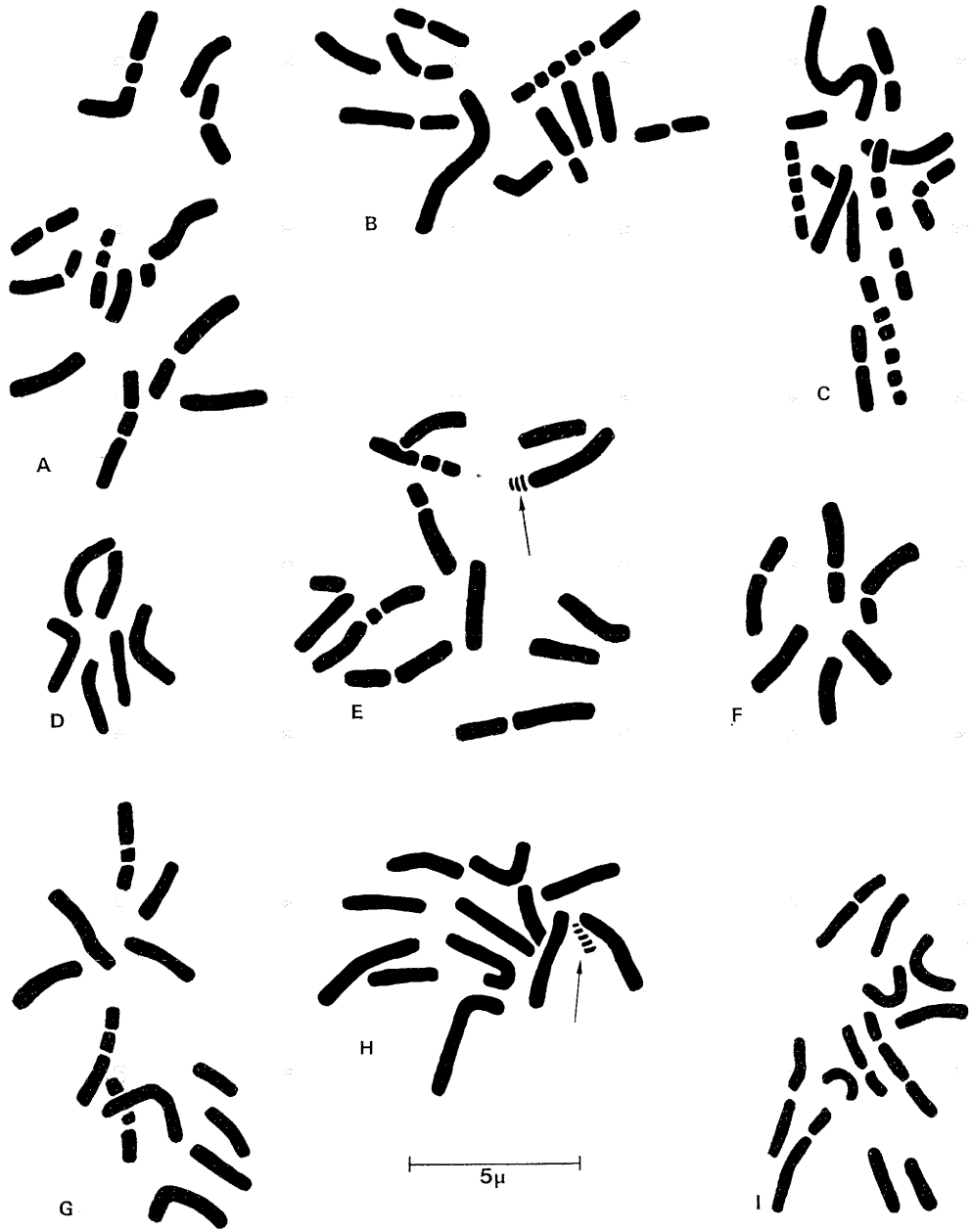

Fig. 3. Mitotic chromosomes. — A—C, E, G—I: *B. rutabulum* (n=12). — D, F: *B. rivulare* (n=6). — A: 72-528 (cf. Fig. 5 B). — B: 71-505. — C: 71-509. — D: 71-171. — E: 72-285. — F: 71-371. — G: 71-665 (cf. Fig. 5 A). — H: 71-491. — I: 71-441. — The arrows show negatively heteropycnotic end segment.

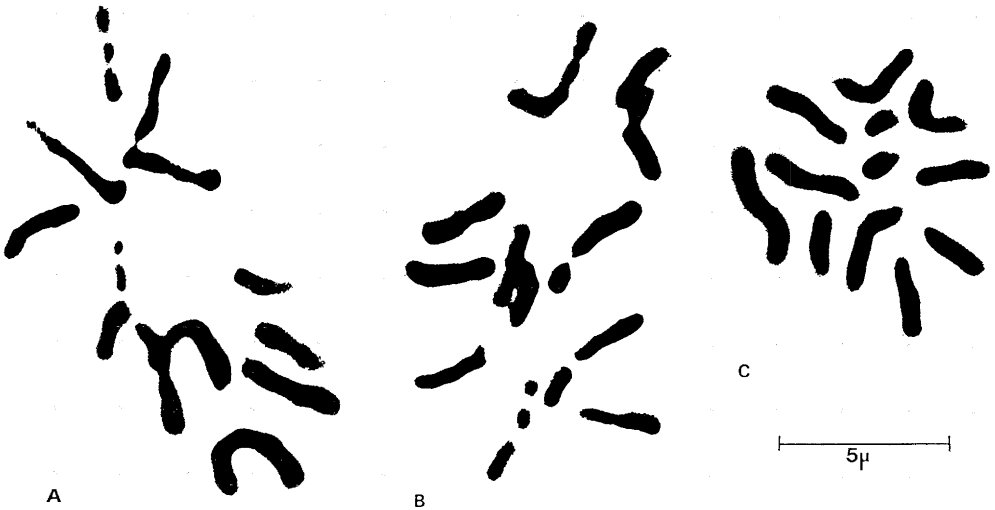

Fig. 4. Photomicrographs of mitotic chromosomes of *Brachythecium rutabulum*. — A: 71-665 (cf. Fig. 3 G). — B: 72-528 (cf. Fig. 3 A). — C: 72-481.

varies. Each nucleus contains one or two large bodies and a varying number of small bodies (Fig. 5 A—C). As a rule there are two large bodies but these sometimes fuse (Fig. 5 C), so that there appears to be only one. All stages in this fusion can be studied. These large heteropycnotic bodies are often designated H by Japanese cytologists. H stands for a large heteropycnotic body and h for the small ones. In the *Brachythecium rutabulum—B. rivulare* complex one large body denotes that the species is haploid and two large bodies that it is diploid. Moreover one body occurs in dioecious species and two in autoecious species.

The differences between heteropycnotic bodies in *B. rutabulum* and *B. rivulare* is discussed on p. 491.

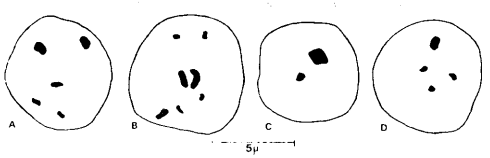

Fig. 5. Heteropycnotic bodies in resting nuclei. — A—C: *Brachythecium rutabulum*. — D: *B. rivulare*. — A: Two large bodies and three small ones. — B: The two larger bodies just before fusion, together with five small bodies. — C: The two large bodies have fused. One additional small body. — D: One large body and three small ones.

Chromosome Numbers Previously Published

n= 5 HOLMEN (1958) Denmark.

n= 6 VISOTSKA (1967) and LAZARENKO et al. (1971) the Ukrainian SSR (as *B. eurhynchioides*). — LAZARENKO et al. (1971) the Latvian SSR and the Estonian SSR, 2 populations.

n=10 MOUTSCHEN (1955) Belgium. — HOLMEN (1958) Denmark.

n=11 SINOIR (1952) probably France. — CHOPRA & KUMAR (1967) India. — BRYAN (1973) Austria.

n=12 WILSON & BURNETT (1961) Scotland. — SMITH & NEWTON (1967) the British Isles, 29 populations. — VISOTSKA (1967) and LAZARENKO et al. (1971) Ukrainian SSR, 4 populations (one population as *B. eurhynchioides*). — RAMSAY (1969) the British Isles. — VYSOTSKAYA & FETISOVA (1969) and LAZARENKO et al. (1971) the Latvian

SSR. — VYSOTSKAYA (1970) and LAZARENKO et al. (1971) the Georgian SSR. — WIGH & STRANDHEDE (1971) Denmark and Sweden, 9 populations (two of the populations as *B. rivulare*). — LAZARENKO et al. (1971) the Estonian SSR.

n=13 VISOTSKA (1967) and LAZARENKO et al. (1971) the Ukrainian SSR, 2 populations.

n=20 RAMSAY (1969) the British Isles, 2 populations.

n=22 LAZARENKO et al. (1971) the Byelorussian SSR, 2 populations.

Some of the above-mentioned populations have been studied by the author. The gathering studied by SMITH & NEWTON (1967) and RAMSAY (1969) with the chromosome number n=12 are all typical *B. rutabulum*. The two gatherings with the chromosome number n=20 reported by RAMSAY (1969) diverge somewhat from the nomenclatural type of the species, particularly in the small size of the plants and leaves. In the most important characters the two populations agree with *B. rutabulum*. As only limited material of this cytotype has been available it cannot be stated with certainty whether it belongs to another taxon in the *B. rutabulum* — *B. rivulare* complex until further material of the cytotype has been found. Until then the two gatherings must be treated as a form of *B. rutabulum*. This cytotype has not been observed elsewhere and it is with all certainty uncommon, at least in Scandinavia.

The Latvian and Estonian gatherings with the chromosome number n=6 proved to be a mixture of *B. rutabulum* and *B. rivulare* so that it seems likely that the chromosome numbers refer to *B. rivulare*. The population with n=6 published under the name of *B. eurhynchioides* has not been available for study.

Two of the Ukrainian populations with n=12 have been studied and they are both typical *B. rutabulum* as are the populations from the Latvian SSR, the Georgian SSR and the Estonian SSR.

One population of *B. rutabulum* with n=13 has also been studied and is in all characters wholly in accordance with the nomenclatural type of the species.

As the other non-Scandinavian populations that have been cytologically studied have not been available to the author, it is not possible to comment on the chromosome numbers. It is evident that the dominating cytotype in *B. rutabulum* has the chromosome number n=12. Chromosome races probably exist in this species, p. 492, but it seems most likely that some of the chromosome counts are incorrect and that some populations have been erroneously determined or that the chromosome numbers refer to mixed gatherings.

There can sometimes be difficulties in spreading and staining which may explain erroneous counts. This may also be due to the bivalents sticking together or to meiotic irregularities, p. 489.

Two European species of *Brachythecium*, *B. salebrosum* and *B. mildeanum* have the chromosome number n=13. As forms of these species can sometimes be difficult to distinguish from *B. rutabulum*, p. 484 this may perhaps explain the chromosome count n=13 reported for *B. rutabulum*. The chromosome count n=22 may have arisen from confusion with *B. curtum* as small forms of *B. rutabulum* can be difficult to distinguish from that species, p. 485.

The chromosome numbers reported for *B. rutabulum* are given in Fig. 6.

Chromosome Numbers in Scandinavian Populations

In Scandinavian populations of *B. rutabulum* three chromosome numbers have been reported, viz. n=5, 10 and 12. The first numbers have been published by HOLMEN (1958) in two Danish populations with the reference numbers 636 and 702 respectively, the latter referring to an autoecious population and the number 636

to a probably dioecious one. The population with n=10 (no. 702) has larger leaves, longer leaf cells and larger spores, 13 μ instead of 10 μ as found in the other gathering (no. 636). The seta is also longer and the capsule smaller in no. 702. According to HOLMEN population 702 is morphologically closely related to *B. curtum*.

The small size of the capsule indicates such a relationship (Table 3) but this is contradicted by the chromosome number. All populations of *B. curtum* that have been studied cytologically by the author have the chromosome number n=22.

No dioecious form of *B. rutabulum* has been observed by the author. In the probably dioecious population, no. 636, the leaves are smaller indicating that it may be a form of *B. rivulare*. This is, however, contradicted by the size of the spores which is only 10 μ.

As these two populations have not been available to the author it is difficult to discuss the morphology in any detail. In Scandinavia some dioecious species of *Brachythecium* are known but none with n=5 has been found by the author. The lowest numbers known are n=6 in *B. rivulare* and n=7 in some species of the *B. albicans* complex (WIGH 1974). This complex is, however, morphologically very divergent from the *B. rutabulum* — *B. rivulare* complex and can thus be excluded from the discussion.

The chromosome numbers in these two populations are thus problematic. The cytological methods used (the sporophytes were embedded in paraffin and cut on a microtome) can perhaps cause the loss of one or more chromosomes so that the chromosome number would be higher than reported. Of course there is a possibility that cytotypes of *B. rutabulum* exist in Scandinavia with n=5 and n=10. It seems, however, more likely that the chromosome numbers are due to erroneous counts, p. 492.

WIGH & STRANDHEDE (1971) reported the chromosome number n=12 in two Scandinavian populations of *B. rivulare*. These reports, however, refer to *B. rutabulum*. The taxonomic determinations were based on the rather well-delimited angular cells, a character that must not be overemphasized. The leaves of two populations are longly pointed in a manner wholly characteristic of *B. rutabulum* and the two populations are autoecious which also supports this latter determination. The other 7 populations studied by the authors are typical *B. rutabulum*.

Meiotic chromosomes in Scandinavian populations of *B. rutabulum* have been studied by VAARAMA (unpubl.) who observed 12 bivalents in a Finnish population.

Meiotic Irregularities

Several meiotic irregularities have been observed in particular in the n=12 cytotype of *B. rutabulum*. RAMSAY (1969) reported for example non-synchronous separations of bivalents, laggards at telophase I and II, micronuclei and irregular spore tetrads. SMITH & NEWTON (1967) reported irregularities such as failure of pairing, bridges, fragments, lagging bivalents or semi-bivalents. LAZARENKO et al. (1971) observed 12 and 13 bivalents in one single sporophyte. In mitotic divisions in the capsule they observed 24 and 26 chromosome bodies, each body consisting of two chromosomes, the chromosome number thus being 2n=48 or 52. Unfortunately they did not study the chromosomes in the gametophyte so that it is difficult to explain this mixoploidy. These irregularities, together with the sticky bivalents, can easily give rise to erroneous chromosome counts.

Origin

According to WILSON & BURNETT (1961) and other authors *B. rutabulum* is an autoploid species. SMITH & NEWTON (1967) did not agree with this as they found neither trivalents nor quadrivalents and as

no cytotype with n=6 is known it must at least be very uncommon. They thought that there would be selection against an autopolyploid species since it would imply the occurrence of tri- and quadrivalents which would give rise to unbalanced spores.

As so few cytological experiments have been carried out in mosses it is difficult to discuss autopolyploidy and allopolyploidy. Through experimental apospory it is possible to produce a polyploid series in mosses, for instance from n=6 to 12 etc. In a number of species it is fairly easy to obtain these polyploids, as the regenerative capacity is very high. It is thus possible to generate a gametophyte with the double chromosome number from a sporophyte, if the sporophyte is cultivated in a suitable nutritional medium.

In the classic work by MARCHAL (1912) a diploid form of *Amblystegium*, *A. serpens bivalens*, was produced through apospory. According to him the basic chromosome number in this species is n=12, and the *bivalens* form thus had n=24. The behaviour of the chromosomes was studied during meiosis. In no sporophyte was a regular pairing of the chromosomes observed. In every sporophyte there was a mixture of quadri-, bi- and univalents, resulting in unbalanced chromosome numbers in the spores. Such a diploid form would thus not be able to compete in nature with the haploid form of the species.

Brachythecium rutabulum may be an autopolyploid species, but if so, the formation of quadri- and trivalents has been suppressed in some way. The species may have originated through autopolyploidy a long time ago and the formation of quadri- and trivalents been suppressed by natural selection. It seems probable that diploid forms of mosses arise in nature through apospory but that these forms presumably have difficulty in establishing themselves if they cannot multiply vegetatively, and thus cannot become widespread if there is no mechanism to ensure more regular meiosis. Autopolyploid species can also arise through endomitosis.

It seems, however, more likely that *B. rutabulum* is an allopolyploid species that has evolved from cytotypes with n=6.

Euploidy and Aneuploidy

The polyploid series n=5, 10 and 20 in *B. rutabulum* has been much discussed. The cytotypes with n=5 and n=10 are discussed here on p. 488. The author cannot support this theory of the basic number n=5 in the species (Fig. 6).

As has been already mentioned some of the chromosome numbers reported in *B. rutabulum* are probably erroneous and others probably refer to other taxa, but this does not explain all the diverging chromosome numbers. Although chromosome races have not been observed by the author in the Scandinavian populations of *B. rutabulum* studied, their existence is supported by the interesting investigation carried out by MOUTSCHEN (1955). Through irradiation of the sporophytes a series of viable aneuploid mutants was obtained. The irradiation resulted in a number of fusions and the number of chromosomes was thus reduced. This investigation shows that *B. rutabulum* can survive radical chromosome mutations. Such changes may occur in nature and it seems likely that the chromosome number can be lower than n=12 as a result of translocations or fusions of whole or almost whole chromosomes.

Only one detailed investigation of the centromere conditions in mosses has been carried out. In a most important investigation VAARAMA (1954) studied the kinetic activity of one easily identifiable chromosome in *Pleurozium schreberi* (BRID.) MITT. This study shows that the particular chromosome has more than one site of active mobility.

As no other investigations of the centromere conditions in mosses have been carried out it is not possible to say if there

is the same type of centromeric activity in other moss chromosomes. In the family Brachytheciaceae accessory chromosomes are known in three genera comprising five species, viz. *Homalothecium lutescens* (HEDW.) ROBINS., *H. sericeum* (HEDW.) B.S.G., *Brachythecium glareosum* (SPRUCE) B.S.G., *B. velutinum* (HEDW.) B.S.G. and *Rhynchostegium megapolitanum* (WEB. & MOHR) B.S.G. (WIGH 1973 a, NYHOLM & WIGH 1973). The accessory chromosomes in all these species behave in the same way as the A-chromosomes. They undergo divisions quite normally and they are never eliminated in mitosis, which denotes kinetic activity.

Chromosome fragmentation or fusion has been observed by VAARAMA (1953) in *Orthotrichum tenellum* BRUCH. In one sporophyte a large bivalent with a subterminal constriction was observed. In another there was no such bivalent but instead there was an additional small bivalent presumed to have derived from the large bivalent. VAARAMA did not exclude the possibility of the large bivalent having arisen through the fusion of two smaller bivalents.

Available information points to the likelihood in certain mosses at least of one or more of the chromosomes having more than one centromere. Furthermore the chromosome number in a population of a species can apparently increase as the result of fragmentation and decrease through translocations or fusion of whole or almost whole chromosomes.

CYTOLOGY OF BRACHYTHECIUM RIVULARE

Chromosome Complement

Only one chromosome number, n=6 has been observed in this species (Fig. 3 D, F). Unlike *B. rutabulum* no chromosome with a negatively heteropycnotic end segment has been observed. This may be due to the fact that fewer gatherings of this species have been studied.

The centromeres are seldom observed in this species, but in one metaphase plate the centromeres in three chromosomes were seen (Fig. 3 F). These three chromosomes have submedian centromeres. All six chromosomes are of about equal size as observed by HOLMEN (1958).

Heteropycnosis

In this dioecious species only one large positively heteropycnotic body is present in the resting nuclei (Fig. 5 D). Apart from this body a varying number of smaller bodies can be observed.

Resting nuclei of *B. rutabulum* and *B. rivulare* can be readily distinguished. Only when the large heteropycnotic bodies in the former species have fused can it sometimes be problematic if only a few cells are available.

Chromosome Numbers Previously Published

n= 6 HOLMEN (1958) Denmark. — SMITH & NEWTON (1968) the British Isles. — VYSOTSKAYA & FETISOVA (1969) and LAZARENKO et al. (1971) the Latvian SSR and the Estonian SSR 3 populations. — WIGH & STRANDHEDE (1971) Denmark. — WIGH (1972 a) Spain, 2 populations.

n=11 INOUE (1967) Japan.

n=12 FETISOVA & VYSOTZKAYA (1970) and LAZARENKO et al. (1971) the Estonian SSR and the Latvian SSR, 2 populations. — The report by WIGH & STRANDHEDE (1971) is erroneous because of incorrect taxonomical determination. The two populations belong to *B. rutabulum*.

n=13 VISOTSKA (1967, 1970) and LAZARENKO et al. (1971) the Ukrainian SSR and Georgian SSR, 4 populations.

n=16 ANDERSON & BRYAN (1958) North Carolina, USA.

The population with n=6 investigated by SMITH & NEWTON (1968) has been studied by the author. It is a typical form of *B. rivulare*, as are the two Spanish populations studied by WIGH (1972 a).

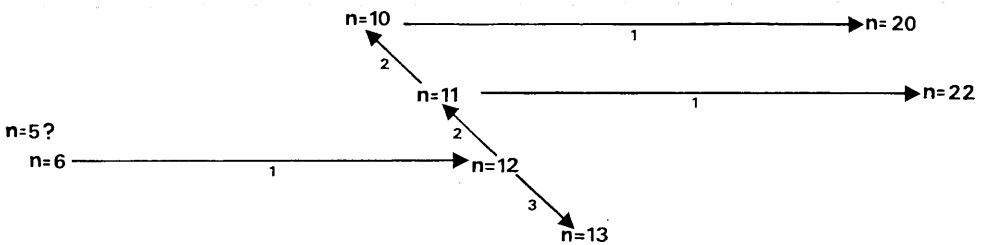

Fig. 6. Chromosome numbers published for *Brachythecium rutabulum*. — Arrow 1 indicates chromosome doubling. — Arrow 2 indicates reduction of chromosome number. — Arrow 3 indicates increase in chromosome number. — For explanation see text.

One of the Latvian populations with n=6 has been investigated and was found to belong to *B. rivulare*. The populations with the chromosome number n=12 from the Latvian SSR and the Estonian SSR both proved to be mixed gatherings of *B. rivulare* and *B. rutabulum* so that the chromosome number presumably refers to *B. rutabulum*.

One of the Ukrainian populations with n=13 has been available. It combines characters typical of both *B. rivulare* and *B. rutabulum*. In the habit, shape and length of leaves and length of nerves it agrees with *B. rivulare*, but in the poorly developed angular cells and the shortly decurrent leaves it resembles more closely *B. rutabulum*. Archegonia only have been found indicating that it may be a dioecious specimen which supports regarding it as a divergent form of *B. rivulare* until additional material is available.

Chromosome Numbers in Scandinavian Populations

Chromosome numbers in *B. rivulare* have been published by HOLMEN (1958) who reported n=6 in a Danish population and WIGH & STRANDHEDE (1971) who published n=6 in a Danish population and n=12 in two other populations. The taxonomic determinations of these last two populations are erroneous and the report refers to *B. rutabulum*.

The chromosome number n=6 has also been observed by ALMGREN (unpubl.) in a Swedish population of *B. rivulare*. In all characters this population is typical of *B. rivulare* as is the population studied by WIGH & STRANDHEDE (1971). It seems thus likely that there is only one cytotype of *B. rivulare* in Scandinavia or at least that the other cytotypes are uncommon.

A WORKING HYPOTHESIS FOR EXPLANATION OF CHROMOSOME NUMBERS IN B. RUTABULUM AND RIVULARE

In Figs. 6 and 7 the chromosome numbers reported in *B. rutabulum* and *B. rivulare* are given.

In *B. rutabulum* n=5 has been published by HOLMEN (1958). At first meiotic metaphase 5 large bivalents of about the same size are shown. In the same species LAZARENKO et al. (1971) reported n=6. At first meiotic metaphase they found 6 large bivalents about equal in size. If the n=5 cytotype has arisen through the fusion of two chromosomes in the n=6 cytotype, one of the chromosomes in the n=5 cytotype would be conspicuously larger than the others. As this is not the case the author presumes that the chromosome number n=5 is an erroneous count. It does not seem likely that it is due to misdetermination as no morphologically related species is known with the chromosome number n=5, p. 489.

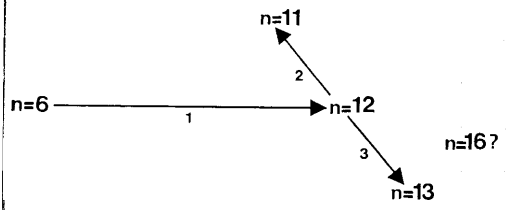

Fig. 7. Chromosome numbers published for *Brachythecium rivulare*. — Arrow 1 indicates chromosome doubling. — Arrow 2 indicates reduction in chromosome number. — Arrow 3 indicates increase in chromosome number. — For explanation see text.

It must be noted that two of the populations of *B. rutabulum* with n=6 published by LAZARENKO et al. (1971) are mixed populations, p. 492.

B. rutabulum probably originates from a cytotype with n=6. This hypothetical cytotype would probably be dioecious and the doubling of the chromosome number would have caused a change from the dioecious to the autoecious state. The n=12 cytotype dominates in this species and structural chromosome changes of this cytotype have given rise to the other cytotypes. Such changes can cause an increase in the chromosome number through fragmentation, if the fragments are centric and display no tendency to fuse with the other chromosomes. This would indicate that the n=13 cytotype could be karyologically heterogeneous and polyphyletic as it seems likely that fragmentation may arise several times and in different chromosomes.

Through translocation of whole or almost whole chromosomes the chromosome number could be lower than n=12. Such changes could comprise one or more chromosomes and also give rise to different karyotypes.

Chromosome doubling of the n=11 and n=10 cytotypes have given rise to the n=22 and n=20 cytotypes respectively.

These chromosome changes have evidently not given rise to any great morphological difference as the cytotypes are still identifiable as belonging to the species *B. rutabulum*. The cytotypes with chromosome numbers other than n=12 are probably not so widespread nor so common as the n=12 cytotype. This is so in Scandinavia at least.

In *B. rivulare* the basic number is n=6. The chromosome number n=12, 13 and 11 can be explained in the same way as in *B. rutabulum*. The chromosome number n=16, however, does not seem to fit into the pattern and its origin is difficult to explain. This chromosome number is uncommon in the genus *Brachytheicum* and exists in a few species only (WIGH 1974).

It must be stressed that this is merely a hypothesis and that perhaps some of the chromosome numbers reported are erroneous. The only cytotypes seen by the author, except for mixed populations with n=6, are n=12, n=13 and n=20 in *B. rutabulum* and n=6 and n=13 in *B. rivulare*.

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APPENDIX. Localities of Cytologically Studied Material

Brachythecium rutabulum

FINLAND. Nyland. Ingå, Fagervik (70—213, 70—215, 70—217, 70—218); Karjalohja, Pyöli (70—191, 70—192, 70—197); Lohja, Ahtiala (70—177, 70—178, 70—181, 70—184), Outamo (70—67); Tenala, Lindö (70—228). — Regio Aboënsis. Salo, Viitta (70—153); Särkisalo, Bastböle (70—85, 70—89), Förby (70—78, 70—163); Turku, Kaarina, Tuorla (70—110).

NORGE. Hordaland. Arna (70—329). — Rogaland. Bryne, Nordheim (71—186, 71—187, 71—188), Orre (71—181, 71—182, 71—184); Eigersund, Helleland (71—135, 71—137, 71—138); Gjestal, Dirdal (71—156); Hå, Ogna (71—147); Karmöy, Avaldsnes (70—427), Stokkastrand (70—416); Kleppe (71—151, 71—152, 71—153); Sandnes, Ålgård (71—164, 71—165); Sauda, 4 km S of Saudasjöen (70—378, 70—392); Stavanger, near the church (71—91), Rennesöy (71—105, 71—106, 71—107, 71—111). — Östfold. Fredrikstad, Veumengen (72—127); Onsöy, Hurröd (72—108, 72—110), Kjölberg (71—124, 72—136, 72—137), Krökeröy, Enhus (72—163, 72—164, 72—166, 72—167), Krökeröy, the quarry near Femdal (72—189), Kråkeröy, Holte (72—196, 72—197), Kråkeröy, Röd (72—44, 72—55, 72—56, 72—63, 72—64, 72—65, 72—142, 72—144, 72—146, 72—150), Kråkeröy, Tangen (72—169, 72—170, 72—171, 72—172), Torgauten (72—38, 72—39, 72—41), Trondalen (72—72, 72—74, 72—77, 72—78, 72—83), Åle (72—90, 72—91), Örebekk (72—119, 72—120, 72—121).

SVERIGE. Bohuslän. Backa, Fridhem (70—479, 70—481, 70—482, 71—3), leg. M. NEUENDORF (71—3); Björlanda, Högåsa (71—12); Kungälv, Stubbhult (71—59 leg. T. HALLINGBÄCK); Skepplanda, Skår (73—01 leg. T. HALLINGBÄCK); Säve, Lindesnäs (72—4, 72—12); Tanum, Knäm (70—374); Torsby, Lilla Överön (70—510); Uddevalla, Kristinedal (71—239, 71—240, 71—244, 71—245, 71—246, 71—247, 71—248, 71—249, 71—250), Kuröd (71—90); Ytterby, Ragnhildsholmen (71—10, 72—7, 72—8). — Dalsland. Ånimskog, Skållebyn (71—15 leg. D. NILSSON). — Gotland. Gotska Sandön, Gamla gården (71—720, 71—722 leg. S. SUNHEDE), Stora Idemoren (71—719 leg. S. SUNHEDE); Västerhejde, Fridhem (72—227 leg. B. PETTERSSON); Västkinde, Nors (71—622 leg. B. PETTERSSON). — Halland. Fjärås, Tjolöholm (71—507, 71—508, 71—509, 71—510); Släp, Särö (70—25), Särö, Västerskog (71—17 leg. D. NILSSON); Skogaby, Ebbarp (70—35, 70—36). — Närke. Gällersta, Attersta (72—576); Kumla (70—272); Vintrosa, Lannafors, limestone quarry (71—457, 71—458). — Skåne. Araslöv, Ullstorp, pond (71—513, 71—514, 71—521), Ullstorp, limestone quarry (71—500, 71—501, 71—502, 71—503, 71—504, 71—505); Bromölla, Edenryd (71—730); Brönnestad, Hovdala (73—20); Fjälkinge, Ivön, limestone quarry (71—489, 71—490, 71—491, 71—492), Näsum kaolin quarry (72—639, 72—641, 72—642). — Småland. Huskvarna, Ådalsfallen (71—27, 71—28 leg. T. HALLINGBÄCK); Lagan, near the river Lagan (73—24 leg. S. SUNHEDE); Visingsö, near the harbour (72—285). — Uppland. Bogesund (71—127); Danmark, Tjocksta (72—481); Gamla Uppsala (72—430); Huddunge (71—697 leg. G. EEN); Uppsala. Röbo, the brick-yard (72—445, 72—453); Vaksala, Skälby (72—469); Vattholma, Åsby (72—412); Vaxholm, Skägga (70—274); Värmdö (70—281). — Västergötland. Askim, St. Amundön (71—19 leg. D. NILSSON); Berg, Postgården (70—517, 70—518, 70—523); Bredsäter, Lugnås (70—249, 70—255, 70—262); Broddetorp, Hornborga (70—550, 70—557, 70—558); Göteborg, Botaniska trädgården (70—461, 70—610, 71—482), Långedrag (70—452), Tynnered (70—431, 70—432); Kinnekulle, Österplana (71—538), Råbäck (73—7, 73—8 leg. S. SUNHEDE); Landvetter (70—450); Lerdala, Karlsfors (70—532, 70—542, 70—545); Skövde, Ryd, Åsen (70—487); Våmb, near the church (72—607, 72—609); Timmersdala, Stora Stolan (72—593, 72—597, 72—601, 72—602); Tuve, Stora Holm (71—16 leg. L. ARVIDSSON). — Västmanland. Guldsmedshyttan, Mårdshyttan, the marble quarry (72—544, 72—550), Fanthyttan, the limestone quarry (71—441, 71—442, 71—445, 71—450); Ljusnarberg, Ställdalen, Östra Bom limestone quarry (71—415); Norberg, Klackberg (72—518, 72—523, 72—528, 72—529, 72—530, 72—531); Sala, Skå, limestone quarry (72—511). — Öland. Algutsrum, Gråborg (71—652, 71—653); Borgholm, slottsruinen (71—80, 71—81, 71—608, 71—609, 71—610, 71—611), between Borgholm and Köping (71—563, 71—564, 71—565, 71—566, 71—567, 71—568, 71—570, 71—571, 71—572, 71—573, 71—574); Degerhamn, Albrunna (71—75, 71—77, 71—82 leg. T. HALLINGBÄCK); Högsrum, Halltorp (71—646, 71—647); Knisa, Knisa mosse (71—79 leg. T. HALLINGBÄCK); Köping, 1 km SW of Dalby (71—585, 71—589, 71—590, 71—591); Stenåsa, Frösslunda (71—626, 71—627, 71—628, 71—629, 71—631, 71—632); Torslunda, Arontorp

(71—685, 71—686), Eriksöre (71—664, 71—665, 71—666, 71—667, 71—668). — Östergötland. Borensberg, brick-yard (72—228, 72—229); Godegård, Blommedal (72—238); Krokek, marble quarry (72—255, 72—256, 72—260, 72—264, 72—265, 72—275, 72—280, 72—292); Ringarum, Sätterbo (72—324, 72—326, 72—327); Törnevalla, limestone quarry (72—244, 72—245); Vånga, Glan limestone quarry (72—304).

Brachythecium rivulare

FINLAND. Nyland. Ingå, Fagervik (70—211, 70—212).

NORGE. Akershus. Asker, Groset (72—201, 72—204), Sem (71—127); Baerum, Skui (70—309, 70—313). — Aust-Agder. Tvedestrand, Tveite (70—349). — Hordaland. Arna, Herland (70—316, 70—321, 70—324). — Rogaland. Frafjord, Brålandsforsen (71—169, 71—171); Hå, Ogna (71—146); Sandnes, Trodal (71—166); Stavanger, Rennesöy (71—109, 71—110). — Telemark. Bamle, Feset (70—354, 70—361). — Vest-Agder. Flekkefjord, Ystabö (71—142).

SVERIGE. Bohuslän. Säve, Lindesnäs (72—11); Uddevalla, Kristinedal (71—237, 71—243). — Jämtland. Åre, Åreskutan (71—367, 71—368, 71—370, 71—371, 71—372). — Skåne. Brönnestad, Hovdala (73—17, 73—18); Dalby, Fågelsångsdalen (71—72 leg. T. HALLINGBÄCK). — Västergötland. Berg, Postgården (70—521, 70—522); Broddetorp, Hornborga (70—560); Falköping, Karleby, Djupadalsbäcken (70—573, 70—579, 70—580); Lerdala, Karlsfors (70—543); Skövde, Ryd, Skåningstorp (70—569), Ryd, Åsen (70—488, 70—489). — Östergötland. Vånga, Glan, limestone quarry (72—299).

Nomenclatural Notes on Arctic Plants

Áskell Löve and Doris Löve

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Nine genera, three species and two subspecies of arctic plants are described as new, one new name is validated, and a change in rank of 49 taxa and new combinations of 124 taxa are validated.

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In connection with the compilation of a cytotaxonomical atlas and checklist of the arctic flora (LÖVE & LÖVE 1975 a), we made efforts to arrive at a uniform classification for as many as possible of the 404 genera, 1629 species and 270 additional subspecies of higher plants which are known to occur within the tundra of the circumpolar northlands. As a norm for the classification, we followed the Linnaean species concept as adopted by Scandinavian and Russian botanists working with these plants and strengthened by the biological or cytogenetical approach. According to this paradigm, the family in its traditional sense is defined as a collection of genera that are likely to have evolved from a common ancestor as far as indicated by morphological and cytological characteristics. The natural genera should show morphological and cytological evidence of linear, and therefore strictly monophyletic, evolution of their species from a single prototype. They must also have certain crossability barriers towards other such groups, although that biological requirement sometimes needs to be relaxed because of taxonomical expediency for very large genera (LÖVE & LÖVE 1974). A good biological species is reproductively isolated from other such taxa, but it is identified by aid of morphological and geographical distinctions. However, within the species miscibility is not only allowed but directly required, irrespective of the magnitude of the morphological distinction of various races. Therefore, sexual subspecies and varieties are defined as interfertile major or minor geographical races that are capable of mixing freely whenever they meet. Since these concepts are at least very close to those followed by the majority of botanists working with arctic plants, only a limited number of adjustments were found to be needed to attain a reasonable closeness to the uniformity endeavoured. They are mainly caused by redefinition of a few generic limits.

In order to save space when validating new names for the arctic taxa for which this is justified, short descriptions are given for the new taxon, or a citation only to the name-giving basionym, except when the rank-deciding combination needs to be added for clarification. Synonyms are neglected unless necessary for identification, and other information is included sparingly for particular cases.

Gymnocarpium disjunctum (RUPRECHT) LÖVE & LÖVE, comb. nov., based on *Polypodium Dryopteris* L. var. *disjunctum* RUPRECHT, in Beitr. Pflanzenk. Russ. Reiches 3 (1845), p. 52; *Dryopteris disjuncta* (RUPR.) C. V. MORTON, p. p.

This is a Pacific species with 2n=80

chromosomes, corresponding to the more widespread Atlantic taxon *G. dryopteris* (L.) NEWMAN with 2n=160 chromosomes (cf. LÖVE & LÖVE 1967).

Festuca rubra L. ssp. **fraterculae** (RASM.) LÖVE & LÖVE, comb. nov., based on *Festuca rubra* L. var. *Fraterculae* RASMUSSEN, in Nytt Mag. f. Naturvid. 66 (1927), p. 110; *F. Richardsonii* HOOK. ssp. *fraterculae* (RASM.) LÖVE & LÖVE.

This rare but very distinct taxon of birdcliffs in northern Norway, the Faeroes and Iceland and perhaps elsewhere in the North Atlantic region, was originally described as a variety only by RASMUSSEN (1927), but later elevated to subspecific rank under *F. richardsonii* HOOK. by LÖVE & LÖVE (1956). Additional observations by us and by BRYNJÓLFSSON (1974) indicate that it is correctly classified as a subspecies equivalent to but younger and therefore less widespread than ssp. *arctica* (HACK.) GOVOR., which is an older name for ssp. *richardsonii* (HOOK.) HULTÉN of the *F. rubra* complex.

Poa supina SCHRAD. ssp. **ustulata** (FRÖHNER) LÖVE & LÖVE, stat. & comb. nov., based on *Poa ustulata* FRÖHNER, in Bot. Jahrb. 88 (1968), p. 437.

This is the widespread Asiatic race of *Poa supina,* rather than a species in its own right as maintained by FRÖHNER (1968), differing most clearly from the European typical race by its lack of long stolons so it grows in tufts, by its dark spikes and the dark-violet anthers, and in its later and longer flowering time, its distinctly shorter lifespan, and several other characters which together make it an easily distinguishable taxon. Naturally, both races are characterized by the same diploid chromosome number, and, in our experience, they are easily hybridized and then give rise to later generations in which their distinguishing characters show a clearly Mendelian segregation, as could be expected of well-defined races at this level of classification.

Phippsia R. BR.

It was pointed out by LÖVE (1970 a), that the morphological characters traditionally employed to distinguish the large grass genus *Puccinellia* PARL. from the small arctic-subarctic genus *Phippsia* R. BR. are of little significance for the separation of taxa at that level. Biologically still more important is the fact, observed by several students in recent decades, that the crossability between these two taxa is no more inhibited than between the species of *Puccinellia* itself. Therefore, following either the classical and purely morphological standard (cf. HARTMAN 1832) or the biological definition of the generic category, these groups must be regarded as being congeneric, as earlier concluded by LÖVE (1970 a, b) and LÖVE & LÖVE (1975 b). The name *Phippsia* has priority and so must be accepted as the valid name for the united group. The following new transfers, changes in rank, and descriptions are required for the taxa occurring in the Arctic:

Phippsia agrostoidea (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia agrostoidea* TH. SÖRENSEN, in PORSILD in Natl. Mus. Canada Bull. 135 (1955), p. 78.

Phippsia anderssonii (SWALLEN) LÖVE & LÖVE, comb. nov., based on *Puccinellia anderssonii* SWALLEN, in Journ. Wash. Acad. Sci. 34 (1944), p. 21.

Phippsia angustata (R. BR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia angustata* R. BROWN, Chloris Melvilliana (1823), p. 29.

Phippsia angustata ssp. **palibinii** (TH. SÖR.) LÖVE & LÖVE, stat. & comb. nov., based on *Puccinellia palibinii* TH. SÖRENSEN, in Medd. om Grönl. 136,3 (1953), p. 74.

Phippsia arctica (HOOK.) LÖVE & LÖVE, comb. nov., based on *Puccinellia arctica* W. J. HOOKER, Fl. Bor. Amer. 2 (1840), p. 248.

Phippsia borealis (SWALLEN) LÖVE & LÖVE, comb. nov., based on *Puccinellia*

borealis SWALLEN, in Journ. Wash. Acad. Sci. 34 (1944), p. 19.

Phippsia borealis ssp. **neglecta** (TZVELEV) LÖVE & LÖVE, comb. nov., based on *Puccinellia borealis* ssp. *neglecta* TZVELEV, in Arkt. Fl. SSSR 2 (1964), p. 206.

Phippsia bruggemannii (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia bruggemannii* TH. SÖRENSEN, in PORSILD in Natl. Mus. Canada Bull. 135 (1955), p. 80.

Phippsia capillaris (LILJEBL.) LÖVE & LÖVE ssp. **pulvinata** (FR.) LÖVE & LÖVE, stat. & comb. nov., based on *Glyceria distans* (L.) WG. var. *pulvinata* FRIES, Mant. 2 (1839), p. 11, pro parte; *Atropis pulvinata* V. KRECZETOVICH, Fl. SSSR 2 (1934), p. 761.

Phippsia deschampsioides (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia deschampsioides* TH. SÖRENSEN, in Medd. om Grönl. 136,3 (1953), p. 73.

Phippsia fragiliflora (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia fragiliflora* TH. SÖRENSEN, in Medd. om Grönl. 136,3 (1953), p. 73.

Phippsia gorodkovii (TZVELEV) LÖVE & LÖVE, comb. nov., based on *Puccinellia gorodkovii* TZVELEV, in Arkt. Fl. SSSR 2 (1964), p. 199.

Phippsia groenlandica (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia groenlandica* TH. SÖRENSEN, in Medd. om Grönl. 136,3 (1953), p. 37.

Phippsia hauptiana (V. KRECZ.) LÖVE & LÖVE, comb. nov., based on *Atropis Hauptiana* V. KRECZETOVICH, in Fl. SSSR 2 (1934), p. 763.

Phippsia interior (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia interior* TH. SÖRENSEN, in HULTÉN, Fl. Alaska & Yukon X (1950), p. 1713.

Phippsia langeana (BERL.) LÖVE & LÖVE, comb. nov., based on *Glyceria Langeana* BERLIN, Öfvers. Kongl. Vet.-Akad. Förh. 1884, No. 7, p. 79.

Phippsia langeana ssp. **alaskana** (SCRIBN. & MERR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia alaskana* SCRIBNER & MERRILL, in Contrib. U. S. Natl. Herb. 13,3 (1910), p. 78; *Puccinellia Langeana* ssp. *alaskana* (SCRIBN. & MERR.) TH. SÖR.

Phippsia langeana ssp. **asiatica** (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia Langeana* ssp. *asiatica* TH. SÖRENSEN, in HULTÉN, Flora Alaska & Yukon X (1950), p. 1710.

Phippsia laurentiana (FERN. & WEATH.) LÖVE & LÖVE, comb. nov., based on *Puccinellia laurentiana* FERNALD & WEATHERBY, in Rhodora 18 (1916), p. 14.

Phippsia lenensis (HOLMB.) LÖVE & LÖVE, comb. nov., based on *Puccinellia sibirica* HOLMB. var. *lenensis* HOLMBERG, in Bot. Not. 1927, p. 207; *Puccinellia lenensis* (HOLMB.) TZVELEV.

Phippsia neoarctica LÖVE & LÖVE, spec. nov.

Planta perennis, caespitosa, foliis glaucescentibus, stolonifera, stolonibus epigeis. Culmi 10—15 cm longi, procumbentes. Folia caulinaria duo, longivaginata; lamina stricta, plicata, 1—3 cm longa, 1.5—2.0 mm lata, apice acuta, glabra. Ligula 1.0—1.3 mm longa, acuta, vel abrupte acuminata. Panicula macilenta, diluto-purpurascens, 3—6 cm longa; rami e nodo inferiore 2—3, tenues, rigidi ascendentes, demum reflexi, spiculis 1—3; pedicelli non incrassati. Spiculae oblongae, 6—11 mm longae, 3—6-florae. Gluma inferior 1.5—2.0 mm longa, lanceolata, obtusa, 3-nervia. Lemmata 3.5—4.5 mm longa, obtusa vel plus minusve emarginata. Palea bifida, lemmatis longitudinis, carinis sine spiculis. Antherae 1.5—2.0 mm longae, sterilis, non dehiscentes. Sine granis.

Chromosomatum numerus 2n=21.

Holotypus: West Greenland, Sydostbugt, leg. N. HARTZ, July 1880, in Herb. Copenhagen, cf. SÖRENSEN, in Medd. om Grönland 136,3 (1953), p. 51—52.

A perennial and caespitose plant with glaucescent leaves and with epiterranean stolons. The flowering culms are procumbent, 10—15 cm long, with two leaves; the upper sheath is elongated; the blades are rigid, folded, 1—3 cm long and 1.5—2.0 mm broad, abruptly pointed at the apex, and glabrous. The ligule is 1.0—1.3 mm long, acute or abruptly pointed. The panicle is meager, dilute-purple, 3—6 cm

long; branches 2—3 from the lower node, slender, stiffly ascending, later on reflexed, bearing 1—3 spikelets; the pedicels are scarcely thickened. Spikelets oblong, 6—11 mm long, 3—6-flowered. The first glume is 1.5—2.0 mm long, lanceolate, obtuse or slightly emarginate, glabrous at the base. The palea is bifid, as long as the lemma or a little longer, the keels are without spinules. The anthers are 1.5—2.0 mm long, sterile and not dehiscent. No seeds develop. Chromosome number 2n=21.

This taxon, which is the socalled "Greenland type" of *P. phryganodes* sensu TH. SÖRENSEN, is distributed throughout arctic North America from Greenland to eastern Alaska. It is apparently a completely sterile and triploid hybrid of unknown parentage that is capable of effective vegetative reproduction, although its wide distribution also may be the result of that it is produced frequently and in many places and survives for a long time.

Phippsia nutkaënsis (K. PRESL) LÖVE & LÖVE, comb. nov., based on *Poa nutkaënsis* K. PRESL, Reliq. Haenk. 1 (1830), p. 272; *Puccinellia nutkaënsis* FERN. & WEATH.

Phippsia nutkaënsis ssp. **borealis** (HOLMB.) LÖVE & LÖVE, comb. nov., based on *Puccinellia retroflexa* (CURT.) HOLMB. ssp. *borealis* HOLMBERG, Bot. Not. 1926, p. 182; *Puccinellia coarctata* FERN. & WEATH.

The new combination at the subspecies level is required because hybridization experiments, still unpublished, between the Beringian taxon and the Atlantic plant have confirmed the suggestion by SÖRENSEN (1953) that these taxa are conspecific, since the hybrids are fully fertile and their meiotic divisions without even the slightest disturbance so a reproductive barrier is absent. Since some slight morphological differences are connected with the geographical separation, however, we find it reasonable to accept the Atlantic taxon as a subspecies in its own right, although its distinction is, admittedly, not always very obvious. It is our belief that this and some other plants and animals that are common to the North Atlantic region and the Beringian area have dispersed over the still open Polar Sea by aid of ocean currents after the formation of the Bering Strait in the Pliocene (cf. EINARSSON, HOPKINS & DOELL 1967).

Phippsia phryganodes (TRIN.) LÖVE & LÖVE, comb. nov., based on *Poa phryganodes* TRINIUS, in Mém. Acad. Pétersb., sér. 6, 1 (1830), p. 389; *Puccinellia geniculata* V. KRECZETOVICH.

This taxon, in its strict sense, is a diploid and sexual species of the Beringian region. Its epithet should not be misapplied as a collective name for the circumpolar arctic complex which here is included in *P. vilfoidea* and *P. neoarctica,* although this has been done by SÖRENSEN (1953) and others.

Phippsia poacea (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia poacea* TH. SÖRENSEN, in PORSILD, in Natl. Mus. Canada. Bull. 135 (1955), p. 78.

Phippsia porsildii (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia porsildii* TH. SÖRENSEN, in Medd. om Grönl. 136,3 (1953), p. 35.

Phippsia rosenkrantzii (TH. SÖR.) LÖVE & LÖVE, comb. nov., based on *Puccinellia rosenkrantzii* TH. SÖRENSEN, in Medd. om Grönl. 136,3 (1953), p. 33.

Phippsia sibirica (HOLMB.) LÖVE & LÖVE, comb. nov., based on *Puccinellia sibirica* HOLMBERG, in Bot. Not. 1927, p. 206, excl. var.

Phippsia svalbardensis (RÖNNING) LÖVE & LÖVE, comb. nov., based on *Puccinellia svalbardensis* RÖNNING, in Kgl. Norske Vidensk. Selsk. Skrifter 1961, Nr. 4 (1962), p. 10.

Phippsia tenella (LGE) LÖVE & LÖVE, comb. nov., based on *Glyceria tenella* LANGE, in KJELLMAN & LUNDSTRÖM, Vega-Exp. Vetensk. Iakttag. 1 (1882), p. 313.

Phippsia vaginata (LGE) LÖVE & LÖVE, comb. nov., based on *Glyceria vaginata*

LANGE, Flora danica, fasc. 44 (1858), tab. 2583.

Phippsia vahliana (LIEBM.) LÖVE & LÖVE, comb. nov., based on *Poa Vahliana* LIEBMANN, Flora danica, fasc. 41 (1845), tab. 2401.

Phippsia vahliana ssp. **byrrangensis** (TZVELEV) LÖVE & LÖVE, stat. & comb. nov., based on *Puccinellia byrrangensis* TZVELEV, in Novit. Syst. Plant. Vasc. 8 (1971), p. 80.

Phippsia vahliana ssp. **colpodioides** (TZVELEV) LÖVE & LÖVE, stat. & comb. nov., based on *Puccinellia colpodioides* TZVELEV, in Arkt. Flora SSSR 2 (1964), p. 194.

Phippsia vahliana ssp. **jenisseiensis** (ROSHEV.) LÖVE & LÖVE, stat. & comb. nov., based on *Atropis jenisseiensis* ROSHEVICH, in Izv. Bot. Sada Akad. Nauk SSSR 30 (1932), p. 300.

Phippsia vilfoidea (ANDERSS.) LÖVE & LÖVE, comb. nov., based on *Catabrosa vilfoidea* ANDERSSON, in MALMGREN, in Öfvers. Kgl. Vet.-Akad. Förhandl. 19 (1862), p. 254; *Puccinellia vilfoidea* (ANDERSS.) LÖVE & LÖVE.

This is the variable tetraploid circumpolar taxon which has frequently but erroneously been identified with the diploid eastern Asiatic and Beringian species *P. phryganodes*. It includes three subspecies of which ssp. *vilfoidea* occupies the European arctic area.

Phippsia vilfoidea ssp. **beringensis** LÖVE & LÖVE, ssp. nov.

Planta stolonifera, stolones foliiferae superficiales praesunt. Palearum carinae papillosae. Cellulae epidermale folii in pagina superiore semper tumidae, saepe guttiforme, interdum item inconspicue papillosae.

Chromosomatum numerus 2n=28.

Holotypus: Bering Sea district, Qiqertariaq, A. E. PORSILD 1069, in Herb. Mus. Canada.

A stoloniferous plant, the stolons with superficial leaves. The keels of the palea are papillose. The cells of the epidermis of the upper leaf surface are always tumid and often dropshaped, sometimes also inconspicuously papillose. Chromosome number 2n=28.

This race, which is the "Beringian type" of *P. phryganodes* sensu SÖRENSEN, grows on the coasts around the Bering Sea and the Bering Strait.

Phippsia vilfoidea ssp. **sibirica** (HADAČ & LÖVE) LÖVE & LÖVE, comb. nov., based on *Puccinellia vilfoidea* ssp. *sibirica* HADAČ & LÖVE, in Bot. Not. 114 (1961), p. 36; *P. phryganodes* ssp. *asiatica* TZVELEV, in Arkt. Fl. SSSR 2 (1964), p. 186.

Phippsia wrightii (SCRIBN. & MERR.) LÖVE & LÖVE, comb. nov., based on *Colpodium Wrightii* SCRIBNER & MERRILL, in Contrib. U.S. Natl. Herb. 13,3 (1910), p. 74.

Bromopsis FOURR.

As recently shown by HOLUB (1973), the generic name *Bromopsis* FOURR. is the correct name for the perennial group of the collective genus *Bromus,* when separated as a distinct genus, and not the frequently used but invalid name *Zerna* PANZER. The following taxa of the eastern Asiatic or western North American Arctic are in a need of transfer to this name, some at a new rank:

Bromopsis dicksonii (MITCH. & WILT.) LÖVE & LÖVE, stat. & comb. nov., based on *Bromus Pumpellianus* SCRIBN. ssp. *dicksonii* MITCHELL & WILTON, in Brittonia 18 (1966), p. 163.

Bromopsis ircutensis (KOM.) LÖVE & LÖVE, comb. nov., based on *Bromus ircutensis* KOMAROV, in Bot. Mat. Herb. Petersb. Bot. Sada 2 (1921), p. 130.

Bromopsis pumpelliana (SCRIBN.) HOLUB ssp. **arctica** (SHEAR) LÖVE & LÖVE, stat. & comb. nov., based on *Bromus arcticus* SHEAR, in SCRIBNER & MERRILL, Grass. Alaska (1910), p. 83.

Bromopsis vogulica (SOCZ.) HOLUB. By an oversight, LÖVE & LÖVE (1975 a) re-

placed the name of the latter author of this combination with their own. It is also worth noting, that TZVELEV (1974) regards this taxon as a subspecies only of *B. pumpelliana,* perhaps a likely proposition which then might logically also require that level for *B. ircutensis.* Lacking experimental evidence, we prefer to keep these taxa at the species level, despite their cytological similarity to the also octoploid *B. pumpelliana.*

Elymus L.

Following numerous experimental observations of the Triticeae group, LÖVE & LÖVE (1961, 1965), LÖVE (1970 a, b), TZVELEV (1973) and DEWEY (1974) have advocated the acceptance of the generic name *Elymus* L. for most of the perennial taxa that have been traditionally included in that genus or in *Agropyron* s. l., *Anthosachne, Clinelymus, Hystrix, Roegneria* and *Sitanion,* excluding as distinct genera *Elytrigia, Leymus* and *Agropyron* s. str. and some annual genera. This proposal has been accepted also in part by RUNEMARK & HENEEN (1968), although they included also *Elytrigia* and *Leymus* in their then much more collective genus *Elymus.* The great majority of arctic taxa of the genus so circumscribed have already been transferred to this group by TZVELEV (1973 and earlier) and others. However, a change in rank or new combinations are required for the following entities:

Elymus alaskanus (SCRIBN. & MERR.) LÖVE & LÖVE ssp. **borealis** (TURCZ.) LÖVE & LÖVE, comb. nov., based on *Triticum boreale* TURCZANINOV, in Bull. Soc. Nat. Moscou 29 (1856), p. 58; *Elymus kronokensis* (KOM.) TZVELEV ssp. *borealis* (TURCZ.) TZVELEV; non *Elymus borealis* SCRIBN.

Elymus alaskanus ssp. **hyperarcticus** (POLUNIN) LÖVE & LÖVE, comb. nov., based on *Agropyron violaceum* HORNEM. var. *hyperarcticum* POLUNIN, in Bull. Natl. Mus. Canada 92 (1940), p. 95; *Roegneria borealis* (TURCZ.) NEVSKI ssp. *hyperarcticum* (POLUNIN) LÖVE & LÖVE; *Elymus sajanensis* (NEVSKI) TZVELEV ssp. *hyperarcticus* (POLUNIN) TZVELEV.

Elymus alaskanus ssp. **islandicus** (MELD.) LÖVE & LÖVE, comb. nov., based on *Roegneria borealis* var. *islandica* MELDERIS, in Svensk Bot. Tidskr. 44 (1950), p. 163; *Roegneria borealis* ssp. *islandica* (MELD.) LÖVE & LÖVE.

Elymus alaskanus ssp. **subalpinus** (L. NEUM.) LÖVE & LÖVE, comb. nov., based on *Triticum violaceum* HORNEM. f. *subalpinum* L. NEUMAN, Sveriges Flora (1901), p. 726; *Agropyron latiglume* (SCRIBN. & SM.) RYDB. ssp. *subalpinum* (L. NEUM.) VESTERGREN.

Elymus alaskanus ssp. **villosus** (V. VASSIL.) LÖVE & LÖVE, comb. nov., based on *Roegneria villosa* V. VASSILIEV, in Bot. Mat. 16 (1954), p. 57; *Elymus sajanensis* (NEVSKI) TZVELEV ssp. *villosus* (V. VASSIL.) TZVELEV; non *Elymus villosus* MUEHL.

Elymus trachycaulus (LINK) GOULD ssp. **andinus** (SCRIBN. & SM.) LÖVE & LÖVE, comb. nov., based on *Agropyron violaceum* (HORNEM.) LGE var *andinum* SCRIBNER & SMITH, in U. S. Dept. Agric., Div. Agrostol. Bull. 4 (1897), p. 30; *Agropyron violaceum* ssp. *andinum* (SCRIBN. & SM.) MELD.

Elymus trachycaulus ssp. **subsecundus** (LINK) LÖVE & LÖVE, stat. & comb. nov., based on *Triticum subsecundum* LINK, Hort. Berol. 2 (1833), p. 190.

Elymus trachycaulus ssp. **stefanssonii** (MELD.) LÖVE & LÖVE, comb. nov., based on *Roegneria Doniana* (WHITE) MELD. var. *Stefanssonii* MELDERIS, in Svensk Bot. Tidskr. 44 (1950), p. 158; *Roegneria Doniana* ssp. *Stefanssonii* (MELD.) LÖVE & LÖVE.

Elymus trachycaulus ssp. **violaceus** (HORNEM.) LÖVE & LÖVE, stat. & comb. nov., based on *Triticum violaceum* HORNEMANN, Flora danica, fasc. 35 (1832), tab. 2044.

Elymus trachycaulus ssp. **virescens** (LGE) LÖVE & LÖVE, comb. nov., based on *Agro-*

pyron violaceum ß *virescens* LANGE, in Medd. om Grönl. 3 (1880), p. 155; *Roegneria Doniana* ssp. *virescens* (LGE) LÖVE & LÖVE.

Critesion RAFIN.

It is our settled belief based on studies by numerous authors and also on our own, still unpublished, cytogenetical experiments, that the genus *Hordeum* L. in its traditional circumscription is an unnatural assemblage of taxa which are composed of haplomes (LÖVE & LÖVE 1975 c) that are too distantly related to be united in a single genus, even at the subgeneric or sectional levels as accepted by TZVELEV (1973). This view is especially supported by the observation that hybridization between these taxa is absent even under ideal experimental conditions, and also by the fact that both annual and perennial taxa are involved, differing morphologically in numerous characters that have been found to be of utmost importance for separating groups at higher levels in other taxa of the Triticeae. Therefore, we find it logical to accept the generic name *Hordeum* L. in a restricted sence, including only the annual species of the subgenus *Hordeum* of TZVELEV (l.c.) or of the section *Crithe* DOELL., typified by *Hordeum vulgare* L. We are not ready to propose what is the correct generic name for the two perennial sections *Hordeastrum* DOELL. and *Bulbohordeum* NEVSKI, hybrids between which seem to indicate haplomic relationships of a congeneric significance (LÖVE & LÖVE, unpubl.), but the section *Stenostachys* NEVSKI differs so substantially from all these groups in its haplomic arrangement that a generic separation is well substantiated, as it also seems to be on purely morphological grounds. At that level, its valid name is *Critesion* RAFIN. Only the single species *C. jubatum* (L.) NEVSKI reaches the Arctic, where it is represented by the following race:

Critesion jubatum (L.) NEVSKI ssp. **breviaristatum** (BOWDEN) LÖVE & LÖVE, comb. nov., based on *Hordeum jubatum* L. ssp. *breviaristatum* BOWDEN, in Canad. Journ. Bot. 40 (1962), p. 1691.

Leymus HOCHST.

The most widespread species of the genus *Leymus* is the tetraploid *L. mollis* (TRIN.) PILGER, which with its subspecies is circumpolar both in the boreal and arctic regions. In the Arctic that species is represented by its typical race and also by the two following races:

Leymus mollis (TRIN.) PILGER ssp. **interior** (HULTÉN) LÖVE & LÖVE, comb. nov., based on *Elymus interior* HULTÉN, Flora of Alaska and Yukon II (1942), p. 270; *Elymus mollis* TRIN. ssp. *interior* (HULTÉN) BOWDEN.

Leymus mollis ssp. **villosissimus** (SCRIBN.) LÖVE & LÖVE, comb. nov., based on *Elymus villosissimus* SCRIBNER, in U. S. Dept. Agric., Div. Agrostol. Bull. 17 (1899), p. 326; *Elymus mollis* ssp. *villosissimus* (SCRIBN.) Á. LÖVE.

Leymus velutinus (BOWDEN) LÖVE & LÖVE, stat. nov., based on *Elymus innovatus* BEAL ssp. *velutinus* BOWDEN, in Canad. Journ. Bot. 37 (1959), p. 1146.

Since this taxon is octoploid with 2n=56 chromosomes, as contrasted to the tetraploid *L. innovatus* from which it is, thus, separated by a reproductive barrier in addition to clear morphological and geographical differences, it is hardly logical to regard it as a subordinate race of the latter. Therefore this change of rank.

Deschampsia caespitosa (L.) PB. ssp. **anadyrensis** (V. VASSIL.) LÖVE & LÖVE, stat. & comb. nov., based on *Deschampsia anadyrensis* V. VASSILIEV, in Bot. Mat. 8 (1940), p. 68.

Calamagrostis maltei (POLUNIN) LÖVE & LÖVE, stat. & comb. nov., based on *Calamagrostis purpurascens* R. BR. var. *Maltei* POLUNIN, in Natl. Mus. Canada Bull. 92

(1940), p. 51; *Calamagrostis purpurascens* ssp. *Maltei* (POLUNIN) A. E. PORSILD.

We are unable to propose a natural division of the very variable and collective taxon *Calamagrostis purpurascens* R. BR. into species that conform with various degrees of polyploidy, mainly because the chromosome reports have not been accompanied by close morphological comparisons of the material. However, we find it to be a step in the right direction to distinguish as separate species those units that are most clearly recognizable. One of these is the taxon above, which has recently been closely analysed and lifted from its originally tentative level of variety to that of subspecies (PORSILD 1975), although that is certainly no improvement in the understanding of its distinctness, which certainly is greater than that of a major geographical race.

Agrostis scabra WILLD. ssp. **septentrionalis** (FERN.) LÖVE & LÖVE, stat. nov., based on *Agrostis scabra* var. *septentrionalis* FERNALD, in Rhodora 35 (1933), p. 209.

The variety category as used by FERNALD for this and many other taxa is clearly that of a major geographical race, or a subspecies in our definition.

Hierochloë orthantha TH. SÖR. We find it difficult to follow WEIMARCK (1971) in placing the strictly apomictic 63-chromosome North American taxon as a subspecies of the predominantly sexual 56-chromosome circumpolar *H. alpina* (SW.) R. & S. LÖVE & LÖVE (1965) found this taxon to be identical with a plant described from Mt Washington by BIGELOW (1816) as *Holcus monticola* and transferred this name to *Hierochloë* (in LÖVE & SOLBRIG 1964). The taxon is listed as *Hierochloë monticola* (BIGEL.) LÖVE & LÖVE by LÖVE & LÖVE (1975 a). We overlooked, however, that this is a homonym of the Australian *H. monticola* MEZ, which in turn is a synonym of *H. submutica* F. MUELL. (cf. VICKERY 1975). Therefore, the correct name for the taxon at the level of species must be *H. orthantha* TH. SÖR., or the same name as applied at the subspecific level by WEIMARCK (1971).

Carex capillaris L. ssp. **fuscidula** (V. KRECZ.) LÖVE & LÖVE, stat. & comb. nov., based on *Carex fuscidula* V. KRECZETOVICH, in EGOROVA, in Novit. Syst. Plant. Vasc. 1 (1964), p. 36.

We are of the opinion that EGOROVA (1964) errs in identifying the southern Eurasiatic-North American tall-grown race ssp. *chlorostachys* (STEV.) LÖVE, LÖVE & RAYMOND with the typical Atlantic-Scandinavian ssp. *capillaris,* but she is evidently correct in distinguishing a low-grown arctic-alpine Eurasiatic-North American taxon from the typical boreal race, since the species was obviously described from the lowlands of Central Sweden to where neither ssp. *chlorostachys* nor the arctic-alpine race reach. However, there is no reason to believe that the taxon in question is a species in its own right, as proposed by EGOROVA (l.c.) with reference to a nomen nudum on a map by KRECZETOVICH (1952), but we find it reasonable to accept it as a major geographical race at the subspecific level.

Carex gaudichaudiana KÜK. ssp. **appendiculata** (TRAUTV. & MEY.) LÖVE & LÖVE, stat. & comb. nov., based on *Carex acuta* L. var. *appendiculata* TRAUTVETTER & MEYER, Flor. Ochot. phaen. (1856), p. 100; *Carex appendiculata* (TRAUTV. & MEY.) KÜK.

We follow KOYAMA (1959) in regarding this northern taxon as a race only of the Asiatic *C. gaudichaudiana*; however, we find it warranted to transfer it to a higher level, since we prefer to distinguish between varieties and subspecies on basis of their geographical distinction.

Carex nigra (L.) REICHARD

The cytological similarities between the morphologically distinguishable races of this widespread species are corroborated

by the ease with which they hybridize where they come together and also under experimental conditions (LÖVE & LÖVE, unpubl.). Therefore, we find it reasonable to accept the three taxa reaching the Arctic only at the subspecific level, to which two need to be transferred:

Carex nigra ssp. **juncea** (FR.) LÖVE & LÖVE, comb. nov., based on *Carex vulgaris* FR. * (ssp.) *juncea* FRIES, Mant. 3 (1842), p. 154.

Carex nigra ssp. **wiluica** (MEINSH.) LÖVE & LÖVE, comb. nov., based on *Carex wiluica* MEINSHAUSEN, in MAAK, Vilyusk. Okr. Yakutsk. Obl. 2 (1886), p. 308; *Carex juncella* (FR.) TH. FR. ssp. *wiluica* (MEINSH.) EGOROVA.

Calla L.

The genus *Calla* is usually regarded as a monotypic taxon with a circumpolar distribution. However, cytotaxonomical studies have revealed, that the north and central European populations, which certainly belong to the species *C. palustris* L. s.str., are characterized by the octoploid chromosome number 2n=72, whereas the North American plant, which is smaller in all respects, is a tetraploid with 2n=36. It was accepted as a distinct species, *brevis,* of the genus *Provenzalia* by RAFINESQUE (1836) but later ignored. In *Calla* its correct name is:

Calla brevis (RAFIN.) LÖVE & LÖVE, comb. nov., based on *Provenzalia brevis* RAFINESQUE, New Fl. North Amer. 2 (1836), p. 67.

Populus tremula L. ssp. **tremuloides** (MICHX.) LÖVE & LÖVE, stat. & comb. nov., based on *Populus tremuloides* MICHAUX, Flora Bor. Amer. 2 (1803), p. 243.

The North American taxon is morphologically very close to the typical *P. tremula* L. of Eurasia, from which it differs technically in having regularly crenate-serrulate and usually short acuminate leaves, as contrasted to the irregularly sinuate-dentate and often obtuse leaves of the Eurasiatic plant. They are ecologically and cytologically identical, and numerous experiments have shown them to be completely interfertile. Therefore, we find it illogical to retain them as distinct species despite their large and distinct geographical areas, and propose the transfer of the North American taxon to the subspecific level of the Eurasiatic species.

Salix brachycarpa NUTT. ssp. **fullertonensis** (C. K. SCHNEIDER) LÖVE & LÖVE, stat. & comb. nov. based on *Salix fullertonensis* C. K. SCHNEIDER, in Bot. Gazette 66 (1918), p. 340.

The northwestern American species *S. brachycarpa* is composed of a few races, two of which reach the arctic regions. The more widespread one of these, ssp. *niphoclada* (RYDB.) ARGUS, is rather common in arctic-alpine areas west of the Hudson's Bay, but in the northern Keewatin District it is replaced by the distinct but less widespread and more prostrate and smaller leaved *S. fullertonensis,* which certainly ought to be reduced to the subspecific level.

Betula nana L. ssp. **perfiljevii** (V. VASSIL.) LÖVE & LÖVE, stat. & comb. nov., based on *Betula Perfiljevii* V. VASSILJEV, in Novit. Syst. Plant. Vasc. 3 (1966), p. 75.

Betula nana ssp. **tundrarum** (PERF.) LÖVE & LÖVE, stat. & comb. nov., based on *Betula tundrarum* PERFILJEV, in Bot. Zhurn. 48 (1963), p. 1139.

In conformity with the acceptance of the widespread Eurasiatic and North American races of *Betula nana* as the ssp. *nana* and ssp. *exilis* (SUKACZ.) HULTÉN, we find it necessary to propose subspecific status also for the two morphologically distinct races above, both of which were originally described as species of a restricted distribution.

Alnus incana (L.) MOENCH ssp. **hirsuta** (SPACH) LÖVE & LÖVE, stat. nov., based on *Alnus incana* var. *hirsuta* SPACH, in Ann. Sci. Nat., 2 sér., 15 (1841), p. 207.

We prefer to regard the species *Alnus incana* as a complex of distinct major

geographical races, since they have been shown by numerous experimenters to be easily hybridized without a reduction in fertility and with later generations giving clearly Mendelian segregations. Of the four races reaching the Arctic, only the above one from eastern Asia has not earlier been validated as a subspecies.

Urtica gracilis AIT. ssp. **sondenii** (SIMM.) LÖVE & LÖVE, comb. nov., based on *Urtica dioica* L. var. *Sondenii* SIMMONS, in LINDMAN, Svensk fanerogamfl. (1918), p. 208; *Urtica dioica* ssp. *Sondenii* (SIMM.) HYLANDER.

Recent cytological investigations have demonstrated beyond doubt that the mainly eastern North American *Urtica gracilis* and its far northern outposts in Scandinavia differ not only morphologically and geographically from the Eurasiatic *Urtica dioica* L. and from other dioecious North American species, but also cytologically, since the latter are distinctly tetraploid with 2n=52 chromosomes (we have reason to doubt records of 2n=48 because reexamination of the slides on which our own reports of this number were based showed that these numbers were caused by a too low estimation of crowded metaphase plates), and the former taxon is diploid with 2n=26. The diploid species reaches the Arctic only in northern Scandinavia and the adjacent Soviet Union, where it is represented by the above race.

Rumex L.

We see no reason to retain the genus *Rumex* in its traditionally very collective sense, and so accept for the dioecious arctic plants the generic names *Acetosella* FOURR. and *Acetosa* MILL. Only the following recently described species need to be transferred to these genera, since valid combinations are available for the other taxa of the northlands:

Acetosella beringensis (JURTSEV & PETROVSKY) LÖVE & LÖVE, comb. nov., based on *Rumex beringensis* JURTSEV & PETROVSKY, in YURTSEV, SYTIN & SEKRETAREVA, in Bot. Zhurn. 58 (1973), p. 1745 (note).

Acetosella krausei (JURTSEV & PETROVSKY) LÖVE & LÖVE, comb. nov., based on *Rumex Krausei* JURTSEV & PETROVSKY, in YURTSEV, SYTIN & SEKRETAREVA, in Bot. Zhurn. 58 (1973), p. 1745.

Acetosa oblongifolia (TOLM.) LÖVE & LÖVE, comb. nov., based on *Rumex oblongifolius* TOLMACHEV, in Arkt. Flora SSSR 5 (1966), p. 154.

Koenigia hadacii LÖVE & LÖVE, spec. nov., based on *Koenigia islandica* L. var. *arctica* HADAČ, in Studia Bot. Čechica 5 (1942), p. 3.

This small diploid taxon is apparently an Asiatic plant that reaches Svalbard. It is distinguished from typical and tetraploid *K. islandica* by being diploid and having smaller flowers and smaller achenes but since this is a modifiable character requiring completely ripe seeds for secure identification, other less modifiable characters need to be searched for. When compared under controlled experimental conditions, the floral and fruit size differences are always reliable, and then the diploid also ripens its seeds significantly earlier than the tetraploid. Both species seem to be almost obligately autogamous and hybridization rarely succeeds even under controlled conditions because of the difficulties of emasculating the flowers. However, triploids derived from pollinations of the tetraploid by pollen from the diploid were found to have a rather high frequency of trivalents at meiosis, perhaps indicating an autoploid origin of the tetraploid species (LÖVE & LÖVE, unpubl.).

Polygonum L.

It is our opinion based on long-time studies of various features of numerous taxa belonging to this very collective genus, that it ought to be divided into more

clearly defined genera, as proposed by many previous authors though generally ignored by authors of manuals. Cytologically, this is well substantiated by variations in chromosome morphology and by the occurrence of at least three basic chromosome numbers that coincide with the morphological characters that have been used to define the restricted genera. Following this view, *Polygonum* is restricted to the annual groups belonging to the section or subgenus *Avicularia,* whereas other genera represented in the Arctic are *Bistorta* SCOP. (not MILL. as inadvertently given by LÖVE & LÖVE, 1975 a), *Persicaria* MILL., *Aconogonon* RCHB. and *Fallopia* ADANS.

According to HULTÉN (1968), who does not subdivide the collective genus, the northern Pacific populations of the wide taxon *P. bistorta* L. all belong to the ssp. *plumosum* (SMALL) HULTÉN, which then includes the ssp. *ellipticum* (WILLD.) PETROVSKY. Recent cytological evidence, however, casts a doubt on this conclusion, since the former apparently strictly American taxon has been found to be hexaploid with 2n=72 chromosomes, whereas the latter eastern Asiatic and Alaskan plant is a tetraploid with 2n=48 chromosomes, as is also the typical race of the species. Therefore, we accept the latter as a subspecies of the Eurasiatic species in the genus *Bistorta* and the former as a species in its own right, *B. plumosa* (SMALL) GREENE (not LÖVE & LÖVE as in LÖVE & LÖVE 1975 a). Likewise, the genus *Aconogonon* is represented in the Arctic by some species, only one of which requires a transfer.

Bistorta major S. F. GRAY ssp. **elliptica** (WILLD.) LÖVE & LÖVE, comb. nov., based on *Polygonum ellipticum* WILLDENOW ex SPRENGEL, Syst. veget. ed. 16, 2 (1825), p. 253; *Polygonum bistorta* L. ssp. *ellipticum* (WILLD.) PETROVSKY.

Aconogonon laxmannii (LEPECH.) LÖVE & LÖVE, comb. nov., based on *Polygonum Laxmannii* LEPECHIN, Nova Acta Petrop. 10 (1797), p. 414.

Dichodon (BARTL.) RCHB.

The genus *Dichodon,* as recently resusciated by IKONNIKOV (1973) to accomodate the species *Cerastium dubium* (BAST.) O. SCHWARZ and *C. cerastoides* (L.) BRITTON and their close relatives, which represent the sections *Dichodon* and *Perennia* IKONN. respectively, ought also to include the section *Strephodon* SER. of the collective genus *Cerastium,* as shown by observations made by SÖLLNER (1954). Both groups are morphologically related and are characterized by the same rare basic chromosome number x=19, as contrasted to x=9 of *Cerastium* proper. This conclusion requires the following transfers:

Dichodon sect. **Strephodon** (SERINGE) LÖVE & LÖVE, comb. nov., based on *Cerastium* sect. *Strephodon* SERINGE, in DC. Prodr. 1 (1824), p. 414.

Dichodon chlorifolium (FISCH. & MEY.) LÖVE & LÖVE, comb. nov., based on *Cerastium chlorifolium* FISCHER & MEYER, in Index IV Sem. Hort. Petrop. (1837), p. 34.

Dichodon dahuricum (FISCH.) LÖVE & LÖVE, comb. nov., based on *Cerastium dahuricum* FISCHER ex SPRENGEL, Pl. minus cognit. Pug. II (1815), p. 65.

Dichodon maximum (L.) LÖVE & LÖVE, comb. nov., based on *Cerastium maximum* LINNAEUS, Spec. plant. (1753), p. 439.

Dichodon perfoliatum (L.) LÖVE & LÖVE, comb. nov., based on *Cerastium perfoliatum* LINNAEUS, Spec. plant. (1753), p. 437.

Sagina L.

Although some botanists of the last century had shown that the collective genus *Sagina* could be divided into at least three more homogeneous genera on basis of floral and fruit characters, this advise has not been heeded by later authors, probably because other technical characters for this separation are somewhat confusing. Since recent cytological evidence, however, shows that these three groups

differ also drastically in their basic chromosome numbers and chromosome morphology, there is a reason now to accept these opinions. In that case, the annual boreal species are assigned to the genus *Saginella* KOCH, s.str. which is characterized by the basic number x=6 and typified by *S. apetala* ARD. The boreal and arctic-alpine group of perennial species similar to *S. nodosa* L. are classified as representing the genus *Spergella* RCHB., s.str. which has the basic number x=7, but the perennial *S. procumbens* L. and its relatives are retained in the genus *Sagina* L., s.str. which is cytologically characterized by the basic number x=11. The acceptance of this division requires the transfer of two arctic-alpine species to the genus *Spergella:*

Spergella caespitosa (J. VAHL) LÖVE & LÖVE, comb. nov., based on *Arenaria caespitosa* J. VAHL, in Flora danica, fasc. 39 (1840), tab. 2389; *Sagina caespitosa* (J. VAHL) LGE.

Spergella intermedia (FENZL) LÖVE & LÖVE, comb. nov., based on *Sagina intermedia* FENZL, in LEDEBOUR, Flora ross. I (1842), p. 339.

Minuartia L.

The redefinition of the strictly Mediterranean genus *Minuartia* L. by HIERN (1899), which made it possible to accomodate within its limits even arctic species, certainly was caused by a misunderstanding of considerable magnitude, although later authors and even two monographers (MATTFELD 1921, 1922; MCNEILL 1962) seem to have accepted this without hesitation. The group so widely defined is highly unnatural from whatever modern point of view it is looked upon, as shown most clearly be the apparent difficulties experienced by MCNEILL (l.c.) in dividing it into subgenera, sections and even subsections and series some of which are not only morphologically heterogeneous but also characterized by distinct basic chromosome numbers and by karyomorphology different from that of their supposedly closest relatives. *Minuartia* s.str. is known to have the basic number x=15, whereas other groups within the collective genus have been reported to have basic numbers as variable as x=8, 9, 10, 11, 12, 13, and 23. We have had the opportunity to make cytotaxonomical studies, still mainly unpublished, of considerable living and herbarium material of numerous species from arctic and boreal regions in Eurasia and North America and also of populations from the Mediterranean and the southwestern Asiatic area of the collective genus. These studies, which also include detailed observations on pollen and seed coat morphology, have convinced us that this unnatural assemblage needs to be divided into groups that better fit the modern biological definition of a genus. Therefore, in the Cytotaxonomical Atlas of the Arctic Flora (LÖVE & LÖVE 1975 a) we have resusciated some long ignored but well-defined and more restricted genera that are represented in the tundra of the northlands, and proposed new names for a couple of groups for which valid names at that level were not available.

One of the most distinct groups within this unnatural assemblage is the section *Uninerviae* which in its strict sense includes a single species with two races that are distributed from southern Greenland to the mountains of Tennessee, with some outposts in South America. Since the taxon has not previously received recognition as a genus, we are pleased to be able to name it in honour of A. ERLING PORSILD, the most outstanding Canadian specialist on arctic plants who received his basic training in Greenland.

Another well-defined group requiring a new name at the generic level is named in honour of JOHANNES and DAGNY TANDE LID of Oslo, he an ardent student of arctic-alpine plants and the author of arctic floras and of the best recent manual of Scandinavian plants, and she the most

outstanding illustrator of arctic and boreal and even subtropical plants.

Additional and revived genera of this complex that reach arctic lands are *Alsinanthe* (FENZL) RCHB., *Neumayera* RCHB., *Tryphane* (FENZL) RCHB. and *Wierzbickia* RCHB., whereas the bulk of genera in need of reseparation from this confused complex are distributed in more southern mountains of the boreal zone. Instead of furnishing exact and detailed descriptions of each of the arctic genera, we provide below a key for their identification, which we have lifted out of the good comprehensive key by MCNEILL (1962), followed by validations of the new taxa of various ranks required for some of the arctic populations.

1 Annual or biennial herbs; petals more or less emarginate, twice as long as the calyx; sepals obscurely or reticulately nerved, erect at anthesis; leaves one-nerved (or almost three-nerved), slender or rather fleshy; seeds obscurely tuberculate to tuberculate, sometimes echinate ..... *Porsildia*, x=10
1 Suffruticose or herbaceous perennials; petals entire, very rarely shortly emarginate .. 2
2 Sepals rounded to obtuse at apex, linear; calyx cylindrical; sterile shoots gradually passing into flowering shoots, rarely flowering shoots distinct and then bearing large fascicles; leaves fleshy, rarely rather rigid, traversed by one more or less prominent nerve 3
2 Sepats acute or acuminate, rarely obtuse and then ovate; calyx ovoid or urceolate; leaves of the sterile rosettes closely fasciculate, or even spreading, slender 4
3 Leaves flat, lanceolate or linear-lanceolate; entire leaf, or the margin near the base, setose, bearing long acute hairs; seeds with a fimbriate crest on the dorsal ridge ..... *Wierzbickia*, x=23
3 Leaves linear-subulate, the margin near the base more or less scabrid with short and obtuse hairs, rarely glabrous; seeds obscurely reticulate to obscurely tuberculate all over ..... *Lidia*, x=13
4 Petals shorter than sepals; sepals erect at anthesis; leaves one-nerved; seeds obscurely tuberculate; perennial herbs with elongate pedicels ..... *Alsinanthe*, x=15
4 Petals longer than sepals, or if shorter, then sepals spreading at anthesis; plant perennial; sepals 3—5(—9)-nerved with a rather narrow membranous or scarious margin; calyx not hardened at the base 5
5 Sepals 5—7(—9)-nerved, rarely 3-nerved and then the seeds are fimbriate; leaves linear-subulate or setaceous; sepals spreading at anthesis; seeds obscurely tuberculate or muricate ..... *Tryphane*, x=12
5 Sepals 3-nerved, acuminate, erect at anthesis; petals obovate or oblong, gradually narrowing to the base, 1.5—2 times as long as sepals; seeds obscurely tuberculate and sometimes echinate ..... *Neumayera*, x=13

Alsinanthe rossii (R. BR.) LÖVE & LÖVE, comb. nov., based on *Arenaria Rossii* R. BROWN, in RICHARDSON, in FRANKLIN, Narr. Journ. Polar Sea, App. VII (1823), p. 738; *Minuartia Rossii* (R. BR.) GRAEBNER, s.str.; *Minuartia Rolfii* NANNF.

Alsinanthe elegans (CHAM. & SCHLECHT.) LÖVE & LÖVE, comb. nov., based on *Arenaria elegans* CHAMISSO & SCHLECHTENDAL, in Linnaea 1 (1826), p. 57; *Minuartia elegans* (CHAM. & SCHLECHT.) SCHISCHKIN.

Porsildia LÖVE & LÖVE, gen. nov.

Based on *Alsine* 12 *Uninerviae* FENZL, in ENDLICHER, Gen. plant. (1840), p. 965; *Minuartia* sect. *Uninerviae* (FENZL) MATTFELD, in Bot. Jahrb. 57, Beih. 126 (1921), p. 28, p. p., excl. *M. uniflora* (WALT.) MATTF. Type species: *Porsildia groenlandica* (RETZ.) LÖVE & LÖVE.

Porsildia groenlandica (RETZ.) LÖVE & LÖVE, comb. nov., based on *Stellaria groenlandica* RETZIUS, Flora Scand. Prodr. ed. 2 (1795), p. 107; *Minuartia groenlandica* (RETZ.) OSTENF.

Porsildia groenlandica ssp. **glabra** (MICHX.) LÖVE & LÖVE, comb. nov., based on *Arenaria glabra* MICHAUX, Flora Bor. Amer. 1 (1803), p. 274; *Minuartia groenlandica* ssp. *glabra* (MICHX.) LÖVE & LÖVE.

Lidia LÖVE & LÖVE, gen. nov.

Based on *Minuartia* sect. *Spectabilis* series *Biflorae* MATTFELD, in Feddes Repert., Beih. 15 (1922), p. 182, diagn. in clavae. Type species: *Lidia biflora* (L.) LÖVE & LÖVE.

Lidia arctica (STEV.) LÖVE & LÖVE, comb. nov., based on *Arenaria arctica* STEVEN, ex SÉRINGE, in DC. Prodr. 1 (1824), p. 104; *Minuartia arctica* (STEV.) A. & GR.

Lidia biflora (L.) LÖVE & LÖVE, comb. nov., based on *Stellaria biflora* LINNAEUS, Spec. plant. (1753), p. 422; *Minuartia biflora* (L.) SCHINZ & THELL.

Lidia obtusiloba (RYDB.) LÖVE & LÖVE, comb. nov., based on *Alsinopsis obtusiloba* RYDBERG, in Bull. Torrey Bot. Club 33 (1906), p. 132; *Minuartia obtusiloba* (RYDB.) HOUSE.

Lidia yukonensis (HULTÉN) LÖVE & LÖVE, comb. nov., based on *Minuartia yukonensis* HULTÉN, in Arkiv f. Bot. II, 7 (1967), p. 52.

Gastrolychnis RCHB.

The arctic-alpine hermaphroditic taxa that traditionally have been treated as a section of either the otherwise dioecious genus *Melandrium* ROEHL. or of the then much too inclusive genus *Silene* L. are more appropriately included in the well-defined genus *Gastrolychnis* (TOLMACHEV & KOZHANCHIKOV, in TOLMACHEV 1971), a procedure based on morphological distinctions but strongly supported by cytological observations of the behavior of haplomes and of genomic relationships in the Caryophyllaceae (LÖVE & LÖVE, unpubl.). Most of the arctic taxa have already been transferred to this genus by previous authors, but new combinations are needed for the following:

Gastrolychnis apetala (L.) TOLM. & KOZH. ssp. **arctica** (FR.) LÖVE & LÖVE, comb. nov., based on *Wahlbergella apetala* (L.) FR. ß *arctica* TH. M. FRIES, in Öfvers. Vetensk.-Akad. Förhandl. 2 (1869), p. 133; *Melandrium apetalum* (L.) FENZL ssp. *arcticum* (FR.) HULTÉN.

This race is endemic in Svalbard.

Gastrolychnis apetala ssp. **uralensis** (RUPR.) LÖVE & LÖVE, stat. & comb. nov., based on *Gastrolychnis uralense* RUPRECHT, in Beitr. Pflanzenk. Russ. Reiches 7 (1850), p. 30; *Silene uralensis* (RUPR.) BOCQUET ssp. *apetala* (L.) BOCQUET.

This circumpolar arctic-subarctic race is frequently confused with the endemic Svalbard race above, even by HULTÉN (1968, 1971).

Gastrolychnis involucrata (CHAM. & SCHLECHT.) LÖVE & LÖVE, comb. nov., based on *Lychnis apetala* L. γ *involucrata* CHAMISSO & SCHLECHTENDAL, in Linnaea 1 (1826), p. 43; *Melandrium involucratum* (CHAM. & SCHLECHT.) ROHRBACH; *Melandrium furcatum* (RAFIN.) HADAČ.

Gastrolychnis involucrata ssp. **elatior** (REGEL) LÖVE & LÖVE, comb. nov., based on *Lychnis apetala* var. *elatior* REGEL, in Bull. Soc. Imp. Nat. Moscou 34 (1862), p. p. emend. MAGUIRE, in Rhodora 52 (1950), p. 240; *Silene involucrata* ssp. *elatior* (REGEL) BOCQUET.

Gastrolychnis involucrata ssp. **tenella** (TOLM.) LÖVE & LÖVE, comb. nov., based on *Melandrium affine* J. VAHL ssp. *tenellum* TOLMACHEV, in Trud. Bot. Muz. 24 (1932), p. 258.

Gastrolychnis soczaviana (SCHISCHKIN) TOLM. & KOZH. ssp. **ogilviensis** (A. E. PORSILD) LÖVE & LÖVE, comb. nov., based on *Melandrium apetalum* ssp. *ogilviense* A. E. PORSILD, in Natl. Mus. Canada Publ. Bot. 4 (1975), p. 23.

Gastrolychnis triflora (R. BR.) TOLM. & KOZH. ssp. **dawsonii** (ROBINS.) LÖVE & LÖVE, stat. & comb. nov., based on *Lychnis triflora* R. BR. var. *Dawsonii* ROBINSON, in Proc. Amer. Acad. 28 (1893), p. 149.

Caltha minor MILL. ssp. **arctica** (R. BR.) LÖVE & LÖVE, comb. nov., based on *Caltha arctica* R. BR., Suppl. to App.

PARRY's Voy. (1824), p. 265; *Caltha palustris* L. ssp. *arctica* (R. BR.) HULTÉN.

Morphological and cytological observations support the opinion that the conventionally circumscribed collective species *Caltha palustris* actually consists of two good species, the Linnaean taxon in its strict sense, which is a plant with 2n=32 chromosomes that is represented in the Eurasiatic Arctic by its ssp. *palustris* and in northwestern Alaska by ssp. *asarifolia* (DC.) HULTÉN, and a circumpolar arctic-alpine polyploid with a variable chromosome number and perhaps partially apomictic. The latter has been given various names in the past, but the oldest valid name for the complex is *C. minor* MILL., described from the mountains of Great Britain, of which the arctic populations are best regarded as a single subspecies.

Anemone drummondii S. WATS. ssp. **heimburgeri** LÖVE & LÖVE, subsp. nov.

Stylus filiformis, firmus, non fragilis. Holotypus: Alaska, Bering Strait district, Teller; Walpole 2006 in U.S. Natl. Herb.

This northern race has a filiform style, which is firm and not fragile as in the more southern typical subspecies. We name it in honour of Dr MARGARET HEIMBURGER, an ardent student of the cytology of the collective genus *Anemone*.

Jurtsevia LÖVE & LÖVE, gen. nov.

Based on *Anemone* subgenus *Rivularidium* JANCZEWSKI, in Revue gén. Bot. 4 (1892), p. 251.

As pointed out by HOLUB (1973), the genus *Anemone* L. represents an unnatural aggregate even after the exclusion of *Hepatica* MILL. and *Pulsatilla* MILL. He defined it strictly as typified by *A. coronaria* L. (x=8) and separated from it the genera *Anemonoides* MILL. (x=8, 15) and *Anemonastrum* HOLUB (x=7). Even after this division, the genus remains heterogeneous, since the monotypic subgenus *Rivularidium* also deviates strongly in its morphology from the so restricted genus *Anemone* from which it also differs in having the basic chromosome number x=7 and morphologically different chromosomes. Its only species is a slender and delicate plant with filiform rootstocks, sparingly hirsute with deeply five-cleft basal leaves and three-cleft involucral leaves; the stems are 5—20 cm high and terminate in a solitary yellow flower which is 1.5—2.5 cm in diameter; the fruiting heads are subglobose, and the achenes are few and globose with a slender and hooked beak. It is a plant of snow-patches, herb-slopes and moist willow thickets in the northlands from Taimyr to Greenland, although LÖVE & LÖVE (1975 a) mistakingly omitted the number 6 (Greenland) from the information of its latitudinal distribution. We find it logical to propose the separation of this taxon under a new generic name. As such, we name it in honour of the very active arctic botanist, BORIS YURTSEV, and transfer its only species to the new genus:

Jurtsevia richardsonii (HOOK.) LÖVE & LÖVE, comb. nov., based on *Anemone Richardsonii* W. J. HOOKER, Flora Bor. Amer. 1 (1829), p. 6.

Anemonastrum narcissiflorum (L.) HOLUB

The widespread and variable species *Anemonastrum narcissiflorum* comprises sixteen major geographical races (HULTÉN 1944; LÖVE, LÖVE & KAPOOR 1971) of which three with outposts in the Arctic are in need of transfer:

Anemonastrum narcissiflorum ssp. **calvum** (JUZ.) LÖVE & LÖVE, stat. & comb. nov., based on *Anemone calva* JUZEPCZUK, in Flora SSSR 7 (1937), p. 279.

Anemonastrum narcissiflorum ssp. **sibiricum** (L.) LÖVE & LÖVE, comb. nov., based on *Anemone sibirica* L., Spec. plant. (1753), p. 541; *Anemone narcissiflora* L. ssp. *sibirica* (L.) HULTÉN.

Anemonastrum narcissiflorum ssp. **villosissimum** (DC.) LÖVE & LÖVE, comb. nov., based on *Anemone narcissiflora* ς

villosissima DE CANDOLLE, Prodr. 1 (1828), p. 22; *Anemone narcissiflora* ssp. *villosissima* (DC.) HULTÉN.

Atragene alpina L. ssp. **sibirica** (L.) LÖVE & LÖVE, comb. nov., based on *Atragene sibirica* LINNAEUS, Spec. plant. (1753), p. 343; *Clematis alpina* (L.) MILL. ssp. *sibirica* (L.) O. KUNTZE.

Since we favour the splitting of the genus *Clematis* L. of recent authors but agree that the Eurasiatic taxon reaching the Arctic is only a race of the alpine species, this transfer is required.

Batrachium circinatum (SIBTH.) SPACH ssp. **subrigidum** (DREW) LÖVE & LÖVE, stat. & comb. nov., based on *Ranunculus subrigidus* DREW, in Rhodora 38 (1936), p. 39.

This is the vicarious North American race of the Eurasiatic species.

Beckwithia glacialis (L.) LÖVE & LÖVE ssp. **chamissonis** (SCHLECHT.) LÖVE & LÖVE, comb. nov., based on *Ranunculus Chamissonis* SCHLECHTENDAL, Animadv. Ranunc. 1 (1819), p. 12; *Ranunculus glacialis* L. ssp. *Chamissonis* (SCHLECHT.) HULTÉN.

We agree with HULTÉN (1944) that the arctic Pacific taxon is most appropriately regarded as a subspecies of the Atlantic arctic-alpine species, which, however, we place in a distinct genus of its own. That requires the present transfer.

Cyrtorhyncha cymbalaria (PURSH) BRITT. ssp. **alpina** (HOOK.) LÖVE & LÖVE, comb. & stat. nov., based on *Ranunculus cymbalaria* PURSH var. *alpina* W. J. HOOKER, Flora Bor. Amer. 1 (1829), p. 11.

The representatives of the species in the western American mountains and in the Arctic from Alaska to Greenland clearly constitute a major rather than a minor geographical race.

Ranunculus hyperboreus ROTTB. ssp. **tricrenatus** (RUPR.) LÖVE & LÖVE, stat. nov., based on *Ranunculus hyperboreus* var. *tricrenatus* RUPRECHT, in Beitr. Pflanzenk. Russ. Reiches 2 (1845), p. 19.

This geographical race has been regarded as a variety only as recently as in the Flora Arctica USSR, although it certainly is no less distinct morphologically and geographically than are the generally accepted arctic races ssp. *hyperboreus* and ssp. *arnellii* SCHEUTZ. Therefore its validation at this level.

Ranunculus acris L.

We agree with ORLOVA (1956) that in addition to the more widespread and distinct low-grown race, ssp. *pumilus* (WG) LÖVE & LÖVE of this species of the arctic regions, two more taxa of this complex in northwestern Eurasia are worthy of recognition, although we are of the opinion that they are more correctly classified as subspecies than as species. At that level their names are:

Ranunculus acris ssp. **glabriusculus** (RUPR.) LÖVE & LÖVE, stat. & comb. nov., based on *Ranunculus glabriusculus* RUPRECHT, in Beitr. Pflanzenk. Russ. Reiches 2 (1845), p. 19.

Ranunculus acris ssp. **scandinavicus** (ORLOVA) LÖVE & LÖVE, stat. & comb. nov., based on *Ranunculus scandinavicus* ORLOVA, in Flora Murm. Obl. 3 (1956), p. 288; *Ranunculus silvaticus* FRIES, non THUILLIER; *Ranunculus acris* ssp. *stevenii* auct. scand., non ANDRZ., nec KORSH.

Papaver relictum (LUNDSTR.) NORDH. ssp. **hyperboreum** (NORDH.) LÖVE & LÖVE, comb. nov., based on *Papaver radicatum* ROTTB. ssp. *hyperboreum* NORDHAGEN, in Bergens Mus. Årbok 1931, Naturv. rekke 2, p. 48; *Papaver Nordhagenianum* Á. LÖVE ssp. *Nordhagenianum*.

This is the northern Scandinavian major race of the 70-chromosome Eurasiatic species of the genus.

Torularia (COSS.) O. E. SCHULZ

We regard it as advisable to accept the genus *Torularia* as distinct from *Braya* STERNB. & HOPPE to avoid heterogeneity of the latter. We also find it necessary to

divide the collective species *humilis* into units restricted by their morphology and single chromosome numbers. So defined, the genus includes two species in the Arctic, here validated:

Torularia arctica (BÖCHER) LÖVE & LÖVE, stat. & comb. nov., based on *Torularia humilis* (C. A. MEY.) O. E. SCHULZ ssp. *arctica* BÖCHER, in Medd. om Grönland 147,7 (1950), p. 29.

Torularia richardsonii (RYDB.) LÖVE & LÖVE, comb. nov., based on *Pilosella Richardsonii* RYDBERG, in Torreya 7 (1907), p. 159.

Boechera LÖVE & LÖVE, gen. nov.

Folia caulina integra, sagittata vel auriculata, amplectia, inferiora dense stellato-pilosa. Corolla alba ab purpurea. Pedicelli maturescentes deflexi vel appressi. Semina alata.

Numerus basicus chromosomatum x=7.

Typus generis: *Boechera holboellii* (HORNEM.) LÖVE & LÖVE.

Cauline leaves entire, sagittate or auriculate, clasping. Leaves of lower part of stem densely covered with minute stellate hairs. Corolla red-violet to white. Ripe fruiting pedicels distinctly deflexed or appressed to the rachis. Seeds winged. Basic chromosome number x=7.

This taxon, which traditionally has been included in the then very collective and heterogeneous genus *Arabis* L., is morphologically as well as cytologically (x=7 versus x=8) clearly distinct, especially when fruiting specimens are compared. We name it in honour of TYGE W. BÖCHER, an arctic botanist of great reputation who has studied this group in detail from various points of view for several decades. The genus includes several species of boreal and mountainous areas in North America, of which the following occur in the Arctic:

Boechera divaricarpa (A. NELSON) LÖVE & LÖVE, comb. nov., based on *Arabis divaricarpa* A. NELSON, in Bot. Gazette 30 (1900), p. 193.

Boechera drummondii (A. GRAY) LÖVE & LÖVE, comb. nov., based on *Arabis Drummondii* A. GRAY, in Proc. Amer. Acad. 6 (1862), p. 187.

Boechera holboellii (HORNEM.) LÖVE & LÖVE, comb. nov., based on *Arabis Holboellii* HORNEMANN, in Flora danica, fasc. 11 (1827), tab. 1879.

Boechera tenuis (BÖCHER) LÖVE & LÖVE, stat. & comb. nov., based on *Arabis Holboellii* var. *tenuis* BÖCHER, in Svensk Bot. Tidskr. 48 (1954), p. 38.

Noccaea MOENCH

The genus *Thlaspi* L. as treated in recent manuals is a heterogeneous group, and some of its socalled sections or subgenera are so distinct that their species never produce hybrids with those of other sections even under experimental pressure. Since the explanation of this lack of crossability of at least the morphologically well-defined section *Pterotropis* DC. is connected with certain features of the chromosomes that indicate a profound haplomic distinction, the separation of this section under the restricted generic name *Noccaea* seems to be well warranted. Two taxa reaching the arctic regions then require to be transferred to this genus:

Noccaea cochleariforme (DC.) LÖVE & LÖVE, comb. nov., based on *Thlaspi cochleariforme* DE CANDOLLE, Syst. nat. 2 (1821), p. 381.

Noccaea montana (L.) F. K. MEYER ssp. **arctica** (A. E. PORSILD) LÖVE & LÖVE, stat. & comb. nov., based on *Thlaspi arcticum* A. E. PORSILD, in Sargentia 4 (1943), p. 40.

Cochleariopsis LÖVE & LÖVE, gen. nov.

Plantae perennis humilis, 2—12 cm alta, multicaulis, rhizomate verticale, a basi ramosa et vix inflata, carnosa; caulibus saepius prostratis, folia radicalia longe petiolata, ovala vel ovata, obtusa, basi rotundata vel reniformi-cordata, post florationem mox emarcida. Folia caulinaria rhomboideo-elliptica, integra vel subhastato-trilobata. Racemi florentes densi, fructiferentes elongati. Flores

minores; stylus brevissimus, pedicelli patuli, capsula subglobosa vel elliptico-ovalis, laevis vel obsolete venosa, 2—3-plo longior quam lata. Siculae globosae, ellipsoideae, obovatae vel ambitu angustatae.

Numerus basicus chromosomatum x=7.

Typus generis: *Cochleariopsis groenlandica* (L.) LÖVE & LÖVE.

A low-growing perennial, 2—12 cm high, the rhizomes vertical with many stems, branched at the base and slightly inflated, fleshy; the stems are often prostrate; the basal leaves have long petioles, and are oval or ovate, obtuse, with a round or reniform-cordate base, withering soon after the flowers have fallen off. The blades of the stem leaves are shorter than the petioles, rhomboid-elliptic, entire or subhastate-trilobed. The racemes are densely covered with flowers and elongate when the fruits ripen. The flowers are small, with short styles, the pedicels spreading; the capsule is subglobose or elliptic-oval, veinless or scarcely veined and 2—3 times longer than broad. The silicules are globose, elliptic, obovate or in extreme cases also narrowed. Basic chromosome number x=7.

The collective nature of the genus *Cochlearia* L. as traditionally circumscribed has become evident through intensive cytotaxonomical studies, which have shown that the taxon actually consists of two morphologically and geographically distinct groups which also differ in their basic chromosome numbers and chromosome morphology and never hybridize, whereas crosses between taxa of each group are more easily produced and also occur in nature. Since the Linnaean genus is typified by *C. officinalis* L., the group with x=6 must be retained as *Cochlearia* s. str., whereas we propose the new name *Cochleariopsis* for the arctic taxon with x=7. The latter includes only a single diploid species with three variable subspecies, in contrast to several distinct species of a polyploid series of the restricted Linnaean genus. The following taxa need to be transferred to the new genus:

Cochleariopsis groenlandica (L.) LÖVE & LÖVE, comb. nov., based on *Cochlearia groenlandica* LINNAEUS, Spec. plant. (1753), p. 647.

Cochleariopsis groenlandica ssp. **arctica** SCHLECHT.) LÖVE & LÖVE, comb. nov., based on *Cochlearia arctica* SCHLECHTENDAL, in DC. Reg. Veg. Syst. Nat. 2 (1821), p. 367; *Cochlearia officinalis* L. ssp. *arctica* (SCHLECHT.) HULTÉN.

Cochleariopsis groenlandica ssp. **oblongifolia** (DC.) LÖVE & LÖVE, comb. nov., based on *Cochlearia oblongifolia* DE CANDOLLE, Reg. Veg. Syst. Nat. 2 (1821), p. 363; *Cochlearia officinalis* ssp. *oblongifolia* (DC.) HULTÉN.

Tolmachevia LÖVE & LÖVE, gen. nov.

Plantae perennis. Caudex crassus ramosus; caulibus plerumque paucis. Folia obovata, lanceolata vel oblonga ovata, approximata. Inflorescentia cymosa, densa, terminalis; flores polygami, pentameri raro tetrameri, purpureo-rosei vel viridi-purpurei vel flavi. Folliculi apocarpa.

Numerus basicus chromosomatum x=9.

Typus generis: *Tolmachevia integrifolia* (RAFIN.) LÖVE & LÖVE.

Perennial plants. The rootstock is thick and branched; the stems are often few. The leaves are obovate-lanceolate or oblong-ovate, close together. The inflorescences are a terminal and dense cyme. The flowers are polygamous, pentamerous or rarely tetramerous, purple-red or greenish-purple or yellow. The follicles are apocarpous. Basic chromosome number x=9.

This western North American and eastern Asiatic genus is biologically most clearly distinguished from *Rhodiola* L. by having polygamous flowers and the basic chromosome number x=9 as contrasted to the dioecious character of the Linnaean genus with its basic number x=11. Its polygamous condition also separates it from the arctic-alpine Eurasiatic *Kirpicznikovia* validated below and from the apparently monotypic Rocky Mountain *Clementsia rhodantha* (A. GRAY) ROSE, both of which have hermaphroditic flowers and

seem to be characterized by the basic chromosome number x=7. We have the pleasure of naming this beautiful arctic-alpine genus in honour of ALEKSANDR I. TOLMACHEV, the eminent master of Russian arctic botany and a longtime friend. It includes the following three species:

Tolmachevia atropurpurea (TURCZ.) LÖVE & LÖVE, comb. nov., based on *Sedum atropurpureum* TURCZANINOV, in Bull. Soc. Mosc. 1 (1840), p. 13, 70.

Tolmachevia integrifolia (RAFIN.) LÖVE & LÖVE, comb. nov., based on *Rhodiola integrifolia* RAFINESQUE, Atl. Journ. 1 (1832), p. 146.

Tolmachevia krivochzhinii (SIPL.) LÖVE & LÖVE, comb. nov., based on *Rhodiola Krivochzhinii* SIPLIVINSKY, in KRIVOCHZHIN & SIPLIVINSKY, in Novit. Syst. Plant. Vasc. 11 (1974), p. 313.

Kirpicznikovia LÖVE & LÖVE, gen. nov.

Based on *Rhodiola* sect. *Chamae-Rhodiola* BORISSOVA, in Novit. Syst. Plant. Vasc. 6 (1969), p. 114.

Typus generis: *Kirpicznikovia quadrifida* (PALL.) LÖVE & LÖVE.

This genus of seven alpine species of which the single one reaching the Arctic is transferred below, is distinguished by its hermaphroditic usually pentamerous and large white, red or rarely yellowish flowers with the stamens attached to the upper part of the petals; it has a thick and branched rootstock, the leaves are linear to oblong and entire, and the numerous stems are short, clustered and persistent. We have the pleasure of naming it after our longtime friend, M. E. KIRPICZNIKOV, who is a specialist on Asiatic plants and one of the good contributors to the Flora SSSR.

Kirpicznikovia quadrifida (PALL.) LÖVE & LÖVE, comb. nov., based on *Sedum quadrifidum* PALLAS, Reise III, Anh. (1776), p. 730.

Saxifraga monticola (SMALL) LÖVE & LÖVE, comb. nov., based on *Muscaria monticola* SMALL, in North Amer. Flora 22 (1905), p. 130.

This arctic eastern Asiatic and Canadian taxon of the group related to *S. caespitosa* L. is apparently a species in its own right, differing morphologically, geographically and cytologically from the circumpolar decaploid complex since it is only a hexaploid.

Alchemilla L.

It seems advisable to regard the apomictic microspecies of *Alchemilla* that reach the arctic regions only as subspecies of the species *A. vulgaris* L., since they are morphologically and geographically comparable to that category of other species, despite being obligately apomictic. The following three taxa are then in need of being transferred to that level:

Alchemilla vulgaris ssp. **oxyodonta** (BUSER) LÖVE & LÖVE, comb. nov., based on *Alchemilla acutidens* BUSER ssp. *oxyodonta* BUSER, in Bot. Not. 1906, p. 141.

Alchemilla vulgaris ssp. **transpolaris** (JUZ.) LÖVE & LÖVE, stat. & comb. nov., based on *Alchemilla transpolaris* JUZEPCZUK, in Bot. Mat. 16 (1954), p. 179.

Alchemilla vulgaris ssp. **vestita** (BUSER) LÖVE & LÖVE, stat. & comb. nov., based on *Alchemilla filicaulis* BUSER var. *vestita* BUSER, in Bull. Herb. Boissier 1 (1893), Appendix 2, p. 22.

Astragalus astragalinus (HOOK.) LÖVE & LÖVE, comb. nov., based on *Phaca astragalina* W. J. HOOKER, Flora Bor. Amer. 1 (1833), p. 145; *Astragalus alpinus* L. ssp. *alaskanus* HULTÉN.

This taxon was reduced to the subspecific level of *A. alpinus* by HULTÉN (1947), and two decades later, HULTÉN (1968) claimed that it and ssp. *alpinus* "form introgression". This is clearly based on the same misuse of this term for morphological indications of alloploidy as by HULTÉN (1956), since *A. alpinus* s. str. is a diploid plant, whereas ssp. *alaskanus* is a tetraploid of which *A. alpinus* may

be one of the parental species. It is evident that the taxon is a species in its own right and so we transfer its name to that level.

Oxytropis taimyrensis (JURTSEV) LÖVE & LÖVE, stat. & comb. nov., based on *Oxytropis arctica* R. BR. ssp. *taimyrensis* JURTSEV, in Bot. Mat. 19 (1959), p. 239.

Recent studies have shown that this taxon is an octoploid plant with 2n=64 chromosomes, whereas *O. arctica* is a dodecaploid with 2n=96, thus indicating that their relationship may be more remote than originally surmised and their taxonomical level similar. Therefore this transfer to a higher level.

Callitriche anceps FERN. ssp. **subanceps** (V. PETR.) LÖVE & LÖVE, stat. & comb. nov., based on *Callitriche subanceps* V. PETROV, in Izvest. Glavn. Bot. Sada 27 (1928), p. 359.

The North American species *C. anceps*, which reaches from Greenland to Alaska in the American northlands, is represented in easternmost Asia by this morphologically and cytologically very closely related vicarious taxon, which certainly is best regarded as a subspecies only.

Viola epipsiloides LÖVE & LÖVE, nom. nov., based on *Viola repens* TURCZANINOV ex TRAUTVETTER & MEYER, in MIDDENDORF, Reise Sibir. 1,2,2 (1856), p. 18; non *Viola repens* SCHWEINITZ.

A new name is required for this species of the eastern Siberian and western North American arctic-alpine regions, because of an earlier homonym. It has frequently been wrongly identified with the Eurasiatic *V. epipsila* LEDEB. to which it does not seem to be even remotely related.

Viola aduncoides LÖVE & LÖVE, spec. nov.

Planta perennis; folia longi-petiolata, subcoriacea, ovata, cordata, glabrata vel dense pubescentia, pilis brevis (minus 0.2 mm longi); stipulae lineari-lanceolatae, integrae vel spinulosi-dentatae; corolla caerulea-purpurea, 10—15 mm longa. Projectura in styli capitata globosa, 1/10 vel minus latitudo capitis; capsula 4—5 mm longa; semina atrofusca. Numerus chromosomatum 2n=40.

Holotypus: Canada, Manitoba, Árnes, meadow along poplar shrub, May 5, 1953, LÖVE & LÖVE 5744 in Herb. Winnipeg.

A perennial plant with long-petioled leaves which are subcoriaceous, ovate and cordate, glabrous or densely pubescent with short hairs (less than 0.2 mm long); the stipules are linear-lanceolate, entire or spinulose-dentate; the corolla is bluish-purple, 10—15 mm long. Projections on the upper tip of the style head are short-conical or globular, 1/10 or less the width of the style head. The capsule is 4—5 mm long; the seeds are dark-brown. Chromosome number 2n=40.

This North American tetraploid species differs from the diploid *V. adunca* SM. in the form of the style head and the smaller projections on it, the shorter hairs on the leaves when present, and in the size of guard cells and pollen grains (MCPHERSON & PACKER 1974). It is apparently an hemiautoploid (LÖVE & LÖVE 1975 c) of Pleistocene origin as indicated by its distribution.

Chamerion platyphyllum (DANIELS) LÖVE & LÖVE, comb. nov., based on *Chamaenerion angustifolium* (L.) SCOP. var. *platyphyllum* DANIELS, in Univ. Missouri Studies 2,2 (1911), p. 176; *Epilobium Danielsii* D. LÖVE; *Epilobium platyphyllum* (DANIELS) LÖVE & LÖVE, non RYDBERG.

This is the octoploid (2n=72) taxon of southern boreal mountains in eastern North America and the western mountains north to the arctic regions, corresponding to the more northern circumpolar *C. angustifolium* (L.) HOLUB. For a discussion of the genus and its correct name, see HOLUB (1972).

Chamerion subdentatum (RYDB.) LÖVE & LÖVE, comb. nov., based on *Chamaenerion subdentatum* RYDBERG, Flora Rocky Mts. (1917), p. 585.

This is the tetraploid mainly western American and eastern Asiatic alpine taxon corresponding to the more widespread and almost circumpolar arctic-alpine octoploid species *C. latifolium* (L.) HOLUB.

Coelopleurum lucidum (L.) FERN. ssp. **gmelinii** (DC.) LÖVE & LÖVE, stat. & comb. nov., based on *Archangelica Gmelinii* DE CANDOLLE, Prodr. 4 (1830), p. 170.

This is the Pacific vicarious race of the otherwise eastern North American species.

Conioselinum chinense (L.) B.S.P. ssp. **boreale** (SCHISCHKIN) LÖVE & LÖVE, stat. & comb. nov., based on *Conioselinum boreale* SCHISCHKIN, in Flora SSSR 17 (1951), p. 351.

This race is the northernmost European population of this widespread and variable species.

Pyrola rotundifolia L. ssp. **asarifolia** (MICHX.) LÖVE & LÖVE, stat. & comb. nov., based on *Pyrola asarifolia* MICHAUX, Flora Bor. Amer. 1 (1803), p. 251.

This vicarious race replaces the ssp. *rotundifolia* of Eurasia in North America and eastern Asia.

Douglasia LINDL.

This genus is closely related to *Androsace* L. from which it differs in some technical characters and also in the apparently derived basic chromosome number x=19 as contrasted to x=10. It is represented in the northlands by three taxa which we believe are most adequately classified as subspecies only of the species *D. ochotensis* (WILLD.) HULTÉN. Two of these are here transferred to this level:

Douglasia ochotensis ssp. **arctica** (CHAM. & SCHLECHT.) LÖVE & LÖVE, stat. & comb. nov., based on *Androsace arctica* CHAMISSO & SCHLECHTENDAL, in Linnaea 1 (1826), p. 220.

Douglasia ochotensis ssp. **gormanii** (GREENE) LÖVE & LÖVE, stat. & comb. nov., based on *Androsace Gormanii* GREENE, in Pittonia 4 (1900), p. 149; *Douglasia Gormanii* (GREENE) CONSTANCE.

Primula tschuktschorum KJELLM. ssp. **arctica** (KOIDZ.) LÖVE & LÖVE, stat. & comb. nov., based on *Primula arctica* KOIDZUMI, in Bot. Mag. Tokyo 25 (1911), p. 216.

We believe that the three rather distinct variations of this Beringian species are correctly classified as three subspecies, although the opinion could also be defended that they may be minor geographical races and then only varieties. A transfer is needed for one of these taxa that has even been described as a species under three different names.

Gentiana L.

The collective genus *Gentiana* needs to be divided into several more natural genera, as demonstrated by several authors during the past two decades. Of these groups, *Ciminalis* ADANS.; HOLUB, *Calathiana* DELARBRE, *Comastoma* (WETTST.) TOYOKUNI, *Gentianella* MOENCH, *Gentianodes* LÖVE & LÖVE, *Gentianopsis* MA and *Lomatogonium* R. BR. are represented in the arctic regions, but only one species and one subspecies of these are in need of a transfer:

Ciminalis prostrata (HAENKE) LÖVE & LÖVE, comb. nov., based on *Gentiana prostrata* HAENKE, in JACQUIN, Collectanea 2 (1788), p. 66.

Gentianopsis detonsa (ROTTB.) MA ssp. **raupii** (A. E. PORSILD) LÖVE & LÖVE, comb. nov., based on *Gentiana Raupii* A. E. PORSILD, in Sargentia 4 (1943), p. 60; *Gentianella detonsa* (ROTTB.) G. DON ssp. *Raupii* (A. E. PORSILD) J. M. GILLETT.

Polemonium boreale ADAMS ssp. **humile** (WILLD.) LÖVE & LÖVE, stat. & comb. nov., based on *Polemonium humile* WILLDENOW ex ROEMER & SCHULTES, Syst. Veget. 4 (1819), p. 792, non SALISBURY; *Polemonium Hultenii* HARA.

This is the northern Siberian race of the species.

Polemonium pulcherrimum HOOK. ssp. **hyperboreum** (TOLM.) LÖVE & LÖVE, stat. & comb. nov., based on *Polemonium hyperboreum* TOLMACHEV, in Feddes Repert. 23 (1927), p. 273.

This is the Siberian subspecies of the species, the typical race of which is met with in the mountains and northlands of North America.

Phlox sibirica L. ssp. **alaskensis** (JORDAL) LÖVE & LÖVE, comb. nov., based on *Phlox alaskensis* JORDAL, in Rhodora 54 (1952), p. 38; *Phlox Richardsonii* HOOK. ssp. *alaskensis* (JORDAL) WHERRY.

Pseudolysimachium OPIZ

The splitting of the collective genus *Veronica* L. has been made on basis of morphological differences only, but these are strongly supported also by differences in basic chromosome numbers, since *Veronica* L., s. str. is characterized by x=8, 9, whereas *Veronicastrum* MOENCH has x=7 and *Pseudolysimachium* OPIZ has x=17. Two of the species belonging to the last genus and occurring in the northlands require a transfer:

Pseudolysimachium maritimum (L.) LÖVE & LÖVE, comb. nov., based on *Veronica maritima* LINNAEUS, Spec. plant. (1753), p. 10.

Pseudolysimachium septentrionale (BORISS.) LÖVE & LÖVE, comb. nov., based on *Veronica septentrionalis* BORISSOVA, in Flora SSSR 22 (1955), p. 369.

Castilleja pallida (L.) KUNTH

This northern species is represented in the arctic tundra by three evidently major geographical races, which REBRISTAIA (1964) regarded as distinct species. Although they are admittedly rather distinct morphologically, this seems to be the result of an almost obligate autogamy rather than of the occurrence of reproductive isolation, so we see no reason to classify them higher than as subspecies, as here validated:

Castilleja pallida ssp. **hyparctica** (REBR.) LÖVE & LÖVE, stat. & comb. nov., based on *Castilleja hyparctica* REBRISTAIA, in Novit. Syst. Plant. Vasc. 1 (1964), p. 289.

Castilleja pallida ssp. **lapponica** (GANDOGER) LÖVE & LÖVE, stat. & comb. nov., based on *Castilleja lapponica* GANDOGER, Flora Europ. 18 (1889), p. 25.

Castilleja pallida ssp. **pavlovii** (REBR.) LÖVE & LÖVE, stat. & comb. nov., based on *Castilleja Pavlovii* REBRISTAIA, in Novit. Syst. Plant. Vasc. 1 (1964), p. 294.

Pedicullariopsis LÖVE & LÖVE, gen. nov.

Plantae perennis, humilis, superne pilosa vel glabra; foliis profunde pinnatifidis pinnatipartisve, laciniis ovatis oblongisve pinnatopinnatifidis, lobis dentatis; spicis interruptis; calycis dentibus abbreviatis integerrimis serrulatisve; corolla tubo basi infracto; galea erostrata, obtusa, labium duplo superans.

Numerus basicus chromosomatum x=6.

Typus generis: *Pedicullariopsis verticillata* (L.) LÖVE & LÖVE.

Perennial plants, erect but low growing, above pilose or glabrous. The stem leaves are in 3—4 whorls, deeply pinnatifid or pinnately partite, and the divisions are ovate-oblongish pinnato-pinnatifid, the lobes are toothed. The spikes are interrupted; the calyx has short teeth that are entire or finely serrate; the corolla tube is sharply bent at the base, the helmet is beakless and obtuse and twice the size of the lower lip. Basic chromosome number x=6.

The new genus differs from *Pedicularis* L. in several characters of the flowers, the arrangement of the spike and in leaf morphology, but the most profound difference is in its chromosome morphology and in the basic number x=6 as contrasted to x=8 of the Linnaean genus. It includes a single but not very variable species of considerable arctic-alpine distribution:

Pedicullariopsis verticillata (L.) LÖVE & LÖVE, comb. nov., based on *Pedicularis verticillata* LINNAEUS, Spec. plant. (1753), p. 846.

Chlorocrepis tristis (WILLD.) LÖVE & LÖVE, comb. nov., based on *Hieracium*

triste WILLDENOW ex SPRENGEL, Syst. veget. 3 (1826), p. 640.

This transfer is needed when the three traditionally accepted subgenera of *Hieracium* L. are elevated to generic rank.

Crepis tectorum L. ssp. **nigrescens** (POHLE) LÖVE & LÖVE, stat & comb. nov., based on *Crepis nigrescens* POHLE, in Acta Hort. Jurjev. 3 (1903), p. 231.

This taxon of northernmost Europe and western Siberia is often regarded as a synonym only of *C. tectorum,* even if some authors accept it as a species in its own right. Although some of its few characteristics are perhaps only modifications of no taxonomical importance, others seem to be genetically conditioned. Since it also has a distinct area of its own, we find it logical to accept it as a race at the subspecific level rather than to ignore it.

Antennaria canescens (LGE) MALTE ssp. **porsildii** (E. EKM.) LÖVE & LÖVE, stat. & comb. nov., based on *Antennaria Porsildii* E. EKMAN, in Svensk Bot. Tidskr. 21 (1927), p. 51.

This is an apomictic and endemic Greenland population of a rather widespread apomictic complex, which certainly was given too high a rank when described as a species. It might even be more correctly classified as a variety only or as a hybrid that has survived simply thanks to its being apomictic.

Nardosmia arctica (A. E. PORSILD) LÖVE & LÖVE, comb. nov., based on *Petasites arcticus* A. E. PORSILD, in Sargentia 4 (1943), p. 74.

The certainly good reasons for keeping this genus as separate from *Petasites* in a more strict sense, given by KUPRIYANOVA (1961), require a transfer of this arctic Canadian taxon.

Nardosmia vitifolia (GREENE) LÖVE & LÖVE, comb. nov., based on *Petasites vitifolius* GREENE, in Leafl. West. Bot. 1 (1906), p. 180.

Another Canadian taxon requiring transfer to this restricted genus.

Endocellion TURCZ.

There are valid morphological and cytological reasons to distinguish the genus *Nardosmia* CASS. from *Petasites* MILL., although both are characterized by the same basic number, x=10. However, we find it illogical to attach to the former the small Asiatic group that has been described as the genus *Endocellion,* even as a subgenus as done by KUPRIYANOVA (1961), since it is not only morphologically distinct but differs also in having the basic number x=7 in addition to a considerably different chromosome morphology. The following two of its three eastern Asiatic arctic-alpine species require a transfer:

Endocellion glacialis (LEDEB.) LÖVE & LÖVE, comb. nov., based on *Nardosmia glacialis* LEDEBOUR, Flora rossica 2,2 (1845), p. 466.

Endocellion gmelinii (TURCZ.) LÖVE & LÖVE, comb. nov., based on *Nardosma Gmelinii* TURCZANINOV, ex DC., Prodr. 7,1 (1838), p. 271.

Tephroseris (RCHB.) RCHB.

As shown by HOLUB (1973), this boreal group which is traditionally included in the then very collective genus *Senecio* L., is morphologically best distinguished by its absence of outer involucral bracts, in addition to several less obvious technical characters. Its most profound biological difference that clearly sets it apart as an evolutionary unit of considerable distinction is, however, the fact that its basic chromosome number is x=8 as contrasted to x=10 of *Senecio* proper. HOLUB (l.c.) recommends that the group be accepted as a genus of its own, an opinion which we endorse on basis of longtime observations of its European and North American representatives. The following new combinations for taxa of the northlands are required:

Tephroseris aquilonaris (SCHISCHKIN) LÖVE & LÖVE, comb. nov., based on *Senecio aquilonaris* SCHISCHKIN, in Flora SSSR 26 (1961), p. 884.

Tephroseris atropurpurea (LEDEB.) HOLUB ssp. **frigida** (RICHARDS.) LÖVE & LÖVE, stat. & comb. nov., based on *Cineraria frigida* RICHARDSON, in Bot. Appendix to FRANKLIN, Narr. of Journ. (1823), p. 748.

Tephroseris atropurpurea ssp. **tomentosa** (KJELLM.) LÖVE & LÖVE, comb. nov., based on *Cineraria frigida* f. *tomentosa* KJELLM., in Vega Exp. Vetensk. Iaktt. 2 (1883), p. 13; *Senecio atropurpureus* (LEDEB.) FEDTSCH. ssp. *tomentosus* (KJELLM.) HULTÉN.

Tephroseris lindstroemii (OSTENF.) LÖVE & LÖVE, comb. nov., based on *Senecio integrifolius* (L.) CLAIRV. var. *Lindstroemii* OSTENFELD, Christiania Vidensk. Selsk. Skr. 1909, No. 8 (1910), p. 70; *Senecio Lindstroemii* A. E. PORSILD.

Packera LÖVE & LÖVE, gen. nov.

Plantae perennis, herbaceae. Caules non rite foliosi. Caudex sine rhizoma repens vel suberectus. Folia simplicia et integra ad lyrato-pinnatifida, folia radicalia petiolata, caulinaria amilia vel minora. Plantae glabratae alteruter ab initium vel plus minusve permanentes tomentosae; pubescentia nunquam e pilis longis articulatisque.

Numerus basicus chromosomatum x=23.

Typus generis: *Packera aurea* (L.) LÖVE & LÖVE.

Herbaceous perennials. Stems not uniformly leafy to the inflorescences, arising from a horizontal to suberect caudex or rhizome. Leaves simple and entire to lyrate-pinnatifid, those at the base petiolate, gradually reduced upwards, or uniform throughout. Plants either quite glabrous from the beginning or more or less permanently tomentose; pubescence never of long jointed hairs. Basic chromosome number x=23.

This mainly North and South American genus with a few representatives in Asia comprises the groups *Aurei, Lobati* and *Tomentosi* of the collective genus *Senecio* as described by RYDBERG (1900) and GREENMAN (1916), which stand apart from the other divisions of the collective aggregate by having prolonged rhizomes, and if pubescence is present it is a tomentum of more or less arachnoid and never of long and jointed hairs, but persistent as flocculent tufts. Its morphological and geographical distinctions are enhanced by its basic chromosome number, which differs markedly from that of *Senecio* L. s. str. (x=10) and *Tephroseris* (RCHB.) RCHB. (x=8) so that its distinction as a genus is biologically well substantiated. It is our pleasure to name the new genus in honour of JOHN G. PACKER, an oldtime friend who has contributed much to the clarification of the status of the arctic-alpine North American members of the taxon. Its arctic taxa are:

Packera aurea (L.) LÖVE & LÖVE, comb. nov., based on *Senecio aurea* LINNAEUS, Spec. plant. (1753), p. 270.

Packera fernaldii (GREENM.) LÖVE & LÖVE, comb. nov., based on *Senecio Fernaldii* GREENMAN, in Ann. Missouri Bot. Gard. 3 (1916), p. 90.

Packera hyperborealis (GREENM.) LÖVE & LÖVE, comb. nov., based on *Senecio hyperborealis* GREENMAN, in Ann. Missouri Bot. Gard. 3 (1916), p. 98.

Packera indecora (GREENE) LÖVE & LÖVE, comb. nov., based on *Senecio indecorus* GREENE, Flora Franciscana (1897), p. 470.

Packera ogotorukensis (PACKER) LÖVE & LÖVE, comb. nov., based on *Senecio ogotorukensis* PACKER, in Canad. Journ. Bot. 50 (1972), p. 511; *Senecio conterminus* auct. Alaska, non GREENMAN.

Packera pauciflora (PURSH) LÖVE & LÖVE, comb. nov., based on *Senecio pauciflorus* PURSH, Flora Amer. Sept. 2 (1814), p. 529.

Packera paupercula (MICHX.) LÖVE & LÖVE, comb. nov., based on *Senecio pauperculus* MICHAUX, Flora Bor. Amer. 2 (1803), p. 120.

Packera resedifolia (LESS.) LÖVE & LÖVE, comb. nov., based on *Senecio resedifolius* LESSING, in Linnaea 6 (1831), p. 243.

Aster L.

We find it more logical to regard the five taxa of arctic *Aster* as representing three and two subspecies only of the two species *A. sibiricus* L. and *A. alpinus* L., rather than as species as accepted in recent manuals. As such the following new levels and combinations are validated:

Aster sibiricus L. ssp. **pygmaeus** (LINDLEY) LÖVE & LÖVE, stat. & comb. nov., based on *Aster pygmaeus* LINDLEY, in W. J. HOOKER, Flora Bor. Amer. 2 (1834), p. 6.

Aster sibiricus ssp. **richardsonii** (SPRENG.) LÖVE & LÖVE, stat. & comb. nov., based on *Aster Richardsonii* SPRENGEL, Syst. Veg. 3 (1826), p. 258.

Aster sibiricus ssp. **subintegerrimus** (TRAUTV.) LÖVE & LÖVE, stat. nov., based on *Aster sibiricus* var. *subintegerrima* TRAUTVETTER, in MIDDENDORF, Reise 1 (1847), p. 161.

Aster alpinus L. ssp. **serpentimontanus** (TAMAMSCH.) LÖVE & LÖVE, stat. & comb. nov., based on *Aster serpentimontanus* TAMAMSCHAN, in Flora SSSR 25 (1959), p. 108, and *Aster cyllenius* ONNO, in Bibl. Bot. 106 (1932), p. 38, p.p., non HALACSY.

Aster alpinus ssp. **tolmatschevii** TAMAMSCH.) LÖVE & LÖVE, stat. & comb. nov., based on *Aster Tolmatschevii* TAMAMSCHAN, in Flora SSSR 25 (1959), p. 107, and *Aster chryzocomoides* DE CANDOLLE, Prodr. 7 (1838), non DESFONTAINES.

Matricaria maritima L. ssp. **boreale** (HARTM.) LÖVE & LÖVE, comb. nov., based on *Tripleurospermum inodorum* SCHULZ-BIP. β *borealis* C. J. HARTMAN, Handb. i Skand. Flora, ed. 5 (1849), p. 2; *Tripleurospermum maritimum* (L.) KOCH ssp. *borealis* (HARTM.) A. PEDERSEN.

We follow the typification of the genus by RAUSCHERT (1974), and refer to HÄMET-AHTI (1967) and PEDERSEN (1972) for clarification of the North Atlantic races of *M. maritima.*

Erigeron thunbergii A. GRAY ssp. **komarovii** (BOTSCH.) LÖVE & LÖVE, stat. & comb. nov., based on *Erigeron Komarovii* BOTSCHANTSEV, in Flora SSSR 25 (1959), p. 213.

Erigeron thunbergii ssp. **koraginensis** (KOM.) LÖVE & LÖVE, stat. & comb. nov., based on *Aster koraginensis* KOMAROV, Flora Kamch. 3 (1930), p. 125.

Erigeron uniflorum L. ssp. **eriocalyx** (LEDEB.) LÖVE & LÖVE, stat. & comb. nov., based on *Erigeron alpinus* L. β *eriocalyx* LEDEBOUR, Flora Altai 4 (1833), p. 91.

Tanacetum vulgare L. ssp. **boreale** (FISCH.) LÖVE & LÖVE, stat. & comb. nov., based on *Tanacetum boreale* FISCHER, ex DC. Prodr. 6 (1838), p. 128.

This is a distinct eastern Asiatic arctic-alpine major race of this common boreal Eurasiatic species, distinguished by its more dissected leaves with narrow and sharply serrulated segments.

Oligosporus groenlandicus (HORNEM.) LÖVE & LÖVE, comb. nov., based on *Artemisia groenlandica* HORNEMANN, Flora danica, fasc. 27 (1818), tab. 1585; *Artemisia borealis* PALL. ssp. *Purshii* (BESS.) HULTÉN; *Artemisia campestris* L. ssp. *spithamea* HALL & CLEM., non *Artemisia spithamea* PURSH.

We find it logical to break up the very heterogeneous *Artemisia* L. into more natural units, as advocated by POLYAKOV (1961), and so accept the generic name *Oligosporus* CASS. for the species traditionally constituting the section or subgenus *Dracunculus.* That genus is characterized by having a smooth and not hairy receptacle and disc-flowers with both stamens and pistils but sterile because of an abortive ovary, and by having an entire or nearly entire style, in addition to other technical differences.

As shown by HULTÉN (1950), the considerable diversity of the arctic-alpine populations that are usually included in the species *Artemisia borealis,* falls nicely into two major groups, which he regarded as major geographical races and separated as the typical taxon and its ssp. *purshii.* Since these taxa have been found to differ in chromosome number so they are certainly reproductively isolated, we find it more appropriate to accept them as distinct species and adopt for the latter its old and validly published name *groenlandicus.* Typical *Oligosporus borealis* (PALL.) POLYAK., as its name must be in the restricted genus, was described from the neighborhood of the Ob river of Siberia. It is a plant with more or less densely and loosely pubescent leaves, the upper ones lobed and the lower ones small with a few broad lobes, and with relatively large (5—6 mm broad) heads with a glabrous involucrum and forming dense and usually unbranched spikes. *O. groenlandicus,* however, which was originally described from western Greenland, is a plant with densely sericeous or pubescent basal leaves which are 2—3 times pinnatifid with narrow lobes, and with smaller (3—4 mm broad) globular heads with pubescent or glabrous involucrum and forming thin spikes. The former taxon is tetraploid with 2n=36 chromosomes, but the latter is diploid with 2n=18. Both are arctic-alpine. The tetraploid reaches from northern European Russia over Siberia to Labrador and western Greenland, where it is relatively common. The diploid is met with from lower Yenissei east to Baffin Island and western Greenland, where it is rare; however, it seems to reach farther north in North America than the tetraploid and grows also in southern mountains in Asia and in Gaspé and the Rocky Mountains of Colorado in North America.

SOME CORRECTIONS

A few obvious misprints have crept in on a few pages of LÖVE & LÖVE (1975 a), but only the following omissions and oversights need to be pointed out:

p. XIV: The important reference to DOROGOSTAISKAYA (1972) has been omitted.

p. 9: The author of the family Botrychiaceae is NAKAI.

p. 320: The reference year 1969 b has fallen out after MULLIGAN & PORSILD for the chromosome report for *Saxifraga adscendens* ssp. *oregonensis.*

p. 596: Lagotis 433 has been omitted from the index.

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Botanical Literature

LÖVE, Á. & LÖVE, D.: Cytotaxonomic Atlas of the Arctic flora. — J. Cramer, Vaduz 1975. ISBN 3-7682-0976-8. xxiii+598 pp. Price (subscription) DM 160:—; (regular) DM 200:—.

The second of a projected series of cytotaxonomic atlases by Á. and D. LÖVE has appeared. (Why, it could be asked, are they called atlases?) The first is that on Slovenian plants reviewed by me in Botaniska Notiser 128: 551—553, where I stressed the significance of the Slovenian list. This in my opinion lies in its usefulness as a source of references to the literature dealing with all vascular plants found in Slovenia (using the taxonomic concept of the authors). In addition, however, I delivered a somewhat lengthy criticism of some of the basic principles presented and exemplified the disadvantages of the "critical" method employed. As the same criticism applies to this volume the reader is referred to the former review.

I have studied the new Atlas of Arctic plants with particular interest, both by reason of my experience of the first Atlas and because my own research has at times brought me into contact with Arctic botany. The book serves the dual purpose of being both a check-list of Arctic taxa and a critical review of their chromosome numbers. The area covered is rather more extensive than the term "arctic" usually implies which is scarcely a disadvantage in this context. This is, however, not the only reason why the number of genera presented has increased by 75 % and the number of species by over 80 % as compared with those dealt with by POLUNIN in his Circumpolar Arctic Flora (1959). The main reason for the discrepancy is of course the difference in taxonomic concepts adopted. POLUNIN used a somewhat collective concept whereas LÖVE and LÖVE are splitters in the extreme. They employ a "biological" or "evolutionary" concept, which implies that a taxon at generic level or lower is defined "biologically" but identified morphologically. More than one basic chromosome number is not tolerated within a single genus, and a correctly and exactly defined species must have one single chromosome number only. In most cases this does not give rise to conflict but the outcome can at times be surprising. *Minuartia*, for example, has been virtually reduced to fragments, and several other genera have been split up. There has also rarely been some lumping, an example being the merging of *Puccinellia* and *Phippsia* with the latter name having been given priority. For practical reasons it might have been wiser to have proposed the conservation of *Puccinellia*. The taxonomic and nomenclatural changes will probably provoke considerable irritation but should perhaps not be regarded as being controversial as they mainly reflect differences of personal opinion. Validations of new taxa and combinations are made in a paper appearing in this issue of Botaniska Notiser (pp. 497—523).

My own limited knowledge of the vast field of the cytotaxonomy of Arctic plants does not permit me to check the overall reliability of the information in the list. As when reviewing the first Atlas I chose to check a genus with which I am familiar, in this case the grass genus *Hierochloë*. The result was both astonishing and disturbing. There is, for instance, no reference to ZHUKOVA's report (1967) on the chromosome number 2n=56 in *H. alpina* nor to my report (1970) on 2n=66 in the same taxon, nor to my report (1971) on 2n=58 in *H. monticola* (*H. orthantha*, *H. alpina* ssp. *orthantha*), nor to my reports (1971, 1973) on 2n=72, 75, 76 and 77 in *H. alpina*. All these reports except ZHUKOVA's represent deviations from the

normal euploid conditions within the taxa. *H. odorata* has not been listed for Greenland where it has been collected from one place (voucher at C). In *H. hirta* ssp. *arctica*, 2n=56 (WEIMARCK 1971) should have been underlined as it has been determined from Arctic material as geographically delimited here. If the omissions are due to oversight there is a severe risk that there may be other accidental omissions and mistakes in the list which would diminish its value catastrophically. On the other hand I must react adversely if the authors should have omitted the information as being "apparently incorrect or inexact", "obviously wrong or taxonomically suspect" or "scientifically worthless and . . . directly misleading to those less familiar with the cytotaxonomical method" (quoted from the reasons given for the exclusion of certain references). I consider that it is the author's responsibility to decide whether the information he publishes is correct, and that no attempt at screening should be made by the compilers of a list of this type.

It is to be hoped that this one unfortunate example is not a measure of the reliability of the book as a whole. If this were so the total number of possible mistakes would be somewhere in the region of 1,500.

As to general appearance I consider that this Atlas, which is typewritten, is more attractive than the first volume, which was a crude computer outprint. It is perhaps regrettable that both volumes are not of the same format.

GUNNAR WEIMARCK

LÖVE, Á. & LÖVE, D.: Plant Chromosomes. — J. Cramer, Vaduz 1975. ISBN 3-7682-0966-0. xv+184 pp. Price DM 36: —.

This is the first of a projected series of volumes on Plant Science. First the microscopic structure of chromosomes is described and their behaviour at mitosis and meiosis surveyed. The theoretical basis of chromosome study is outlined and there is a short section dealing with tissues suitable for cytological study. The microscope and other equipment are briefly presented together with some simple techniques of observation. Practical cytotechnology is described in greater detail with a number of selected methods.

The little book is handy to use and is in general attractive. Most terms are adequately explained and their philologic derivations given. However, I should have preferred the terms "centromere" and "kinetochore" to have been kept separate, using "centromere" to denote the visual constriction and "kinetochore" for the submicroscopic organelle for chromosome movement. This is a practice that has been introduced into modern literature and is to my mind a commendable one. A short section on the submicroscopic structure and biochemistry of chromosomes would have been warranted although admittedly it is somewhat peripheral in view of the limited scope of the book. As it is now the book is predominantly descriptive with rather little of the functional aspect. Some emphasis is laid on chromosome number. Techniques for karyotype analysis, the detailed study of meiosis, etc. are more superficially treated. I admit to being astonished that sectioned material is so strongly recommended for karyotype analysis rather than squashes. In spite of the fact that much current literature is cited, the impression might be received that little has happened in the field of karyology since the 40s. In particular I find it regrettable that the new banding techniques such as the Giemsa technique are so briefly mentioned and no practical details discussed. Although only very recently taken into use by botanists these techniques will undoubtedly assume great importance. I also searched in vain for mention of certain other methods of which my own experience has been satisfactory.

I cannot agree with the statement on p. 93 that the chromosome number counted at meiosis is n. The number 2n is obtained when counting the two groups at anaphase I (they should be added together to avoid a miscount if non-disjunction has occurred) as well as at, for example, diakinesis and metaphase I where bivalents are usually counted (consisting, of course, of two chromosomes each).

Figures 15, 25 and 26 are wrongly oriented which could be misleading.

So much negative criticism is perhaps hardly fair, for what book conforms wholly with the demands of the prospective reviewer. I am convinced that this volume will serve favourably as a short introduction to chromosome study. A great advantage is that it comprises both theory and practice whereas the comprehensive textbooks usually deal with only the one or the other.

GUNNAR WEIMARCK