Systematics of Gynandriris (Iridaceae), a Mediterranean–southern African disjunct

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Gynandriris is a small genus of Iridaceae, defined partly by a shortly stalked ovary with a long sterile beak on which the flower is borne, a corm, and also by membranous, semi-transparent, prominently ribbed inflorescence spathes. It is allied to the large African genus *Moraea* and has an unusual distribution with species in the Mediterranean Basin–Middle East and in southern Africa. The most well known species, *G. sisyrinchium*, distributed from Morocco to Pakistan, is frequently included in *Iris*, but is clearly closely related to the southern African species of the genus, and thus more closely allied to *Moraea* than to *Iris*. Seven species are recognized in southern Africa, four of which are new. Two species are recognized in the Northern Hemisphere, a departure from the traditional treatments which recognize only a single species. Chromosome counts are provided for several species, and the distinctive karyotype with a base number of x=6 supports the contention based on morphology, that northern and southern species are closely allied.

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Gynandriris, a small genus of the Iridaceae, is treated here as comprising seven species in southern Africa and two more in the Mediterranean–Middle East. It is closely related to *Moraea* and belongs with it in the Iridoideae-Irideae. I have included *Gynandriris* with *Moraea* and several other genera in the subtribe Homeriinae (Goldblatt 1976 b), a group which is characterized by a bifacial leaf and a corm of a type unique to this alliance. Homeriinae are predominantly African in distribution, *Gynandriris* being the only genus in the subtribe which extends north of the Sahara Desert. The common northern hemisphere species, *G. sisyrinchium*, is the most widespread, ranging from Morocco to Pakistan, with the other northern species, *G. monophylla*, having a more restricted distribution in the eastern Mediterranean (Fig. 1). In southern Africa, *Gynandriris* extends from southeastern Zimbabwe and Botswana to the southwestern tip of South Africa (Fig. 1). Species are concentrated in the south and southwest which has a winter rainfall–dry summer (i.e. mediterranean type) climate. *Gynandriris simulans* alone occurs in the summer rainfall parts of southern Africa, where it is found mainly in semiarid parts of the interior.

Relationships

As treated here *Gynandriris* is clearly a natural assemblage. The species all appear to be very closely related, and comparatively difficult to distinguish even for a petaloid monocot group. The distinguishing features of the genus are first, the shortly stalked ovary, enclosed in the inflorescence spathes, which has a long sterile extension, the beak, on which the flower is borne (Figs. 3, 5); second, a tunicate corm; third, very distinctive membranous inflorescence spathes which are almost transparent between the prominent pale vertical veins. The capsules are also transparent and when in fruit the characteristically large dark seeds can usually be seen through the dry spathes. The flower is similar in basic structure in all species, and very like that of *Moraea*, with large outer tepals, smaller inner tepals, partly united filaments, and flattened petaloid style branches with paired crests. Unlike

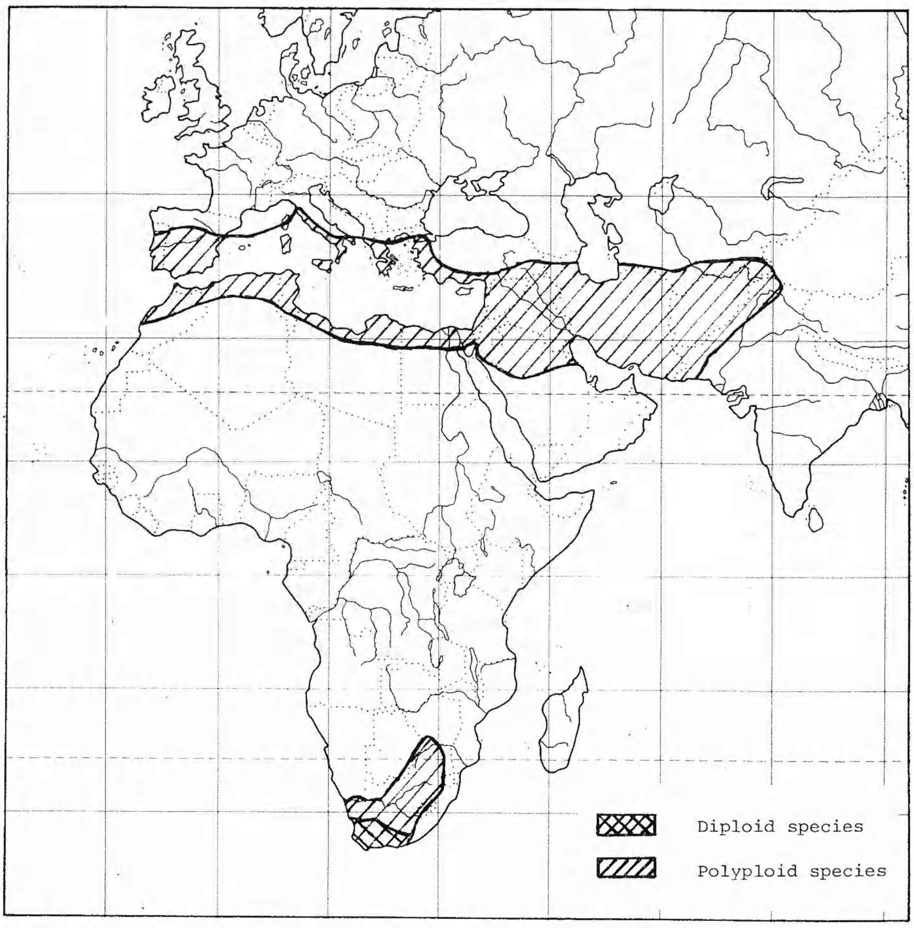

Fig. 1. Distribution of *Gynandriris*. Ranges of diploid and polyploid species are shaded differentially. (Although the southern African *G. simulans* is known cytologically from only two chromosome counts, it is assumed here to be a polyploid species).

Iris the tepals are free, thus a perianth tube is lacking.

The unusual ovary with its sterile tube is not unique in the Iridoideae, but is found also in the recently described *Barnardiella* (Goldblatt 1976 c), a monotypic genus from Namaqualand, South Africa. *Barnardiella* does not have the peculiar spathes of *Gynandriris*, and has quite different flowers with subequal spreading tepals and filiform style branches. It also has a different chromosome number, x=10, from *Gynandriris* which has x=6 and as I have suggested (Goldblatt 1976 c) it is fairly certain that *Barnardiella* and *Gynandriris* are not directly related in spite of having such a distinctive character as the beaked ovary in common.

Gynandriris sisyrinchium, the well known northern hemisphere species and type species of *Gynandriris*, is often associated with *Iris*, a genus which occurs throughout the temperate northern hemisphere. *G. sisyrinchium* is still commonly known today as *Iris sisyrinchium* in many countries (see Taxonomic history). The majority of systematists in the past treated this species as the sole member of *Iris* section *Gynandriris* (Bentham and Hooker 1882, Dykes 1913) ignoring its southern relatives even though the affinities of this species to the African genus *Moraea* were pointed out early in the nineteenth century by Ker (Ker-Gawler) (1805). The similarities between *Gynandriris sisyrinchium* (and its several southern African allies of subtribe Homeriinae) and *Moraea* are in fact very strong and can hardly be regarded as having evolved independently in *Iris*. The shared features include: the corm of a single internode, described elsewhere in detail (Goldblatt 1976 b); the linear, bifacial, channeled leaf found in most species of *Moraea*; a flower lacking a perianth tube (typical of *Moraea* but present in most species of *Iris*); and partially united filaments (typical of *Moraea*, but not found in *Iris*).

Cytology

Gynandriris has until now been fairly poorly known cytologically with several counts only for *G. sisyrinchium* and one each for *G. setifolia* and *G. pritzeliana* (published under *G. torta*) (Goldblatt 1971). Comparison of karyotypes of the northern and two southern species showed several striking similarities and led me to the conclusion that the northern and southern species were indeed congeneric, and even closely related (Goldblatt 1971 p. 375). Subsequently I have made every effort to obtain more material of *Gynandriris* for cytological study and several new counts are reported here (Table 1). Counts are now known for six of the seven southern African species recognized while in the Northern Hemisphere, *G. monophylla* and *G. sisyrinchium* have been counted, the latter over much of its wide range. A base number for the genus of x=6 can be confidently accepted. Both northern species are tetraploid, 2n=24, with *G. sisyrinchium* having been counted from Morocco, Corsica, Portugal, Italy, Greece, Israel, Lebanon, Iran and Pakistan. The southern African winter rainfall species are diploid, 2n=12, while the wide ranging summer rainfall area species *G. simulans* is evidently polyploid with 2n=24 and 36 recorded for two widely separate populations.

Karyotypes are similar in all species, polyploids having the basic pattern repeated. Usually the largest pair of chromosomes are metacentric, the remainder acrocentric (Fig. 2). Frequently a pair, and often two pairs of satellites are visible, on the second largest and one of the smaller chromosome pairs. The satellites are always very large, much longer than the adjacent chromosome arm, and often the satellites appear separated for some distance from the parent chromosome. This pattern is true for *G. setifolia, G. cedarmontana, G. simulans, G. australis, G.*

Table 1. Chromosome numbers in *Gynandriris*. New counts are in bold print. Goldblatt collections cited are at MO.

Species	Haploid number	Collection data or literature reference
G. pritzeliana	6	(Goldblatt 1971; S. Africa, Cape Nieuwoudtville)
	6	S. Africa, Cape, Calvinia-Middelpos, Goldblatt 4275
	6	S. Africa, Cape, S. Nieuwoudtville, Goldblatt s.n. no voucher
G. hesperantha	**6**	S. Africa, Cape, Glenlyon, Nieuwoudtville, Goldblatt 4371
G. cedarmontana	**6**	S. Africa, Cape, E. Pakhuis Pass, Goldblatt 4287
G. setifolia	6	(Goldblatt 1971; S. Africa, Cape, Worcester district)
	6	S. Africa, Cape, near Swellendam, Goldblatt 5084
	6	S. Africa, Cape, Matjesfontein, Goldblatt 5083
	6	S. Africa, Cape, Kenilworth, Cape Town, Goldblatt 5082
G. australis	**6**	S. Africa, Cape, Cape St. Francis, Goldblatt 5081
G. simulans	**12**	S. Africa, Cape, Victoria West, Goldblatt 5085
	18	S. Africa, O. F. S., Brandfort, Goldblatt 4506A
G. sisyrinchium	12	(Simonet 1932; source unknown)
	12	(Fernandes et al. 1948; Portugal, Evora "var albiflora")
	12	(Fernandes et al. 1948; Portugal, Evora)
	12	(Fernandes & Queirós 1970–71; Portugal, Setubal)
	12	(Delay & Petit 1971; Morocco, El Harhoura)
	12	Pakistan, Lower Swat, Nasir s.n. cult. MBG, Goldblatt 5080
	12	Iran, Kuh Alwend, S. W. Hamadan, Furse 2009 (K)
	12	Greece, Paros, Young 344 (K)
	12	Greece, Athens, Filipapou hill, Goldblatt 5055
	12	Israel, Dimona-Yeroham, Goldblatt 5001
	12	Israel, Negev, Givat Hagar, Goldblatt 5033
	12	Israel, Upper Galilee, Galil s.n. no voucher
	12	Israel, Jordan Valley, Avishai s.n. cult. MBG, Goldblatt 5075
	12	Italy, Sicily, Eloro, Goldblatt 5072
	12	Italy, Sicily, Peninsula Madalena, Goldblatt 5069
	12	Malta, Lanfranco 5479/86 (MO).
	12	France, Corsica, Tamberg s.n. cult. MBG, Goldblatt 5079
	12	Lebanon, Mt. Sanane, Astlet s.n. cult. MBG, Goldblatt 5078
G. monophylla	**12**	Libya, Cyrenaica, near Marawa, McKrill s.n. cult. MBG, Goldblatt 5077
	12	Greece, Athens, Filipapou hill, Goldblatt 5054
	12	Greece, Athens, Lycabetos, Goldblatt 5052
	12	Greece, Cape Sounion, Goldblatt 5064

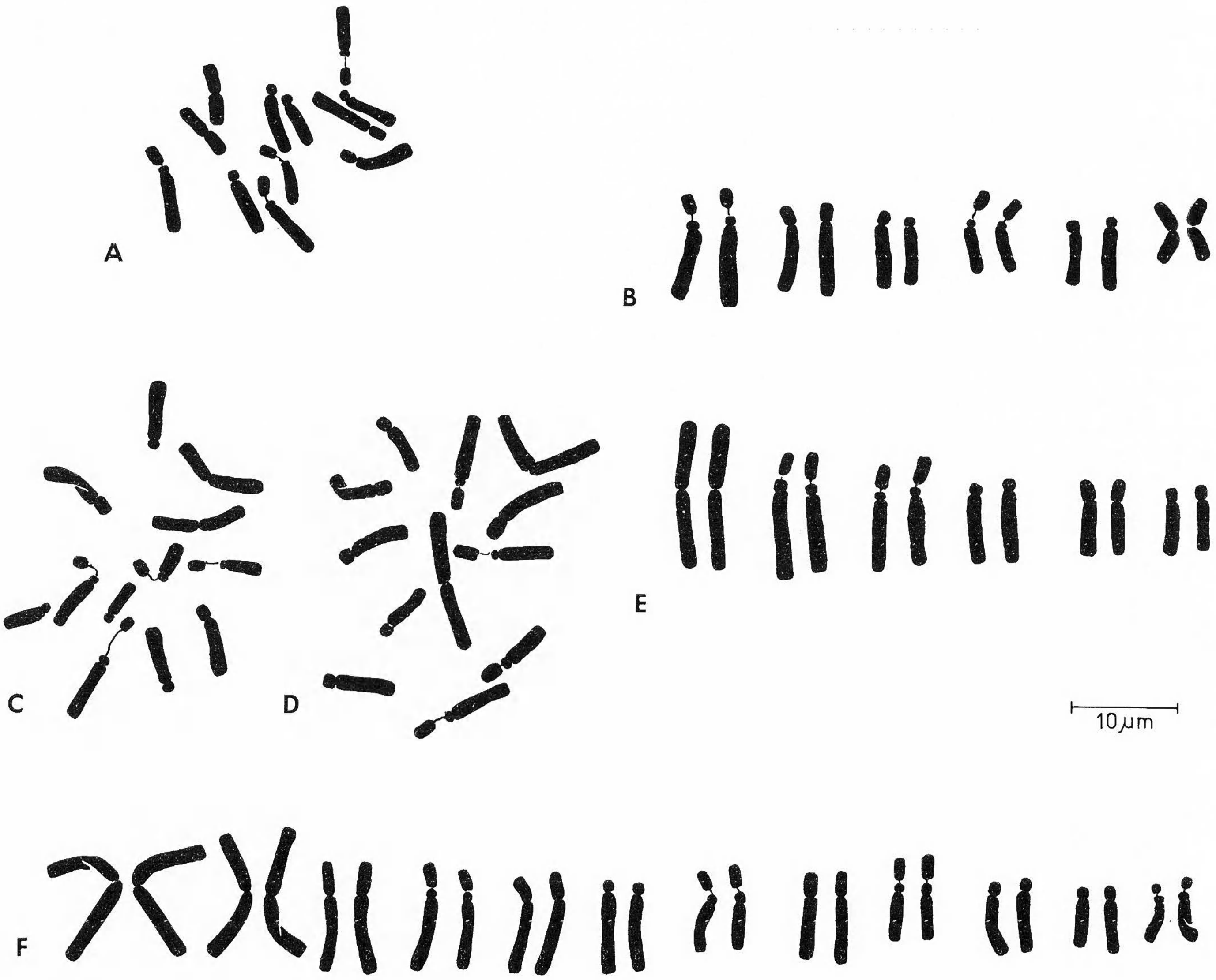

Fig. 2. Chromosome cytology of the diploid S. African species of *Gynandriris*, and the Mediterranean polyploid *G. monophylla*. — A: Mitotic metaphase in *G. hesperantha*. — B: Karyotype of *G. pritzeliana*. — C: Mitotic metaphase in *G. setifolia*. — D: *G australis*; — E: Karyotype of *G. cedarmontana*. — F: Karyotype of *G. monophylla*.

monophylla and *G. sisyrinchium* (Fig. 2 C–E). In the other two species examined, *G. hesperantha* and *G. pritzeliana* (Fig. 2 A, B), the metacentric pair is amongst the smallest of the chromosomes and the satellites are on the first and third longest chromosome pairs. It is not always possible to demonstrate two pairs of satellites but they appear with sufficient frequency to make it seem likely that they are part of the normal karyotype for all species even though not visible in every preparation. Published illustrations of karyotypes of *G. sisyrinchium* by Fernandes & Queirós (1970–71), Fernandes et al. (1948), Ricci (1970–71), and Simonet (1932) agree with the above description in general, making allowances for differences in cytological techniques, and also show four pairs of satellites as would be expected in the tetraploids. Ricci (1970–71) reported small differences between karyotypes of typical *G. sisyrinchium* and a south Sicily race of the species.

The base number of x=6 is suggestive of a relationship of *Gynandriris* to *Moraea* subgenus *Vieusseuxia*, one of the two subgenera of *Moraea* with x=6 (Goldblatt 1976 a, 1976 b) and the only subgenus of *Moraea* with x=6 where branched and multi-leafed species occur. The present center of subgenus *Vieusseuxia* is in southern and eastern South Africa. Most species of *Gynandriris*, and all the diploid species occur in this same general area which thus seems likely to be the place where the genus originated. The distribution of *Gynandriris* in Eurasia–North Africa is secondary, being remote from the presumed center of origin of the genus and from the center for the whole tribe Homeriinae.

Habitat

Gynandriris is, in general, adapted to arid habitats and tends to be found in areas of poor soil, often where vegatation has been disturbed, as well as in semi-desert conditions. *Gynandriris setifolia*, the well known Cape species, which grows in fairly mesic habitats nevertheless conforms to this pattern and is one of the few species of Iridaceae that is distinctly adventive. Thus it often occurs in unfavorable habitats, and is frequently recorded along roadsides, in cracks in paving, and it has been observed by the writer as a lawn weed in the south western Cape in infertile sandy soil. It is also recorded as a weed from South Australia. Other southern African species do not appear to have a capacity for weediness, but within their ranges tend to grow in poor soils and in exposed and arid situations.

Gynandriris sisyrinchium grows in a variety of habitats over its very great range and is reported from hill slopes, sand littoral and in desert conditions. It occurs on waste sites, in fields and near cultivated areas (Wendelbo & Mathew 1975) and roadsides and dry ditches (Täckholm & Drar 1954) which suggests a capacity for adventiveness. It is apparently easily distributed and may in fact have achieved its great range in more recent history and have spread from the Mediterranean basin with primitive agriculture. The second Northern Hemisphere species, *G. monophylla*, is distinctly coastal over most of its range, and grows best where there is little other vegetation, and in trampled areas.

Reproduction

Sexual reproduction occurs in all species of *Gynandriris*. Self-incompatibility is the rule in tribe Homeriinae, with this condition well known in *Moraea, Homeria* and *Galaxia* (unpublished data) but of the species of *Gynandriris* examined, only *G. pritzeliana* and *G. sisyrinchium* appear to be self-incompatible (data not known for *G. hesperantha, G. australis* or *G. anomala); G. cedarbergensis* is self-compatible, but at least in the experimental greenhouse does not set seed normally by its own pollen. *G. setifolia, G. monophylla* and *G. simulans* are all autogamous in the greenhouse, and produce large amounts of viable seed. Interspecific hybrids can be produced between all four of the southern African species that I have grown, namely, *G. pritzeliana*, *G. setifolia*, *G. simulans* and *G. cedarmontana*. Flowering times of the southern African and Eurasian species overlap very little, even in greenhouse conditions, but several attempted crosses between southern species and *G. sisyrinchium* failed. All species reproduce asexually by means of basal cormlets produced in small numbers annually alongside the main corm. In *G. simulans* a cormlet is also often produced in the axil of a basal leaf.

Interspecific relationships

All species of *Gynandriris* appear closely allied and inter-relationships are not clear. Primitive and derived characteristics are difficult to evaluate amongst the species with minor exceptions. The single leaf is likely to be derived from the two-leafed condition, while spreading inner tepals may be ancestral to erect tepals. Also diploidy precedes polyploidy, and self-compatibility and autogamy are specializations from self-incompatibility in general and probably so in *Gynandriris*. Thus in the southern African species *G. pritzeliana* may come closest to the ancestral type, with its large flower, outspread inner tepals, diploidy and self-incompatibility. The coiled leaves of this species are, though specialized, a very superficial character. The localized *G. hesperantha* is obviously closely related to, and perhaps derived from *G. pritzeliana*. *G. anomala*, with its single leaf, also appears most closely related to *G. pritzeliana*. The diploid and self-compatible *G. cedarmontana*, with erect inner tepals, seems more specialized than the preceeding. *G. setifolia*, the small flowered Cape species, has spreading inner tepals, but reproductively appears specialized, and the other southern African species *G. simulans*, which is polyploid and autogamous, has what may be the most specialized flowers in the group, with spotted markings, narrow tepals, and short duration of blooming (Table 2). This very speculative rationale is the basis for the species arrangement in the systematic treatment.

The two Northern Hemisphere species, presumably derived from southern African ancestors, are treated last and are tentatively regarded as the most specialized of the genus. Thier consistenly erect inner tepals and polyploidy support the placement as the most advanced species of *Gynandriris*.

Systematics

Taxonomic history

Gynandriris sisyrinchium (L.) Parl., the first species of *Gynandriris* to be described, was initially referred to *Iris* (Linnaeus 1753). At the end of the Linnaean period, the younger Linnaeus described the Cape species *G. setifolia* (L. fil.) Foster, also placing it in *Iris*. This species is typified by a collection made by C. P. Thunberg at the Cape and the description was in fact copied from Thunberg's ms. description of *Iris setacea* which was later published by Thunberg (1782). Both *I. sisyrinchium* and *I. setifolia* were assigned by Ker (1805) to *Moraea* when he revised and redefined this African genus according to Linnaeus' original circumscription.

Salisbury was the first botanist to suggest separate generic status for *Gynandriris* when in 1812 he proposed *Diaphane* to include *Iris sisyrinchium* as well as *I. juncifolia* (a true *Iris*). *Diaphane* was not provided with a description and is therefore invalid, as is the name *D. edulis* (a superfluous synonym for *G sisyrinchium*). *Diaphane* was never validated and thus has no taxonomic status.

At the same time Salisbury first used the name *Helixyra*, also a nomen nudum, as a new genus for the very strange *Moraea longiflora* Ker. This species collected by Niven in South Africa in about 1800 was only recently rediscovered in 1976 (Goldblatt 1976 b). It is unusual, but not unique in *Moraea* in having a true perianth tube. The nature of this tube was not, however, apparent to Baker (1878, 1896) who used Salisbury's *Helixyra* as a subgenus of *Moraea*, for the South African species of *Gynandriris* including as well *M. longiflora*. Baker described several new species of *Gynandriris* all of which he referred to *Moraea*, all but one being reduced to synonymy in this treatment.

Brown (1929) raised *Helixyra* to generic rank and validated the name with a full description. He also described four new species from the Transvaal, all of which are placed in synonymy here under *G. simulans*. However, as Foster (1936) pointed out. *Helixyra* Salisb. ex N. E. Br. was only validated in 1929 while *Gynandriris* Parl. (Parlatore 1854) is a much earlier name. If considered as synonyms, *Gynandriris* thus has precedence. In fact the type species of *Helixyra, H. flava* a superfluous name for *Moraea longiflora*, is a true *Moraea* with a perianth tube as its recent rediscovery in South Africa has revealed beyond doubt (Goldblatt 1976 b) and *Helixyra* is thus a nomenclatural synonym of *Moraea*.

Both Baker (1878, but not later) and Brown (1929) included the Northern Hemispere *G. sisyrinchium* together with the southern African species in their concepts of the alliance (at subgeneric or generic level, as *Helixyra)* thus implicitly agreeing with Ker, Klatt and others in separating *Gynandriris* from *Iris* and recognizing its closer affinities with *Moraea*. Many other European botanists were however unaware of, or preferred to ignore the existence of southern African representatives of the genus. This led to the peculiar situation in Baker's (1892) Handbook of the Irideae, where *G. sisyrinchium* is treated as the sole specis of *Iris* subgenus *Gynandriris* while southern African species are placed in *Moraea* subg. *Helixyra*. Baker (1896) continued this treatment in Flora Capensis where he admitted six species to the subgenus. Subsequently most important works on southern African flora recognized northern and southern species as congeneric (Brown 1929; Foster 1936).

In Europe, North Africa and the Middle East, treatment of *Gynandriris* has been and still is unsettled. Many important floristic and revisionary treatments, especially in the later nineteenth and early twentieth century treat *G. sisyrinchium* as *Iris*, notably Boissier (1884), Foster (1892), Ascherson & Graebner (1907), Dykes (1913) and Komarov (1935). Several more recent works also adhere to this treatment, such as Lawrence (1953), Täckholm & Drar (1954), Maire (1959), Baroni (1969), Polunin (1969, 1972), Zángheri (1976) and Guinochet & Vilmorin (1978).

Gynandriris was recognized first in Italy (Parlatore 1854) and several Italian works, e. g. Lojacono (1908) and Fiori (1925) continued to maintain the genus distinct from *Iris*, although more recent Italian floras do not (Zángheri 1976). A number of recent floras recognize *Gynandriris* amongst which Mouterde (1966) and Wendelbo & Mathew (1975) are notable, while Rodionenko

(1961) in his study of *Iris* also upholds *Gynandriris*. The close relationship of *Gynandriris* to *Moraea* has also been stressed by Burtt (1971) when dealing with distribution of southern African and Mediterranean floras.

Morphological characters

Rootstock. The rootstock is a corm of the *Moraea* type (Goldblatt 1976 b) which is a single internode long and is derived from a swollen lateral bud. At the top of the enlarged internode is a distinct growing apex and it is from this point that the adventitious roots emerge, rather than from the base as in the *Crocus* type corm. The corm is comparatively large in *Gynandriris*, 1–2 cm in diameter, except in the dwarf *G. monophylla* which has corms usually less than 1 cm in diameter. The corms are covered by brittle, rather papery inner tunics and tougher fibrous outer layers. The tunic fibers are often pale, and sometimes covered by a mealy substance, especially in *G. pritzeliana*, which when scraped away reveals the very dark, tough fibers found in this species.

Cataphylls. The 3–4 cataphylls which sheath the underground part of the stem and leaves, are pale and membranous, and hardly differ throughout the genus.

Leaves. There are either one or two produced leaves, and both are inserted near the base of the plant. The leaves are long, and slender, and much exceed the stem, though often become bent or broken. Except in *Gynandriris pritzeliana*, the leaves are channeled and straight to slightly twisted, and erect or trailing. Leaves of *G. pritzeliana* are coiled in corkscrew fashion either throughout or at least distally. This coiling is poorly developed in cultivated plants, but seems constant in all wild populations. The leaf blade in this species is also distinctive in having a broad hyaline band along the adaxial surface. Leaf number is variable in *Gynandriris sisyrinchium*, *G. setifolia* and *G. simulans*, and to a lesser extent in *G. monophylla*, where both one or two leafed plants occur, often side by side and in the same collection. There seems no consistent pattern in leaf number though more often young or depauperate plants have a single leaf. *Gynandriris monophylla* typically has a single leaf but occasionally two leafed plants occur, and in some populations almost all plants have a small second leaf. The variation in leaf number in these species has no taxonomic significance. *Gynandriris hesperantha*, *G. pritzeliana* and *G. cedarmontana* always have two well developed leaves even in collections made in very dry seasons, when plants are otherwise very stunted. In the two collections known of *G. anomala* all plants have a single leaf.

Stem. The stem is usually branched, and in one of two different ways. The scape may be quite short and contracted, with branches then being borne at the same level in semi-umbellate manner. This pattern often appears in plants growing in open ground amongst other very short vegetation or in drought affected plants. More often the stem is elongated and short lateral branches are carried in the axils of stem bracts. In some plants there may be more than one major branch, and these are then produced near the stem base. Each branch bears an inflorescence at its apex and dry bract leaves at the nodes which partly enclose the lateral branches. There seems to be no significance to the branching pattern, which is very variable in some species. In *G. simulans*, the entire range of branching patterns may occur and there seems no taxonomic value to this character. Thus Brown's *G.* (*Helixyra*) *spicata* based on a very tall specimen with a single main axis cannot be recognized and is placed in synonymy here, under *G. simulans*.

Inflorescence. As in almost all members of subfamily Iridoideae, the several flowered inflorescence is enclosed in two large opposed bractlike structures, here called spathes. These in fact resemble very closely the bract leaves, borne at nodes, and are thus distinguished by their position. The spathes of *Gynandriris* are distinctive in being membranous and semi-transparent with very prominent pale vertical veins. The inner spathe is always slightly longer than the outer, and the spathes of *Gynandriris* differ between species only in overall size. The polyploid *G. sisyrinchium* has the largest, and the tiny flowered *G. setifolia* and *G. monophylla*, the smallest (Figs. 3, 6). Size, however, varies considerably even on the same plant, with the main spathes usually larger than lateral spathes.

Flowers. The flowers are the most distinctive features of each species but are difficult to study in dried material. Flowers vary in size, colour and relative orientation of the tepals. These features are partly obscured even in carefully pressed material, and sometimes are quite impossible to detect, as when partly wilted flowers are pressed without further attention. Ideally, some features such as colour and petal orientation should be recorded on labels and all parts of several flowers should be laid out and pressed individually.

The flowers are fugaceous, lasting a single day each. The timing of flowering is characteristic in each species and varies within small limits (Table 2). Flowers range in colour from deep blue-violet, through pale blue to lilac or white usually with a white nectar guide. This whole range is known in *G. sisyrinchium* but the species usually has light to dark blue flowers. *Gynandriris cedarmontana* is the only species in the genus in which flowers are consistently white but in other species white forms appear to occur occasionally as mutants, which I have noted in populations of *G. setifolia*, which otherwise usually has pale blue-purple flowers. The variety *alba* Fernandes and Garcia (not recognized in this treatment) of *Gynandriris sisyrinchium*, which evidently differs from the type only in its white flowers is apparently another example of the occasional occurrence of white flowers in a blue flowered species. Flowers of *G. simulans* are unusual in being speckled so that the very pale purple ground colour is mottled with small spots of darker colour. This speckling fades entirely in dry material.

In general form the flowers are *Iris*-like, with larger, unguiculate outer tepals, smaller inner tepals and petaloid style branches with paired crests above the stigmatic surfaces. The outer tepals are always marked with either white, less often yellow-orange or sometimes white and orange, nectar guides at the base of the limb of the outer tepals. Tepals vary in size in different species and tepal length is a good indicator of flower size. The largest flowers are found in *Gynandriris sisyrinchium*, tepals ranging from (20–)25–40 mm. Intermediate in size are flowers of *G. pritzeliana, G. australis, G. cedarmontana, G hesperantha* and *G. anomala* (tepals 22–30 mm long), while the smallest flowers are found in *G. simulans*(17–25 mm), *G. setifolia* and G. monophylla (11–19 mm long).

Table 2. Flower phenology in *Gynandriris*.

Species	Opening	Fading
G. setifolia	12–1 p.m.	5–6 p.m.
G. australis	not known	not known
G. cedarmontana	12:30–1:30 p.m.	6–6:30 p.m.
G. pritzeliana	11–12 noon	4–4:30 p.m.
G. hesperantha	4–4:30 p.m.	7–7:30 p.m.
G. anomala	ca 11–12 noon	not known
G. simulans	3:30–4:30 p.m.	6:30–7 p.m.
G. sisyrinchium	1:30–2:30 p.m. (in some forms 11:30–12:30)	6–7 p.m. (in some forms 5–5:30)
G. monophylla	1–2 p.m.	5–5:30

Orientation of tepals appears to be a significant character but can seldom be determined from dried specimens. The limb of the outer tepals is outspread either horizontally or reflexed up to 45° below horizontal.

The inner tepals are erect in *G. sisyrinchium, G. monophylla, G. cedarmontana* and *G. hesperantha,* and outspread in the other southern African species. The inner tepals are consistently smaller than the outer tepals and may be contiguous with the outer tepals at the knee.

Androecium. Each of the three stamens lies appressed to a style branch and is only slightly shorter than each branch, with the anther apex lying just below the stigma lobes. The filaments are partly united, usually for one third to one half their length. This feature appears to be of some significance, with *Gynandriris simulans* having filaments united for ± 1.5 mm, less than one fourth their length.

The anthers, like the tepals, are a good measure of flower size. The largest anthers are found in *G. sisyrinchium* (5–10 mm) and *G. anomala* (8–10 mm). The smallest anthers are found in *G. setifolia* and *G. monophylla* (2.5–4.0 mm) with other southern species intermediate in this character.

Gynoecium. The sessile ovary with its sterile beak, the character which partly defines *Gynandriris*, is of limited use in the taxonomy of the genus. It varies only in size and is proportional to spathe length and flower size (Figs. 3, 5).

The style branches and crests are, like the stamens, useful indicators of flower size. However, size of these two characters is not always proportional to overall flower size. *Gynandriris simulans* thus stands out as having very short crests in comparison to the other floral parts. Its style branches are quite long, but also narrow, and with its small crests, the flowers of this species have a slender and delicate appearance. The style character is often useful in the identification of *G. simulans*. Also unusual is *G. cedarmontana* which has remarkably large style crests (12–13 mm) on a flower of intermediate size.

Capsule. The capsules of *Gynandriris* are distinctive in having thin membranous walls and, like the spathes, are transparent. The seeds are comparatively large and dark and are visible when ripe through the spathes.

Taxonomy

Gynandriris Parl.

Parlatore, Nuov. Gen. et Sp. 49. 1854. — Type species: *G. sisyrinchium* (L.) Parl.

Iris sect. *Gynandriris* (Parl.) Benth. & Hook., Gen. Pl. 3: 687. 1882 — *Iris* subg. *Gynandriris* (Parl.) Lawrence. Gentes Herb. 8: 366. 1953.

Moraea subg. *Helixyra* Salisb. ex Baker, Jour. Linn. Soc. Bot. 16: 132. 1878, non sensu Salisb. — Type species: *M. longiflora* Ker. (*Helixyra* Salisb. nom. nud., an invalid name, typified by the cited species *Helixyra flava*, an illegitimate, superfluous name for *Moraea longiflora* Ker, was believed by Baker and later by N. E. Brown to represent the earliest name for *Gynandriris*, and they included under this both the southern African and northern hemisphere species of this genus.)

Helixyra Salisb. ex N. E. Br., Trans. Roy. Soc. S. Afr. 17: 348. 1929, non sensu Salisb.; nom superfl. pro *Gynandriris* Parl. Type species: *H. longiflora* (Ker) N. E. Br., (= *Moraea longiflora* Ker).

Diaphane Salisb., Trans. Hort. Soc. 1: 304. 1812, nom. nud. Species cited *D. edulis* nom. illeg. superfl. pro *Iris sisyrinchium* L. (= *Gynandriris*) and *D. stylosa* nom. illeg. superfl. pro *Iris juncea* Desf. (= *Iris*).

Plants small to medium perennial herbs. *Rootstock* a tunicate corm. *Cataphylls* 2–4, membranous. *Leaves* 1 or 2, bifacial, either linear and canaliculate or helically coiled. *Stem* either contracted with branches clustered near base or extended with short sessile branches; bract leaves sheathing, dry and membranous. *Inflorescence* spathes membranous, transparent between vertical ribs. *Flowers* blue to white; outer tepals larger than inner, spreading to reflexed; inner tepals erect or reflexed. *Filaments* united in lower half to quarter; *anthers* linear-oblong. *Ovary* ± sessile enclosed in inflorescence spathes, fertile in lower third only and extended upwards as a slender sterile beak; *style* short with flattened petaloid branches appressed to stamens bearing paired crests above the transverse bilobed stigma. *Capsule* enclosed, transparent with membranous walls; seeds many, dark, angular *Basic chromosome number* x=6.

Distribution. Southern Africa: Zimbabwe, Botswana, Lesotho and South Africa and north of the Sahara in the Mediterranean basin, eastwards through the Middle East to Pakistan (Fig. 1).

Key to the Northern Hemisphere species

1. Flowers small, pale slate-blue, with outer tepals 11–16(–19) mm long; anthers 2.5–4.0 mm; leaf usually solitary, occasionally with a small, or full sized second leaf .... 9. *G. monophylla*
– Flowers medium to very large, pale to dark blue, violet, lilac or rose purple, with outer tepals (20–)25–40 mm long; anthers 4.5–10.0 mm; leaves usually two, or solitary .... 8. *G. sisyrinchium*

Keys to the southern African species

Two keys are provided, one for herbarium material and one for live plants.

Key to herbarium material

1. Leaves 2, helically coiled .... 1. *G. pritzeliana*
– Leaves 1–2, linear, canaliculate 2
2. Anthers 2.5–4.0 mm long; outer tepals 12–18 mm .... 5. *G. setifolia*
– Anthers (4–)5–8 mm long; outer tepals (17–)19–30 mm long 3
3. Inner tepals (18–)22–26 mm long; style crests (4–)7–12 mm long (outer tepal limb not spotted) 4
– Inner tepals 9–20 mm long; style crests 3–6 mm long (outer tepal limb spotted throughout) .... 7. *G. simulans*
4. Anthers 7–8 mm long; flowers dark blue-purple .... 2. *G. hesperantha*
– Anthers 5–7 mm long; flowers pale blue-purple or white 5
5. Inner tepals erect, to 5 mm wide; flowers white .... 4. *G. cedarmontana*
– Inner tepals reflexed, 6–7 mm wide; flowers blue–blue purple 6
6. Claw of outer tepals 7–8 mm long . 3. *G. anomala*
– Claw of outer tepals 11–12 mm long 6. *G. australis*

Key to live plants

1. Flowers with inner tepals erect or ascending; leaves straight not coiled 2
– Flowers with inner tepals outspread to reflexed; leaves straight or coiled 3

2. Flowers white; style crests 12–13 mm long .... 4. *G. cedarmontana*
– Flowers dark blue-purple; style crests 7–10 mm long .... 2. *G. hesperantha*
3. Tepals speckled throughout; filaments united for less than one fourth their length ... 7. *G. simulans*
– Tepals not speckled throughout; filaments united for one third to one half their length 4
4. Leaves straight, channeled 5
– Leaves coiled for entire length or in upper half .... 1. *G. pritzeliana*
5. Outer tepals 12–18 mm long; anthers to 4 mm long; leaves 1 or 2 .... 5. *G. setifolia*
– Outer tepals 18–28 mm long; anthers 5–7 mm long; leaves solitary 6
6. Claw of outer tepals 7–8 mm long . 6. *G. anomala*
– Claw of outer tepals 11–12 mm long 6. *G australis*

1. **Gynandriris pritzeliana** (Diels) Goldbl., Fig. 3 I

Goldblatt, Ann. Missouri Bot. Gard. 63: 781. 1976.

Moraea pritzeliana Diels, Engl. Bot. Jahrb. 44: 17. 1910. — Type: South Africa, Cape, Calvinia, Diels 694 (B, holotype).

Moraea torta L. Bol., S. Afr. Gard. 17: 418. 1927. — Type: South Africa, Cape, near Calvinia, Compton. s.n. (BOL, holotype). — *Helixyra torta* (L. Bol.) Barnard, Iris Yearbk. (1932): 52 (Iris Soc. Engl.). — *Gynandriris torta* (L. Bol.) Foster, Contr. Gray Herb. Harv. 114: 41. 1936.

Plants medium, (7–)12–35 cm high. *Corm* 1.5–2.0 cm in diameter, tunics dark, or often mealy covered and appearing pale: fibers coarse and rigid. *Leaves* 2, linear, flat in cross section and helically coiled from the base, or in upper half; either upright and exceeding the stem, or horizontal; 2.5–5.0 mm wide, usually with two prominent submarginal veins and a broad hyaline band along the midline of the adaxial surface. *Stem* either contracted, with branches produced near ground, or extended with branches produced from the base and at each aerial node. *Spathes* herbaceous, becoming dry above, or completely dry, often red-flushed; inner spathe (34–)37–45 mm long, outer slightly shorter. *Flowers* dark blue-violet, with yellow nectar guide; *outer tepals* 21–30 mm long, limb half again as long as the claw and 10–15 mm wide, reflexed to ± 45°; *inner tepals* 20–26 mm long, up to 7 mm wide, also reflexed. *Filaments* 5–6 mm long, joined in lower 1.5–3.0 mm; *anthers* 4.5–6.5 mm long. *Style branches* 8–10 mm, crests (4–)7–11 mm long. *Capsule* narrow, 1.5–2.0 cm long; *seeds* angular, relatively large. *Chromosome number* 2n=12.

Flowering time. Mid September–November.

Distribution. From Loeriesfontein and Calvinia in the north, through the Roggeveld to the Koedoes Mountains and the Komsberg escarpment in the south. Fig. 3.

Gynandriris pritzeliana is a very distinctive species having strongly coiled leaves, a very easily recognized character, and large very dark blue to violet flowers with broad reflexed inner and outer tepals. The species was for a long time known by a synonym *G. torta*, the name it was given (as *Moraea*) by Louisa Bolus in 1927. Only recently, when the types of all species of *Moraea* were examined in the course of a revision of this genus (Goldblatt 1976 b) did it emerge that *M. pritzeliana* was in fact a species of *Gynandriris*, and identical with *G. torta*.

It is quite common in dry situations in the interior of the Cape west coast, particularly around Nieuwoudtville and Calvinia, though it extends well to the south and has been recorded in the Koedoes Mountains and at the foot of the Komsberg between Sutherland and Laingsburg. *G. pritzeliana* is a diploid species like the other western Karoo-Cape species, and it is strongly self-incompatible, in contrast with the related *G. cedarmontana* and *G. setifolia*. Because of its unspecialized flower with spreading inner tepals as well as diploidy and self-incompatibility, *G. pritzeliana* is assigned to a basal position in the genus. Its spirally coiled leaves, although obviously derived, are regarded as less fundamental and overlaid on a basically unspecialized species.

2. **Gynandriris hesperantha** Goldbl. sp. nov.

Type: South Africa, Cape, Glenlyon, Nieuwoudtville, rocky hills, Goldblatt 4371 (MO, holotype, K, NBG, isotypes).

Planta robusta, 40–60 cm alta. Cormus 2–3 cm in diametro. Folia 2, lineares, canaliculata. Spatha 45–60 mm longa. Flores purpureo-violacei; tepala exteriora 26–29 mm longa, ungues ca 10 mm, limbus reflexus ca 10 mm latus; tepala interiora 22–26 mm longa, erecta, ca 5 mm lata. Filamenta 5–6,5 mm longa, connata 2–3 mm; antherae 7–8 mm. Rami styli 9–12 mm longi, cristae 7–10 mm.

Plants 40–60 cm high. Corm 2–3 cm in diameter with pale mealy tunics. *Leaves* 2, linear, channelled, 6–8 mm wide, much longer than the stem and trailing. *Stem* erect, tall, with short branches

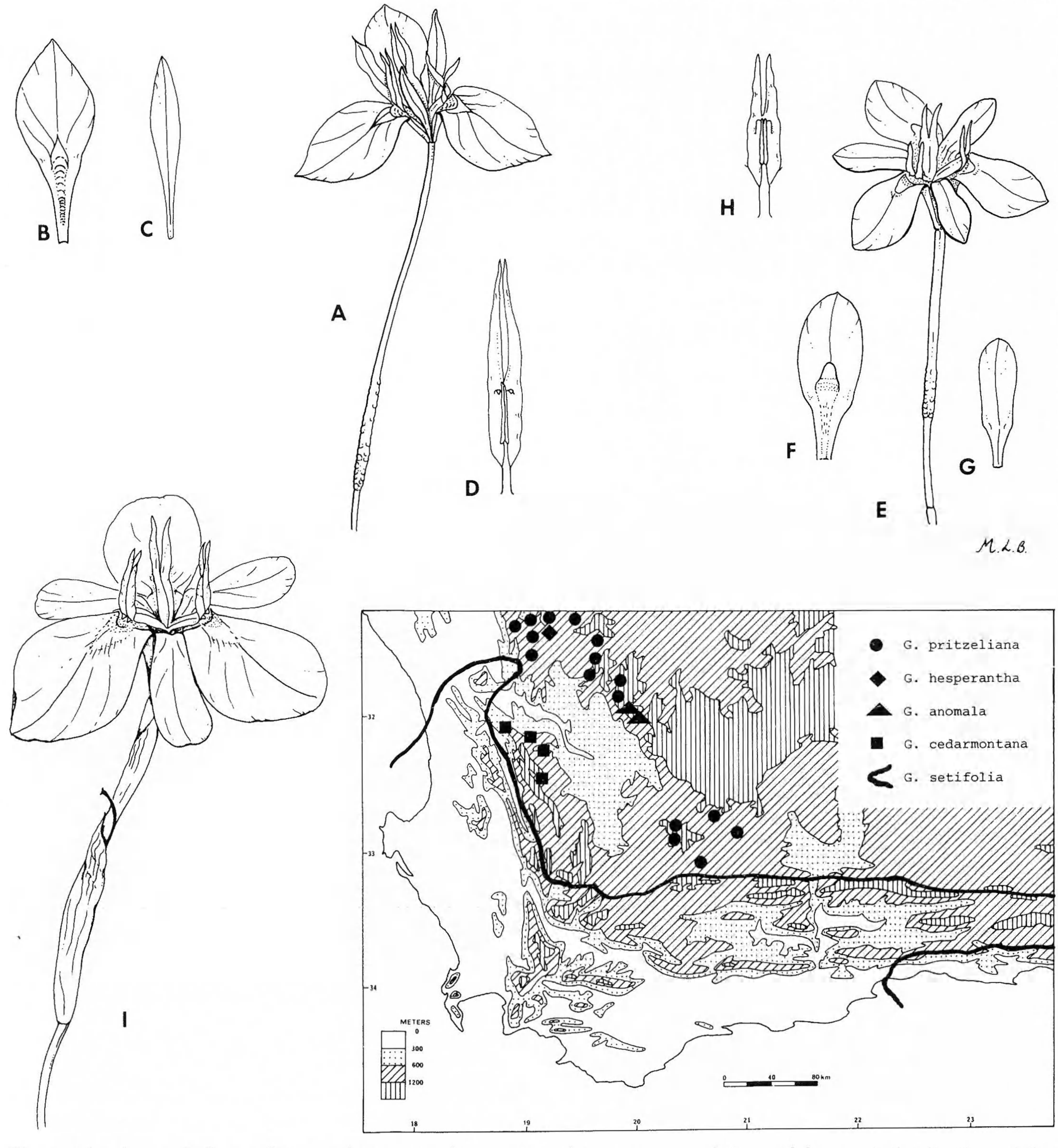

Fig. 3. Floral morphology of *Gynandriris pritzeliana, G. cedarmontana* and *G. setifolia*, and distribution of the five western Cape species (*G. setifolia*, partial range only). A–D: *G. cedarmontana*. — A: Flower. — B: Outer tepals. — C: Inner tepal. — D: Style branch and stamen. — E–H: *G. setifolia*. — E: Flower; — F: Outer tepal. — G: inner tepal. — H: Style branch and stamen. — I: *G. pritzeliana*. Flowers and tepals ± life size, style branch and stamens × 2.

at the nodes. *Spathes* dry, 45–60 mm long, inner slightly longer than outer. *Flowers* purple-violet, with yellow nectar guides; outer tepals 26–29 mm long, claw 10 mm, limb reflexed to ± 45°, ca 10 mm wide; *inner tepals* 22–26 mm long, erect, ca 5 mm wide. *Filaments* 5–6.5 mm long, joined 2–3 mm; anthers 7–8 mm. *Style branches* 9–12 mm long, crests 7–10 mm. *Capsule* large, *seeds* brown. *Chromosome number* 2n=12.

Flowering time. Late spring, October–November.

Distribution. Very local, on the rocky hills east of Nieuwoudtville in heavy clay soil. Fig. 3.

Gynandriris hesperantha is the tallest and one of the most robust species of the genus. It is confined to the low rocky hills to the east of Nieuwoudtville in the Calvinia district, and grows only in the heavy red clay soil found in this area. It most resembles *G. pritzeliana*, which is probably its closest relative, and it occurs entirely within the range of this more widespread species. *Gynandriris hesperantha* differs from *G. pritzeliana* in several characters, being taller, and having straight leaves in contrast to the coiled leaves of the latter. The two species differ in floral details also, *G. hesperantha* having larger spathes and anthers, and erect inner tepals. *Gynandriris hesperantha* is evening blooming, flowers opening at about 4:30 p.m., at about the time that flowers of *G. pritzeliana* begin to fade, and its flowers last till well after dark, fading at about 7:30 p.m.

3. **Gynandriris anomala** Goldbl. sp. nov.

Type: South Africa, Cape, Roggeveld W. of Middelpos, Goldblatt 4396 (MO, holotype, K, NBG, PRE, isotypes).

Planta ca 30 cm alta. Folium solitarium, linear, canaliculatum, ad 7 mm latum, caulis excedentum. Spatha 36–45 mm longa. Flores caerulei; tepala exteriora 21–26 mm longa, ungues 8–9 mm, limbus reflexus, 10–12 mm latus; interiora ca 22 mm longa, reflexa. Filamenta 4,5–6 mm longa, connata 2–3 mm; antherae 5–7 mm longae. Rami styli 8–10 mm longi; cristae ad 10 mm longae.

Plants ca 30 cm high. *Corm* not known. *Leaf* solitary, linear, canaliculate, to 7 mm wide, much longer than the stem. *Stem* erect, branching at the nodes. *Spathes* dry, membranous, sometimes herbaceous below, 36–45 cm long, inner slightly longer than outer. *Flowers* blue with white nectar guides, strong and sweet scented; *outer tepals* 21–26 mm long, claw 8–9 mm, limb reflexed at ca 45°, 10–12 mm wide; *inner tepals* ca 22 mm long, also reflexed, ca 7 mm wide. *Filaments* 4.5–6 mm long, joined for about half their length; *anthers* 5–7 mm long. *Style branches* 8–10 mm long, crests to 10 mm. *Capsule* and *seeds* not known. *Chromosome number* not known.

Flowering time. October.

Distribution. Apparently local in the Roggeveld between Calvinia and Middelpos. Fig. 3.

Gynandriris anomala, though known from only two collections, seems quite clearly a distinct species. It appears to be most closely related to *G. pritzeliana*. *G. anomala* is found along a small part of the Roggeveld escarpment, and entirely within the range of *G. pritzeliana*. The two differ in serveral important features, although their flowers are similar in structure, *G. anomala* has pale blue flowers that have a strong sweet scent while those of *G. pritzeliana* are dark in color and have no apparent scent. Vegetative differences are more pronounced, as *G. anomala* has a single, linear channelled leaf, in contrast to the very distinctive pair of coiled leaves of *G. pritzeliana*. Cytology and reproductive biology of *G. anomala* are unknown.

4. **Gynandriris cedarmontana** Goldbl. sp. nov., Fig. 3 A–D

Type: South Africa, Cape, Welbedacht, Bidouw Valley, Goldblatt 4287 (MO, holotype, K, NBG, PRE, S, US, WAG, isotypes).

Planta 10–30 cm alta. Tunici cormi pallidi, farinosi. Folia 2, canaliculata, lineares. Caulis erecta, rami sessiles. Spathae siccae, interior 40–60 mm longa, exterior brevior. Flores albi; tepala exteriora 24–27 mm longa, limbis 14–16 mm longis; tepala interiora 20–25 mm longa lineares-lanceolata, erecta. Filamenta 5–6 mm longa, antherae 5–6 mm. Rami styli 8–11 mm longi, cristae ± 12.5 mm longae.

Plants 10 to 30 cm high. *Corm* 1–1.5 cm in diameter, with dark tunics of stiff, coarse fibers covered by mealy substance. *Leaves* 2, linear, canaliculate, ± erect or trailing, longer than the stem. *Stem* with one main axis and few to several ± sessile branches. *Spathes* membranous, dry at flowering time; inner 40–60 mm long, outer slightly shorter. *Flower* white; *outer tepals* lanceolate, 24–27 mm long, limb 14–16 mm long, and 10–12 mm wide, outspread, horizontal to somewhat reflexed; *inner tepals* 20–25 mm long, linear-lanceolate, 3–5 mm wide, erect. *Filaments* 5–6 mm long, free in upper half to two thirds; *anthers* 5–6 mm. *Style branches* 7–11 mm long, crests 11–13 mm long. *Capsule* and *seeds* not known. *Chromosome number* 2n=12.

Flowering time. September–October.

Distribution. Southwestern Cape, moist sites in the arid valleys of the northern Cedarberg and Nardouw Mts. Fig. 3.

Gynandriris cedarmontana is a fairly local species, occurring in the dry, interior valleys of the northern Cedarberg and Nardouw Mountains of the southwestern Cape. It apparently growns in moist sites only, either in seeps or along ditches or stream banks. Like *G. setifolia*, which occurs to the west and *G. pritzeliana* which occurs to the northeast of its range, it is diploid, but it resembles neither of these species very closely. It is characterized by a relatively large flower which unlike any other species of the genus is white. Floral structure is also distinctive. The inner tepals are erect and comparatively narrow and although the flower is large the style crests are disproportionate in being larger than might be expected from the overall size (Fig. 3 A–D). *Gynandriris cedarmontana* is self-compatible but self fertilization does not normally occur. In contrast, the short and tiny flowered *G. setifolia*, probably its closest relative, is apparently consistently autogamous.

5. **Gynandriris setifolia** (L. fil.) Foster, Fig. 3 F–H

Foster, contr. Gray Herb. Harv. 114: 40. 1936.

Iris setifolia L. fil., Suppl.: 99. 1781. — Type: South Africa, Cape Province, without precise locality, Thunberg s.n. (Herb. Thunb. 1163, UPS, holotype). — *Moraea setifolia* (L. fil.) Druce, Rep. Bot. Exch. Club Br. Isles 1916: 363. 1917. — *Helixyra setifolia* (L. fil.) N. E. Br., Trans. Roy. Soc. S. Afr. 17: 349. 1929.

Iris setacea Thunb., Diss. Irid.: 20, Tab. 1. 1782 nom. illeg. superfl. pro *I. setifolia* L. fil., Suppl.: 99. 1781. — *Moraea setacea* (Thunb.) Ker, Konig & Sims, Ann. Bot. 1: 240. 1805.

Moraea humilis Eckl., Top Verz. 15. 1827. nom nud.

Moraea xerospatha MacOwan ex Baker, Fl. Cap. 6: 529. 1897. — Type: South Africa, Cape Town, MacOwan 3118 (K, lectotype, BOL, isotype).

Moraea rogersii Baker, Handbook Irid. 57. 1892. — Type: South Africa, Cape, Mossel Bay, Rogers s.n. (K, holotype). — *Helixyra rogersii* (Baker) N. E. Br., Trans. Roy. Soc. S. Africa 17: 349. 1929. — *Gynandriris rogersii* (Baker) Foster, Contrib. Gray Herb. Harv. 114: 40. 1936, syn. nov.

Plants small, 5–18(–25) cm high. *Corm* 1(–1.5) cm in diameter with pale tunics. *Leaves* one or two, linear, canaliculate, 2–3 mm wide, much longer than the inflorescence. *Stems* usually branched, either very short with nodes condensed, or elongated. *Spathes* usually dry at flowering time, inner 20–35(–40) mm long, outer slightly shorter. *Flowers* small, pale blue-mauve, occasionally white, with yellow-orange nectarguides; *outer tepals* 12–18 mm long, limb equal or slightly exceeding the claw, sharply reflexed, 5–9 mm wide; *inner tepals* 12–16 mm long, also reflexed. *Filaments* 3.5–6 mm long, united in lower third to half; *anthers* 2.5–4 mm. *Style branches* 4–7 mm long, crests 4–7 mm. *Capsule* ± 1 cm long, *seeds* dark, angular. *Chromosome number* 2n=12.

Flowering time. Late spring, September–early November.

Distribution. Southwestern Cape, from Van Rhynsdorp in the north to Grahamstown in the east, but absent from the sea coast between Mossel Bay and Port Elizabeth; often adventive and in waste places, roadsides, lawns: naturalized in Australia. Figs. 3, 4.

Gynandriris setifolia is readily distinguished from the rest of the genus by its small size and tiny flowers (Fig. 3). Although it is fairly variable, and occasionally plants with larger than usual spathes of flowers do occur, it can always be recognized by the small size of most, if not always all, of the floral parts.

This species is native to the southwestern and southern Cape and occurs under relatively high rainfall conditions along the south and west coasts from Mossel Bay to Van Rhynsdorp, extending inland to Matjesfontein and the Swartberg. It is replaced in the Cedarberg by the closely related, white flowered *Gynandriris cedarmontana*. *G. setifolia* is easily recognized by its very small, pale blue–purple flowers, sharply reflexed inner and outer tepals, and short anthers. The flowers open between noon and 1:00 p.m. and fade towards sunset.

Gynandriris setifolia is distinctly weedy, and is occasionally found in lawns, and roadsides within its range. It is also recorded as an introduced and naturalized weed in Australia. It is a diploid species, but in all populations I have examined the plants are autogamous, and produce much seed. The reproductive mode is unexpected in the family, but explains the success of the species as a weed.

6. **Gynandriris australis** Goldbl. sp. nov.

Type: South Africa, Cape, Humansdorp Div., Jeffreys

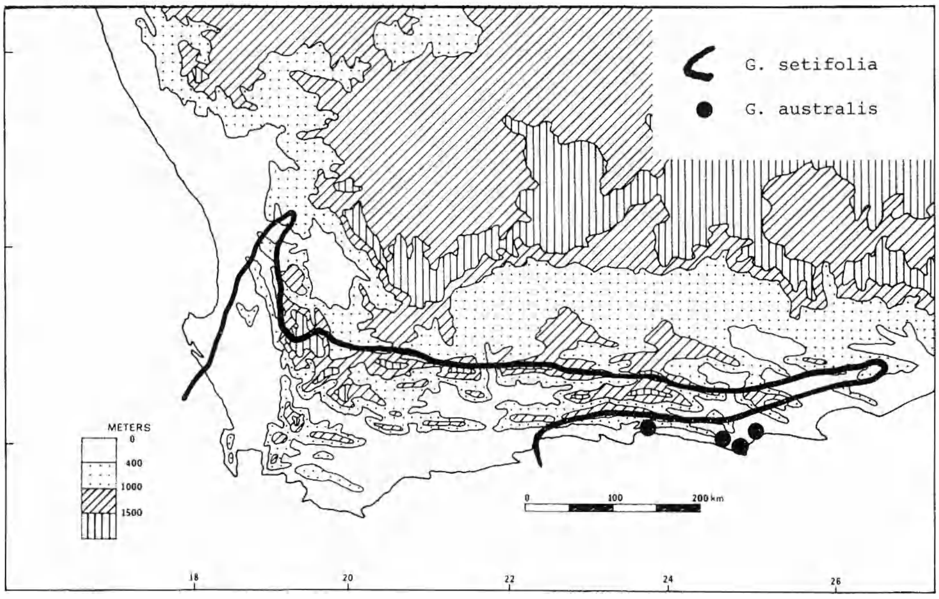

Fig. 4. Distribution of *Gynandriris setifolia* and *G. australis*.

Bay, duineveld, Fourcade 3309 (BOL, holotype, K, isotype).

Planta 6–25 cm alta. Tunici cormi pallidi. Folium unum, linear. Caulis erecta, ramosa. Spathae 35–60 mm longae. Flores caerulo-purpurei; tepala exteriora 23–28 mm longa, limbis 13–18 mm longis; tepala interiora 18–22 mm longa. Filamenta 5–5,5 mm longa; antherae 5 mm longae. Rami styli 8–9 mm, cristae 8–12 mm longae.

Plants 6–25 cm high. *Corm* ca 1.5 cm in diameter with soft, pale tunics. *Leaf* solitary, channeled, erect to trailing. *Stem* usually branching, elongate or barely produced above ground, then with branches clustered near base. *Spathes* dry-membranous; inner 35–60 mm long, outer slightly shorter. *Flowers* pale blue, nectar guide white with orange at base; *outer tepals* lanceolate, 23–28 mm long, limb 13–18 mm, spreading horizontally to slightly reflexed; *inner tepals* 18–22 mm long, to 5 mm wide, ? outspread. *Filaments* 5–5.5 mm long united for 1 mm; *anthers* ca 5 mm long. *Style* branches 8–9 mm long, crests 8–12 mm. *Capsule* and seeds not known. *Chromosome number* 2n=12.

Flowering time. Late September–early November.

Distribution. Southern Cape between Mossel Bay and Jeffreys Bay, in coastal sand dune vegetation. Fig. 4.

Gynandriris australis is probably most closely related to the more widespread *G. setifolia*, from which it differs mainly in its very much larger flower. It has in the past been regarded as *G. setifolia* but I believe its flower, well beyond the range of variation in flower size found in *G. setifolia*, and characteristic habitat in coastal sand dunes indicate the need for specific recognition. *Gynandriris australis* has a restricted distribution only along the southern Cape coast between Mossel Bay and Jeffreys Bay. It is diploid, like the other southwestern Cape–western Karoo species, but its reproductive biology has not been studied.

7. **Gynandriris simulans** (Baker) Foster, Fig. 5

Foster, Contrib. Gray Herb. Harv. 114: 40. 1936.

Moraea simulans Baker, Handbook. Irid. 58. 1892. —Types: South Africa, Transvaal, Bloemhof, Nelson 203 (K, lectotype); syntype, without locality, Scott Elliot 1250 (K). — *Helixyra simulans* (Baker) N. E. Br., Trans. Roy. Soc. S. Africa 17: 350. 1929.

Moraea cladostachya Baker, Handbook, Irid. 58. 1892. — Types: South Africa, Verleptpram, Orange R., N. Namaqualand, Drége 2610 (K, lectotype, L, LE, MO, S, isotypes); syntype, Cape, eastern frontier, Barber s.n. (K). — *Helixyra cladostachya* (Baker) N. E. Br., Trans. Roy. Soc. S. Africa 17: 349. 1929 — *Gynandriris cladostachya* (Baker) Foster, Contrib. Gray Herb. Harv. 114: 40. 1936, syn. nov.

Moraea burchellii Baker, Handbook Irid. 57. 1892. — Type: South Africa, Cape "Bechuanaland, Jabrins fountain", Burchell 2250 (K, holotype). — *Helixyra burchellii* (Baker) N. E. Br., Trans. Roy. Soc. S. Africa 17: 349. 1929 — *Gynandriris burchellii* (Baker) Foster, Contrib. Gray Herb. Harv. 114: 40. 1936, syn. nov.

Helixyra elata N. E. Br., Trans. Roy. Soc. S. Africa 17: 349. 1929. — Type: South Africa, Transvaal, Standerton, Rogers 14799 (K, holotype). — *Gynandriris elata* (N. E. Br.) Foster, Contrib. Gray Herb. Harv. 114: 40. 1936, syn. nov.

Helixyra mossii N. E. Br., Trans. Roy. Soc. S. Afri-

Fig. 5. Floral morphology and distribution of *Gynandriris simulans*: — A: Whole plant (life size). — B: Androecium and gynoecium (× 2). — C: Corm (× 0.5).

ca 17: 350. 1929. — Type: South Africa, Transvaal, Geduld, Moss 15607 (K, holotype, S, P, isotypes). — *Gynandriris mossii* (N. E. Br.) Foster, Contrib. Gray Herb. Harv. 114: 40. 1936, syn. nov.

Helixyra propinqua N. E. Br., Trans. Roy. Soc. S. Africa 17: 349. 1929. — Type: South Africa, Transvaal, Zoutpansberg, DvS s.n. (PRE 2462) (K, holotype). — *Gynandriris propinqua* (N. E. Br.) Foster, Contrib. Gray Herb. Harv. 114: 40. 1936, syn. nov.

Helixyra spicata N. E. Br., Trans. Roy. Soc. S. Africa 17: 349. 1929. — Type: South Africa, Cape, Griqualand West, Burchell s.n. (K, holotype). — *Gynandriris spicata* (N. E. Br.) Foster, Contrib. Gray Herb. Harv. 114: 41. 1936, syn. nov.

Plants (10–)14–40(–45) cm high. *Corm* 1.5–2 cm in diameter with pale to dark tunics of ± entire layers or coarse fibers; often bearing a cormlet in leaf axil. *Leaves* 1 or 2, linear, channeled, exceeding the stem, and 2–4 mm wide. *Stem* either contracted, sometimes with many basal branches or extended, with short, ± sessile aerial branches and sometimes longer basal branches. *Spathes* usually dry at flowering time, occasionally herbaceous near base; inner (25–)30–55 mm long, outer slightly shorter. *Flower* pale blue–lilac, with darker speckles over entire outer tepal with yellow nectar guides; *outer tepals* (17–)20–28 mm long, limb ± equal or slightly longer than claw, and to 8 mm wide, spreading to reflexed; inner tepals 15–19 mm long, 3–4 mm wide, spreading to reflexed. *Filaments* 5–6 mm long, united near base for 1–1.5 mm; *anthers* (4–)5–8 mm. *Style branches* 8–12 mm, crests 3–6 mm long. *Capsule* oblong, 13–20 mm long, seeds large, black, angular. *Chromosome number* 2n=24, 36.

Flowering time. August–September, at the end of the dry season.

Distribution. South Africa, Lesotho, Botswana and Zimbabwe, usually in xeric grass-bushland mainly in areas of the interior with winter drought, and meagre summer rainfall. It is absent from the moister parts of summer rainfall South Africa. Fig. 5.

There are comparatively few collections of this species for such a wide distribution and it is consequently rather poorly known. Collections are mainly from populated areas, and numerous from the Witwatersrand, Bloemfontein and Kimberley, while the species is represented by single collections from southwestern Zimbabwe, eastern Botswana and the northern Transvaal. Moreover, few of the collections are complete and properly prepared so that floral features are known from relatively few specimens.

As treated here, all plants from the summer rainfall area of southern Africa are regarded as a single species, and the seven species recognized by Brown (1929) are merged under one name. Of the three earliest names available, all dating from 1892, *Gynandriris simulans* was chosen for the taxon because the type specimen (Nelson 203, here selected as lectotype) is from the center of its range and in no way unusual. Brown's species concepts were clearly far to norrow, and he recognized species on the basis of growth form and branching habit which as discussed earlier are now known to be variable even in plants of the same populations, growing close together. Thus *G. elata* is a rather robust southern Transvaal plant with long branches; *G. propinqua* a robust northern Transvaal plant; *G. spicata* a form with very short branches on a long stem from East Griqualand; *G. mossii* and *G. burchellii* are rather diminutive forms; and *G. cladostachya* has a conspicuous cormlet in its basal axil. Brown distinguished *G. simulans* from the above only by height and number of branches, very unsatisfactory specific characters.

Gynandriris simulans has relatively small flowers for the genus, with outer tepals in the 17–27 mm long range. Both inner and outer tepals are rather narrow, and both whorls are laxly outspread to reflexed. The flowers appear to be distinctive in being speckled throughout with darker spots on a pale lilac background but this speckling rapidly fades in dried material. Only very few collectors have noted coloration, but the speckling is consistently mentioned when flower color is indicated, and this pattern is reported almost throughout the range of the species. Another feature rarely indicated by collectors is flowering time, but some have given 4–5 pm as the time flowers open (see also Brown 1936) and I have noted similar timing in plants cultivated in St. Louis. My plants, from Victoria West in the karoo regularly opened at ± 3:30 pm and faded at about 7 pm. This very short blooming period helps explain why *G. simulans* is so rarely gathered and why flowers are so often lacking or wilted in the available collections.

The species is evidently polyploid, though chromosome number is known from only two collections. A population from Victoria West is tetraploid, 2n=24, while a collection from near Brandfort in the Orange Free State is hexaploid, 2n=36. Differences in ploidy may be correlated with the variation in floral and vegetative characters which seem greater than in most other species of the genus.

8. **Gynandriris sisyrinchium** (L.) Parl., Fig. 6 A.

Parlatore, Nouv. Gen. et Sp. 49. 1854.

Iris sisyrinchium L., Sp. Pl. ed. 1: 40. 1753. — Type: illustration "*Sisyrinchium majus*" in Clusius, Rariorum

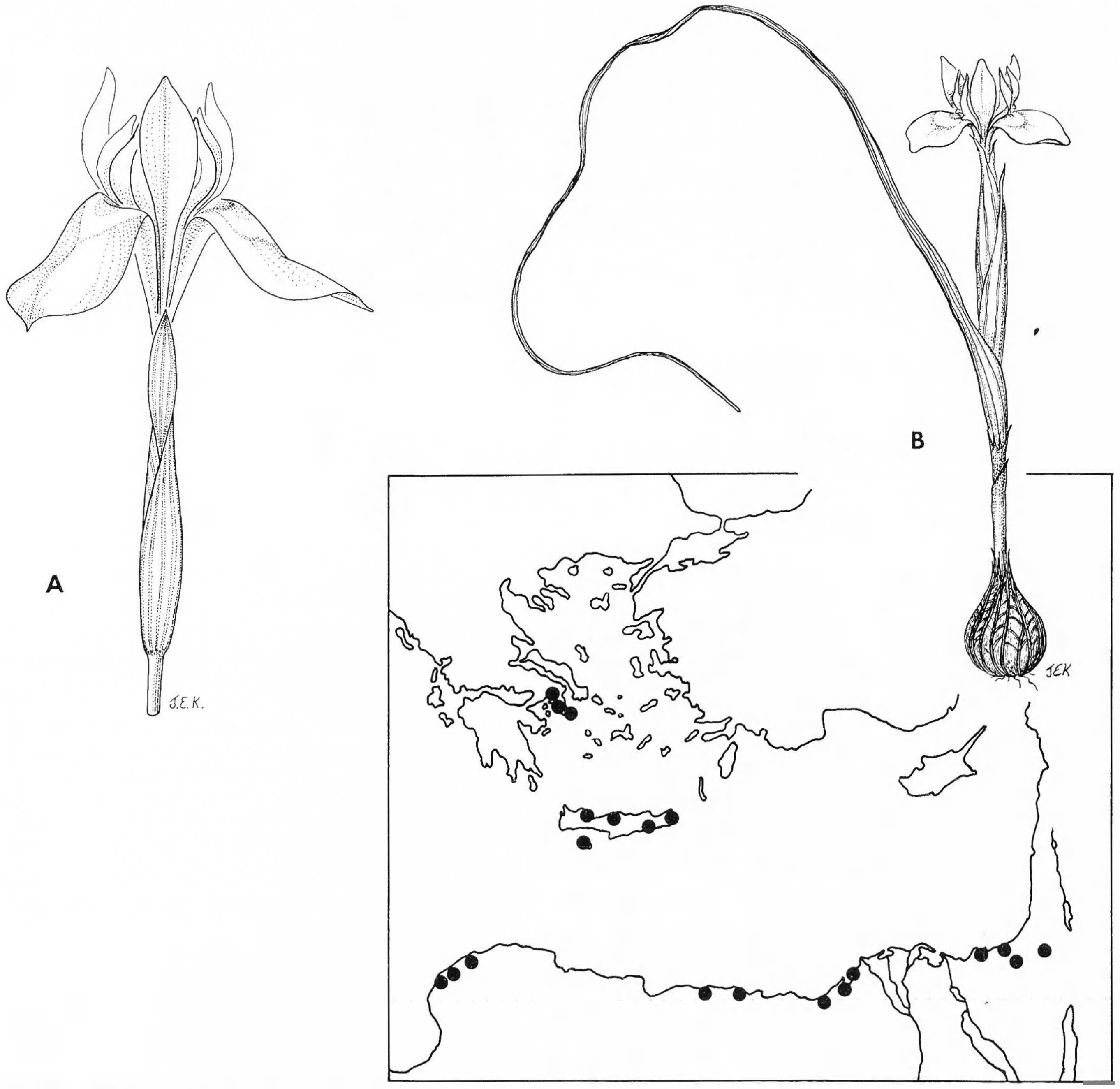

Fig. 6. The Northern Hemisphere species of *Gynandriris* with distribution of *G. monophylla* only: — A: *G. sisyrinchium* (life size). — B: *G. monophylla* (life size). (The complete range of *G. sisyrinchium* is provided in Fig. 1 in which the whole range of the genus in the Northern Hemisphere is the same as that for *G. sisyrinchium*.)

Plantarum Historiae 1: 216. 1601 (lectotype). — *Moraea sisyrinchium* (L.) Ker, Konig & Sims, Ann. Bot. 1: 201. 1805. —*Xiphion sisyrinchium* (L.) Baker, Jour. Bot. 7: 42. 1871. — *Helixyra sisyrinchium* (L.) N. E. Br., Trans. Roy. Soc. S. Africa 17: 349. 1929.

Iris collina Salisb., Prod. Stirp. 45. 1796 nom. illeg. superf. pro. *I. sisyrinchium* L.

Iris fugax Pers. sensu Tenore, Fl. Nap. 1: 15, tab. 4. 1811, non Pers., Syn. 1, 54. 1805 nom illeg. superf. pro *Moraea tricolor* Andr. —*Moraea fugax* (Pers.) Tenore sunsu Tenore, Syll. Fl. Neap.: 26. 1831, nom. illeg. non *M. fugax* (de la Roche) Jacq., 1776.

Moraea tenoreana Sweet sensu Sweet, Brit. Flow. Gard. ser. 1, tab. 110. 1825, superfl. nom. nov. pro *Iris fugax* Pers. (homotypic synonym of *Moraea tricolor* Andr.).

Diaphane edulis Salisb., Trans. Hort. Soc. 1: 304. 1812, nom. illeg. superf. pro *Iris sisyrinchium* L.

Iris syrtica Viviani, Fl. Libycae Spec. 3, t.1, f.1. 1824. — Type: Libya, "Magnae Syrteos", location of specimen not known to me, illustration seen.

Iris sisyrinchium var. *major* Cambessedes, Mém. Mus. Paris 14: 314. 1827. Type: Balearic Is. (not known to me).

Iris sisyrinchium var. *minor* Cambessedes, Mém. Mus. Paris 14: 314. 1827. nom. illeg. superf. pro. *I. sisyrinchium* L.; non sensu Aschers. & Graeb., Syn. Mitteleur. Fl. 3: 517 et auct. (= *G. monophylla* Boiss. & Heldr. ex Klatt).

Iris aegyptica Delile, Frag. Fl. Arab. Petr. 7. 1833. — Type: Egypt, not seen (possible type at LE).

Iris involuta Garzia, Effem. Sci. Sicilia 3: 286. 1834.

— Type: Italy, Sicily (location of type not known to me).

Iris maricoides Regel, Acta Hort. Petrop. 8: 676. 1884. — Type: Soviet Central Asia, near Pishpek, on arm of R. Pyandzh (not seen). — *Gynandriris maricoides* (Regel) Nevska, Acad. Nauk. S. S. R. Bot. Inst. Trudy ser. 1, 4: 217. 1937.

Gynandriris monophylla Jord., Jord. & Four., Ic. Fl. Eur. 2: 27, tab. 291. 1903, nom. illeg. non *G. monophylla* Boiss & Heldr. ex Klatt 1865–66. — Type: Algeria near Algiers (figure only seen).

Gynandriris numidica Jord., Jord & Four., Ic. Fl. Eur. 2: 27, tab. 292. 1903. — Type: Algeria, near Constantine (figure only seen).

Gynandriris littorea Jord., Jord. & Four., Ic. Fl. Eur. 2: 27, tab. 293. 1903. — Type: Algeria, near Algiers (figure only seen).

Gynandriris sisyrinchium var. *alba* Fernandez & Garcia, Biol. Soc. Brot. 21: 8. 1947. — Type: Portugal (not seen).

In synonymy only: *Iris zelantea* Vigo (In Parl., Nouv. Gen. et Sp.: 53. 1854).

Note 1. For a discussion of *Gynandriris sicula* (Todaro) Todaro (syn. *Moraea sicula, Iris todaroana, I. maculata, I. sisyrinchium* var. *sicula*, and *I. sisyrinchium* var. *maculata*) see excluded species.

Note 2. Varieties listed by Baker (1878), Richter (1890), Foster (1892), Pampanini (1936), and Maire (1959) are not included in the synonomy.

Plants medium to large, (6–)10–30 cm high. *Corm* 1–2 cm in diameter with tunics of brown, soft textured or rarely black and wiry, fine to medium fibres. *Leaves* 1 or 2, linear, more or less straight, 3–5 mm wide. *Stem* contracted or extending well above ground, few branched, occasionally simple. *Spathes* usually dry at flowering time, inner (35–)40–65 mm long, outer slightly shorter. *Flowers* pale to deep blue, violet, or rose–purple; *outer tepals* (19–)21–40 mm long, limb sometimes equal to but usually shorter than the claw, spreading; inner tepals erect, 19–28 mm long. *Filaments* (7–)8–14 mm long, united for about one third their length; *anthers* (4.1–)4.5–10.0 mm. *Style branches* 8–20 mm, crests 6–12 mm, shorter than the branches. *Capsule* ca. 2 cm long, seeds black, angular. *Chromosome number*: 2n=24.

Flowering time. Late winter to late spring, January–May.

Distribution. Mediterranean basin and Middle East, from Portugal to northern Pakistan. Fig. 1.

One of only two species of the genus (and of tribe Homeriinae) found in the northern hemisphere, *Gynandriris sisyrinchium* is one of the most widespread species of Iridaceae. It is relatively common in the Mediterranean basin and is consequently well known and much collected. Since its description by Linnaeus in 1753, it has acquired a large number of synonyms. Some of these appear to differ in no significant way from the type, but others have been applied to discrete forms, especially size and colour variants. There appears to be no type specimen, and the species must be typified by the illustration in Clusius' Rar. Pl. Hist. vol. 1, p. 216 entitled "*Sisyrinchium majus*", which Linnaeus cited. Linnaeus himself recognized two forms, a larger flowered and a smaller flowered.

Variation in flower size is apparently common in this species with smaller flowered plants often found in more arid habitats, and also at the end of the flowering season. Several authors have recognized small flowered plants or races as distinct varieties, from Cambessedes (1827), who equated his var. *minor* with Linnaeus' type, to Maire (1959). It is important to distinguish these smaller flowered plants, "var. *minor*," from the very distinct *G. monophylla*, a species of the eastern Mediterranean, with flowers much smaller than the smallest blooms of *G. sisyrinchium*. These two entities have often been confused, and many authors have equated var. *minor* Cambessedes and *G. monophylla* (Aschers. & Graebner 1907; Täckholm & Drar 1954). It is generally quite easy to see the differences between *G. sisyrinchium* and *G. monophylla* in live plants, especially as the two sometimes grow together. The larger flowered *G. sisyrinchium* typically has clear bright blue to violet flowers and *G. monophylla* has tiny pale slate gray–blue flowers. These differences observed in Egypt by Drar (1925) and Täckholm & Drar (1954) have been confirmed in my field studies in Greece. Differences in height and robustness accompany the floral differences, *G. sisyrinchium* usually being taller, larger, and often with two leaves, while *G. monophylla* usually has one leaf. The epithet *monophylla* is somewhat misleading since leaf number is not a specific character, and just as *G. sisyrinchium* may have a single leaf, *G. monophylla* may have two.

Differences in flower size make confusion unlikely between *G. sisyrinchium* and *G. monophylla*. The outer tepal of the former usually ranges from 25–40 mm with occasional specimens as small as 19 mm, while the anthers, another good guide to flower size, usually exceed 5 mm, although in rare examples they may barely exceed 4 mm. *G. monophylla*, in contrast, has outer tepals ranging in size from 11–18 mm and rarely to 19 mm, and anthers less than 4 mm long, and usually about 3 mm.

The plant called *G. sicula*, or *G. sisyrinchium* var. *sicula*, is a variant I find it difficult to deal with. It was illustrated and described in detail by Todaro (1887–92, as *Moraea*) from a cultivated plant in the botanical gardens at Palermo, and apparently originally from southern Sicily. Differences from *G. sisyrinchium* which Todaro also knew well, include leaf number, flower size, and importantly speckled outer tepals in which the limb much exceeds the claw, and short style crests. This plant is often recognized in Italian floristic treatments but there are, as far as I have been able to ascertain, no herbarium collections of it other than the type, which today lacks a flower and as such is virtually indistinguishable from *G. sisyrinchium*. Albo (1919), dealing with the flora of southeastern Sicily, lists numerous localities for this plant which he calls *Iris sisyrinchium* var. *maculata*. With the assistance of Dr. S. Brullo of the University of Catania, I visited two of these sites and found plants with flowers slightly different from typical *G. sisyrinchium* (notably and orange mark at the base of the nectar guide, and an orange line down the outer tepal claw) but not at all similar to Todaro's illustration of *G. sicula*. These southeastern Sicily plants are best regarded merely as a regional race of *G. sisyrinchium*. Until more light can be thrown on *G. sicula*, this species must be excluded. Variant forms of *G. sisyrinchium* illustrated by Ricci (1970–71) from Sicily and Sardinia may relate to the *G. sicula* question, but documentation is inadequate and allows no constructive opinion. These plants, however, also lack the spotted tepals mentioned by Todaro.

Gynandriris sisyrinchium grows in a wide variety of habitats from the sea shore to open woodland to true desert conditions, with soils varying from stony gravel, to rich clay loam, to sand. It often appears as an adventive, and grows in large numbers in disturbed sites, fallow fields, and road verges. It possibly owes its wide distribution to man, who may have inadvertently spread the species along with primitive agriculture.

G. sisyrinchium is apparently tetraploid throughout its range (Table 1), with some variation in karyotype. Ricci (1970–71) has documented minor karyotypic variation in morphologically recognizable forms from mainland Italy, Sicily, and Sardinia. The flowers of the two atypical forms appear, from the illustrations in his article, unusual but are doubtfully of any taxonomic importance.

9. **Gynandriris monophylla** Boiss. & Heldr. ex Klatt, Fig. 6 B

Klatt, Linnaea 34:578, 1865–66. — Type: Greece, "Attica ad Phalerum raro" collector cited as Boissier, but probably Heldreich s.n. (ann. 1853) (C lectotype; L, MO, isotypes); Paratypes: Spain, Majorca, Cambessedes s.n. (K), = *G. sisyrinchium*; S. Africa, Cape, Drège 2599 (not seen) and Ecklon & Zeyher Irid. 33 (LE, MO), = *G. setifolia*; S. Africa, "Trans-Gariepina", Ecklon & Zeyher Irid. 301 (not seen), probably *G. simulans*.

Iris sisyrinchium L. var. *monophylla* Heldr., Atti Congresso Internazionale Botanico, Firenze 234. 1876. — Type: Greece, "Athenas ad Padisha", Heldreich 1891 (ann. 1848) (K lectotype, E isotype); Paratype: Greece, "planitie marit. Phaleri", 1856, Heldriech, Herb. Graec. Normal. no. 51 (G, K, W). — *Gynandriris sisyrinchium* (L.) Parl. var. *monophylla* (Heldr.) Halacsy, Consp. Fl. Graec. 3: 191. 1904.

Iris sisyrinchium var. *minor* Camb. sensu Täckholm & Drar, Flora Egypt vol. 3, 465. 1954, et sensu auct. — *Moraea sisyrinchium* (L.) Ker var. *minor* (Camb.) Bak. sensu Baker, J. Linn. Soc. Bot. 16: 132. 1878, pro parte.

In synonymy only: *Iris monophylla* Boiss. & Heldr. (In Klatt, Linnaea 34: 578, 1865–66; Heldr., Atti Congr. Bot. Fireze 234, 1876.) — *Iris samaritani* Heldr. (In Heldr., Atti Congr. Bot. Firenze 234, 1876; Baker, J. Linn. Soc. Bot. 16: 132. 1878.)

Plants small, seldom more than 4–6 cm above ground including flower. *Corm* 8–10 mm in diameter, tunics dark coloured. *Leaf* usually solitary, 10–15 mm long and trailing, occasionally with a small second leaf, rarely with two fully developed leaves. *Stem* seldom produced above ground, usually simple, but sometimes bearing 1 or 2 lateral inflorescences on side branchs. *Spathes* usually dry, 20–30(–35) mm long, outer slightly shorter than inner. *Flowers* very pale blue with nectar guide orange ringed with white; *outer tepals* 11–17(–20) mm long, claw pale, densely spotted; limb horizontal, slightly shorter than claw; inner tepals erect, 9–15 mm long, lanceolate, to 2 mm at widest. *Filaments* 4–6 mm long, united for ca. 1 mm; *anthers* 2–3(–4) mm long. *Style branches* 5–6 mm long, crests 4–6 mm. *Chromosome number*: $2n=24$.

Flowering time. Mid-March–April.

Distribution. Eastern Mediterranean, mainly coastal, Libya, Egypt, ?southern Israel and Greece in Attica, Aegina, and Crete. Fig. 6.

When he first described *Gynandriris monophylla*, Klatt cited several collections comprising what are today regarded as four different species, Mediterranean and South African, all belonging to *Gynandriris* and having in common a single leaf. I have selected the collection from Greece as lectotype, thus fixing the concept of *G. monophylla* as applicable to the dwarf Greece–N. African species. Other specimens cited are a Cambessedes collection from Majorca, which is a short-stemmed form of *G. sisyrinchium*, and Drège and Ecklon & Zeyher plants from South Africa, not all of which I have seen but which include *G. setifolia* and perhaps *G. simulans*. The Greece collection is chosen as lectotype firstly because the name *monophylla* was clearly taken from the manuscript name given this collection, and secondly, fixing the name *monophylla* for the taxon preserves current usage.

Gynandriris monophylla was redescribed, apparently independently by Heldreich in 1876, the epithet *monophylla* again being used, though at varietal rank, as *Iris sisyrinchium* var. *monophylla*. The species has generally been accorded recognition as a variety of *G. sisyrinchium* in local and regional floras subsequent to its treatment by Heldreich (e. g., Richter 1890, Halacsy 1904, Boissier 1884, Muschler 1912, Drar 1925, Post 1933, Täckholm & Drar 1954 (under the name var. *minor*); Rechinger 1943, etc.). In treatments of larger areas, however, *G. monophylla* has usually been relegated to synonymy as in Dykes' monograph of *Iris* (Dykes 1913), as well as by Baker (1892) and Foster (1936).

My own field observations of *G. sisyrinchium* and *G. monophylla* have convinced me that *G. monophylla* is indeed a distinct plant and worth specific recognition. In mainland Greece it is confined to the Attic peninsula where it ranges from Athens east along the coast, and locally inland, to Cape Sounion. It grows in open areas with shallow soil, or where the vegetation has been much trampled, but is absent from very rocky or heavily vegetated sites. Interestingly, at some places, e.g., Filipapou hill in Athens and around the temple at Sounion, *G. monophylla* grows together with *G. sisyrinchium*, and in these situations the difference between the two species is quite striking. Flowers of *G. monophylla* are pale blue–gray, dull colored, and less than half the size of the large, bright and often deep blue–purple flowers of *G. sisyrinchium*. Where I have seen them growing together there are no signs of intermediate forms and both species are rather uniform morphologically although, as often noted, *G. sisyrinchium* varies in height, though not in these areas in flower size.

Elsewhere in Greece, *Gynandriris monophylla* occurs on Aegina, Crete, and on the small island of Gaudos off southern Crete. It is evidently rare on Aegina and is not known to Pauline Haritonidou, who has studied the island's flora in detail. On Gaudos, Dorfler observed *G. sisyrinchium* growing together with *G. monophylla* (Dorfler 83 [W]). *G. monophylla* has a wider range in North Africa, where it occurs along the coast of Libya and Egypt with an eastern extension into northern Sinai (see Post 1933), and Israel, where it is rare. Al least two collections (Zohary 13335 & 13371) from the Negev seem to belong in this species. *G. monophylla* appears to be more variable in N. Africa, and flowers range from the small size found in Greece to rather larger ones especially in the Nile delta region (e. g., Balls s.n. [E]).

It is usually easy to recognize *Gynandriris monophylla* either live or dry by its very small flowers with tepals, stamens, and style branches all considerably smaller (Fig. 6 A) than in the related but far more common *G. sisyrinchium*. Occasionally problems may be encountered in distinguishing unusually small flowered and dwarfed specimens of *G. sisyrinchium* from larger flowered forms of *G. monophylla*. Colour may be useful here, since *G. monophylla* has pale blue–gray flowers which contrast sharply with the clear and dark blues and blue–purples of *G. sisyrinchium*. In dried material intermediate forms are harder to name though generally anther size is a good guide. Plants with anthers 4 mm or less are almost certainly *G. monophylla*, while those with anthers 4.5 mm or longer are *G. sisyrinchium*.

Excluded species

1. *Gynandriris apetala* (L. Bol.) R. C. Foster, Contrib. Gray Herb. 127: 48. 1939 = *Moraea cooperi* Baker (Goldblatt 1976 b).

2. *Gynandriris italica* (Parl.) Sanguinetti, Prod. Flor. Romae 747. 1864 = *Iris chamaeiris* Bertolini (Dykes 1913).

3. *Gynandriris longiflora* (Ker) Foster. Contrib. Gray Herb. 114: 40. 1936 = *Moraea longiflora* Ker (see Goldblatt 1976 b).

4. *Gynandriris sicula* (Todaro) Todaro, Flora Sicula 3: 73. 1908.

This species was described (as *Moraea*) from a plant found in the botanical gardens in Palermo by Todaro (1887–1892), who knew the related *G. sisyrinchium* well, and contrasted the two species in his description. He distinguished *G. sicula* by a consistently solitary leaf (versus two leaves in common forms of *G. sisyrinchium*), very short outer tepal claws, short style crests, and importantly, speckled markings on the limbs of the outer tepals. This species is often recognized in floristic works of Italy and Sicily, sometimes as a variety of *G. sisyrinchium*, and by various synonyms.

I have attempted to find plants matching the type illustration in Sicily and with the help of Dr. S. Brullo, University of Catania, visited several places where populations, locally thought to match *G. sicula*, occurred, i.e. coastal southeastern Sicily (Albo 1919). Plants located mostly had a solitary leaf, but otherwise differed in no significant way from typical *G. sisyrinchium*, having similar pale blue–purple flowers, and tepal claws about as long, or longer than the limbs. As discussed under *G. sisyrinchium*, I prefer to exclude *G sicula* entirely. Until wild plants matching the type are located, it seems best to assume this plant was a mutant or teratological form of *G. sisyrinchium*. It is, however, relevant to point out that the southern African *G. simulans* has speckled tepals, and unusually short tepal limbs, and the possibility cannot be excluded that this species was in cultivation at Palermo. The type illustration of *G. sicula* does not sufficiently resemble *G. simulans* to permit recognition of these as conspecific.

The synonymy of *G. sicula* is as follows:

Gynandriris sicula (Todaro) Todaro, Fl. Sicula 3: 73. 1908. — *Moraea sicula* Todaro, Hort. Bot. Panorm. 2: 43, Tab. 34. 1887–1892. — Type: Italy, southern Sicily, cult. Hort. Bot. Palermo, Todaro s.n. (FI, holotype).

Iris todaroana Ciferri & Giacomini, Nomenclator. Fl. Ital. vol 1: 150. 1950.

Iris maculata Todaro ex Zangeri, Flora Italica 1, 877. 1976 nom superf. pro *Iris todaroana* Ciferri & Giacomini.

Iris sisyrinchium var. *sicula* Fiori, Nuova Fl. Anal. d'Ital. 303. 1923–25; Borg, Descr. Fl. Maltese Is. 707. 1927.

In synonymy only: *Iris maculata* Todaro. In Lojacono, Fl. Sicula 3: 73. 1908

5. *Gynandriris spiralis* (N. E. Br.) Foster, Contr. Gray Herb. 114: 41. 1936 = *Barnardiella spiralis* N. E. Br.) Goldbl. (Goldblatt 1976 c)

6. *Gynandriris stenocarpa* (Schltr.) R. C. Foster. Contr. Gray Herb. 127: 47. 1939 = *Moraea cooperi* Baker (Goldblatt 1976 b).

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The lichen genera Argopsis and Stereocaulon in New Zealand

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Ten species of *Stereocaulon* Hoffm. are recorded from New Zealand and of this number five (*S. argus* Hook. fil. & Tayl., *S. colensoi* Church. Bab., *S. gregarium* Redinger, *S. fronduliferum* Lamb, *S. loricatum* Lamb) appear to be endemic there. *Argopsis megalospora* Th. Fr., is confined to the subantarctic islands (Campbell Island and the Auckland Islands, but not Macquarie Island) and has not yet been positively identified from the mainland of New Zealand. A key is given to species recognised in the New Zealand flora together with details of chemistry, distribution, habitat, morphology and nomenclature.

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The lichen family Stereocaulaceae was first proposed by Duvigneaud (1944) to comprise the genera *Argopsis* Th. Fr., *Pilophorus* Th. Fr., and *Stereocaulon* Hoffm., which were earlier included in the Cladoniaceae (Zahlbruckner 1926, Smith 1921). Cooke & Hawksworth (1970) record that the first valid publication of the family Stereocaulaceae was by Chevallier, 1826–27, as an "order", with the spelling "Stereocauleae". Duvigneaud's studies on the development of the erect, spore-bearing structures (podetia) of the Cladoniaceae s. lat., showed that in *Argopsis* and *Stereocaulon* the ontogeny of the fertile stalks of the secondary thallus is fundamentally different from that of species of *Cladonia* and *Baeomyces*. He used Vainio's (1890) term, pseudopodetia, to describe the erect, secondary thallus of *Stereocaulon* and later studies (Lamb 1951, 1977, Jahns 1970, Henssen & Jahns 1973) have confirmed and extended this view, adding to the Stereocaulaceae the genus *Compsocladium* Lamb (Lamb 1956).

Species of *Argopsis* and *Stereocaulon* are saxicolous or terricolous and in New Zealand are found colonising a wide range of rock and soil types, with some species being ± restricted to a particular substrate e.g. *S. vesuvianum* occurs mainly on volcanic soils and on lava. The pseudopodetia arising from a crustose or granular-verrucose or scale-like primary thallus which is frequently evanescent, can be erect, tufted, ± copiously branched structures up to 25 cm tall (as in robust forms of *S. ramulosum*), or small, simple and densely crowded-caespitose as in *S. caespitosum* and *S. gregarium*.

The delimitation of *Stereocaulon* was discussed by Dodge (1948) and Lamb (1951, 1977). Lamb (1974) also described the anatomy, chemistry and morphology of *Argopsis* together with distributional data on its three species.

The first collection of *Stereocaulon* from New Zealand was made by Joseph Banks and Daniel Carl Solander, naturalists on Captain James Cook's bark Endeavour during the circumnavigation of 1769–1771. A specimen of *S. ramulosum* (Sw.) Räusch., from an unidentified coastal locality is preserved in BM. In 1791, Archibald Menzies, naturalist to George Vancouver's Discovery expedition of 1791–1795, gathered *S. ramulosum* from the shores of Dusky Sound, specimens of which are preserved in the herbaria of BM, E, LINN-SM and S.

The nineteenth century saw an expansion of collecting and subsequent taxonomic appraisal of New Zealand lichens including species of *Stereocaulon* (see Richard 1832, Cunningham 1836, Hooker & Taylor 1844, Montagne 1845, Raoul 1846, Babington 1855, Nylander 1858, 1860, 1876, 1888, Lindsay 1866, 1868, 1869, Hooker 1867, Krempelhuber 1868, 1870, Knight 1884, Hue 1892–1898, Müller Argoviensis 1894, 1896 a, Hellbom 1896) and at the close of the century the *Stereocaulon* flora of New Zealand (including the subantarctic islands to the south) based largely on the collections of Banks and Solander, Berggren, Buchanan, Colenso, D'Urville, Filhol, Haast, Hector, Helms, Hooker, Knight, Lindsay, Menzies and Sinclair numbered six species: *S. argus* Hook. fil. & Tayl., *S. corticatulum* Nyl., *S. colensoi* Church. Bab., *S. fronduliferum* Lamb (based on Babington's taxon *S. ramulosum* var. *compressum*), *S. ramulosum* and *S. vesuvianum* Pers., with several varieties and forms of *S. ramulosum* accounting for most of the synonyms existing in the literature up to that time. Apart from a few collections of Colenso, Haast, Hector, Monro and Sinclair made from mountainous inland areas in the 1860's, most of the nineteenth century specimens of *Stereocaulon* to be found in European herbaria deriving from New Zealand are from lowland and predominantly coastal localities.

In contrast to the proliferation of published work relating to New Zealand lichens that was characteristic of the last 15 years of the nineteenth century, for the first two decades of the 20th, little or nothing was done. Among the few lichens identified by Lindau (1909) from a collection made in the subantarctic were *S. argus* from the Auckland Islands (recorded as *Sphaerophorus argus*), and *S. argus* (recorded as *S. argodes*) and *S. ramulosum* from the Antipodes Islands, gathered by Leonard Cockayne.

The lichenological riches of New Zealand's mountains (particularly those of South Island) were not explored to any significant extent until the arrival of the Swedish botanists G. Einar and Greta Du Rietz in 1926–27 when the first comprehensive collections of alpine lichens were made. In Du Rietz's herbarium (the lichens will be distributed to S, GB, UPS and LD) copious collections of *Stereocaulon* contain the following species: *S. argus, S. caespitosum* Redinger, *S. corticatulum, S. fronduliferum, S. gregarium* Redinger, *S. ramulosum* and *S. vesuvianum*. Although Du Rietz never published a detailed account of his New Zealand lichen collections, he actively encouraged several local botanists to include lichens in their collections with the result that H. H. Allan (Galloway 1976), G. Simpson and J. S. Thomson collected lichens from many parts of both North and South Islands, duplicates of which were sent to Zahlbruckner (1941) in Vienna for determination.

From these collections Redinger (1936) described two new species from South Island collections of Simpson and Thomson, naming them *S. caespitosum* and *S. gregarium*. Dodge (1948) described *S. pulvinare* Dodge from New Zealand material that is, in my opinion, only a caespitose coastal modification of *S. ramulosum*. His later accounts of New Zealand lichens contain many equivocal taxa, for example his use of *S. argodes* Nyl., refers to *S. loricatum* Lamb, and to *S. argus* (Fineran & Dodge 1970, Fineran 1971) and the nom. nud. *S. traversii* (Hue) Dodge (Fineran 1971) to *S. ramulosum*. The extreme polymorphy of *S. ramulosum* in New Zealand (incidentally not supported by any variation in chemistry) has confused many authors over the years resulting in the establishment of many superfluous names. The accounts of Dodge (1929), Zahlbruckner (1941), Martin (1966) and Martin & Child (1972) perpetuate the burden of irrelevant nomenclature surrounding this highly plastic and adaptable species, and further, present a confused view of speciation in the genus in New Zealand.

A preliminary report on two species new to New Zealand, *S. loricatum* and *S. trachyphloeum* Lamb (Galloway et al. 1976), is a prelude to the present study. In a recent synoptic world treatment of *Stereocaulon*, Lamb (1977) records 11 species and 12 infraspecific taxa from New Zealand including a new species *S. wadei* Lamb which is, in my opinion, merely a chemical strain of *S. corticatulum*. Valuable though Lamb's account is, I feel that it gives too much taxonomic weight to often only minor modifications, usually environmentally induced, and fails to take into account the extreme morphological, and sometimes also chemical variation that is encountered in New Zealand populations of *Stereocaulon*. Indeed it is a matter for regret that so many subspecific taxa are recorded for what I can only regard at present as ecological variants of plastic species.

Material and methods

Collections. In view of the conflicting evidence in the literature regarding speciation in *Stereocaulon* in New Zealand and of the proliferation of poorly defined infraspecific taxa, a revision of the New Zealand species was undertaken. In this revision I have used my own collections made over 18 years from the Three Kings Islands (lat. 34°S) in the north of New Zealand, to southern Stewart Island (lat. 47°S) in the south. In addition, type and other material was examined in, or borrowed from the following herbaria: BM, CANU, CHR, E, FH, H, H-ACH, H-NYL, LD, LINN-SM, MEL, OTA, S, UPS, UPS-ACH, UPS-THUNBERG, UPSV, W and WELT. Most of the published taxa relating to *Stereocaulon* in New Zealand were reexamined as well as all relevant 18th and 19th century collections.

Anatomy and morphology. The taxonomic importance of pseudopodetial branching, phyllocladia, cephalodia, soredia, apothecia and pycnidia are reviewed in detail by Lamb (1951), and for the definition of anatomical and morphological terms the reader is referred to this account. The development of pseudopodetia and also details of ascocarp ontogeny in *Stereocaulon* are discussed by Duvigneaud (1944), Lamb (1951), Jahns (1970) and Henssen & Jahns (1973).

Chemistry. Specimens were extracted in hot acetone and the extracts examined by thin-layer chromatography (TLC) by the method of Culberson (1972). Compounds identified from the New Zealand species of *Stereocaulon* and from *Argopsis megalospora* are detailed in the accounts of Cambie (1968), Culberson (1969, 1970), Culberson et al. (1977), Fox & Huneck (1970), Fox et al. (1970) and Lamb (1974, 1977).

Key to genera

1. Apothecia expanded, to twice as wide as supporting branch, or wider, thalline exciple massive, ± cupuliform, coarsely wrinkled-scabrid, disc slightly concave to plane, spores large, broadly cylindrical-ellipsoid, muriform, 1–3(–6) per ascus .... *Argopsis*
– Apothecia rarely wider than supporting branch, thalline exciple rarely well developed, often obscured by disc which is frequently convex-subglobose, spores narrowly elongate-fusiform, 1–13-septate, 8 per ascus ..... *Stereocaulon*

Argopsis Th. Fr.

Thallus dimorphic. Primary thallus small, verrucose, soon disappearing. *Secondary thallus* of persistent, fruticose, often richly branching pseudopodetia which are firmly attached to the substrate by a stout holdfast, pseudopodetia with inconspicuous cephalodia and with ± scattered phyllocladia. *Apothecia* terminal, often large, expanded, disc plane with a prominent margin and massive thalline exciple. Spores large, muriform, 1–2(–6) per ascus, broadly cylindrical-ellipsoid. *Pycnidia* sometimes present, below apothecia, minute, swollen, clustered, ostiole punctate, black. *Pycnospores* filiform, curved.

Argopsis is a Southern Hemisphere genus of three species (Lamb 1974) which are restricted to the Auckland, Campbell and Crozet Islands and to Kerguelen. One species is known from the New Zealand botanical province and occurs on the Auckland Islands and Campbell Island. It has not yet been positively identified from the New Zealand mainland.

1. **Argopsis megalospora** Th. Fr.

Fries 1858: 335 — Type: Campbell Island. J. D. Hooker (UPS! holotype; BM, E, FH! isotypes).

Anatomy, chemistry, distribution and morphology of *A. megalospora* is discussed by Lamb (1974).

Affinity. *A. megalospora* is scarcely likely to be confused with any other lichen in the New Zealand flora except *Stereocaulon argus*, and in the Auckland Islands and Campbell Island the two species are sympatric. The plane, expanded apothecial disc, the massive, warted thalline exciple, the pale and smooth pseudopodetial cortex and the scarcity of both cephalodia and phyllocladia sufficiently distinguish *A. megalospora* from *S. argus*. Further, the large muriform spores of *A. megalospora* are characteristic.

Habitat and distribution. *A. megalospora* is a subantarctic species found on exposed rock outcrops in subalpine grasslands open shrublands and among fellfield vegetation on the Auckland Islands and on Campbell Island (Lamb 1974). It is not known from further south on Macquarie Island or to the north on Stewart Island or the southern mountain ranges of South Island in New Zealand. It appears to be one of a group of relict species (*Knightiella splachnirima* (Hook. fil. & Tayl.) Gyelnik, *Siphulastrum triste* Müll. Arg., *Siphula subcoriacea* Müll. Arg., *Steinera* spp., and *Stereocaulon argus* are others) restricted to exposed subalpine areas between lat. 44–57°S in the southern Pacific Ocean, which may possibly represent fragments of a once more widespread antarctic flora (representative of the southern margin of Gondwanaland) lost from New Zealand and the Antarctic continent possibly as a result of widespread glaciations in Pleistocene times (Galloway 1979). Specimens of *A. megalospora* were examined in BM, CHR, OTA and UPS.

Stereocaulon Hoffm.

Thallus dimorphic. *Primary thallus* small crustose, granular, verrucose or squamulose soon disappearing, very seldom persistent. *Secondary thallus* erect, of simple or branching pseudopodetia which are firmly attached to the substrate by a ± well developed basal holdfast, pseudopodetia corticate or ± completely decorticate, covered with verrucae or simple or branched phyllocladia which are usually terete and corticate, medulla loosely woven containing colonies of a green protococcoid alga, chondroid axis of thick-walled longitudinal hyphae, cephalodia abundant to rare, containing a blue-green alga. *Apothecia* terminal, lecideine, disc frequently convex, occasionally plane and marginate, brown or red-brown to black, hypothecium usually colourless, brown in some species, paraphyses simple, asci clavate to cylindrical, 8-spored. *Spores* colourless, thin-walled, elongate-ellipsoid to cylindrical-fusiform or vermiform transversely 1–13-septate. *Pycnidia* terminal or lateral, immersed, ovoid to spherical, darkened about the ostiole. *Pycnospores* filiform to cylindrical, straight or curved.

Stereocaulon is a genus of some 123 species of wide distribution, 10 species of which occur in the New Zealand flora. Of this number five appear to be endemic.

Key to Stereocaulon in New Zealand

1. Phyllocladia with dark centres and light margins .... 1. *S. vesuvianum*
– Phyllocladia without dark centres 2
2. Pseudopodetia 0.3–3 (rarely to 6) cm tall 3
– Pseudopodetia (1–)3–25 cm tall 6
3. Pseudopodetia (1–)3–10 mm tall, mainly simple, phyllocladia absent 4
– Pseudopodetia to 3 (rarely to 6) cm tall, phyllocladia present or absent 5
4. Cephalodia persistently pale, wrinkled-scrobiculate, apothecia convex, immarginate, hypothecium colourless .... 9. *S. gregarium*
– Cephalodia brown-black, scabrid, apothecia plane, distinctly marginate, hypothecium brown .... 8. *S. caespitosum*
5. Pseudopodetia simple or sparingly branched, to 3 cm tall, phyllocladia and soredia absent, cortex continuous, distinctly verruculose-areolate .... 10. *S. loricatum*
– Pseudopodetia branched, never simple, phyllocladia present ± sorediate, cortex continuous or in flaky patches .... 4. *S. corticatulum*
6. Phyllocladia flattened, paler on underside, hypothecium brown .... 5. *S. fronduliferum*
– Phyllocladia terete, hypothecium colourless 7
7. Cephalodia distinctly stalked 8
– Cephalodia sessile or only very slightly stalked 9
8. Cortex of pseudopodetia verruculose-areolate, apices and phyllocladia sometimes sorediate, spores (1–)3–4-septate ...... 7. *S. trachyphloeum*
– Cortex of pseudopodetia smooth to wrinkled, apices and phyllocladia never sorediate, spores (5–)6–9(–13)-septate .... 3. *S. colensoi*
9. Phyllocladia numerous, cephalodia large, irregular-wrinkled, apothecia small, disc convex, red-brown .... 6. *S. ramulosum*
– Phyllocladia sparse, cephalodia small, globose, sparse, apothecia large, disc plane to slightly convex, brown-purple to black .... 2. *S. argus*

In the discussion of species which follows, the arrangement of taxa is alphabetical within the system of subgenera, sections and subsections outlined by Lamb (1977).

1. **Stereocaulon vesuvianum** Pers., Fig. 1

Persoon 1810: 19 — Type: Italy. In Monte Vesuvia (H-ACH! isotype; L-PERS holotype not seen). For synonymy see Lamb (1977).

Thallus to 3.5 cm tall. *Pseudopodetia* simple or sparingly branched, tapering from base to apex, decorticate and rather pruinose. *Phyllocladia* on short, thick stems, rounded, peltate, becoming warted-convolute with a prominent dark greenish-grey centre and pale margins, small and crowded at apices of pseudopodetia, larger and more dispersed towards base of pseudopodetia. *Cephalodia* ± sessile, infrequent, dark green, black or brown, rather amorphous, gelatinous, shining, clustered at base of phyllocladia towards the base of pseudopodetia. *Apothecia* rare in New Zealand material, when present mainly at apices of pseudopodetia, to 1 mm in diam., disc pale brown with a prominent concolorous margin when young, occluded at maturity. Spores 3–5(–6) septate, (25–)30–50(–55) × 2.5–3.5 μm (Lamb 1977).

Chemistry. Atranorin and stictic acid, ± norstictic acid.

Affinity. *S. vesuvianum* is distinguished from all other species in the New Zealand flora by characteristic morphological and chemical differences, viz., the clustered peltate phyllocladia with darker centres and pale margins, and the presence of stictic acid in the medulla. Taxonomically it is remote from other species of *Stereocaulon* found in New Zealand, being placed in subgen. *Stereocaulon* sect. *Denudata*, whereas all of the other species are included in subgen. *Holostelidium* (Lamb 1977). The species shows

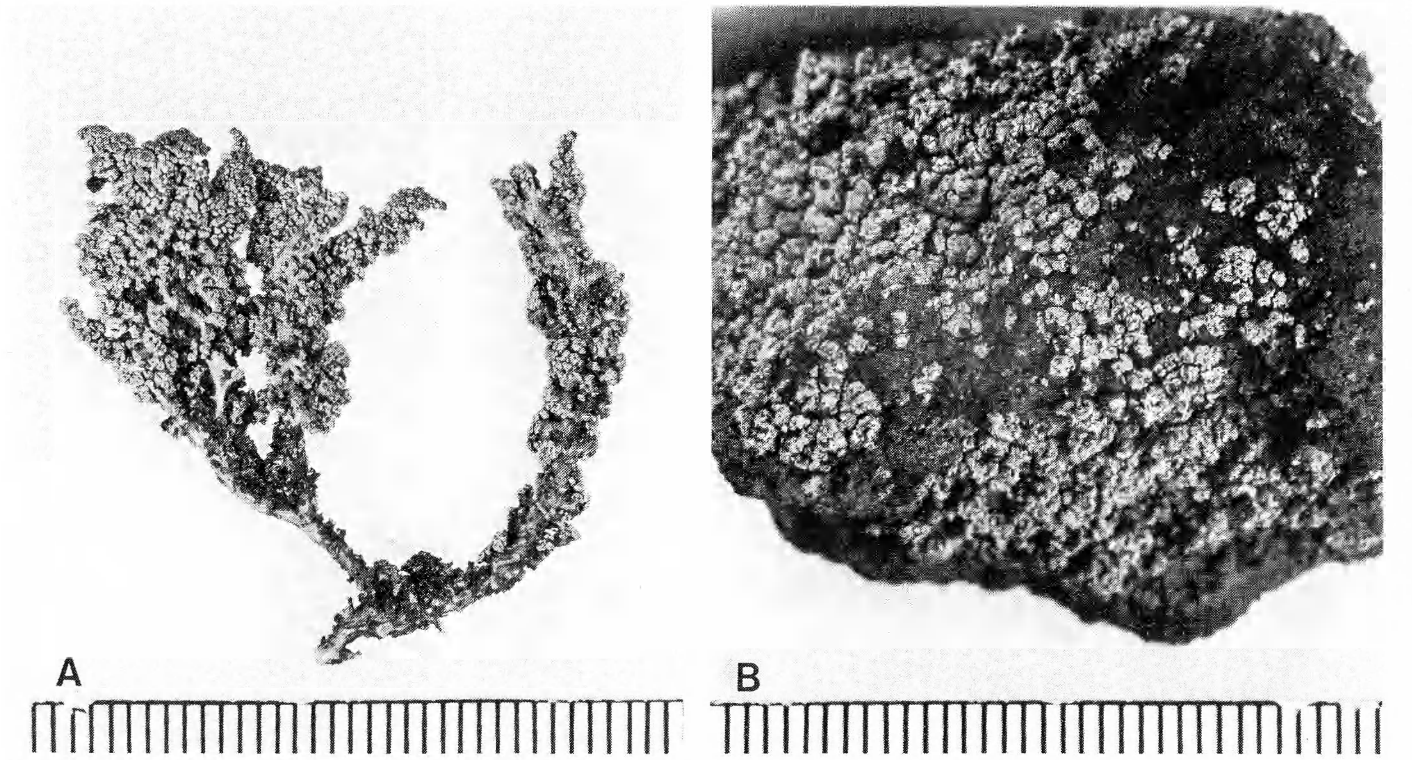

Fig. 1. *Stereocaulon vesuvianum*. — A: New Zealand, Rangitoto Island, H. H. Allan (CHR). — B: New Zealand. Mt Tarawera, A. S. D. King (CHR). — Scale in mm.

considerable variation in its morphology from erect, ± conical clumps or tufts to a scattered, closely appressed crust of phyllocladia on very reduced pseudopodetia. Both forms are illustrated (Fig. 1) and a full range of intermediates exists between these two extremes. Lamb (1977) records *S. vesuvianum* var. *nodulosum* (Wallr.) Lamb f. *umbonatum* (Wallr.) Lamb, and var. *kilimandscharoense* B. Stein, as occurring in New Zealand, but as these taxa appear to define only environmentally induced modifications within the known range of variation of *S. vesuvianum*, I consider such subspecific taxa to be superfluous.

Habitat and distribution. S. vesuvianum is a cosmopolitan species widely distributed in both Northern and Southern Hemispheres being particularly characteristic of volcanic soils. In New Zealand (Fig. 2) it is frequently encountered on lava flows of even quite recent age and on pumice soils of the Volcanic Plateau (North Island), on Mt Egmont and on Rangitoto Island. It is genuinely rare in South Island being known there from only four localities, Waiau Pass on the border of Nelson and Canterbury (Galloway & Simpson 1978), from alpine grasslands above the Lewis Pass on the slopes of Mt Technical, and-

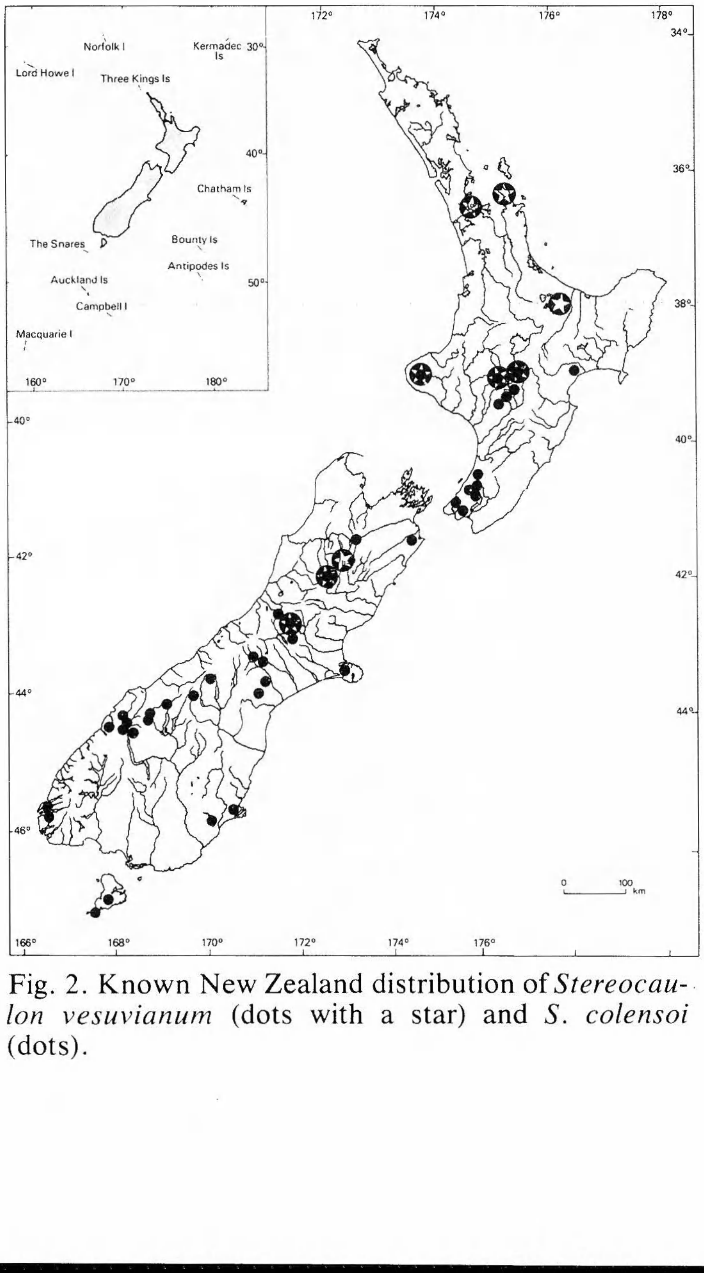

Fig. 2. Known New Zealand distribution of *Stereocaulon vesuvianum* (dots with a star) and *S. colensoi* (dots).

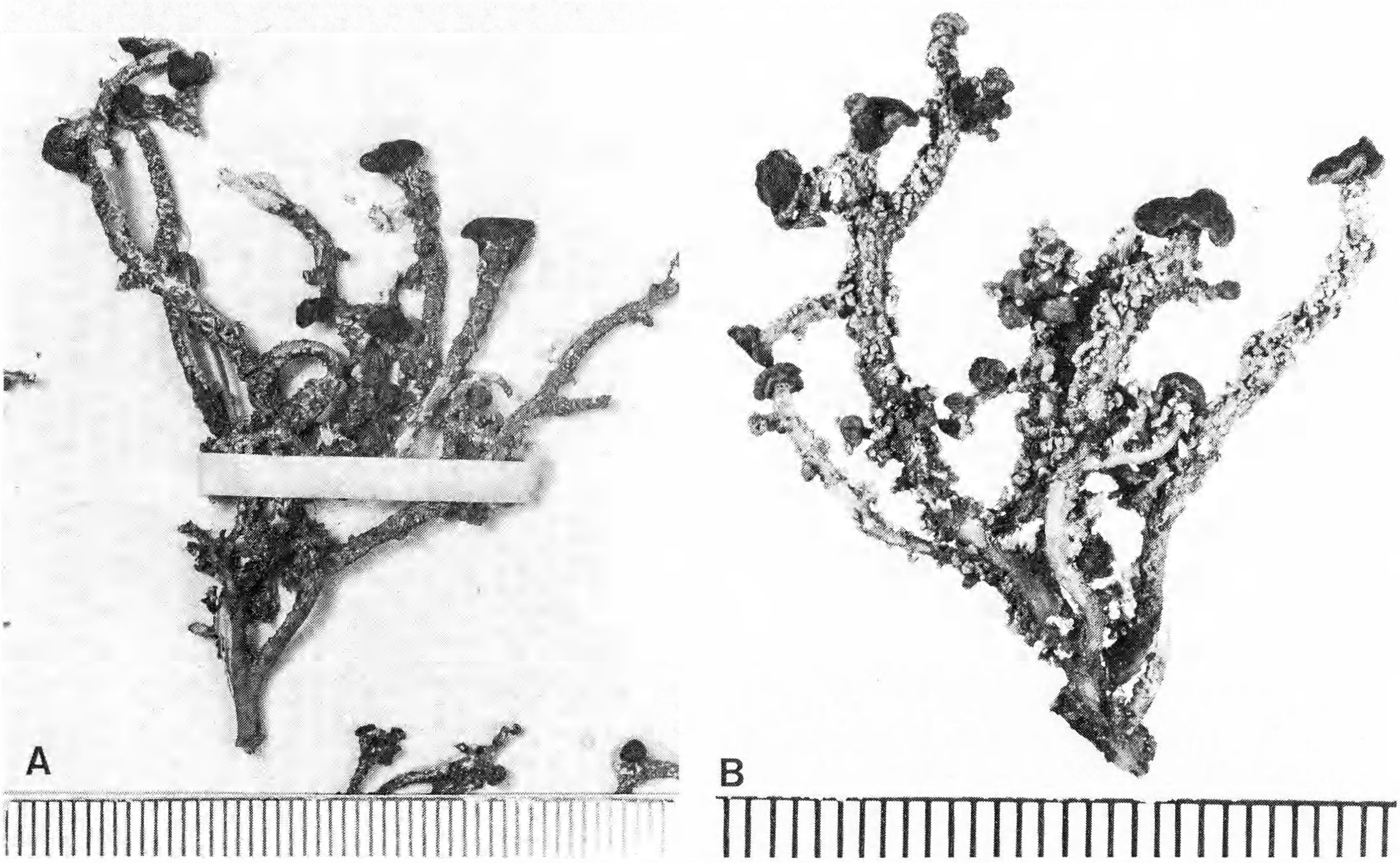

Fig. 3. *Stereocaulon argus*. — A: Campbell Island, J. D. Hooker (BM lectotype). — B: Campbell Island, M. Filhol (H-NYL 40013 p.p. lectotype of *S. argodes* Nyl.). — Scale in mm.

from the slopes of Hill's Peak and Mt Misery near Cass, the last two localities having been discovered by G. Einar and Greta Du Rietz in 1927. The record of *S. vesuvianum* from granite pavement on the summit of Smith's Lookout at the southern and of Stewart Island (Galloway 1968) is in error, the plant concerned being an aberrant form of *S. gregarium*. Specimens of *S. vesuvianum* were examined in BM, CHR, H-ACH and S.

2. **Stereocaulon argus** Hook. fil. & Tayl. Fig. 3

Hooker & Taylor 1844: 653 — Type: Campbell Island. J. D. Hooker (BM, UPS! isolectotypes; FH lectotype not seen). — *Stereocaulon macrocarpum* var. *argus* (Hook. fil. & Tayl.) Th. Fries 1857 p. 22.

Stereocaulon argodes Nylander 1876 p. 87. — Type: Campbell Island. M. Filhol (H-NYL 40013! lectotype here designated).

Thallus large, robust 4–7(–10) cm tall, branching ± dichotomous at base becoming sympodial towards apices. *Pseudopodetia* very firmly attached by a well developed holdfast, basal or primary branches stout 1.5–3(–5) mm wide, often decorticate, smooth, to strongly vertically furrowed and cracked, upper parts of branches mostly corticate although the cortex may extend to the base of pseudopodetia; cortex coarse and strongly rugose to verrucose or areolate-cracked. *Phyllocladia* sparse, corticate, with smooth white shining tips, simple, terete, gnarled, fingerlike at first and often ± restricted to the base of pseudopodetia, becoming flattened, coralloid-branched at maturity (to 7 mm long) and often ridged and cracked, at the apices of pseudopodetia the phyllocladia are smaller and nodular, rounded or flattened. *Cephalodia* developed on large pseudopodetia, small, globose 1.5(–2)–5 mm in diam., smooth or coarsely rugose, sessile or very shortly stalked, greyish-white, surface smooth, matt, never areolate or maculate. *Apothecia* terminal, large (to 5 mm in diam.), disc brownish-purple to black, plane in immature fruits and then with a conspicuous pale margin, becoming convex and immarginate at maturity, hypothecium 75 μm tall, colourless to pale brownish, asci clavate 6–8-spored. *Spores* colourless to pale yellowish, 3–7-septate, 30–50 × 4–6 μm.

Chemistry. Atranorin and perlatolic acid.

Affinity. *S. argus* may be confused with *Argopsis megalospora*, the two species are often sympatric and share a similar geographical distribution and habitat preference (see under the latter species). *S. argus* may also be mistaken for some forms of *S. ramulosum* however the cortex of the pseudopodetia, the structure of the phyllocladia and cephalodia distinguish *S. argus* (the chemistry of the two species is similar) and when it is fertile the fruits of the two species are easily separable.

Habitat and distribution. *S. argus* is a subantarctic species found on rocks in open windswept grasslands in the Auckland Islands, Campbell, Macquarie and Antipodes Islands. There is also a record of the species from the summit of Smith's Lookout on Stewart Island, the most southerly elevated portion of that island (Galloway 1968) however the material is in poor condition and as the immature fruits do not contain spores the possibility exists that the material may be a form of *S. ramulosum*. Although the diagnosis of *S. argus* was confirmed (I. M. Lamb in litt.) the species has yet to be positively identified from the New Zealand mainland.

Specimens examined. Campbell Island: J. D. Hooker (BM, E, H-NYL, UPS) — M. Filhol (BM, H-NYL) — Mt Beeman, 1958 expedition (BM, CHR) — *Auckland Islands*: D. Horning (CHR) — *Macquarie Island*: D. Horning (CHR) — *Antipodes Island*: L. Cockayne (CHR).

3. **Stereocaulon colensoi** Church. Bab., Fig. 4

Babington 1855: 295 — Type: New Zealand. Colenso 2746 (BM! holotype, H-NYL 40133 a, WELT L989! isotypes) Although the holotype (BM) contains no locality data, the Colenso herbarium (WELT) has an isotype collection (Fig. 4) labelled in Colenso's handwriting "... *Stereocaulon*, a truly beautiful species, summit Ruahine. S. botrys W. C.", see also Colenso (1884). — *Pilophoron colensoi* (Church. Bab.) Knight 1884 p. 400. — *Corynophoron colensoi* (Church. Bab.) Nylander 1888 p. 15.

Stereocaulon colensoi var. *caliginosum* Lamb 1977 p. 288 — Type: New Zealand, North Island, Kaimanawa Range, Thunderbolt Peak, 150 m D. J. Galloway 1972 (FH! holotype, CHR! isotype).

Thallus large, robust to 8 cm tall, firmly attached at base by a well developed holdfast and there often conspicuously grooved and longitudinally furrowed with little lateral cracking, branching variable, complex or simple. *Pseudopodetia* stout, often vertically furrowed, corticate or decorticate, cortex cracked and somewhat marbled, smooth or wrinkled or verrucose-areolate, investing pseudopodetia ± completely to the base, or often restricted to near the apices of the pseudopodetia in the vicinity of the fruit. *Phyllocladia* corticate, shining, smooth, slightly cracked, terete, fingerlike at first becoming branched in older parts, numbers very variable, numerous or sparse. *Cephalodia* very distinctly stalked, ficoid (Fig. 5), often numerous, single or clustered, frequently associated with phyllocladia, large, greyish-blue, surface distinctly convoluted and maculate or areolate-scabrid. *Apothecia* common, lateral and terminal, disc black or dark brownish-black, to 5 mm wide, immature fruits plane or concave with a conspicuous pale margin, mature fruits consistently convex and immarginate, hypothecium colourless. *Spores* elongate-fusiform (5–)6–9(–13)-septate, 75–100 × 4–6 µm.

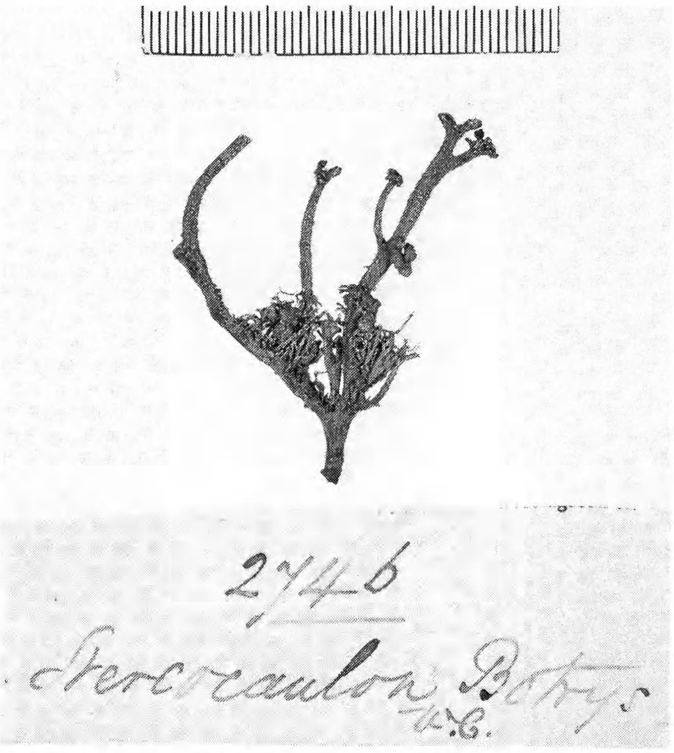

Fig. 4. *Stereocaulon colensoi*, New Zealand, Ruahine Range, W. Colenso (WELT isotype). Scale in mm.

Chemistry. Collections of *S. colensoi* exhibit a rather variable chemistry (Fox & Huneck 1970, Fox et al. 1970). The type contains atranorin and colensoinic acid and this pattern is found consistently in collections from alpine grasslands of central North Island. Collections from other parts of North Island and from all South, and Stewart Island localities contain in addition to

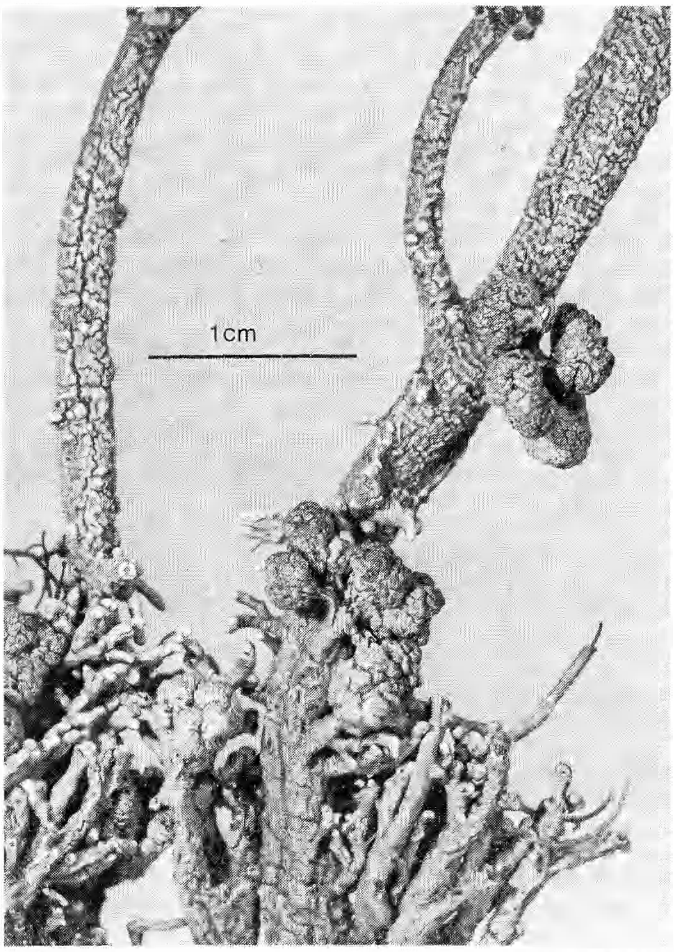

Fig. 5. Cephalodia, phyllocladia and cortex of pseudopodetia of *S. colensoi* (WELT isotype).

atranorin and colensoinic acid, varying quantities of lobaric, divaricatic and perlatolic acids. It has yet to be established conclusively whether the chemical variation shown correlates significantly with any morphological variation dependent on a particular ecology. For the present, at least two chemotypes are recognized from New Zealand populations of *S. colensoi*.

Affinity. *S. colensoi* is most likely to be confused with some robust forms of *S. ramulosum* but it differs from this species in a number of important respects: its cephalodia are always distinctly stalked and the surface of these structures is always wrinkled-scrobiculate, scabrid, maculate, never smooth, the phyllocladia are predominantly simple or furcate not consistently coralloid-branched, and their chemical constituents are different. The pseudopodetia of *S. colensoi* are also, as a rule, shorter and stouter than those of *S. ramulosum*, and the mature fruits of *S. colensoi* are black whereas those of *S. ramulosum* are red-brown. These differences also serve to distinguish *S. colensoi* from *S. argus* and from *S. trachyphloeum*, from the New Guinean species *S. staufferi* Lamb (Frey 1967), and from the South American species *S. implexum* Th. Fr. (Lamb 1977). As mentioned above, the numbers of phyllocladia in specimens of *S. colensoi* is very variable, as is the extent of development of the pseudopodetial cortex and the medullary chemistry. At the northern limit of its range (lat. 39°S) individuals of *S. colensoi* tend to be rather sparsely branched, with short thick pseudopodetia, invested in a wrinkled or verrucose cortex which extends to the base, phyllocladia are sparsely developed and tend to be grouped towards the base of the pseudopodetia along with the cephalodia. Colenso's type (Fig. 4) is of this kind. At lower altitudes in North Island and throughout lowland and subalpine areas in South and Stewart Islands specimens of *S. colensoi* are taller, more richly branching, with a less well developed pseudopodetial cortex and a much greater development of phyllocladia. The internal and external appearance of the apothecia and cephalodia is similar in both types and between these two extremes it is possible to find a full range of intermediate forms. The influence of environment on the morphology of *S. colensoi* needs careful observation in the field. The taxon *S. colensoi* var. *caliginosum* Lamb (Lamb 1977) which is sympatric with typical *S. colensoi* on the summit of the Kaimanawa Range (North Island) is merely an exposed form of the species gathered from the northern limit of its range and does not deserve any separate taxonomic status and for this reason it has been included in the synonymy of *S. colensoi*.

Habitat and distribution.' *S. colensoi* is a subalpine species endemic to New Zealand (Fig. 2) found in primarily undisturbed sites from sea level on subalpine blanket peat in southern Stewart Island, to 2000 m in mountainous areas of both South and North Islands. It has not been collected from any further north than lat. 39°S. It is a light-demanding species being most commonly encountered on rocks in grassland above the treeline or on rocks in grassland in open river flats at lower altitudes. It is very rarely found in deep shade in the interior of forests and seems to be much less tolerant of shade than *S. ramulosum*. Unlike this latter species it is not a particularly aggressive coloniser of roadside cuttings or river shingle, banks etc. On glacial erratics and on rocks alongside streams *S. colensoi* is frequently found in association with species of *Placopsis*, the orange-red terrestrial alga *Trentepohlia* and the moss *Racomitrium lanuginosum*. This particular association of plants is often the substrate for the growth of seedlings of species of *Nothofagus* (*N. menziesii* and *N. solandri* var. *cliffortioides*) in forested areas of South Island both east and west of the Main Divide. Specimens (120) of *S. colensoi* were examined in the following herbaria: BM, CHR, H-NYL, OTA, S, UPS and WELT.

4. **Stereocaulon corticatulum** Nyl., Fig. 6

Nylander 1858: 117 — Type: New Zealand, sine loco. W. Colenso 5144 (H-NYL 40026! holotype, BM, WELT! isotypes). The location of Colenso's collections 5144 is given on the packet of the isotype in his own herbarium (WELT) as "... On rocks Mt Tarahi and Cape Palliser."

Stereocaulon leptaleum Nylander 1860 p. 251 — Type: Tasmania, sine loco. J. D. Hooker (H-NYL 39978! holotype).

Stereocaulon detergens Nylander 1888 p. 16 — Type: New Zealand, sine loco. Ex Herb Jones 1867 (H-NYL 40025! holotype — *S. corticatulum* var. *detergens* (Nyl.) Müller Argoviensis 1894 p. 22.

Stereocaulon humile Müller Argoviensis 1896 b p. 88 — Type: Australia, Victoria. Knight 60 (G! holotype) — *S. corticatulum* var. *humile* (Müll. Arg.) Lamb in Frey 1967 p. 244.

Stereocaulon corticatulum var. *complanatum* Lamb 1977 p. 289 — Type: New Zealand, South Island, Otago. Taieri Mouth. J. Murray 1421, 1958 (OTA! isotype, FH holotype not seen).

Stereocaulon wadei Lamb 1977 p. 305 — Type: New Zealand, North Island. Near Whakapapa, Tongariro National Park. A. E. Wade 1966 (BM! isotype, FH holotype not seen).

Thallus rather small to 2–3 cm as a rule, robust specimens to 6 cm tall, spreading, without a defined holdfast and often forming dense compact colonies amongst mosses or on small boulders and stones in damp places. *Pseudopodetia* smooth, rarely slightly furrowed, mostly ± terete or slightly flattened, becoming branched in upper parts, ± extensively corticate, cortex continuous or in flaky patches. *Phyllocladia* sparse and often poorly developed, ± indistinguishable from finer corticate pseudopodetial branches, or granular papillose, spherical rather variable in shape, sorediate. *Soredia* granular, white, present on most parts of thallus, in part derived from breakdown of phyllocladia. *Cephalodia* attached to main stems, sessile or shortly stalked, pale brownish-grey, rounded globose at first becoming scrobiculate – impressed, cortex smooth or slightly maculate. *Apothecia* rare, terminal, occasionally also lateral, to 1.5 mm in diam., disc convex, brown or blackish-brown, immarginate, hypothecium colourless. *Spores* straight acicular-fusiform, 3-septate, 35–50 × 2–3 µm.

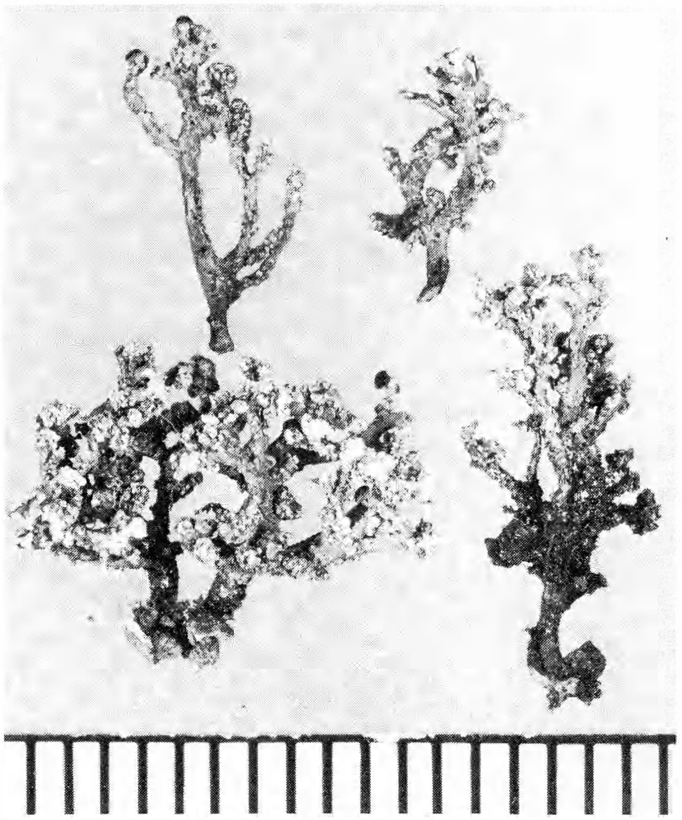

Fig. 6. *Stereocaulon corticatulum*, New Zealand, Cape Palliser, W. Colenso (WELT isotype). — Scale in mm.

Chemistry. Atranorin, rangiformic and norrangiformic acids. The taxon *S. wadei* contains atranorin, perlatolic, glomelliferic and glomellic acids (Lamb 1977) but the specimens of *S. corticatulum* (40 examined) from other parts of New Zealand had the normal chemistry. It is possible that two separate chemical strains exist in *S. corticatulum* as in other species of the genus found in New Zealand.

Affinity. *S. corticatulum* is characterised by the presence of soredia and is the only species of *Stereocaulon* in New Zealand to have these structures consistently present, although the degree of production of soredia is variable ranging from a few erose phyllocladia to a dense granular covering of the whole thallus (Fig. 7). Some collections of *S. trachyphloeum* are sorediate at their apices but soredia seem to be rather incon-

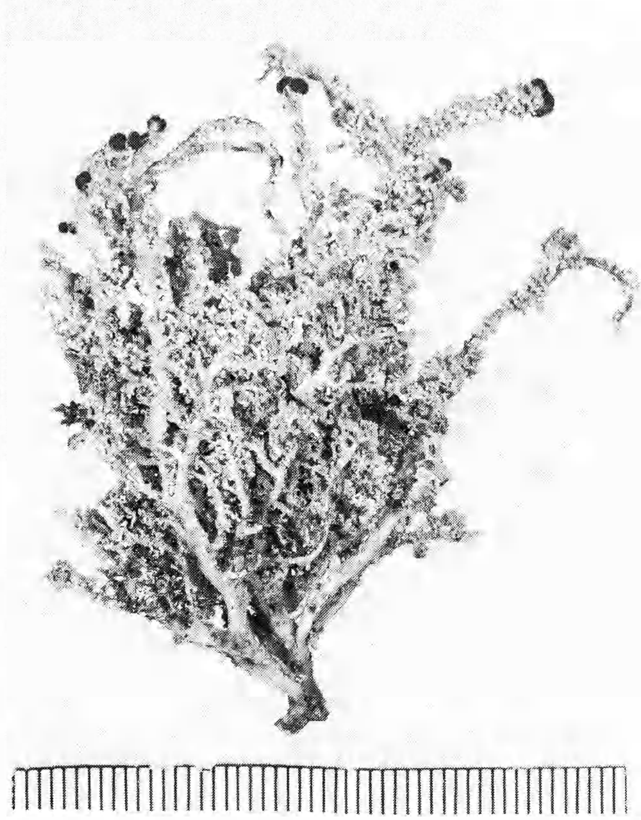

Fig. 7. *Stereocaulon corticatulum*, New Zealand, Mt Peel in grassland, D. J. Galloway (CHR). — Scale in mm.

stant in this species. It is, however, quite distinct from *S. corticatulum* and could not easily be confused with it. *S. corticatulum* is most closely related to *S. delisei* Bory, and *S. melanopotamicum* Lamb, taxa not occurring in New Zealand (Lamb 1977). Apart from the presence of soredia *S. corticatulum* appears similar in morphology to *S. fronduliferum* although there are differences in size, and both spore and chemical characters. As in most species of *Stereocaulon* in New Zealand, *S. corticatulum* has a very variable morphology depending largely on microhabitat and microclimate, ranging from small, appressed almost crustose forms in dry, exposed situations to ± robust luxuriant forms in damp, shaded situations. Some of these forms have been accorded separate taxonomic rank e.g. *S. corticatulum* var. *complanatum*, var. *humile* and *S. wadei* (this last separated only on the basis of differing medullary chemistry) but cannot realistically be supported as good independent entities until comprehensive field studies on the species are undertaken.

Habitat and distribution. S. corticatulum although not a common species is widespread in New Zealand ranging from the Three Kings Islands in the north (lat. 34°S) to the southern parts of Stewart Island (lat. 48°S) and it has been collected on both east and west coasts of both North and South Islands from sea level to 2100 m (Fig. 8). It is known also from Australia (Weber & Wetmore 1972), New Guinea (Frey 1967), Tristan da Cunha (Jørgensen 1976) Argentina, Chile, Gough Islands and South Africa (Lamb 1977), its distribution undoubtedly being effected by wind-blown diaspores.

Although found on exposed rocks in subalpine situations it can tolerate deep shade. However at present scant ecological information is available on this still undercollected species. Orwin (1970) discussed lichen succession on recently deposited rock surfaces in several sites in the Southern Alps of South Island and records that for some rock surfaces exposed for 29–40 years, at 29 years exposure 14 % of the lichen cover was provided by *S. corticatulum* with a 98 % cover of the 40 year old surface. Thus in some situations *S. corticatulum* appears to be an effective coloniser of newly exposed rock surfaces and may play a part in the process of soil formation in recently glaciated environments. Specimens of *S. corticatulum* were examined in the following herbaria: BM, CHR, H-NYL, OTA, S and WELT.

5. **Stereocaulon fronduliferum** Lamb

Lamb 1977: 293 — Type: New Zealand, sine loco. H. Locke Travers (PC-HUE holotype not seen).

Stereocaulon ramulosum var. *compressum* Church. Bab. Babington 1855 p. 294 — Type: New Zealand, North Island, sine loco. W. Colenso (BM! lectotype, WELT L913, L914! isolectotypes).

Thallus small, spreading to 3.5 cm tall. *Pseudopodetia* ± erect, branched, terete or more commonly flattened appearing dorsiventral, corticate, cortex commonly nodular or cracked. *Phyllocladia* conspicuously and characteristically flattened, branched, leaflike, pinnatifidly arranged, paler on the lower side, developed towards the tips of primary and secondary branches and appearing as terminal proliferations of these (Fig. 9). *Cephalodia* yellowish-brown to 3 mm in diam., spherical to subglobose, slightly wrinkled when young becoming areolate and cracked with age, solid-cored. *Apothecia* terminal, small, 1–2 mm wide, disc black with a con-

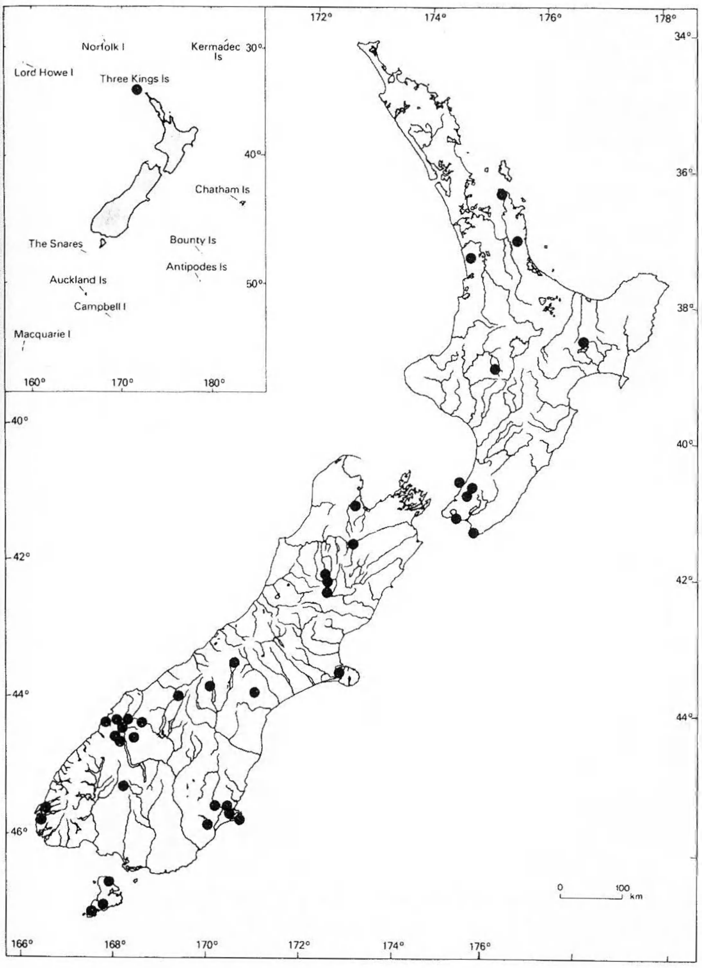

Fig. 8. Known New Zealand distribution of *Stereocaulon corticatulum*.

colorous margin when young becoming occluded at maturity, thalline exciple brown, smooth, hypothecium brown. *Spores* 6–8 per ascus, cylindrical-fusiform, 5–10-septate, 40–78 × 3.5–4 µm.

Chemistry. Atranorin and fumarprotocetraric acid.

Affinity. *S. fronduliferum* is a characteristic endemic species at once distinguished from all other species in New Zealand by the laterally compressed pseudopodetia with flattened leaf-like phyllocladia which are pale on their lower surface. The species may possibly be related to the sorediate species *S. corticatulum* as some individuals of that species may be conspicuously flattened although *S. fronduliferum* is never sorediate and has a different chemistry. The reasons for the rejection of Colenso's specimens as the type of a species *S. compressum*, are discussed by Lamb (1977).

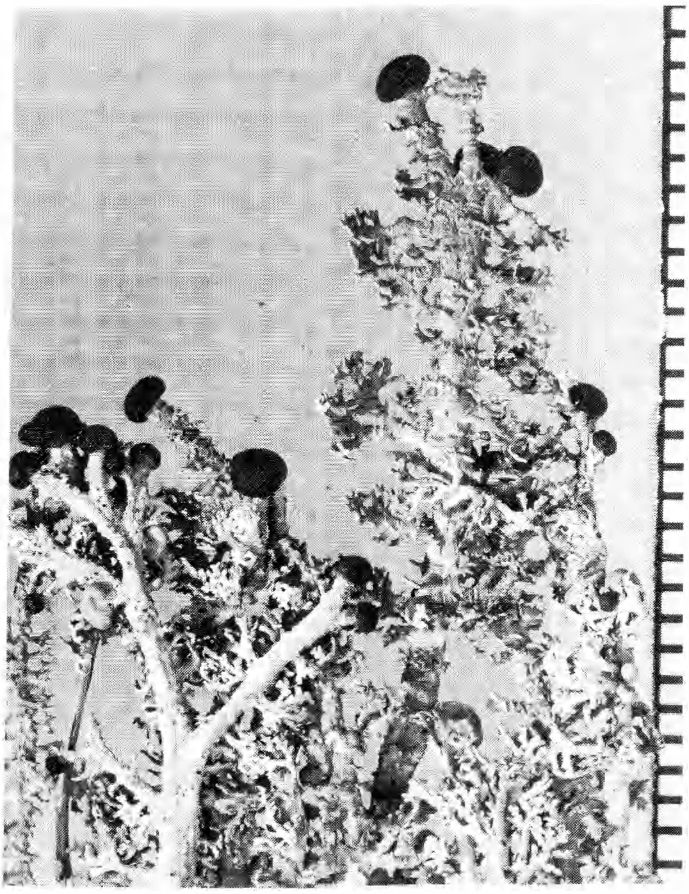

Fig. 9. *Stereocaulon fronduliferum*, New Zealand, Routeburn Valley, G. Einar and Greta Du Rietz (S). — Scale in mm.

Habitat and distribution. *S. fronduliferum* is still rather poorly known from New Zealand and is much in need of further study and collection. It is known from North, South and Stewart Islands (Fig. 10) and ranges from sea level to 2100 m. It has been gathered from deep shade in forested areas (where the whole thallus is bright green on the upper surface and pale yellowish-green or whitish below) to exposed subalpine grassland habitats in high rainfall areas (here the thallus is uniformly creamish-white or greyish). 14 specimens were examined from the following herbaria: BM, CHR, S and WELT.

6. **Stereocaulon ramulosum** (Sw.) Räusch., Fig. 11

Räuschel 1797: 328 — *Lichen ramulosus* Swartz 1788 p. 147 — Type: Jamaica. Swartz (S! holotype, H-ACH, UPS-ACH, UPS-THUNBERG! isotypes).

Stereocaulon furcatum Fries 1825 p. 285 — Type: Indiae Occidentalis. Ded. Casstrom (UPS! holotype) — *S. ramulosum* var. *furcatum* (Fr.) Nylander 1857 p. 96.

Stereocaulon macrocarpum Richard 1832 p. 34 — Type: New Zealand. "Havre de l'*Astrolabe* (Kaiteriteri, Nelson). A. Richard (PC-HUE holotype not seen) — *S. ramulosum* var. *macrocarpum* (Rich.) Church. Bab. Babington 1855 p. 294.

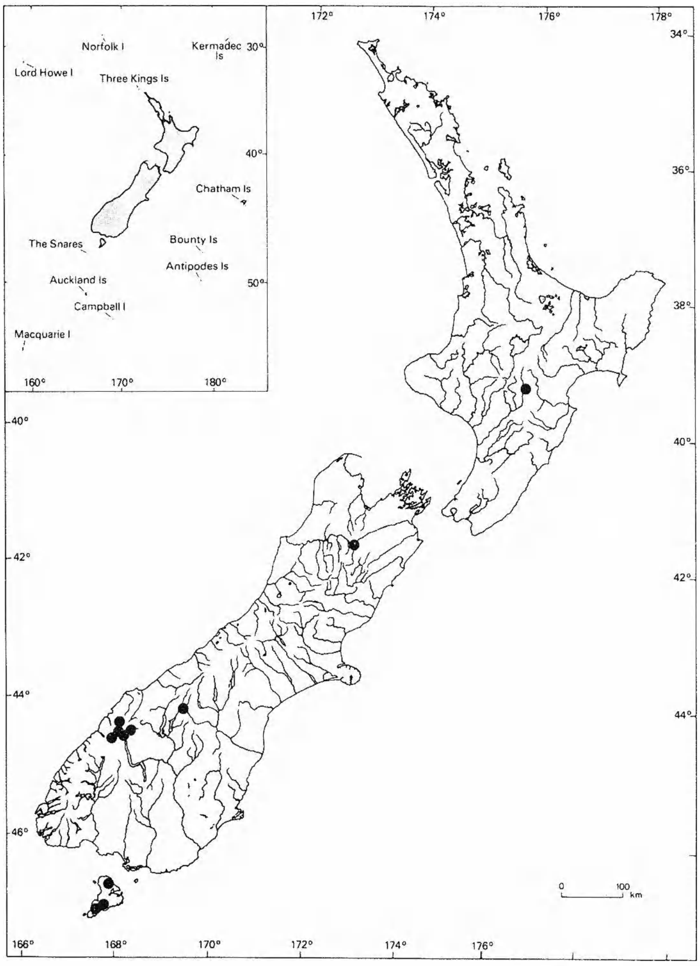

Fig. 10. Known New Zealand distribution of *Stereocaulon fronduliferum*.

Stereocaulon ramulosum f. *elegans* Th. Fries 1857 p. 12 — Type: Straits of Magellan. N. J. Andersson (UPS! lectotype).

Stereocaulon ramulosum f. *strigosum* Th. Fries 1857 p. 12 — Type: "Söderhafsländerna". A. Sparrmann (UPS! lectotype).

Stereocaulon vimineum Th. Fries 1857 p. 13 — Type: In alpibus Mexicanis ad Tiuzutlan, 6/47. F. Liebmann (UPS! lectotype) — *S. ramulosum* var. *vimineum* (Th. Fr.) Nylander 1859 p. 209 — *S. ramulosum* f. *vimineum* (Th. Fr.) Hue 1890 p. 245.

Stereocaulon proximum Nylander 1859 p. 210 — Type: Paramo de Talima, Lind. 1005 (H-NYL 40039! lectotype) — *S. ramulosum* f. *proximum* (Nyl.) Tuckerman 1886 p. 228.

Stereocaulon mixtum Nylander 1859 p. 210 — Type: Bolivia. Weddell. (H-NYL 40085! lectotype).

Stereocaulon macrocarpoides Nylander 1860 p. 238 — Type: Tasmania. Ex Herb. Hooker. (H-NYL 40029! lectotype) – *S. proximum* var. *macrocarpoides* (Nyl.) Nylander 1861 p. 371 — *S. ramulosum* var. *macrocarpoides* (Nyl.) Krempelhuber 1870 p. 124.

Stereocaulon submollescens Nylander 1876 p. 88 — Type: Campbell Island. M. Filhol 1874 (H-NYL 40089! holotype) — *S. ramulosum* var. *submollescens* (Nyl.) Lamb 1977 p. 325.

Stereocaulon pulvinare Dodge 1948 p. 139 — Type: New Zealand, Otago, Dunedin. Mac's Valley. J. S. Thomson (CHR! isotype) — *S. ramulosum* var. *pulvinare* (Dodge) Lamb 1977 p. 283.

Stereocaulon macquariense Dodge 1968 p. 289 — Type: Macquarie Island. H. Hamilton 108 (Herb. Dodge holotype not seen).

Stereocaulon ramulosum var. *pulvinare* f. *crebratum* Lamb 1977 p. 283 — Type: New Zealand, Otago. Port Chalmers. J. S. Thomson (CHR! holotype).

Stereocaulon traversii (Hue) Dodge in Fineran 1971 p. 222 nom. nud. — *Stereocaulon proximum* f. *traversii* Hue 1898 p. 245 — Type: New Zealand, sine loco. Travers (PC-HUE holotype not seen).

Stereocaulon proximum var. *nudatum* Müller Argoviensis 1886 p. 252 — Type: Australia. Broger's Creek. Bauerlen 1884 (G! lectotype) — *S. ramulosum* var. *nudatum* (Müll. Arg.) Müller Argoviensis 1896 b p. 199 — *S. ramulosum* f. *nudatum* (Müll. Arg.) Lamb 1977 p. 281.

Stereocaulon ramulosum f. *subcompressum* Lamb 1977: 282 — Type: Tasmania. Mt Wellington. Bastow (LD! holotype).

Stereocaulon ramulosum f. *tomentosulum* Lamb 1977 p. 282 — Type: Colombia. Dept Santander, W slope of Paramo Rico 3600 m. E. P. Killip & A. C. Smith 1927 (S! holotype). For additional synonyms see Lamb (1977).

Thallus variable in size though predominantly very large and well developed, to 25 cm tall, with a very prominent holdfast, yellowish-brown and devoid of cortex and phyllocladia. *Pseudopodetia* ± complexly branching of stout primary branches and smaller more richly branched secondary branches towards apices, primary branches white, ± decorticate with prominent exposed fungal hyphae visible giving a tomentose, ± fibrillose appearance (×10 lens) with occasional shallow vertical grooves, often lightly invested with a thin layer of algae, secondary branches ± covered with a distinctly greenish algal layer. *Phyllocladia* terete, corticate, conspicuously green when fresh, simple and nodular or fingerlike at first (often densely clothing young pseudopodetia) soon becoming complex, coralloid-branched, most conspicuous towards apices of pseudopodetia. *Cephalodia* numerous, sessile or occasionally shortly stalked, prominent, bluish-grey when fresh, folded indented or wrinkled, surface smooth never areolate or maculate or scabrid. *Apothecia* usually terminal but also subterminal and lateral, small, usually not wider than the width of the supporting branch, disc always convex light red-brown to dark brown never black, thalline exciple smooth, light yellowish-brown. *Spores* 3–5(–7)-septate, 28–40 (–90) × 3–4 μm.

Chemistry. Atranorin and perlatolic acid, often

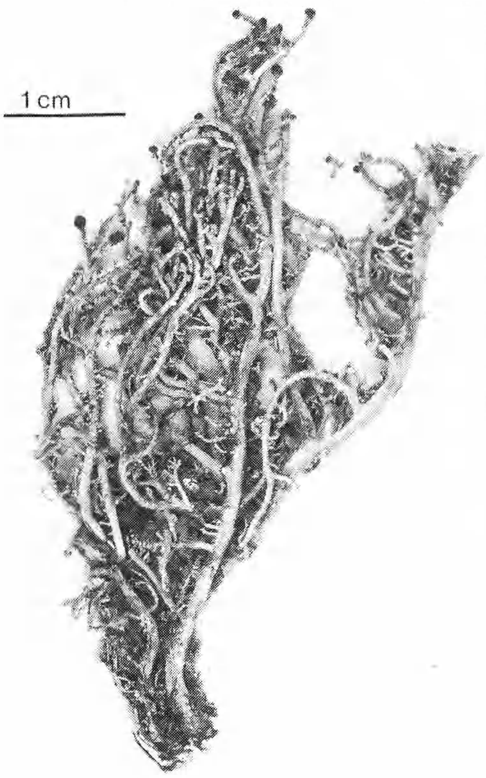

Fig. 11. *Stereocaulon ramulosum*, Jamaica, Swartz (UPS-THUNBERG isotype).

with anziaic acid. Chemical variation in the species is discussed by Lamb (1977).

Affinity. *S. ramulosum* is the most widespread species of *Stereocaulon* in the New Zealand flora and also the species exhibiting the widest range of morphological variation. It is remarkably successful as an early coloniser of disturbed ground and this success in adapting to a wide range of habitats has resulted in a profusion of growth forms, reflected alas in an extensive taxonomic synonymy (see above). The morphological variation observed in New Zealand populations is not supported by an equivalent variation in chemistry. A combination of several morphological characters, viz., the sessile, wrinkled, smooth-surfaced cephalodia (Fig. 12 A), coralloid-branched phyllocladia, the large decorticate pseudopodetia and the small red-brown convex apothecial discs (Fig. 12 B) serve to distinguish *S. ramulosum* from all other species of *Stereocaulon* in the New Zealand flora.

Habitat and distribution. *S. ramulosum* is the most widespread species of the genus in New Zealand occurring from the Three Kings Islands in the far north of the country to the subantarctic islands in the south, and is by far the most commonly encountered species of the genus, and certainly one of the most commonly collected of New Zealand lichens. It is an aggressive coloniser of disturbed sites, particularly of roadsides, areas of forest clearance and even penetrating into urban areas onto rocks in gardens and stone walls. It seems to adapt easily and quickly to a variety of microhabitats and microclimates being common on the coast in most parts of the country and reaching inland to subalpine situations as high as 1500 m. It is tolerant of quite dense shade but in damp, shaded environments becomes much elongated and devoid of phyllocladia. It has the most northerly range of the genus in New Zealand (although a few specimens of *S. corticatulum* were collected from the Three Kings Islands) and is one of the most commonly collected lichens of North Auckland (Hayward & Hayward 1973, 1974 a, b, Hayward et al. 1975, 1976).

It is a very widely distributed Southern Hemisphere lichen, reaching the Northern Hemishpere in Hawaii, the West Indies (it was first described from Jamaica by Swartz) Central America and Mexico (Lamb 1977). Its distribution in New Zealand is shown in Fig. 13. 450 specimens of *S. ramulosum* were examined from the following herbaria: BM, CANU, CHR, E, G, H-ACH, H-NYL, H, LD, MEL, OTA, S, UPS, UPS-ACH, UPS-THUNBERG, WELT.

7. **Stereocaulon trachyphloeum** Lamb

Galloway et al. 1976: 64 — Type: Tasmania. Hansen's Peak 1136 m, on quartzite-schist, G. C. Bratt 67/527 (Herb. G. C. Bratt! isotype, FH holotype not seen).

Thallus large, coarse to 9 cm tall, sparingly branched, with a well developed holdfast. *Pseudopodetia* stout, 1–3(–5) mm wide, terete, covered with a ± continuous, coarsely scabrid, verrucose-areolate cortex, apices of pseudopodetia often eroded-sorediate. *Phyllocladia* rather sparse, variable, often most distinct at the apices of small, clustered secondary branchlets, terete, fingerlike at first, becoming coralloid-branched. *Cephalodia* conspicuous, stalked, large (to 3 mm in diam.), wrinkled, scrobiculate, surface minutely areolate, distinctly blue-grey. *Soredia* white or greyish, granular, rather sparse, developed on the ends of pseudopodetia and possibly the result of insect attack. *Apothecia* rare, terminal, 1–3

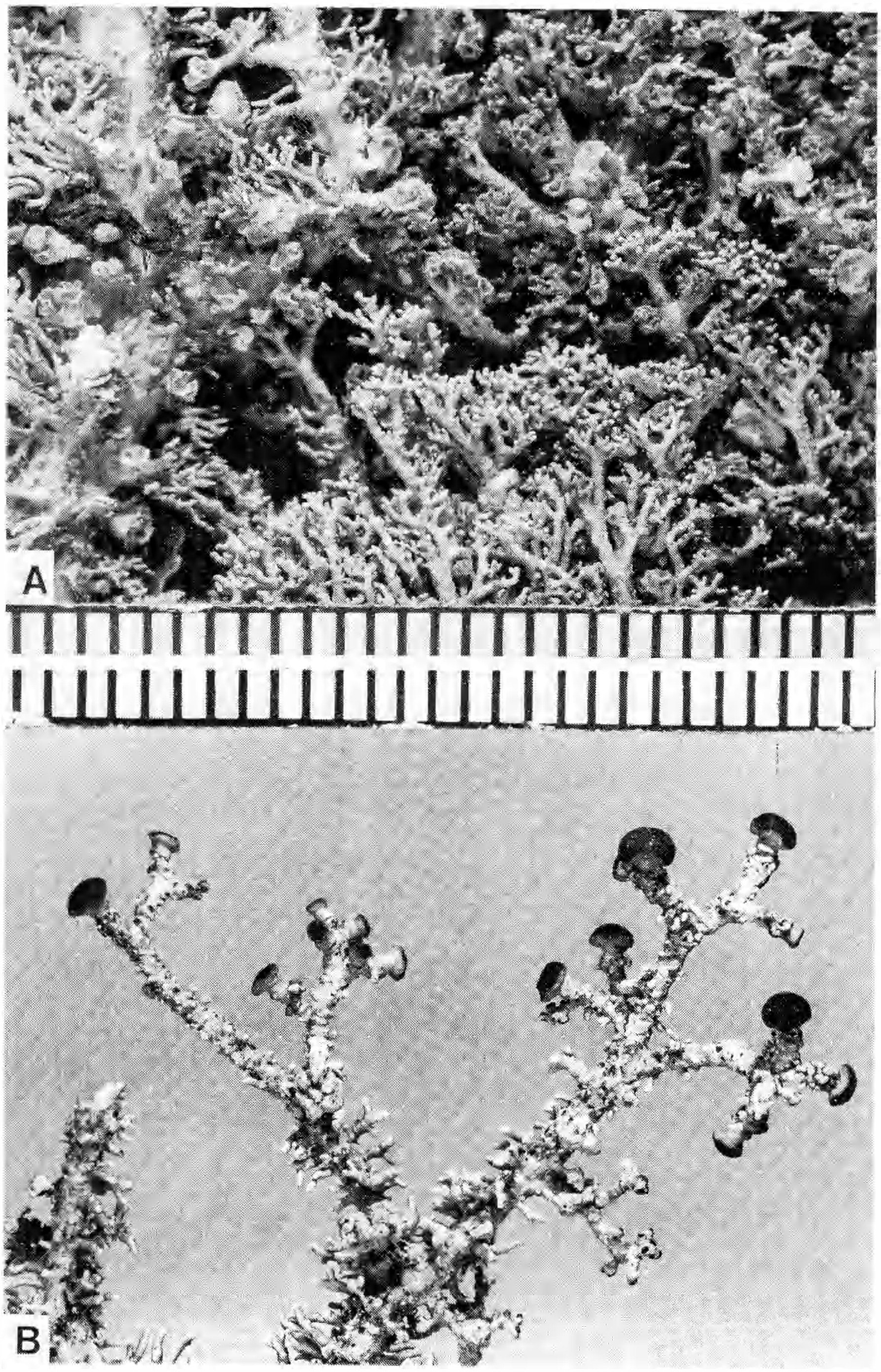

Fig. 12. *Stereocaulon ramulosum*. — A: Cephalodia and phyllocladia. — B: Apothecia and pseudopodetia. — Scale in mm.

mm wide, disc black, plane in young fruits and with a thin margin, becoming convex and immarginate at maturity. *Spores* 2–5 per ascus, clavate-fusiform, 1-3-septate, 25–35 × 5–7 μm.

Chemistry. Atranorin, fumarprotocetraric and protocetraric acids, with perlatolic and anziaic acids in apothecia only.

Affinity. The differences between *S. trachyphloeum, S. corticatulum, S. colensoi, S. ramulosum* and *S. argus* are discussed by Galloway et al. (1976).

Habitat and distribution. *S. trachyphloeum* is a subalpine species with a restricted occurrence in Tasmania and, although rare, occurring from 750–2100 m in North, South and Stewart Islands in New Zealand (Fig. 14). Specimens examined are detailed in Galloway et al. (1976).

8. **Stereocaulon caespitosum** Redinger, Fig. 15

Redinger 1936: 132 — Type: New Zealand. South Island, Otago. Mt Maungatua 900 m, on schist rock. J. S. Thomson ZA 185 (W! lectotype, CHR! isolectotype) — *Gymnocaulon caespitosum* (Redinger) Duvigneaud 1956 p. 14.

Thallus dwarf, to 8 mm tall. *Pseudopodetia*

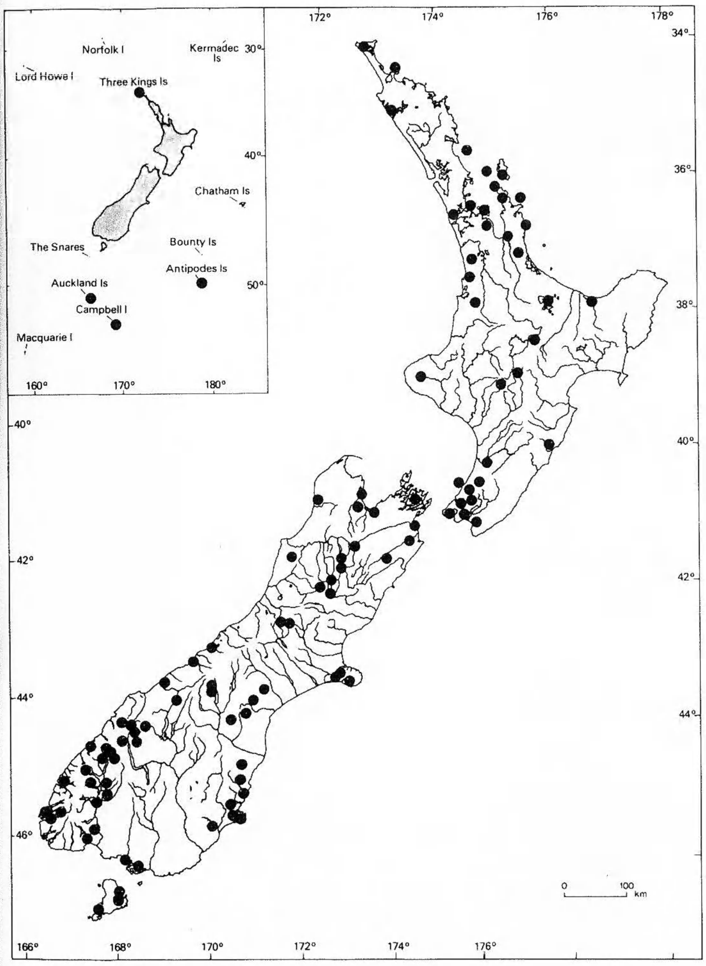

Fig. 13. Known New Zealand distribution of *Stereocaulon ramulosum*.

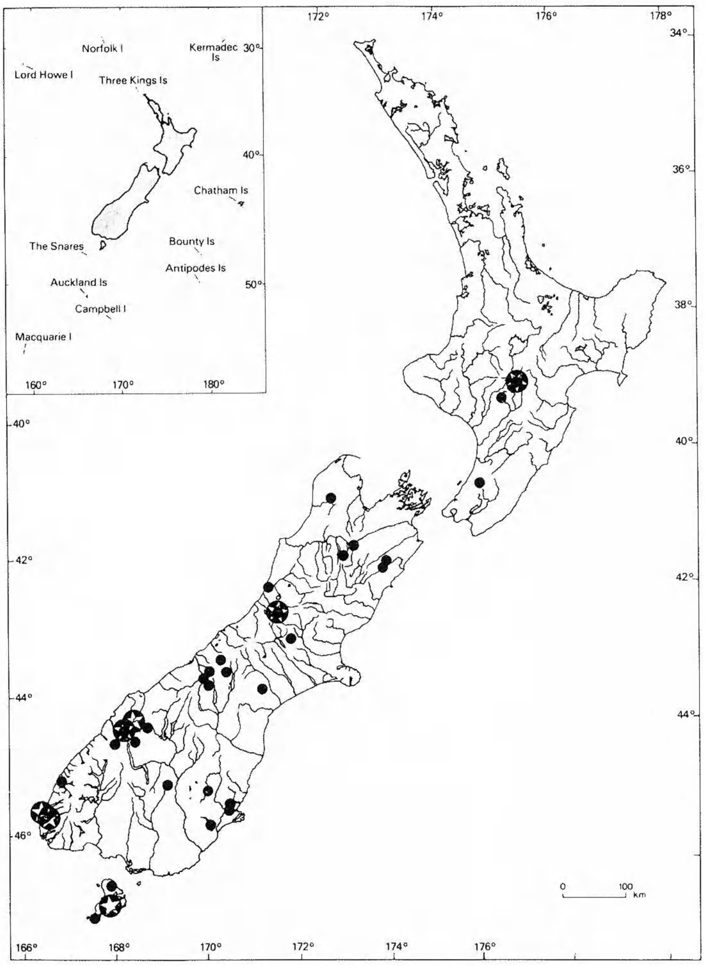

Fig. 14. Known New Zealand distribution of *Stereocaulon trachyphloeum* (dots with a star) and *Stereocaulon caespitosum* (dots).

simple, erect, fingerlike, occasionally bifurcating at the apices, nodular-papillose at first, becoming terete, corticate, cortex continuous, sometimes horizontally cracked, smooth or wrinkled, often shining, greyish-white below becoming purplish-brown above and mottled, with small black pycnidia at apices. *Phyllocladia* absent. *Cephalodia* basal, cerebriform and slightly convoluted, greenish-black, surface rather scabrid. *Apothecia* terminal, disc black 1–5 mm wide, deeply concave at first becoming persistently plane at maturity with a prominent raised light red-brown margin, thalline exciple smooth or wrinkled, red-brown, hypothecium 60–75 μm thick, red-brown. *Spores* broadly fusiform, 8 per ascus, 6–8-septate, 30–50 × 4–7 μm.

Chemistry. Atranorin, protocetraric and fumarprotocetraric acids.

Affinity. *S. caespitosum* is closely related to *S. gregarium* and *S. loricatum* the other two species in the New Zealand flora lacking phyllocladia. They form a natural group which seems to have evolved in New Zealand, primarily in the mountains of South Island. It differs from both *S. gregarium* and *S. loricatum* in the following characters: pseudopodetia smooth, shining, purplish-brown towards apices, cephalodia greenish-black, not pale, apothecia at maturity plane and consistently marginate and hypothecium consistently red-brown.

Habitat and distribution. *S. caespitosum* forms densely compacted patches on rocks in exposed alpine situations from the Kaimanawa Range in North Island to the Auckland Islands (Fig. 14). Its peculiar and immediately recognisable growth form allows it to survive in rigorous environments exposed to the eroding forces of frost, wind and water. In association with species of the moss *Andreaea* and the lichens *Psoroma buchanani*, *P. hirsutulum*, *Siphula decumbens*, *Stereocaulon gregarium* and *Toninia bullata*, it may play an active part in the process of soil consolidation in alpine environments. In addition

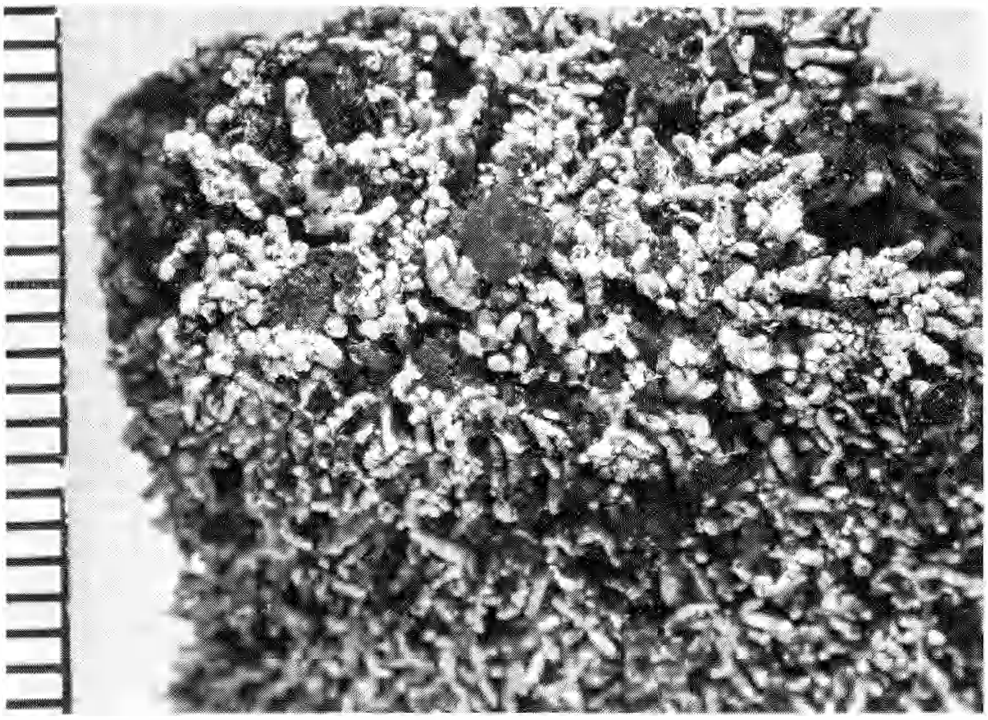

Fig. 15. *Stereocaulon caespitosum*, New Zealand, Tin Range, Stewart Island, D. J. Galloway (CHR). — Scale in mm.

to its occurrence in New Zealand *S. caespitosum* is also known from Australia, Tasmania and Campbell Island (Lamb 1977). 40 specimens of *S. caespitosum* were examined in the following herbaria: BM, CHR, OTA, S and W.

9. **Stereocaulon gregarium** Redinger, Fig. 16

Redinger 1936: 137 — Type: New Zealand. South Island, Otago. Flagstaff Hill, Dunedin 700 m, on schist rock. J. S. Thomson ZA 149 (W! holotype, CHR! isotype) – *Gymnocaulon gregarium* (Redinger) Duvigneaud 1956 p. 14.

Thallus to 15 mm tall, fertile pseudopodetia conspicuously taller than sterile pseudopodetia. *Pseudopodetia* simple, occasionally bifurcating at apices, terete, fingerlike, corticate, cortex continuous, smooth to cracked, verrucose-wrinkled, whitish-cream never purplish-brown, exposed forms greyish, the result of a crazing of fine black lines across the cortex. *Phyllocladia* absent. *Cephalodia* basal, pale yellowish-brown or greenish never black, distinctly cerebriform, convoluted. *Apothecia* terminal, often 2–3 per pseudopodetium, disc black 1–4 mm wide, plane when young with a thin pale margin, becoming convex and immarginate at maturity, thalline exciple smooth, pale yellowish-brown, hypothecium 100–120 μm tall, colourless or pale yellowish-brown. *Spores* 8 per ascus, fusiform, acicular 6–8(–10)-septate, 48–68 × 5–6 μm.

Chemistry. Atranorin and protocetraric acid, with fumarprotocetraric, perlatolic colensoinic and anziaic acids as inconstant accessory compounds.

Affinity. *S. gregarium* is most closely related to *S. loricatum* (see below) and to *S. caespitosum* and appears to be endemic to New Zealand. It is often encountered growing with *S. caespitosum* but is distinguished from that species in the following characters: the pseudopodetia are taller and often branched at the apices, the cortex is matt, wrinkled–verrucose and greyish-white never purplish-brown, the cephalodia are pale, the apothecia at maturity are convex and immarginate, the hypothecium is pale yellowish-brown or colourless and the spores are 6–10-septate.

Habitat and distribution. *S. gregarium* is endemic to New Zealand and occurs there on exposed alpine rocks from Mt Ruapehu in North Island to the summit of Smith's Lookout at the southern tip of Stewart Island (Fig. 17). In many exposed habitats it is associated with the related species *S. caespitosum*, the closely appressed dwarf nature of the two species and their densely compacted pattern of growth making them resistant to fragmentation and dispersal by the eroding forces of frost, wind and water. The two species are frequently found growing with the moss *Andreaea* and it is possible that this asso-

Fig. 16. *Stereocaulon gregarium*, New Zealand. Dusky Sound, Mt Hodges, D. J. Galloway (CHR). — Scale in mm.

ciation may promote the formation of soil in areas of recently exposed rock particularly in glaciated regions. 25 specimens of *S. gregarium* were examined from the following herbaria: BM, CHR, FH, OTA, S and W.

10. **Stereocaulon loricatum** Lamb

Galloway et al. 1976: 61 — Type: New Zealand. South Island, Otago, West Matukituki Valley, Mt French 1600 m on rock. D. J. Galloway 1967 (FH! holotype, BM, CHR! isotypes).

Thallus to 3 cm tall, primary thallus ± persistent of branching ± dorsiventral ascending lobes. *Pseudopodetia* simple, erect, often 1-2-branched at apices, ± continuously corticate, cortex distinctly verrucose-areolate. *Phyllocladia* absent. *Cephalodia* sessile, basal or occasionally inserted above the base of the pseudopodetia, pale yellowish or olive green, rounded, corrugate-scrobiculate or even botryose, alga *Stigonema*. *Apothecia* terminal, often 2–3 clustered at apices of fertile pseudopodetia, disc black to 3 mm in diam., plane or concave at first with a thin margin but consistently convex and immarginate at maturity. *Spores* 6–8 per ascus, elongate-fusiform, 5–9-septate, 40–70 × 4–6 μm.

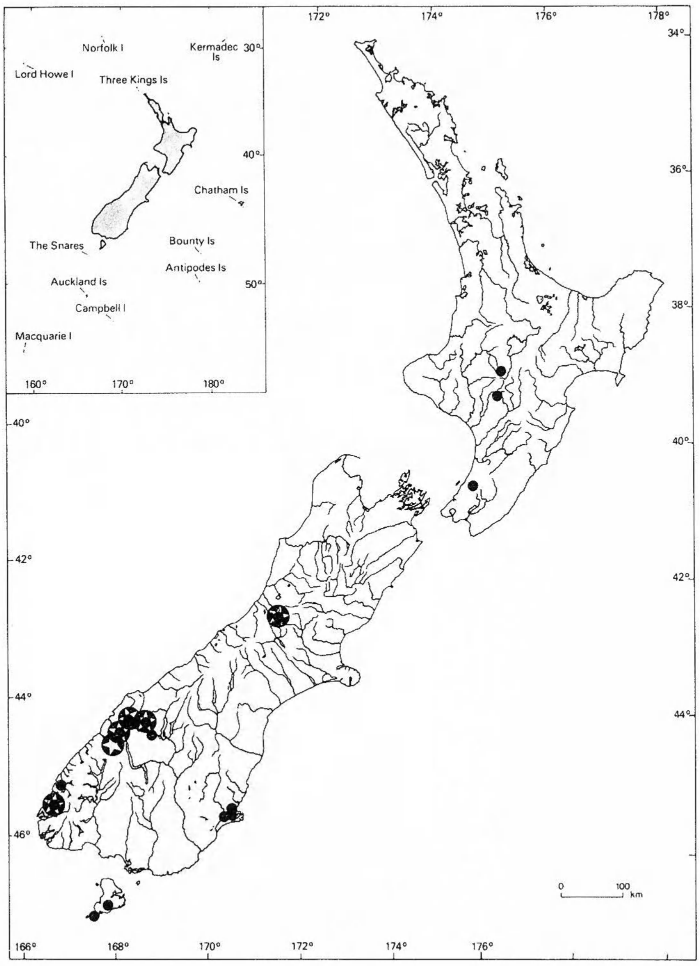

Fig. 17. Known New Zealand distribution of *Stereocaulon loricatum* (dots with a star) and *S. gregarium* (dots).

Chemistry. Atranorin, colensoinic, fumarprotocetraric and salazinic (trace) acids.

Affinity. *S. loricatum* is closely related to *S. gregarium* and is often sympatric with this species and with *S. caespitosum*. The affinities of the species are discussed by Galloway et al. (1976).

Habitat and distribution. *S. loricatum* is an endemic alpine species found on schist rocks in Otago and on grewacke rocks in Canterbury, in areas of high rainfall at altitudes of 850–2200 m (Fig. 17). Specimens of *S. loricatum* examined are recorded in Galloway et al. (1976).

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Botanical literature

De Vogel, E. F. 1980: *Seedlings of dicotyledons. Structure, development, types. Descriptions of 150 woody Malesian taxa.* 465 pp., including 178 drawings and 20 colour plates. Centre for Agricultural Publishing and Documentation, Wageningen, the Netherlands. ISBN 90-220-0696-4.

This beautiful book is the result of a seedling project at the Bogor Botanic Gardens, Indonesia, in cooperation with the Rijksherbarium, Leiden. Seeds of Malesian woody taxa were collected and their germination studied. Most of the book contains detailed descriptions and accurate drawings of about 150 species, so that there is much original information. I have checked the description of a *Memecylon* species against germinating seeds of the same species (which by pure coincidence are germinating in our greenhouses in Stockholm now) and it is exact and exhaustive. There are also general chapters on seedling morphology and seedling ecology and a classification of seedling types with discussions of earlier literature.

De Vogel has classified dicot seedlings in general, i.e. not only those of Malesian taxa, into 16 types named after genera, e.g. *Macaranga type, Cyclamen type, Rhizophora type, Garcinia type, Orobanche type*. It is obvious that the system has been carefully thought out, but I fear that it is too detailed and that the names of the types are too unfamiliar (such as the *Heliciopsis type/ Koordersiodendron subtype*) for it to gain general acceptance.

The most important distinction is between Type 1 (*Macaranga type*) with green assimilating cotyledons and the remaining 15 types with food-storing or haustorial cotyledons. De Vogel launches the new term 'paracotyledons' for the (green assimilating) cotyledons of the first type, whereas he reserves the old term cotyledon for food-storing and haustorial cotyledons only, which he considers primitive. The common and familiar seedlings with green assimilating (para)cotyledons have lost their true cotyledons — their paracotyledons are secondarily evolved and homologous with the first pair of true leaves in the primitive seedling type. This noteworthy hypothesis is derived from observations of *Diospyros* and a number of other genera with various seedling types. Whether it holds for all seedling types with green assimilating (para)cotyledons remains to be conclusively demonstrated.

This comprehensive book should become an important reference work on seedlings not only for the Malesian forester but also for morphologists and taxonomists.

Kåre Bremer

Taxonomic and nomenclatural notes on the genus Limonium in Sicily

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Brullo, S. 1980 09 18: Taxonomic and nomenclatural notes on the genus Limonium in Sicily. *Bot. Notiser 133:* 281–293. Stockholm. ISSN 0006-8195.

Some taxonomic and nomenclatural notes on the Sicilian species of *Limonium* are presented. New species (*L. lopadusanum* Brullo, *L. hyblaeum* Brullo, *L. mazarae* Pignatti, *L. syracusanum* Brullo, *L. zeraphae* Brullo, *L. pignattii* Brullo & Di Martino ex Brullo, *L. furnarii* Brullo, *L. calabrum* Brullo, *L. tauromenitanum* Brullo, *L. ionicum* Brullo, *L. catanzaroi* Brullo, *L. halophilum* Pignatti, *L. lilybaeum* Brullo, *L. selinuntinum* Brullo, *L. aegusae* Brullo, *L. pachynense* Brullo) and a new subspecies (*L. oleifolium* Miller subsp. *algusae* Brullo) are described. Besides, some changes of rank and new combinations (*L. intermedium* (Guss.) Brullo, *L. flagellare* (Lojac.) Brullo, *L. ponzoi* (Fiori & Béguinot) Brullo, *L. divaricatum* (Rouy) Brullo, *L. cyrtostachyum* (Girard) Brullo, *L. balearicum* (Pignatti) Brullo, *L. oleifolium* Miller subsp. *opulentum* (Lojac.) Brullo, *L. catanense* (Tineo ex Lojac.) Brullo) are made and a new name (*L. lojaconi* Brullo) is proposed. A check-list of the species of *Limonium* known from Sicily is also presented.

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In Sicily the genus *Limonium* Miller is very rich in species, many of which, however, either have not been described or have been confused with other species. There are numerous authors who have studied the Sicilian species of *Limonium*, among them are: Gussone (1827, 1832, 1843), Boissier (1848), Lojacono-Pojero (1907), Pignatti (1971, 1972), Brullo & Di Martino (1974), Brullo et al. (1977).

In order to clarify the rank and the taxonomic value of a lot of these critical species, some herbarium research (BOLO, CAT, FI, NAP, PAL, RO, TBS) have been carried out, above all, in the herbaria of Gussone (NAP) and of Lojacono (PAL), in which the types of many *Limonium* species described from Sicily are stored. The presence and distribution of the *Limonium* species on the island and the neighbouring islets have been checked by personal collections (CAT), by means of which it was possible to ascertain the veracity of many indications and to discover new species. In this work, which is the first contribution to the knowledge of the Sicilian species of *Limonium*, the taxonomic rank of many species is clarified and various new taxa are also described.

1. **Limonium lopadusanum** Brullo, sp. nov., Fig. 1

Holotype: Lampedusa, VII.1828, Gussone (NAP).

Statice bellidifolia Guss., Fl. Sic. Syn. 1: 369 (1843), p.p., non Gouan (1765).

Statice psiloclada Boiss. var. *gracilis* Boiss. in DC., Prodr. 12: 651 (1848), p.p.

Statice psiloclada Boiss. var. *albida* Lojac., Fl. Sic. 2(2): 18 (1907), p.p., non Boiss. (1848).

Statice psiloclada Boiss. var. *spathulaefolia* Lojac., Fl. Sic. 2(2): 18 (1907), p.p.

Planta perennis, 7–25 cm alta, caule ramosissimo, pulvinato, ramis foliis vetustis crebissime vestitis. Scapi laeves vel leviter rugosi, exiles, graciles, fragillimi, solitarii, pauci, ramis sterilibus nullis vel nonnullis. Folia glauca, patentia vel reflexo-patentia, obovato-spathulata, 5–12×3–6 mm (vel in planta macrosomatica 25–40×10–16 mm) obtusa, revoluta, 1–3(-5)-nervia. Panicula ampla, fragilis, paulo ramosa, ramis simplicibus rare fasciculatis (2–3 nodo), flexuosis, arcuatis. Spicae 2–8(–10) cm longae. Spiculae 1–3(–4) in 1 cm, 2-3-florae. Bractea interior recta, 4–4,5 mm longa. Bractea exterior 1–1,5 mm longa, 1/6 bracteae interioris obtegens. Calyx 4,5–5 mm longus, 1 mm ex bractea interiore exsertus.

Plant 7–25 cm, pulvinate, much branched. Stems smooth or lightly rugose, slight, delicate, solitary. Leaves glaucous, obovate-spathulate, 5–12 × 3–6 mm (rarely 25–40 × 10–16 mm), 1–3

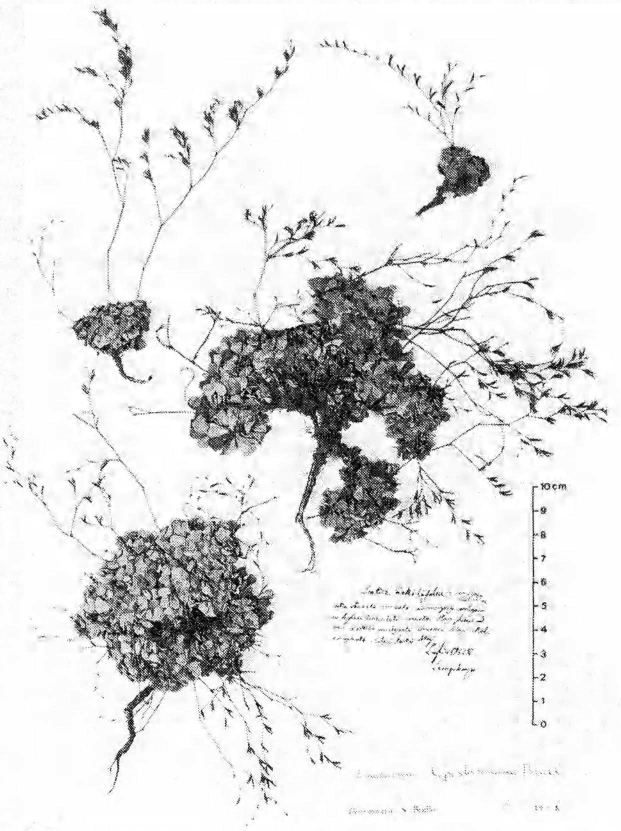

Fig. 1. *L. lopadusanum*. Holotype (Gussone, NAP).

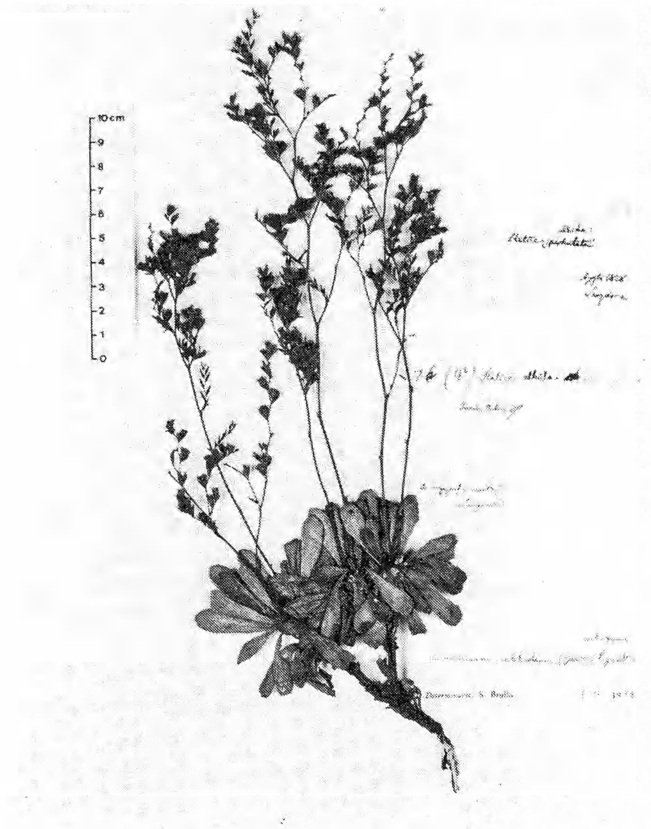

Fig. 2. *L. albidum*. Lectotype (Gussone, NAP).

(–5)-veined, obtuse. Panicle ample, fragile, with branches arcuate, simple, rarely fasciculated. Spikes 2–8(–10) cm. Spikelets 1–3(–4) per cm, 2–3-flowered. Inner bract 4–4.5 mm, straight. Calyx 4.5–5 mm.

Distribution. Islands of Lampedusa (very frequent) and Linosa (rare), along the rocky coast.

Up to now, the species has been confused with *L. albidum* (Guss.) Pignatti; the latter is very distinct and is endemic on Lampione, a small islet in the neighbourhood of Lampedusa. *L. albidum* (Fig. 2) differs from *L. lopadusanum* in the following characters: Plant 20–35 cm with caulis not pulvinate; stems rugose-tuberculate, rigid, two in every rosette, rarely solitary; leaves oblanceolate-spathulate, 25–50 × 5–12 mm; panicle branched also below with branches generally fasciculated (2–6 at every node), straight, crowded; spikes 2–5(–7) cm; spikelets (3–)4–8 per cm, 6–8(–10)-flowered; inner bract 5 mm; calyx 5.5 mm.

2. **Limonium hyblaeum** Brullo, sp. nov., Fig. 3

Holotype: Capo Passero a Scoglitti, in lapidosis maritimis, V–VI, Gussone (NAP).

Statice bellidifolia Guss., Fl. Sic. Prodr. 1: 38 (1827), non Gouan (1765). — *Statice bellidifolia* Guss., Fl. Sic. Syn. 1: 369 (1843), p.p. non Gouan (1765).

Statice psiloclada Boiss. var. *gracilis* Boiss. in DC., Prodr. 12: 651 (1848), p.p.

Statice psiloclada Boiss. var. *spathulaefolia* Lojac., Fl. Sic. 2(2): 18 (1907), p.p.

Planta perennis, 6–25 cm alta, pulvinata, scapis laevis, rigidis, saepe ramulosis sursum, ramis sterilibus nullis. Folia rigidula, punctata, glaucescentia, rugosa, plana vel leviter revoluta, spathulata vel obovato-spathulata, 8–30(–45)×4–16 mm, uninervia vel obscure trinervia, apice rotundata, subito in brevem petiolum 1,5–2,5 mm latum contracta. Panicula ramis divaricatis, rectis vel incurvis, nudis in basi. Spicae 1–3(–5) cm longae. Spiculae 2–3(–4)-florae, 4–6 in 1 cm. Bractea interior 4–4,5 mm longa, lato margine hyalino. Bractea exterior obtusa vel acutiuscula, 1,5–2 mm longa 1/3–1/4 bractea interioris obtegens. Calyx 4–5,5 mm longus, ex bractea interiore exsertus; limbus tubo brevior vel subaequilongus. Corolla coerulea, 5–5,5 mm longa.

Plant 6–25 cm, pulvinate. Leaves glaucescent, rugose, spathulate or obovate-spathulate, 8–30 (–45)×4–16 mm, 1-veined or obscurely 3-veined, rounded at apex. Non-flowering branches absent. Spikes 2–3(–4)-flowered, 4–6 per cm. Inner bract 4–4.5 mm. Calyx 4–5.5 mm.

Distribution. Rocky coast of southern Sicily (between Scoglitti and Capo Passero) and Favignana.

Fig. 3. *L. hyblaeum*. Holotype (Gussone, NAP).

Gussone (1843) has gathered sub nomine *Statice bellidifolia*, plants with their origin in southern Sicily and in Lampedusa. From the examination of the specimens of Herb. Gussone it can be seen that this species has two different taxa which for their remarkable morphological difference made it possible to bring about a separation at the specific rank. These two species, which are represented by *L. hyblaeum* and *L. lopadusanum*, are both attributed to the *L. albidum* group regarding some of their characters.

3. **Limonium mazarae** Pignatti, sp. nov., Fig. 4

Holotype: Sicilia occid. a Mazara, XI.1965, Catanzaro (TSB).

Planta foliis rosulatis numerosis, oblanceolato-spathulatis, 5–8(–9) mm latis, apice plerumque rotundatis. Spicae laxissimae (spiculis dissitis, 2–5 in 1 cm) et elongatae usque ad 5 cm, eleganter virgatae; spiculae 1–2-florae; caetera sicut L. lopadusano cui affinis.

Similar to *L. lopadusanum*, but leaves oblanceolate-spathulate, 7–18(–30) × 5–8(–9) mm, rounded at apex; spikes lax, 1.5–5 cm long; spikelets 1–2-flowered, 2–5 per cm.

Distribution. Rocky coast between Mazara del Vallo and Capo Granitola (W. Sicily).

This species is similar to *L. lopadusanum*, but the narrower and less spathulate leaves are reminiscent of those of *L. minutiflorum* (Guss.) O. Kuntze, from which it can be distinguished by the elongated inflorescence with very lax spikelets (as in all species of the *L. albidum* group). The presence of populations intermediate between *L. albidum* and *L. minutiflorum* in southern Sicily was already mentioned by Pignatti (1972 p. 45). Here they are formally described as a new species. Until now they have only been found in the territory between Mazara del Vallo and Capo Granitola.

Fig. 4. *L. mazarae*. Specimen coming from the type locality (Brullo, CAT).

4. **Limonium intermedium** (Guss.) Brullo, comb. nov., Fig. 5

Lectotype: Lampedusa, in inundatis salsis maritimis, VII.1828, Gussone (NAP). — Basionym: *Statice intermedia* Guss., Fl. Sic. Prodr. Suppl. 1: 87 (1832).
Statice psiloclada Boiss. var. *intermedia* (Guss.) Boiss. in DC., Prodr. 12: 651 (1848).

Distribution. Lampedusa in the salt-marsh near the port.

L. intermedium together with *L. lopadusanum, L. albidum, L. hyblaeum, L. mazarae* and *L. panormitanum* (Tod.) Pignatti belongs to the *L. albidum* group. This group is characterized by: branched caulis with leaves at its entire length, covered below by dry leaves; spathulate leaves; inflorescence fragile, with sterile branches absent or a few at the base, poor, with lax and falling spikes; straight inner bract and calyx.

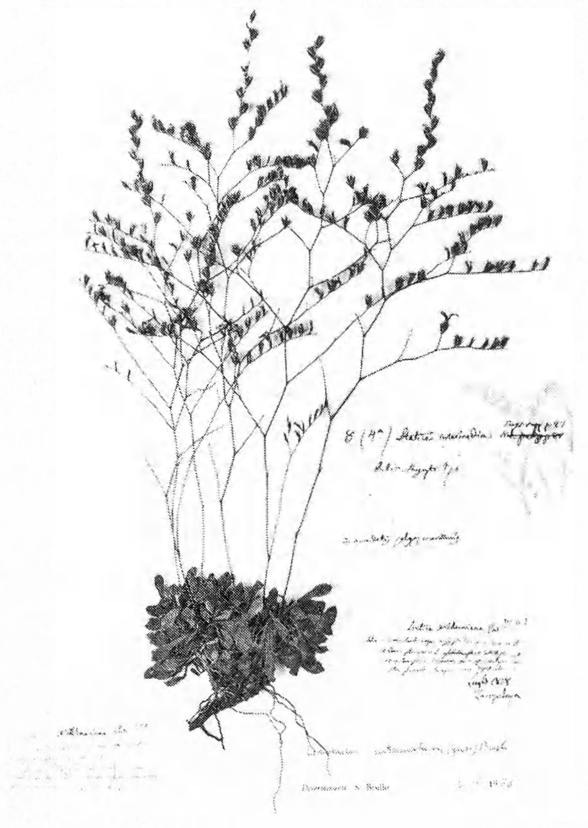

Fig. 5. *L. intermedium*. Lectotype (Gussone, NAP).

5. **Limonium flagellare** (Lojac.) Brullo, comb. nov., Fig. 6

Lectotype: Alcamo, s.d., Tineo (PAL). — Basionym: *Statice flagellaris* Lojac., Fl. Sic. 2(2): 27 (1907).

Distribution. Cliffs near the sea, between Balestrate and Castellammare (Palermo).

6. **Limonium ponzoi** (Fiori & Béguinot) Brullo, comb. et stat. nov.

Lectotype: Drepanum (Trapani), in rupibus calcareis littoreis inter loca Pizzolongo et Bonagia dicta, VI–VII.1923, Ponzo 2922 (FI). — Basionym: *Statice ambigua* Lojac. var. *ponzoi* Fiori & Béguinot, Sched. Fl. Ital. Exs. Forlì, Ser. 3, Cent. XXIX–XXX, 384 (1927). — *Statice ponzoi* Ross ex Fiori & Béguinot, Sched. Fl. Ital. Exs. Forlì, Ser. 3, Cent. XXIX–XXX, 384 (1927), pro syn.

Statice ambigua Tineo ex Lojac., Fl. Sic. 2(2): 26 (1907), non Rouy (1904).

Distribution. Rocky coast near Capo Bonagia (Trapani).

This species is similar to *L. bocconei* (Lojac.) Litard. with which it has in common the numerous, dense and intricate stems, with many sterile branches and few terminal flowering ones. The differential characters of the two species are, however, numerous. *L. ponzoi* has: Caulis with green leaves at anthesis; stems green when dry; leaves obovate-spathulate, up to 25 mm wide; inferior caulis scales 3–5 mm long; spikelets 5–6 per cm, 2–3-flowered; inner bract curved dorsally, 5–5.5 mm long; medium bract 3 mm and outer one 2 mm; calyx 6 mm; corolla 7 mm. *L. bocconei* instead has: Caulis with withered leaves at anthesis; stems blackened when dry; leaves linear-spathulate, up to max. 10 mm wide; inferior caulis scales 2–5 mm; spikelets 6–7 per cm, 1–2-flowered; inner bract straight, 3.5–4 mm; medium bract 2 mm and outer one 1–1.5 mm; calyx 4–5 mm; corolla 5–5.5 mm.

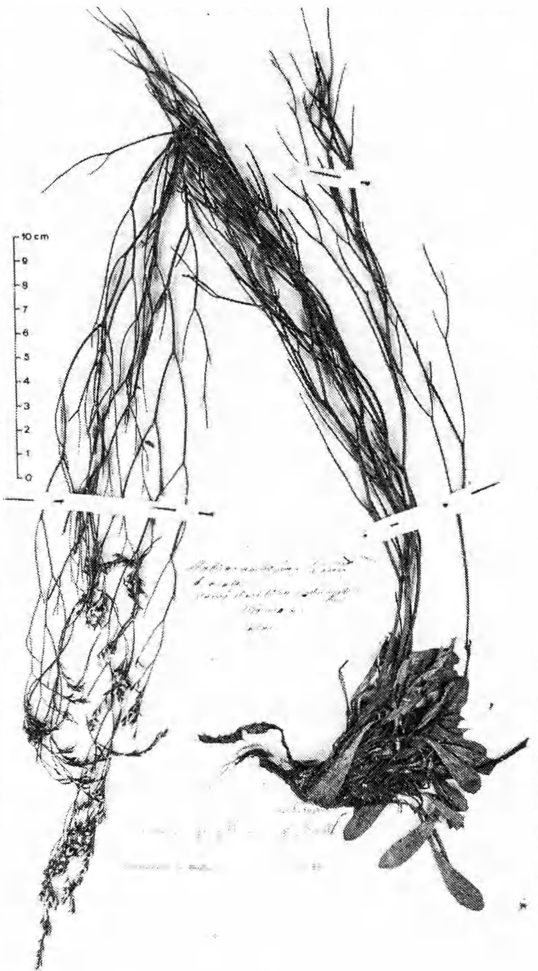

Fig. 6. *L. flagellare*. Lectotype (Tineo, PAL).

7. **Limonium syracusanum** Brullo, sp. nov., Fig. 7

Holotype: S. Panagia (Siracusa), 30.VII.1973, Brullo & Bartolo (CAT).

Planta perennis, 15–50 cm alta. Scapi striati, ramis sterilibus permultis, simplicibus vel paulo ramosis, fragilibus in nodis, articulis curvatis, dimorphi, partim sunt articulis robustis, rigidis, 1–2 cm longis, diametro

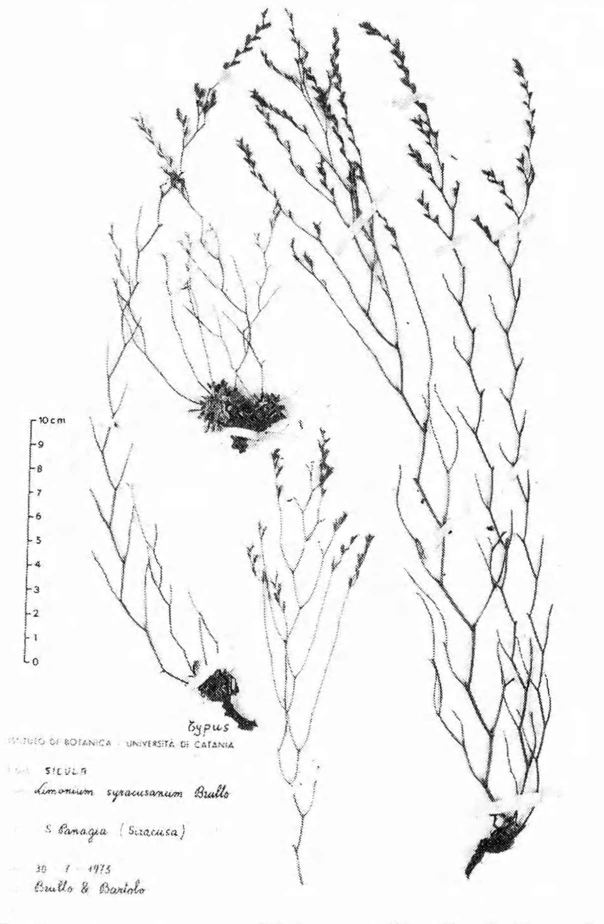

Fig. 7. *L. syracusanum*. Holotype (Brullo & Bartolo, CAT).

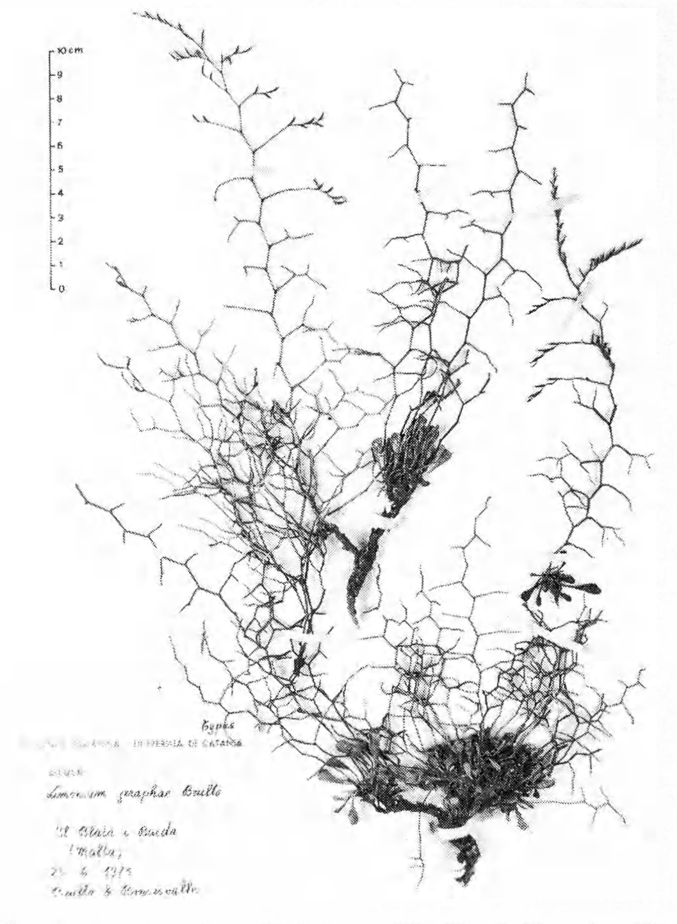

Fig. 8. *L. zeraphae*. Holotype (Brullo & Ronsisvalle, CAT).

non inferiore 1 mm, partim sunt articulis gracilibus, flexuosis, subtilibus, 5–15 mm longis, diametro inferiore 1 mm. Folia linearia-spathulata, rosulata, 10–50× 3–8 mm, uninervia, in petiolum longum attenuata. Spicae 2,5–8(–12) cm longae. Spiculae 2–4-florae, 2–3 in 1 cm. Bractea interior recta, 3,5(–4) mm longa, laxe cingentis flores, lato margine hyalino. Bractea exterior 1–2 mm longa. Calyx 4–5 mm longus, ex bractea interiore exsertus, limbo breviore quam tubo. Corolla coerulea 5–5,5 mm longa.

Plant 15–50 cm. Stems striate, fragile at nodes, dimorphous, some of these with robust, rigid segments 1–2 cm long, more than 1 mm in diameter, other ones with slender, flexuous segments 5–15 mm long, less than 1 mm in diameter. Non-flowering branches numerous, simple. Leaves linear-spathulate, rosulate, 10–50 × 3–8 mm, 1-veined. Spikes 2.5–8(–12) cm. Spikelets 2–4-flowered, 2–3 per cm. Inner bract straight, 3.5(–4) mm. Calyx 4–5 mm.

Distribution. Rocky coast between Augusta and Capo Passero (S.E. Sicily).

This species together with *L. ponzoi*, *L. bocconei* and *L. flagellare* belongs to the *L. bocconei* group. From these species *L. syracusanum* differs in several characters concerning the stems, the leaves, the spikes and spikelets.

8. **Limonium zeraphae** Brullo, sp. nov., Fig. 8

Holotype: Malta, Il Blata i-Baida, 25.VI.1973, Brullo & Ronsisvalle (CAT).

Statice reticulata auct. fl. melit., non. L. (1753).

Statice cancellata auct. fl. melit., non Bernh. ex Bertol. (1827).

Planta perennis, 6–40 cm alta. Scapi scabri, prostrati vel suberecti, ramosissimi, ramis sterilibus permultis, fragilibus in nodis, densis, intricatis, articulis 4–15 mm longis, curvatis, valde divaricatis formantibus angulis (60°–)90°–160°. Folia oblanceolata vel oblanceolato-spathulata, plus minusve revoluta, uninervia, 10–30(–40)×2–6(–9) mm, apice rotundato vel obtuso, anthesi plerumque sicca. Panicula ampla, spicis curvatissimis, divaricato-reflexis, scorpioideis, (2–)3–8 cm longis. Spiculae uniflorae, 2–3 in 1 cm. Bractea interior recta vel leviter curvata in basi, 4,5–5 mm longa, cyllindrica, flores arte amplectens, brunneo-virens exsiccatione. Bractea media 1,5–2 mm longa. Bractea exterior acuta, 1–1,5 mm longa, 1/5 bracteae interioris obtegens. Calyx 5 mm longus, limbo longiore quam tubo, lobis calycinis rotundis, ex bractea interiore longe exsertus. Corolla 6–7 mm longa, coeruleo-lilacina.

Plant 6–40 cm. Stems scabrous, prostrate or suberect, much branched, intricate, with segments 4–15 mm long, fragile at nodes and with branches diverging at an angle of (60°–)90°–160°. Non-flowering branches numerous. Leaves oblanceolate or oblanceolate–spathulate, 10–30(–40)×2–6 (–9) cm. Spikes arcuate (2–)3–8 cm. Spikelets 1-flowered, 2–3 per cm. Inner bract 4.5–5 mm, straight, cylindrical. Calyx 5 mm.

Distribution. Maltese Archipelago, on the coastal rocks.

On the basis of herbarium research and personal collections, *L. zeraphae* is probably the only species of *Limonium* living on the Maltese Islands. In the past, this species was reported as *Statice reticulata* L., but in the Linnean herbarium the specimen labelled with this name (LINN 395.9) is very different from *L. zeraphae*. This species is dedicated to the Maltese botanist Stefano Zerafa.

9. **Limonium divaricatum** (Rouy) Brullo, comb. et stat. nov.

Basionym: *Statice virgata* Willd. var. *divaricata* Rouy, Rev. Bot. Syst. Géogr. Bot. 1(10): 160 (1903). — *Limonium virgatum* (Willd.) Fourr. subsp. *divaricatum* (Rouy) Pignatti, Arch. Bot. (Forlì) 31: 75 (1955). — *Limonium graecum* (Poiret) Rech. fil. subsp. *divaricatum* (Rouy) Pignatti, Bot. Journ. Linn. Soc. 64: 366 (1971).

Distribution. Corsica, Sardinia, Balearic Islands,? Sicily.

L. divaricatum is similar to *L. zeraphae*, from which it differs in the following characters: stems rugose-tuberculate with segments 1–2 cm long and diverging at an angle (45°–)60°–90°(–120°); spikes 1–4 cm long, with spikelets 2–3-flowered; inner bract straight, compressed laterally, 5.5–6 mm long, dark when dry; outer bract 1.5–2 mm long, obtuse, overlapping 1/4 of the inner; calyx 6 mm, with obtuse lobes, limb shorter than the tube.

10. **Limonium pignattii** Brullo & Di Martino ex Brullo, sp. nov.

Holotype: Isola Grande dello Stagnone (Marsala), 14.VII.1974, Brullo & Di Martino (CAT).

Limonium pignattii Brullo & Di Martino, Boll. St. Inform. Giard. Col. Palermo 26: 11 (1974), nomen invalidum cum descr. lat. sed design. typi omissa.

Distribution. Coastal rocks and salt marshes of western Sicily between Marsala and Trapani, islands of Stagnone, Favignana and Levanzo.

11. **Limonium furnarii** Brullo, sp. nov., Fig. 9

Holotype: Capo Granitola (Mazara del Vallo), 26. IX.1973, Brullo (CAT).

Planta perennis, 5–25 cm alta, caule 0,5–6 cm longo, fruticoso, ramoso, folioso, foliis vetustis inferioribus siccis persistentibus. Scapus rugosus sursum, ramis sterilibus nonnullis. Folia viridia, oblanceolata vel linearia-spathulata, 10–45×3–6(–9) mm, erecta vel erecto-patentia, plana, apice obtuso vel rotundato, mucronulata. Panicula pyramidata, ramis subtilibus, flexuosis, longo tractu nudis. Spicae 5–20 mm longae, densiflorae. Spiculae 1–2-florae, 8–10 in 1 cm. Bractea interior 3,5–4,5 mm longa, recta, lato margine scarioso-rufescente. Bractea media et exterior 2 mm longae. Calyx 4–5 mm longus, pilosus in tubo, leviter exsertus ex bractea interiore; limbus tubo subaequilongus. Corolla lilacina, 5–5,5 mm longa.

Plant 5–25 cm. Leaves oblanceolate or linear-spathulate, 10–45×3–6(–9) mm, mucronate. Panicle pyramidal, with few sterile branches. Spikes 5–20 mm. Spikelets 1–2-flowered, 8–10 per cm. Inner bract 3.5–4.5 mm, straight. Calyx 4–5 mm, with pubescent tube.

Distribution. Capo Granitola near Mazara del Vallo, on the coastal rocks.

This species is morphologically very different to the other species of *Limonium* present in Sicily. It only has a weak affinity with the *L. minutiflorum* (Guss.) O. Kuntze, especially regarding the spikelets. This new species is named in honour of Prof. F. Furnari, my dear friend and colleague.

12. **Limonium lojaconi** Brullo, nom. nov., Fig. 10

Lectotype: Trapani presso il Mulino a Vento, 1849, Tineo (PAL).

Statice sicula Tineo ex Lojac., Fl. Sic. 2(2): 20 (1907).

Distribution: W. Sicily at Trapani, Favignana, ?Levanzo.

The epithet *"siculum"* cannot be used as a basionym of this taxon in the genus *Limonium*, because the name *Limonium siculum* has already been used by Miller (1768) in order to describe another species, which is a synonym of *Limoniastrum monopetalum* (L.) Boiss. Therefore, a new name is proposed. *L. lojaconi* is

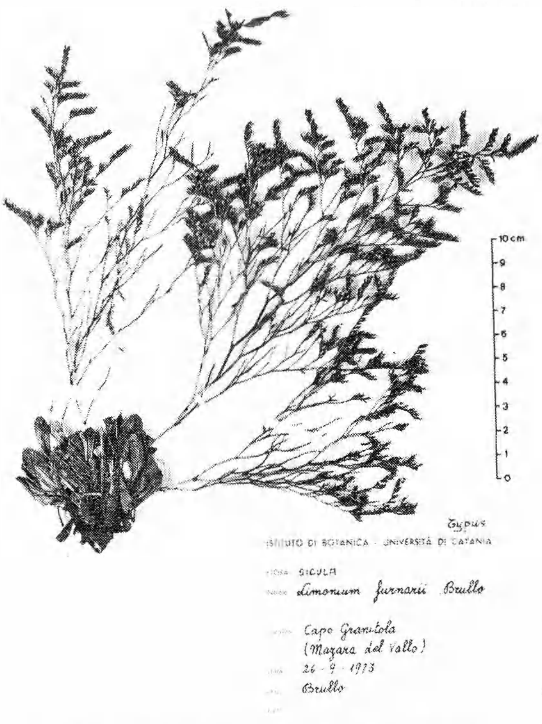

Fig. 9. *L. furnarii*. Holotype (Brullo, CAT).

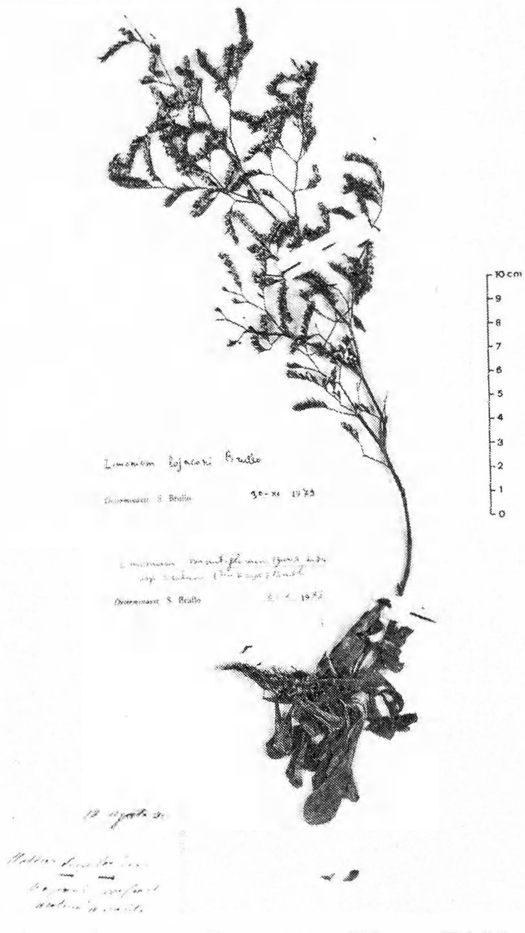

Fig. 10. *L. lojaconi*. Lectotype (Tineo, PAL).

similar to *L. minutiflorum*, from which it differs in the following characters: leaves 3-veined; spikes denser with 4–8 spikelets per cm; inner bract 4–4.5 mm long, slightly incurved at apex; outer bract 1–1.5 mm long, obtuse, overlapping 1/3–1/4 of the inner; calyx 4–4.5 mm, villose in the tube, lobes slightly obtuse. The species is dedicated to the Sicilian botanist M. Lojacono, who first described it as *Statice sicula*.

The four following species (13–16) also belong to the *L. minutiflorum* group:

13. **Limonium minutiflorum** (Guss.) O. Kuntze, Fig. 11

Kuntze, Rev. Gen. 2: 395 (1891).

Lectotype: Filicudi, in lapidosis maritimis, s.d. Gussone (NAP). — Basionym: *Statice minutiflora* Guss., Fl. Sic. Prodr. Suppl. 1: 80 (1832).

Distribution. N. Sicily near Capo Milazzo and the Aeolian Islands.

The species is characterized by: leaves oblanceolate-spathulate, 1–3-veined, 25–40 × 4–11 mm, obtuse or rounded at apex, glaucous; non-flowering branches few; spikes 1–4 cm long with 3–5 spikelets in 1 cm; inner bracht straight, 3.8–4 mm; outer bract acute, 2 mm long, overlapping 1/2 of the inner; calyx 4.5–5 mm, with few hairs in the tube, with rounded or obtuse lobes, limb

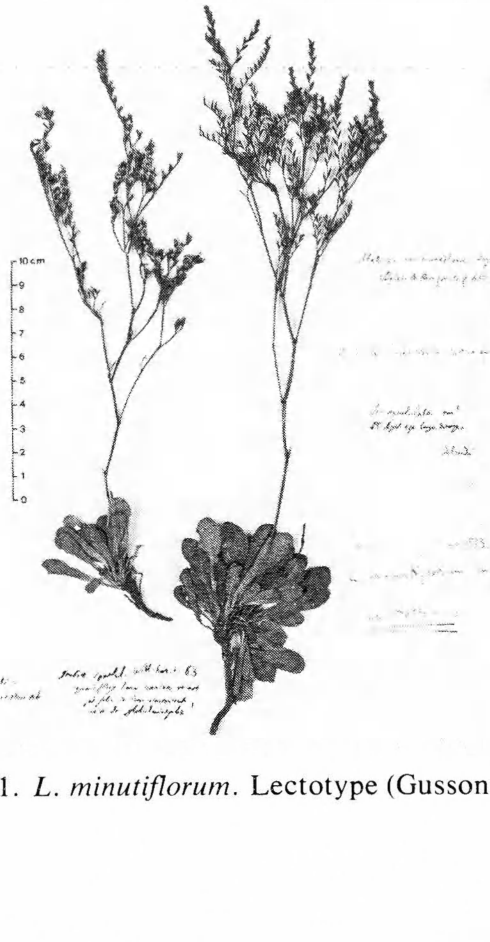

Fig. 11. *L. minutiflorum*. Lectotype (Gussone, NAP).

shorter or equal to the tube, exceeding the inner bract by 1–1.5 mm; corolla 5–6 mm long.

14. **Limonium calabrum** Brullo, sp. nov.

Holotype: Rupi di Copanello (Prov. di Catanzaro), 11.VIII.1883, Fiori (FI).

A Limonio minutifloro differt: folia 40–70 mm longa; spiculae 6 in 1 cm; bractea interior 3–3,5 mm longa; bractea exterior 1 mm longa, 1/4 bractea interioris obtegens; calyx pilosus in tubo, 3,5–3,8 mm longus, limbo breviore quam tubo.

Distribution. Calabria, on the maritime rocks of the Ionic coast near Copanello (Catanzaro).

15. **Limonium cyrtostachyum** (Girard) Brullo, comb. nov.

Basionym: *Statice cyrtostachya* Girard, Ann. Sci. Nat. Ser. 3, 2: 328 (1844).

Distribution. Algeria, rocky coast.

16. **Limonium balearicum** (Pignatti) Brullo, comb. et stat. nov.

Basionym: *Limonium minutiflorum* (Guss.) O. Kuntze subsp. *balearicum* Pignatti, Arch. Bot. (Forlì) 31: 85 (1955).

Distribution. Balearic Islands.

17. **Limonium tauromenitanum** Brullo, sp. nov., Fig. 12

Holotype: Naxos (Taormina), 6.VII.1974, Brullo (CAT).

Planta perennis, 15–40 cm alta, caule fruticoso, foliis rosulatis paulo densis, viridibus anthesi, vetustis rare persistentibus. Scapi fragiles, elongati, pauci, longo tractu nudi, sursum divisi ramis floriferis, ramulis sterilibus nullis vel nonnullis. Folia viridia, rigida, coriacea, erecta, exteriora 3-nervia, interiora uninervia, margine plus minusve revoluto, linearia-spathulata, 15–40×3–6 mm, acuta vel obtusiuscula. Panicula generaliter unilateralis. Spicae 1,5–2,5(–3) cm longae, spiculis bifloris 4–6 in 1 cm. Bractea interior recta, 4 mm longa, angusto margine hyalino. Bractea media 1,2–1,5 mm longa. Bractea exterior 1,5–2 mm longa, 1/3 bracteae interioris obtegens. Calyx 4,5–5 mm longus, leviter pilosus in tubo, ex bractea interiore c. 1,5 mm exsertus; limbus tubo subaequilongus. Corolla coeruleo, 5,5–6 mm longa.

Plant 15–40 cm. Leaves coriaceous, 1–3-veined, linear-spathulate, 15–40×3–6 mm, revolute. Panicle generally unilateral, with sterile branches few or absent. Spikes 1.5–2.5(–3) cm. Spikelets 2-flowered, 4–6 per cm. Inner bract 4 mm, straight. Calyx 4.5–5 mm.

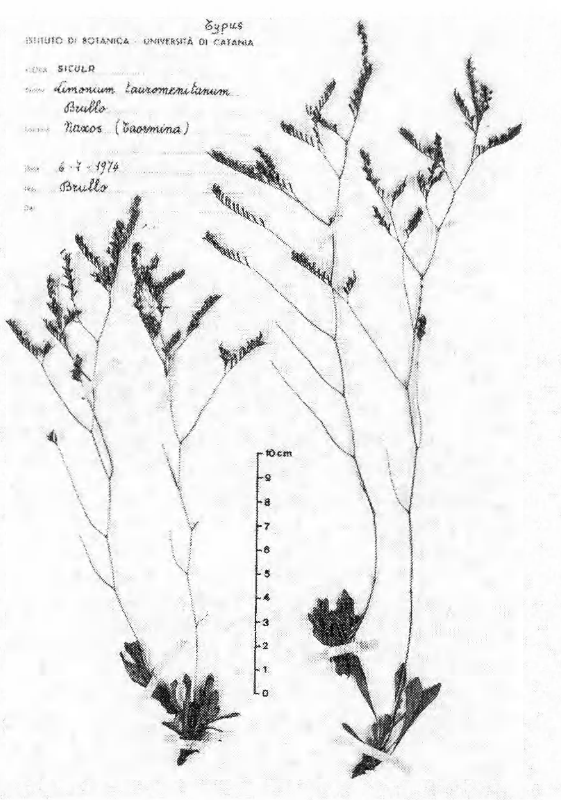

Fig. 12. *L. tauromenitanum*. Holotype (Brullo, NAP).

Distribution. Taormina on the volcanic rocky coast.

Although the characters of the flowers and the type of inflorescence of this species make it similar to *L. minutiflorum*, a lot of other characters nevertheless make it different to the latter.

18. **Limonium ionicum** Brullo, sp. nov., Fig. 13

Holotype: Taormina, Isola Bella, 1.X.1978, Brullo & Pavone (CAT).

Planta perennis, 12–40 cm alta, caule fruticoso, inferne foliorum vetustorum dense vestito, foliis superioribus rosulatis viridibus anthesi. Scapi flexuosi, erecti, elongati, nitidi vel leviter rugosi, ramosi in inflorescentia, ramulis sterilibus nullis. Folia viridia, herbacea, fossulata, rugosa linearia-spathulata, 25–80×(3–)4–9(–11) mm, 3(–5)-nervia, rare uninervia, plana, patentia, lamina in angustum et longum petiolum gradatim attenuata, obtusa vel obtusiuscula. Panicula simplex vel paulo ramosa, bilateralis. Spicae 2–5 mm longae. Spiculae biflorae, 3–5(–7) in 1 cm. Bractea interior 4,5–5 mm longa, recta vel curva a latere, margine anguste hyalino. Bractea media 2–2,2 mm longa. Bractea exterior 2,5–3 mm longa, 1/2 bracteae interioris obtegens. Calyx 5–5,5 mm longus, leviter pilosus in tubo, ex bractea interiore 0,8–1 mm exsertus, limbo quam tubo longiore. Corolla coerulea, 6–6,5 mm longa.

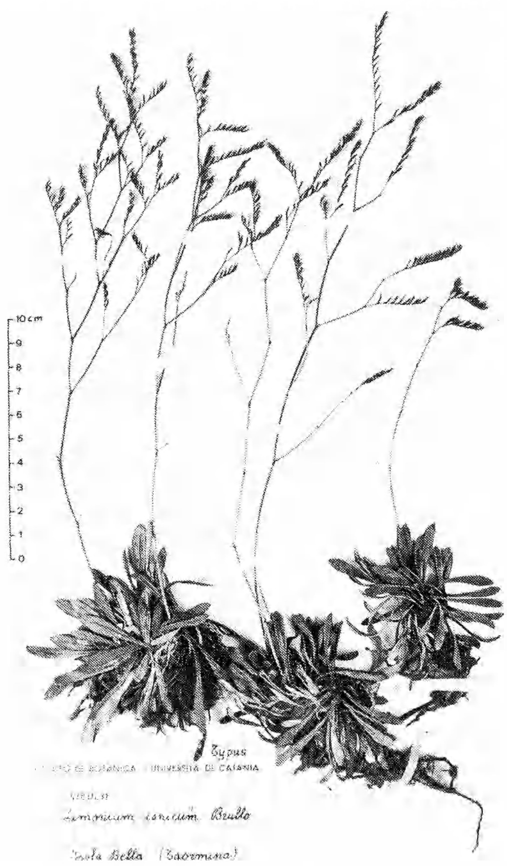

Fig. 13. *L. ionicum*. Holotype (Brullo & Pavone, CAT).

Plant 12–40 cm. Leaves tender, rugose, linear-spathulate, 25–80 × (3–)4–9(–11) mm, (1–)3(–5)-veined, plane. Panicle bilateral, with sterile branches absent. Spikes 2–5 cm. Spikelets 2-flowered, 3–5(–7) per cm. Inner bract 4.5–5 mm. Calyx 5–5.5 mm.

Distribution. Calcareous rocks of the Isola Bella near Taormina.

This species is akin to *L. tauromenitanum*, from which it differs in several important morphological characters and ecologically. In fact, *L. ionicum* is a calcicole species, whereas *L. tauromenitanum* is a calcifuge species localized on the volcanic rocks.

19. **Limonium oleifolium** Miller

Miller, Gard. Dict. ed. 8 no. 3 (1768).

19 a. **Limonium oleifolium** Miller subsp. **algusae** Brullo, subsp. nov

Holotype: Linosa, rupi marine vulcaniche, X.1973, Furnari (CAT).

A typo differt: planta elata usque ad 60 cm alta; folia 1–3-nervia; spicae 4–10 cm longae, spiculis 2–3 in 1 cm; bractea interior 6 mm longa, bractea exterior acuta, 2,5–2,8 mm longa, angusto margine hyalino, 1/3 bracteae interioris obtegens; bractea media 2,5 mm longa; calyx 6 mm longus, tubus calycis brevior vel subaequilongus quam limbus.

Plant tall, up to 60 cm high. Leaves 1–3-veined. Spikes 4–10 cm with 2–3 spikelets per cm. Inner bract 6 mm. Outer bract 2.5–2.8 mm, acute, overlapping 1/3 of the inner. Medium bract 2.5 mm long. Calyx 6 mm.

Distribution. Linosa (Algusa), along the volcanic rocky coast.

Subsp. *oleifolium* differs from subsp. *algusae* in the following characters: Plant 15–45 cm high; leaves 1-veined; spikes 1–4(–6) cm long with 4–5 spikelets in 1 cm; inner bract 4–5 mm long; outer bract obtuse, 1–2 mm long, overlapping 1/4 of the inner; medium bract 1–2 mm long; calyx 4.5–5 mm long, with curved tube longer than the limb.

19 b. **Limonium oleifolium** Miller subsp. **opulentum** (Lojac.) Brullo, comb. et stat. nov.

Lectotype: Porto Empedocle, s.d., Lojacono (PAL). — Basionym: *Statice opulenta* Lojac., Fl. Sic. 2(2): 23 (1907).

Distribution. Coastal marly soils near Porto Empedocle (Agrigento).

This subspecies differs from the type as follows: stem with few sterile branches, stronger, with a base diameter greater than 0.7 mm; caulis-scales less than 4–5 mm; spikelets 6–11-flowered, 4–6 per cm; inner bract 5.5–6.5 mm; outer bract 2–2.5 mm; calyx 5–6 mm.

20. **Limonium catanzaroi** Brullo, sp. nov., Fig. 14

Holotype. Ribera, VIII.1972, Catanzaro (CAT).

Planta perennis, 25–30 cm alta, caule ramoso longe folioso, foliis vetustis caudiculis vestentibus. Scapi fragiles, elongati, ramis inferioribus sterilibus, multis, subsimplicibus, supremis floriferis in paniculam amplam digestis. Folia linearia-rhomboidea, 20–50×2–4 mm, acuta vel obtusiuscula, mucronulata, brunnea anthesi, plana, uninervia, attenuata in angusto petiolo. Spicae 2–6 cm longae, spiculis bifloris, 2–4 in 1 cm. Bractea interior 5 mm longa, recta, large albomarginata, cylindrica, viridis. Bractea exterior acuta vel obtusiuscula, 2 mm longa, amplo margine hyalino, 2/5 bracteae interioris obtegens. Calyx rectus, 5–5,5 mm

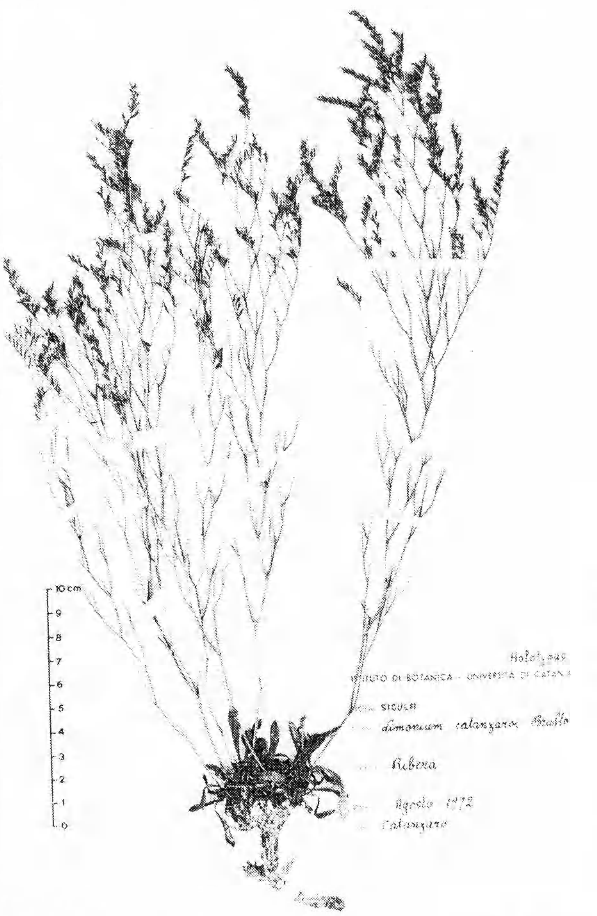

Fig. 14. *L. catanzaroi*. Holotype (Catanzaro, CAT).

longus, tubo subaequilongo vel breviori quam limbo, rubescens versus basim, brevibus et densis pilis sericeis in tubo, limbo omnino albo praeter subtiles nervos usque ad apicem loborum excurrentos, lobis 1 mm longis. Corolla coeruleo-violacea, 6 mm longa.

Plant 25–30 cm. Leaves linear-rhomboidal, 20–50 ×2–4 mm, acute or slightly obtuse, 1-veined. Non-flowering branches numerous. Spikes 2–6 cm. Spikelets 2-flowered, 2–4 per cm. Inner bract 5 mm, straight, with wide hyaline margin. Calyx 5–5.5 mm, straight, with veins reaching apex of the lobe.

Distribution. W. Sicily on the clay soils of the interior near Ribera.

This species seems to be quite isolated taxonomically as fas as its morphological characteristics are concerned. It could be confused with *L. oleifolium*, but the differences between the two species are remarkable. *L. oleifolium* differs from *L. catanzaroi* as follows: robust stem, not fragile at the nodes; leaves linear-spathulate and obtuse; shorter spikes with spikelets more dense; inner bract incurved, compressed laterally with very narrow hyaline margin, dark when dry; outer bract obtuse with very narrow hyaline margin, overlapping 1/4 of the inner; calyx 4.5–5 mm, curved, glabrous or slightly hairy in the tube, limb whitish only at the apex, reddish-brown in the remainder, with veins not reaching apex of the lobe; lobes of the calyx max. 0.5 mm long; calyx with limb shorter than the tube. It is my pleasure to name this beautiful plant after its discoverer Mr. Fr. Catanzaro.

21. **Limonium catanense** (Tineo ex Lojac.) Brullo, comb. nov., Fig. 15

Lectotype: Catania, alla cala nella lava sotto la Conceria, VI.1851, Tineo (PAL). — Basionym: *Statice catanensis* Tineo ex Lojac., Fl. Sic. 2(2): 27 (1907).

Distribution. Catania, on the volcanic maritime cliffs.

This species is very distinct from the other Sicilian species of *Limonium*, particularly where the branchlet of the stem and the morphology of the spikes and the spikelets are concerned.

22. **Limonium halophilum** Pignatti, sp. nov., Fig. 16

Holotype: Mazara del Vallo, estate 1965, Catanzaro (TBS).

Limonium ramosissimum (Poiret) Maire subsp. *siculum* Pignatti, Bot. Journ. Linn. Soc. 64: 366 (1971).

Distribution. Salt-marshes of Capo Feto near Mazara del Vallo (W. Sicily).

The epithet '*siculum*' cannot be used as a basionym for this taxon at the specific level (cf. also no. 12, *L. lojaconi* above). A new name is therefore proposed.

23. **Limonium lilybaeum** Brullo, sp. nov., Fig. 17

Holotype: Isola Grande dello Stagnone, nei pantani salmastri, 14.VII.1974, Brullo (CAT).

Planta perennis 6–35 cm alta, caule contracto folioso. Scapus robustus, rigidus, striatus, ramis sterilibus nonnullis. Folia acuta vel acutiuscula, rigida, plana, oblanceolato-spathulata, mucronulata, 25–50 × 7–13 mm, laevia, glauca, 3-nervia, rosulata. Panicula ampla, pyramidata, ramis subtilibus flexuosis. Spicae 0,5–2,5 cm longae. Spiculae biflorae, 7–8 in 1 cm. Bractea interior 5 mm longa, margine hyalino 0,5–1 mm lato. Bractea exterior obtusa vel acutiuscula, 2,5 mm longa, 1/2 bracteae interioris obtegens. Bractea media 2,5–3 mm longa. Calyx 5 mm longus, limbo ex loto albo aequilongo tubo, lobis obtusis 0,8–1 mm longis.

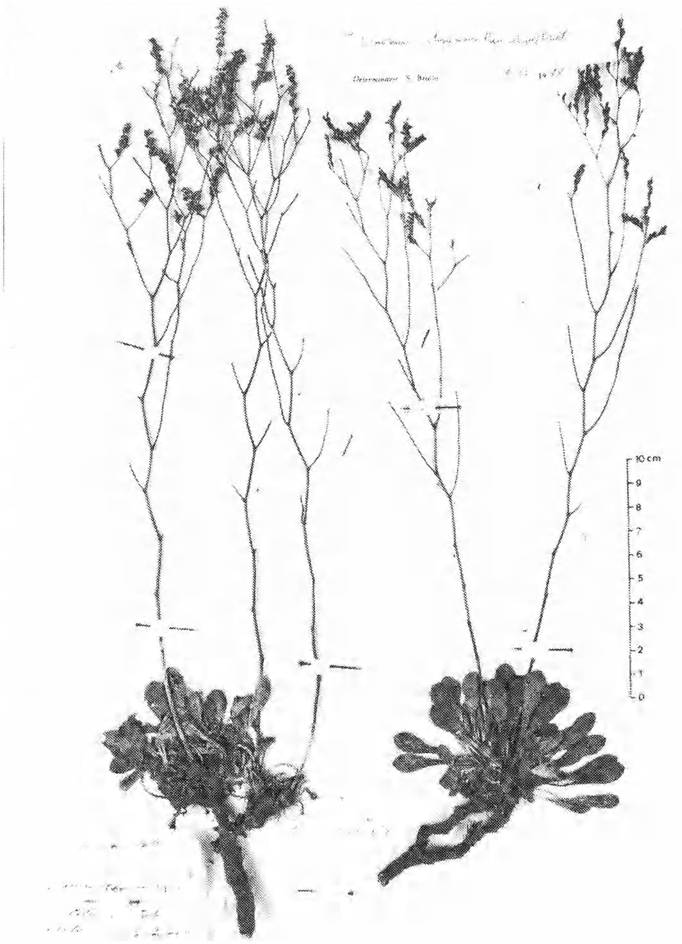

Fig. 15. *L. catanense*. Lectotype (Tineo, PAL).

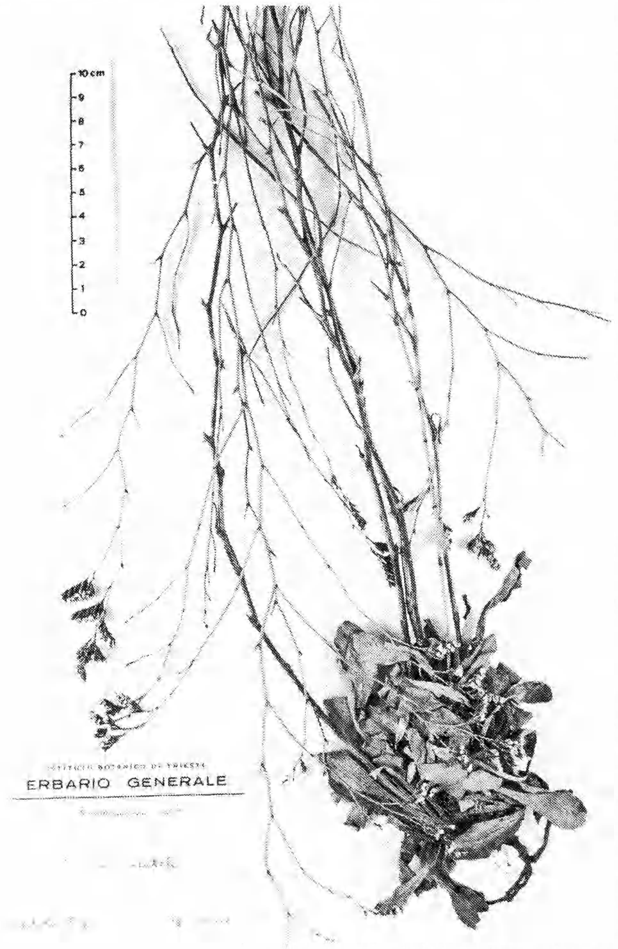

Fig. 16. *L. halophilum*. Isotype (Catanzaro, TSB).

Plant 6–35 cm. Leaves rigid, oblanceolate-spathulate, 25–50 × 7–13 mm, rosulate, 3-veined. Panicle pyramidal with few sterile branches. Spikes 5–25 mm. Spikelets 2-flowered, 7–8 per cm. Inner bract 5 mm. Calyx 5 mm with lobes 0.8–1 mm long.

Distribution. Saline soils of the Isola Grande of the Stagnone Archipelago near Marsala.

24. **Limonium selinuntinum** Brullo, sp. nov., Fig. 18

Holotype: Selinunte, sulle rupi costiere, 27.VIII.1974, Brullo (CAT).

Planta perennis 20–35 cm alta, caule ramoso, contracto, folioso. Scapus ramosus, scabrus, ramis robustis, divaricato-erectis, sterilibus perpauci. Folia oblanceolato-spathulata, glauca, 20–60 × 5–12 mm, plana, acuta vel acutiuscula, 1–3-nervia, sine mucrone vel leviter mucronulata. Panicula ampla, pyramidata, ramis elongatis. Spicae 6–15 mm longae. Spiculae 4–6-florae, 8–10 in 1 cm. Bractea interior 5 mm longa, margine hyalino 0,5 mm lato. Bractea exterior obtusa, 2 mm longa, 2/3 bracteae interioris obtegens. Calyx 5 mm longus, limbo tubo subaequilongo, limbo omnino albo, lobis obtusis 0,5 mm longis.

Plant 20–35 cm. Leaves oblanceolate-spathulate, 20–60 × 5–12 mm, 1–3-veined. Panicle pyramidal with few sterile branches. Spikes 6–15 mm. Spikelets 4–6-flowered, 8–10 per cm. Inner bract 5 mm. Calyx 5 mm with lobes 0.5 mm long.

Distribution. Selinunte on the maritime cliffs.

25. **Limonium aegusae** Brullo, sp. nov., Fig. 19

Holotype: Favignana, presso il Pantano, 31. VII.1973, Brullo & Bartolo (CAT).

Planta perennis, 5–25 cm alta, caule suffruticoso, ramis foliis vetustis stipatis crebissime vestitis. Scapi numerosi, scabri, subtili, graciles, flexuosi vel rigiduli, e ipsissima basi subito ramosi, ramis sterilibus nonnullis. Folia linearia-spathulata, plana, non rigida, scabrorugosa, 10–30 × 4–6(–9) mm, uninervia vel obscure 3-nervia, acuta, mucronulata, gradatim in longum et angustum petiolum attenuata. Ramuli floriferi divaricato-recti, in paniculam depauperatam digesti. Spicae densae, 7–20 mm longae. Spiculae 1–2-florae, 6–8 in 1 cm. Bractea interior 4–4,5 mm longa, recta, leviter albo-marginata. Bractea exterior acutiuscula, 1,5(–2) mm longa, 2/5 bracteae interioris obtegens. Calyx 5–5,5 mm longus, paulo pilosus in tubo, ex bractea interiore breviter exsertus, limbo ex toto albo longiore

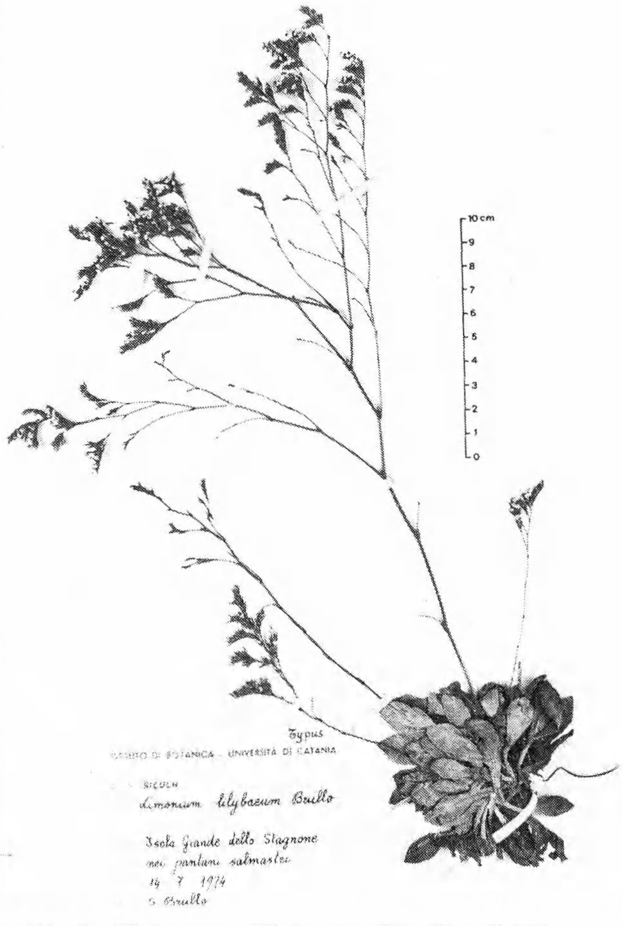

Fig. 17. *L. lilybaeum*. Holotype (Brullo, CAT).

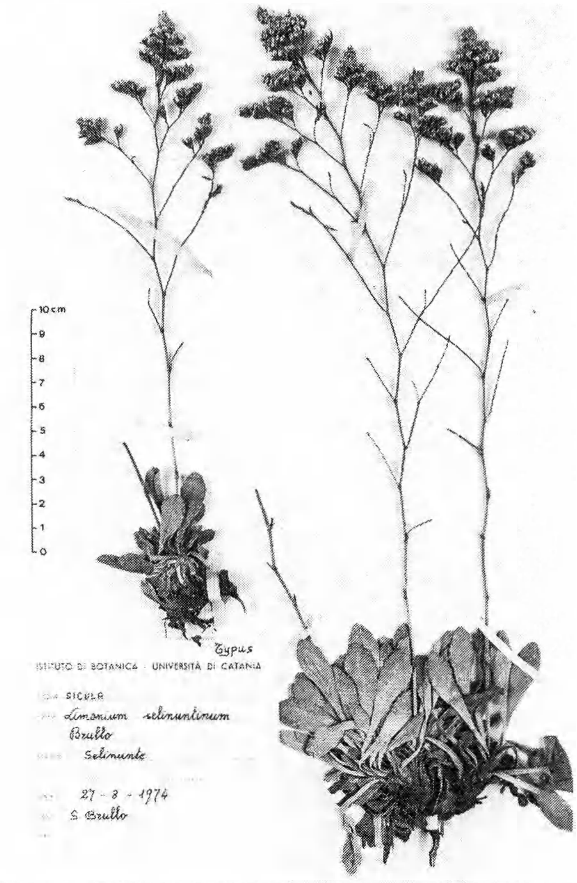

Fig. 18. *L. selinuntinum*. Holotype (Brullo, CAT).

quam tubo, lobis acutis 0,5 mm longis. Corolla 5,5–6 mm longa, coeruleo-lilacina.

Plant 5–25 cm. Stems numerous, scabrous, slender, flexuous, with few sterile branches. Leaves linear-spathulate, 10–30 × 4–6(–9), 1-veined or obscurely 3-veined, acute. Spikes 7–20 mm. Spikelets 1-2-flowered, 6–8 per cm. Inner bract 4–4.5 mm. Calyx 5–5.5 mm.

Distribution. Island of Favignana (Aegusa) near salt-marsh.

26. **Limonium pachynense** Brullo, sp. nov. Fig. 20

Holotype: Pantano Longarini, 21.VIII.1972, Brullo (CAT).

Planta perennis, 6–50 cm alta, caule contracto, ramis foliosis. Scapus robustus, saepe a basi ramosus, ramis sterilibus nonnullis, striatus, diametro articulorum inferiorum 0,5–2 mm. Folia oblanceolato-spathulata, plana, rugosa, viridia-glaucescentia, 15–80×6–16 mm, 3-nervia vel obscure 3-nervia, interiora saepe mucronulata, longe in petiolum latum 1–2,5 mm attenuata. Panicula corymbosa, ramulis divaricato-rectis longe nudis deorsum. Spicae 6–12 mm longae. Spiculae 2–3-florae, 8–10 in 1 cm. Bractea interior recta, 5 mm longa, angusto margine hyalino 0,2–0,3 mm lato, rotundata in apice. Bractea media 2 mm longa. Bractea exterior obtusa, 2–2,5 mm longa, 2/5 bracteae interioris obtegens. Calyx 4–4,5 mm longus, tubo laeviter piloso, ex bractea interiore non exsertus, limbo breviore quam tubo, brunneo-rufescente deorsum, lobis obtusis 0,5 mm longis. Corolla roseo-lilacina, 5–6 mm longa.

Plant 6–50 cm. Stems robust, striate. Leaves oblanceolate-spathulate, 15–80 × 6–16 mm, 3-veined. Panicle corymbose with few sterile branches. Spikes 6–12 mm. Spikelets 2–3-flowered, 8–10 per cm. Inner bract 5 mm. Calyx 4–4.5 mm.

Distribution. Salt-marshes near Pachino (S. Sicily).

L. pachynense, *L. halophilum*, *L. lilybaeum*, *L. selinuntinum*, *L. aegusae* and *L. secundirameum* (Lojac.) Brullo, species very distinct for numerous peculiar characters, all belong to the *L. ramosissimum* group (Pignatti 1971, 1972)

Acknowledgements. I am grateful to Prof. S. Pignatti for generously giving me valuable advice and for publishing two new species in this paper. I also wish to thank Dr M. Erben for his critical reading of the manuscript.

Fig. 19. *L. aegusae*. Holotype (Brullo & Bartolo, CAT).

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Appendix

A current check-list of the genus Limonium in Sicily.

Limonium sinuatum (L.) Miller
Limonium ferulaceum (L.) O. Kuntze
Limonium serotinum (Reichenb.) Pignatti
Limonium calcarae (Tod. ex Janka) Pignatti
Limonium parviflorum (Tineo in Guss.) Pignatti
Limonium cosyrense (Guss.) O. Kuntze
Limonium bocconei (Lojac.) Litard.
Limonium ponzoi (Fiori & Béguinot) Brullo
Limonium flagellare (Lojac.) Brullo

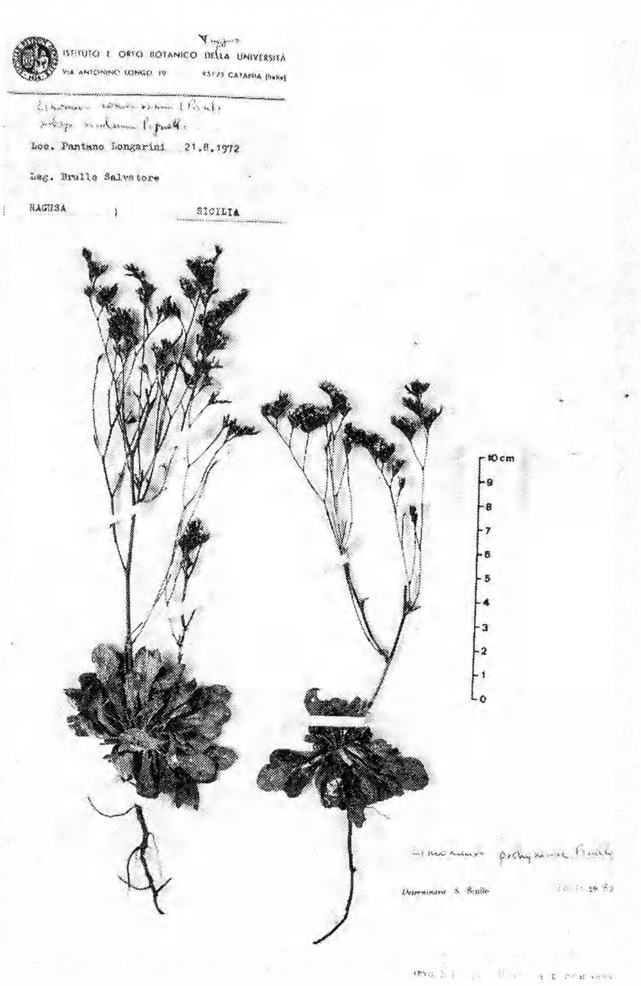

Fig. 20. *L. pachynense*. Holotype (Brullo, CAT).

Limonium syracusanum Brullo
Limonium zeraphae Brullo
Limonium tenuiculum (Tineo ex Guss.) Pignatti
Limonium catanense (Tin. ex Lojac.) Brullo
Limonium pignattii Brullo & Di Martino ex Brullo
Limonium catanzaroi Brullo
Limonium minutiflorum (Guss.) O. Kuntze
Limonium lojaconi Brullo
Limonium tauromenitanum Brullo
Limonium ionicum Brullo
Limonium furnarii Brullo
Limonium albidum (Guss.) Pignatti
Limonium lopadusanum Brullo
Limonium hyblaeum Brullo
Limonium mazarae Pignatti
Limonium panormitanum (Tod.) Pignatti
Limonium intermedium (Guss.) Brullo
Limonium oleifolium Miller subsp. *oleifolium*
Limonium oleifolium Miller subsp. *algusae* Brullo
Limonium oleifolium Miller subsp. *opulentum* (Lojac.) Brullo
Limonium duriusculum (Girard) Fourr.
Limonium halophilum Pignatti
Limonium secundirameum (Lojac.) Brullo
Limonium lilybaeum Brullo
Limonium selinuntinum Brullo
Limonium aegusae Brullo
Limonium pachynense Brullo
Limonium densiflorum (Guss.) O. Kuntze
Limonium sibthorpianum (Guss.) O. Kuntze
Limonium echioides (L.) Miller

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Embryology of Eriocaulon hookerianum Stapf and the systematic position of Eriocaulaceae

GOVINDAPPA D. AREKAL and S. N. RAMASWAMY

Arekal, G. D. & Ramaswamy, S. N. 1980 09 18: Embryology of Eriocaulon hookerianum Stapf and the systematic position of Eriocaulaceae. *Bot. Notiser 133:* 295–309. Stockholm. ISSN 0006-8195.

The embryology of *Eriocaulon hookerianum* is described. The microsporangial wall consists of an endothecium, a middle layer and a glandular tapetum of uninucleate cells in addition to the epidermis. Pollen grains are three-celled and spiraperturate at shedding. The ovary is superior, tricarpellary and syncarpous with three orthotropous tenuinucellate ovules on an axile placenta. Embryo sac development follows the Polygonum type. The three antipodals fuse to form a cyst. The endosperm is nuclear. Early cleavages of embryonal development conform to the Penaea variation, Asterad type. Both integuments contribute to the seedcoat. The innermost layer of the pericarp develops band-like thickenings and helps in seed release. The results have been evaluated for assessing the systematic position of Eriocaulaceae. The elevation of the family to the rank of an order by Hutchinson and Cronquist is justified on embryological grounds.

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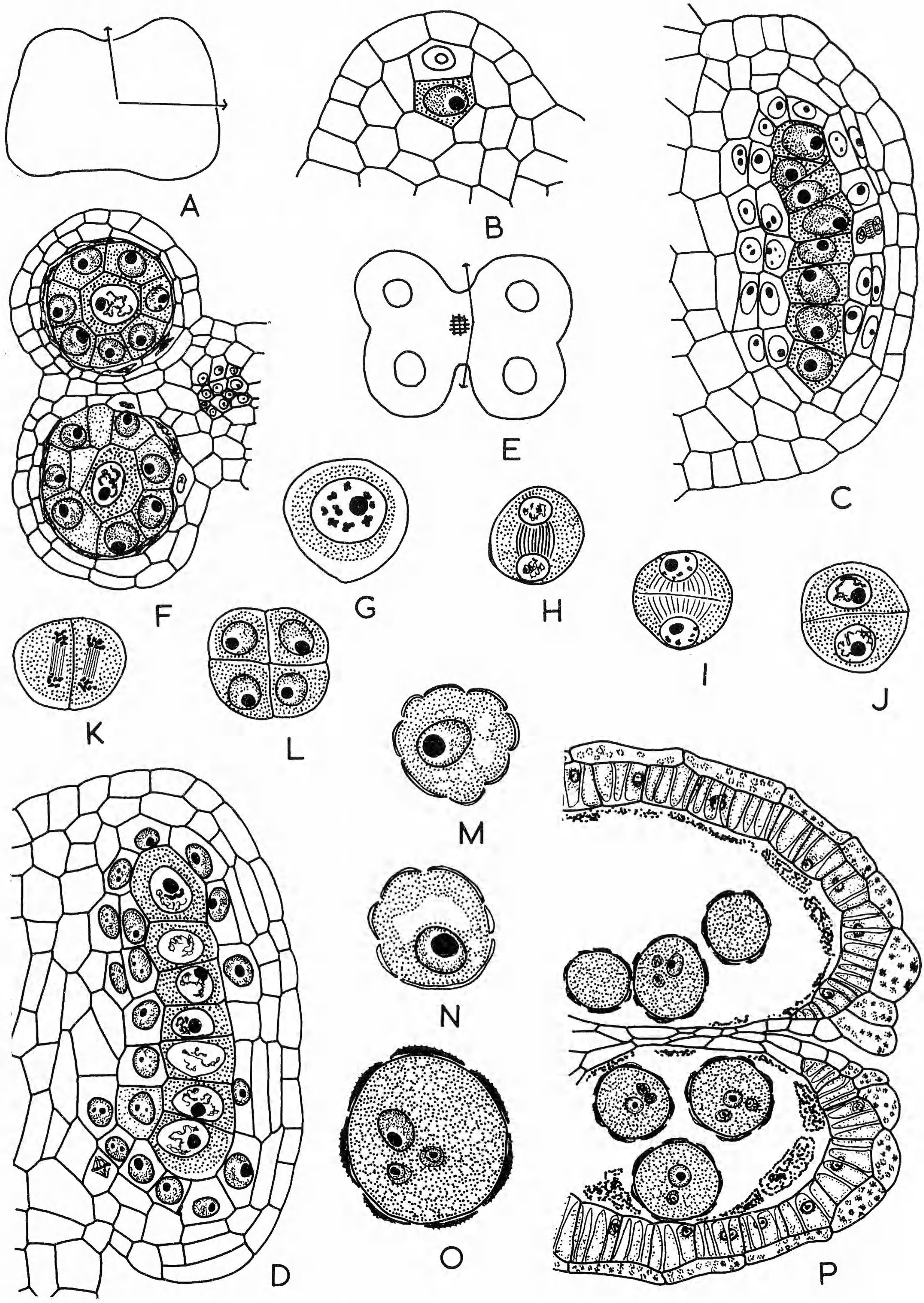
The Eriocaulaceae commonly known as the Pipewort family are a large cosmopolitan assemblage comprising 13 genera and approx. 1500 species, included under two subfamilies, Eriocauloideae and Paepalanthoideae (Moldenke 1971). They are "the Compositae of Monocotyledons" (Rendle 1930). The members are predominantly pantropical, though a few extend even to the temperate zones. Although they possess a wide range of floral structure, all the species together constitute, more or less, a well-defined natural group. In spite of a large number of publications regarding the taxonomy of this family (see Bentham & Hooker 1883, Ruhland 1903, 1930, Moldenke 1959, 1971), there is no unanimity amongst the taxonomists about the systematic position of the family in the Monocotyledons (Bentham & Hooker 1883, Engler & Prantl 1887, Hallier 1912, Bessey 1915, Rendle 1930, Benson 1957, Hutchinson 1959, Takhtajan 1966, Cronquist 1968).

For the past two decades embryological investigations have greatly altered our ideas regarding the importance of embryology in the classification of angiosperms. Nevertheless, more intensive studies are required if a proper basis is to be provided for the formulation of universal laws.

Smith (1910) was the first to investigate the embryology of Eriocaulaceae. He recorded a 4-layered anther wall including a tepetum of uninucleate cells, 3-celled pollen, a Polygonum type of embryo sac with inconspicuous antipodal cells, a nuclear endosperm and an undifferentiated embryo in *Eriocaulon septangulare*. Palm (1920) examined the pollen development in *E. truncatum* and reported that it was 3-celled at shedding. Patel & Patel (1964) studied *E. cinereum* and recorded the occurrence of 3-celled spiraperturate pollen, a Polygonum type of embryo sac with three antipodal cells, a nuclear endosperm and an unorganized embryo. The occurrence of a glandular tapetum containing binucleate cells, a 2-celled triporate pollen at shedding, a Polygonum type of embryo sac containing three superposed antipodal cells, and enveloped by an endothelium, a nuclear endosperm and an undifferentiated embryo, in addition to the structure of seedcoat and fruit wall are subsequently reported by Begum (1968) for *E. quin-*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quangulare. Since the investigations regarding the family are inadequate and the results vary Maheshwari & Kapil (1963) rightly felt that Eriocaulaceae deserved a detailed study. Embryological investigations on the family were undertaken to fill in the large gap. The present paper deals with various embryological aspects of *Eriocaulon hookerianum*.

Material and methods

Material for the present study was collected from marshy areas near Bababudan Hills and Mullaiahnagiri (1550 and 1850 m altitude respectively), Chikkamagalore District, Karnataka State, India. The voucher specimens numbered Swamy (SNR. 1–5) were deposited in the Herbarium of the Post-graduate Department of Botany, Manasa Gangotri, Mysore-6. The entire flowering and fruiting heads were fixed in Formalin-Acetic acid-Alcohol (FAA). The involucral bracts of the heads were removed before fixation. In order to separate the minute flowers the flower heads were dissected under a binocular dissecting microscope. Hard seeds were softened with 15 % hydrofluoric acid (in 70 % ethyl alcohol). An ethanol-xylol-paraffin series was followed during dehydration and imbedding. Serial cross and longitudinal sections were cut 8–14 μm thick and stained in Heidenhain's Iron-alum-haematoxylin using erythrosin as a counterstain.

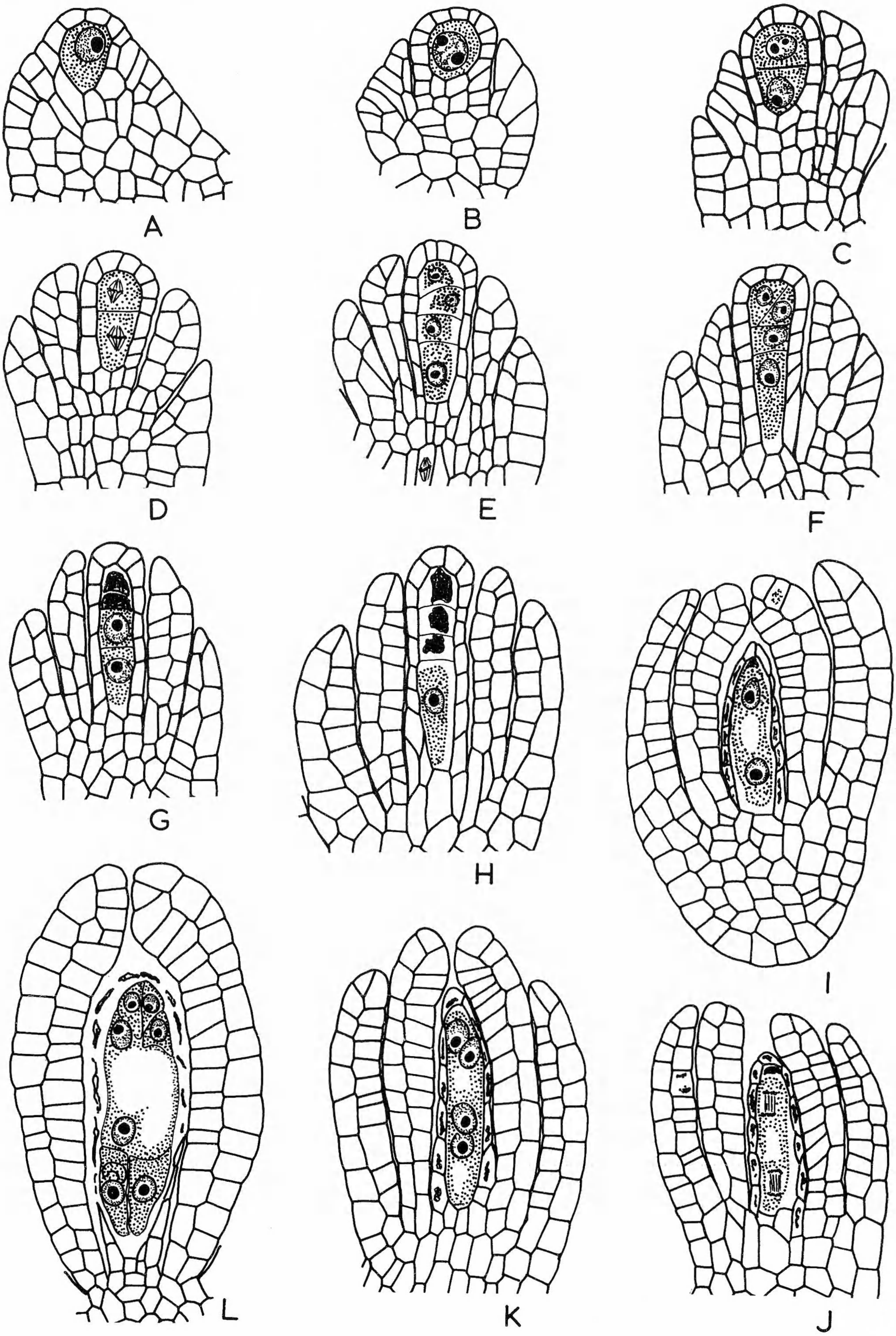
Observations

Microsporangium and male gametophyte. A cross section of a very young anther is 4-lobed and each lobe is the site of a microsporangium (Fig. 1 A). A large-nucleate densely cytoplasmic hypodermal archesporial cell differentiates in each lobe and divides periclinally producing the primary parietal and primary sporogenous layers (Fig. 1 B). The cells of the primary parietal layer, by periclinal division, delimit the endothecium from an inner layer, which in turn and by a similar division, gives rise to the middle layer and tapetum (Fig. 1 C–F). The tapetal cells enlarge in size and become conspicuous by the acquisition of large nuclei and dense cytoplasm. During the later stages of sporangium development the middle layer becomes crushed. The uninucleate tapetal cells break down after providing nourishment for the microsporocytes and pollen grains. The cells of endothecium increase in size and develop fibrillar thickenings on the inner side of their tangential walls. The epidermal cells elongate and increase in size considerably, acquiring dark-staining granular bodies (Fig. 1 P).

Meanwhile, cells of the primary sporogenous layer divide transversely and produce a row of sporogenous cells which soon increase in size, become spherical and function as microspore mother cells (Fig. 1 C–G). Meiotic divisions follow. Quadripartition of the mother cells is successive and the microspore tetrads are isobilateral (Fig. 1 G–L). Soon, the microspores enlarge in size, acquire a spherical shape and separate. A conspicuous vacuole develops in the cytoplasm and pushes the microspore nucleus to one side (Fig. 1 M–N). A mitotic division of this nucleus leads to the organization of a small generative cell and a large tube cell. The generative cell gradually moves into the cytoplasm of the tube cell and divides producing two male gametes. The two adjacent microsporangia coalesce before pollen liberation due to the breakdown of separation layers of cells. At the time of shedding the pollen grain is 3-celled. It is spherical in shape and has a thin intine and a comparatively thick, minutely spinascent, spiraperturate exine (Fig. 1 O).

Megasporogenesis and female gametophyte. A large densely protoplasmic hypodermal archesporial cell is organised very early in the ovular primordium (Fig. 2 A). It increases in size and functions directly as the megaspore mother cell. After meiosis-I, two dyad cells are formed (Fig. 2 B–D). These pass through meiosis-II and together give rise to a linear or obliquely T-shaped tetrad of megaspores (Fig. 2 D–F). Three of the megaspores in the tetrad usually degenerate and the lowermost one functions (Fig. 2 H). It is rare that two megaspores of a tetrad show signs of further development (Fig. 2 G). The functional

Fig. 1. Microsporangium and male gametophyte development in *Eriocaulon hookerianum*. — A: Outline of transverse section of very young anther. × 750. — B: T.s. of an anther lobe showing primary parietal and primary sporogenous layers. × 585. — C, D: Longitudinal sections of microsporangia showing two stages in the development of a 4-layered anther wall enclosing a layer of microspore mother cells. × 1250. — E: Outline of t.s. of anther at spore mother cell stage. × 560. — F: Left part of E to show cellular details. × 625. — G–L: Stages in the formation of a microspore tetrad from a microspore mother cell. × 1670. — M–O: Stages in the development of a 3-celled pollen. × 1670. — P: T.s. of part of a mature anther lobe to show structural details. × 840.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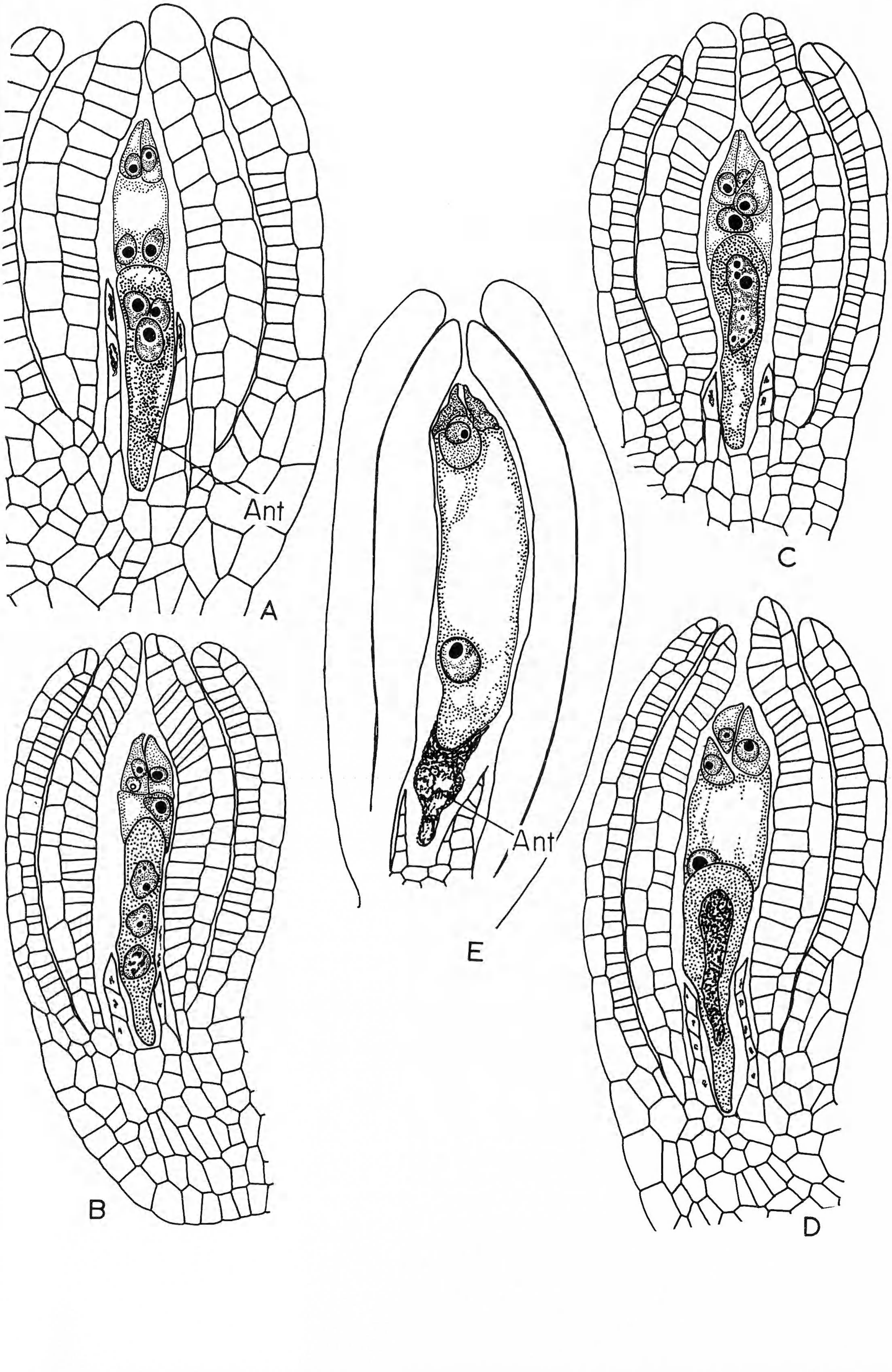
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megaspore develops into an 8-nucleate embryo sac of the Polygonum type (Fig. 2 I–L). The walls of the antipodal cells soon disorganize and their protoplasts fuse together producing an antipodal cyst. This cyst acquires dense cytoplasm and its nuclei increase in size. It elongates towards the egg apparatus, consequently reducing the size of the central cell. Its 3 nuclei meet and fuse together to form a large polyploid nucleus (Fig. 3 A–C). Meanwhile, the two polar nuclei unite forming a secondary nucleus. Marked changes occur in the embryo sac soon after the organization of the secondary nucleus. The central cell begins to elongate towards the chalaza and increases in size, while vacuolization of its cytoplasm becomes prominent (Fig. 3 C–D). The large nucleus of the antipodal cyst breaks down and the entire cyst itself is gradually pressed down by the extending central cell.

The mature embryo sac (Fig. 3 E) is spindle-shaped and is in direct contact with the inner layer of the inner integument. The egg apparatus consists of 2 degenerating synergids and a large egg. The antipodal cyst persists as a dark, intensely staining mass at the lower end of the sac. The secondary nucleus it confined to the chalazal half of the embryo sac.

Endosperm. Fertilization is porogamous. One of the sperm nuclei fuses with the egg and the other unites with the secondary nucleus producing the primary endosperm nucleus (Fig. 4 A).

The primary endosperm nucleus located at the antipodal end of the embryo sac divides and no wall is formed after this division. The two resulting nuclei divide simultaneously (Fig. 4 B–C). After further free nuclear divisions a number of endosperm nuclei are formed. These are distributed throughout the embryo sac in the peripheral cytoplasm, more nuclei being confined to the chalazal end of the young endosperm. Cell wall formation begins at the chalazal end and gradually extends to the micropylar part. When the initial wall formation is complete, a larger amount of endosperm tissue is noticeable at the chalazal part than in the micropylar region, while only two layers of cells are found along the sides. A prominent vacuole occupies the centre of the embryo sac (Fig. 5 A, B). The later growth of the endosperm is centripetal and is by cell division. Ultimately the central vacuole becomes replaced by large isodiametric cells gorged with reserve food in the form of starch gains and oil globules (Fig. 6).

Embryo. The division of the zygote occurs only after the formation of a few endosperm nuclei in the embryo sac and it is transverse (Fig. 7 A, B). The resulting apical cell *Ca* and the basal cell *Cb* divide vertically, each producing two juxtaposed cells, divisions in cell *Cb* being tardy (Fig. 7 C–E). The first proembryonal tetrad is, therefore, of the A_1 category of Souèges (1948). The two cells derived from *Ca* divide vertically at right angles to the previous one and organize the quadrants *q* (Fig. 7 F–H). Periclinal divisions follow in the two tiers of the proembryo delimiting the dermatogen from an inner group of cells (Fig. 7 J–M). Rapid vertical and transverse divisions occur in the inner group of cells in the quadrant region, while anticlinal divisions occur in the dermatogen (Fig. 7 N–T). Division of cells in region *Cb* are very few. During further stages of development the rate of cell division is slow in regions *q* and *Cb* but cells of the upper part of the embryo increase in size. As a result, the region expands (Fig. 7 U–W). The embryo in a ripe seed is comparatively few-celled, bell-shaped and undifferentiated (Fig. 7 X).

Ovule, seedcoat and fruit wall. The ovule is orthotropous, bitegmic and tenuinucellate. Each

Fig. 2. Megasporogenesis and development of female gametophyte in *Eriocaulon hookerianum*. — A: An ovular primordium showing a hypodermal archesporial cell. — B: Megaspore mother cell. — C: Dyad cells. — D: Nuclear division in dyad cells. — E–F: Linear and oblique T-shaped megaspore tetrads respectively. — G: Two functional megaspores of a linear tetrad. — H: Functional megaspore and three degenerating megaspores of a linear tetrad. — I: 2-nucleate embryo sac. — J: Nuclear division in the 2-nucleate embryo sac. — K: 4-nucleate embryo sac. — L: Organized 8-nucleate embryo sac. — × 760. (See p. 298.)

Fig. 3. Stages in the organization of the antipodal cyst in *Eriocaulon hookerianum*. — A: An 8-nucleate embryo sac with walls of antipodal cells disorganized to form a cyst. — B: Embryo sac with an antipodal cyst having 3 superposed nuclei. — C: Embryo sac with an antipodal cyst after fusion of the 3 nuclei in the cyst. — D, E: stages in the development of mature embryo sac showing enlarged and elongated central cell; note degenerating antipodal cyst. — A: × 1150. B–E: × 760. — Ant. Antipodal cyst. (See p. 299.)

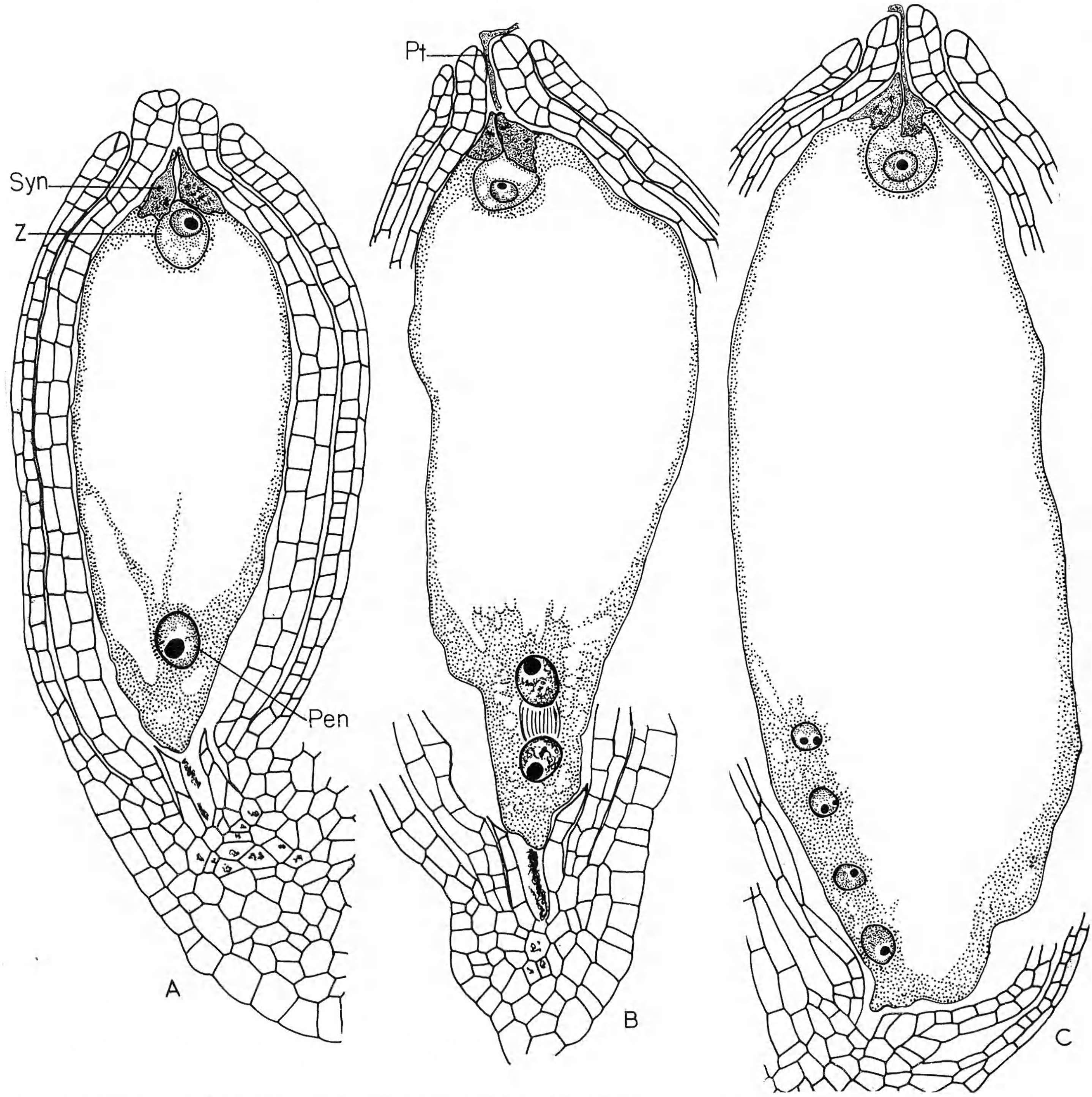

Fig. 4. Endosperm in *Eriocaulon hookerianum*. — A: Fertilized embryo sac showing primary endosperm nucleus located at the chalazal end. — B: First free nuclear division of primary endosperm nucleus. — C: Embryo sac with 4 endosperm nuclei located at the chalazal end. × 560. — Pen Primary endosperm nucleus, Pt Pollen tube, Syn Synergid, Z Zygote.

integument is 2-layered. The cells of the inner layers of both integuments are shorter and more densely cytoplasmic than cells of the outer layers (Fig. 8 A). Marked changes occur in the cells of both layers of each of the integuments during post-fertilization stages. The inner tangential walls of the cells of the inner layers become very thick as the cells increase in length (Fig. 8 B–D). Meanwhile, the cells of the outer layers also elongate and appear to be very narrow but their walls do not thicken. The thickening on the inner tangential walls of the inner layer of the cells increases. Tannin-like substances accumulate in the cells of the inner layer of the inner integument while cells of the inner layer of the outer integument become conspicuously vacuolate and

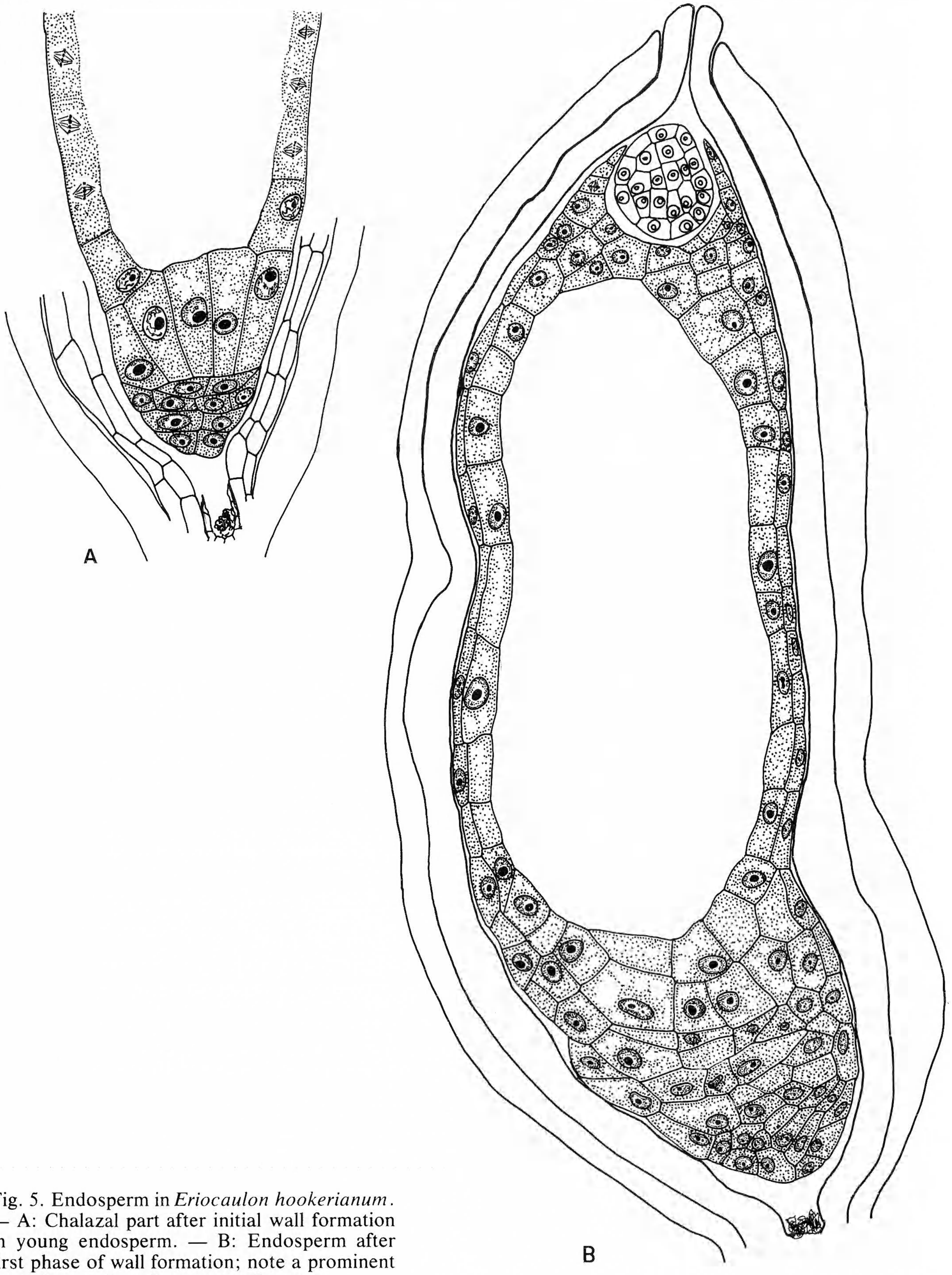

Fig. 5. Endosperm in *Eriocaulon hookerianum*. — A: Chalazal part after initial wall formation in young endosperm. — B: Endosperm after first phase of wall formation; note a prominent central vacuole and presence of greater amount of endosperm tissue at the chalazal end. — × 560.

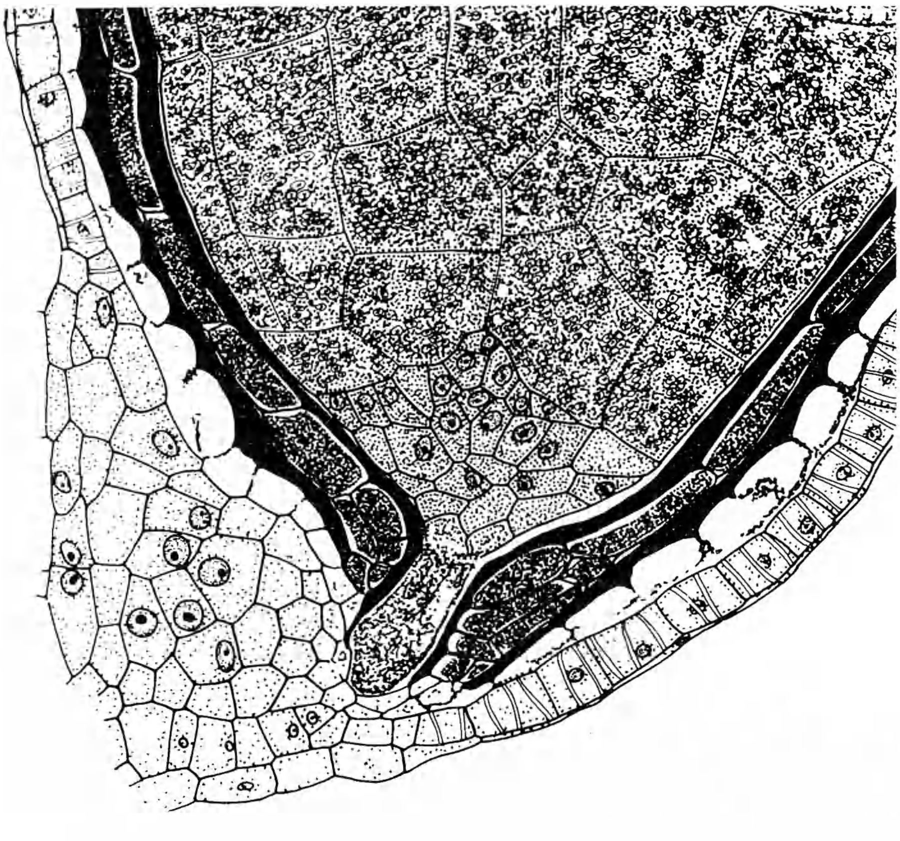

Fig. 6. Chalazal half of a l.s. of seed to show structural details of endosperm tissue. × 560.

increase in size. As the seed ripens and its endosperm increases in volume the outer layers of the two integuments as well as the inner layer of the outer integument become crushed (Fig. 8 E, F). Finally the seedcoat consists of the tannin-containing inner layer of the cells of the inner integument and the remains of the other layers of the cells in addition to the extremely thick inner tangential wall of the inner layer of the outer integument (Fig. 8 F).

The ovarian wall is made up of 2 or 3 layers of elongated cells (Fig. 8 A). During the post-fertilization stages the middle layer, if present, becomes crushed. The cells of the inner layer increase in size and the cells of the outer layer elongate further and appear to be narrow. As the pericarp gets older, prominent band-like thickenings develop on the inner side of the tangential walls belonging to cells of the inner layer. This layer helps in the dehiscence of the capsule (Fig. 8 C–F).

Discussion

In all the species of *Eriocaulon* investigated so far, the structure of the microsporangium and the development of the male gametophyte are essentially similar. A cross section of a very young anther is invariably 4-lobed and each lobe contains the hypodermal archesporium. Nevertheless, the occurrence of two rows of archesporial cells is recorded in *E. cinereum* (Patel & Patel 1964). The presence of the two-rowed archesporium could be considered as a primitive feature and the single-rowed condition derived from simplification. The periclinal division of the

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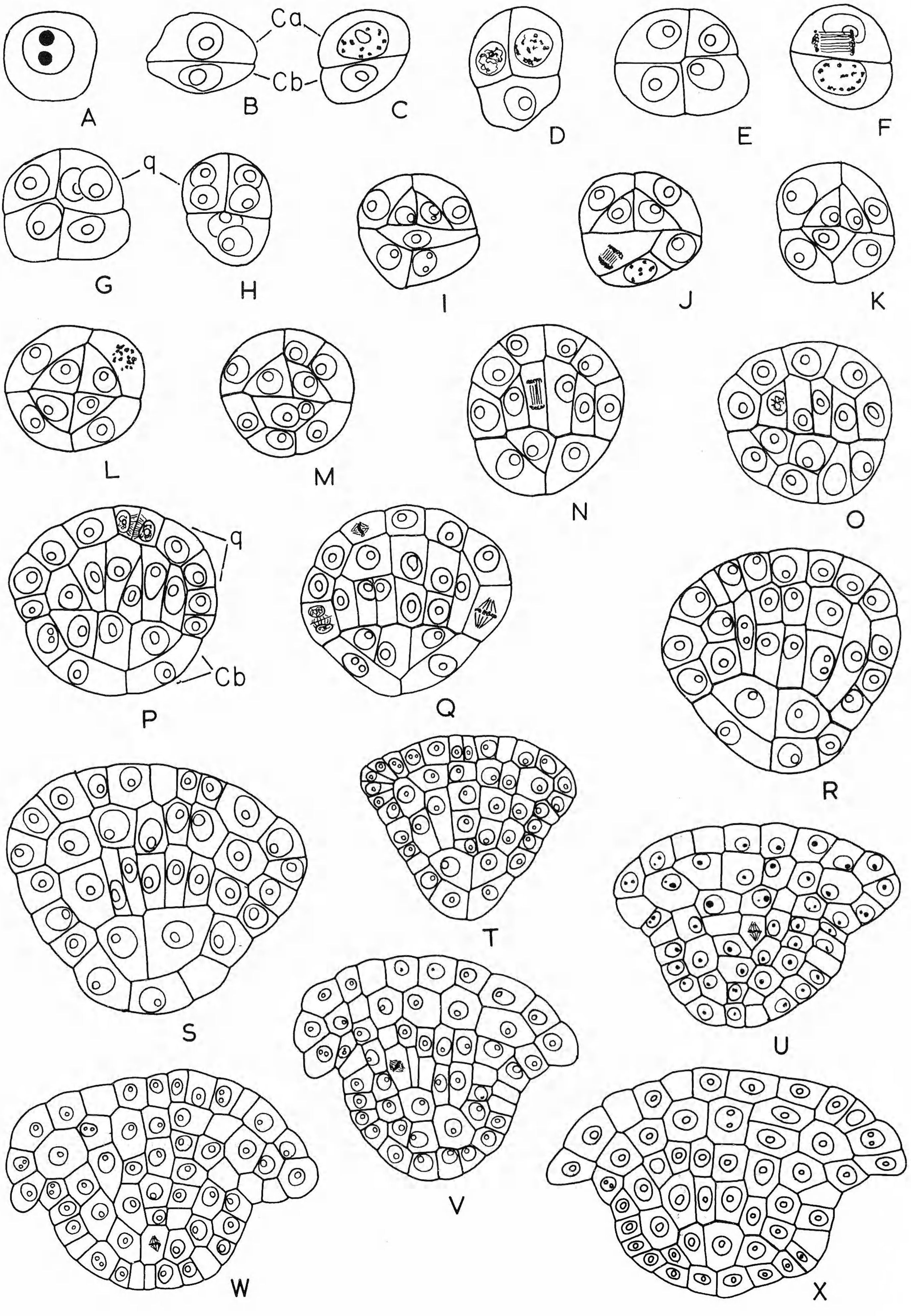
Fig. 7. Development of embryo in *Eriocaulon hookerianum*. — A: Zygote. — B, C: 2-celled proembryos with apical and basal cells. — D: 3-celled proembryo. — E: First proembryonal tetrad. — F–H: Stages in the organization of quadrant. — I–W: Subsequent stages of embryo development. — X: Embryo from mature seed. — A–T: × 990. U–X: × 660. — Ca apical cell, Cb basal cell, q quadrant. (See p. 304.)

Fig. 8. Stages in the development of seedcoat and pericarp in *Eriocaulon hookerianum*. — A: Part of longitudinal section of an ovary at the 8-nucleate stage of the embryo sac to show the structure of integument and ovary wall layers. — B–E: Show changes in integument and ovary wall layers during post-fertilization stages. — F: Shows the structure of seed coat and pericarp at ripe stage. — A–D: × 920. E, F × 1020. — Ii inner integument, Oi outer integument, Ow. ovary wall. (See p. 305.)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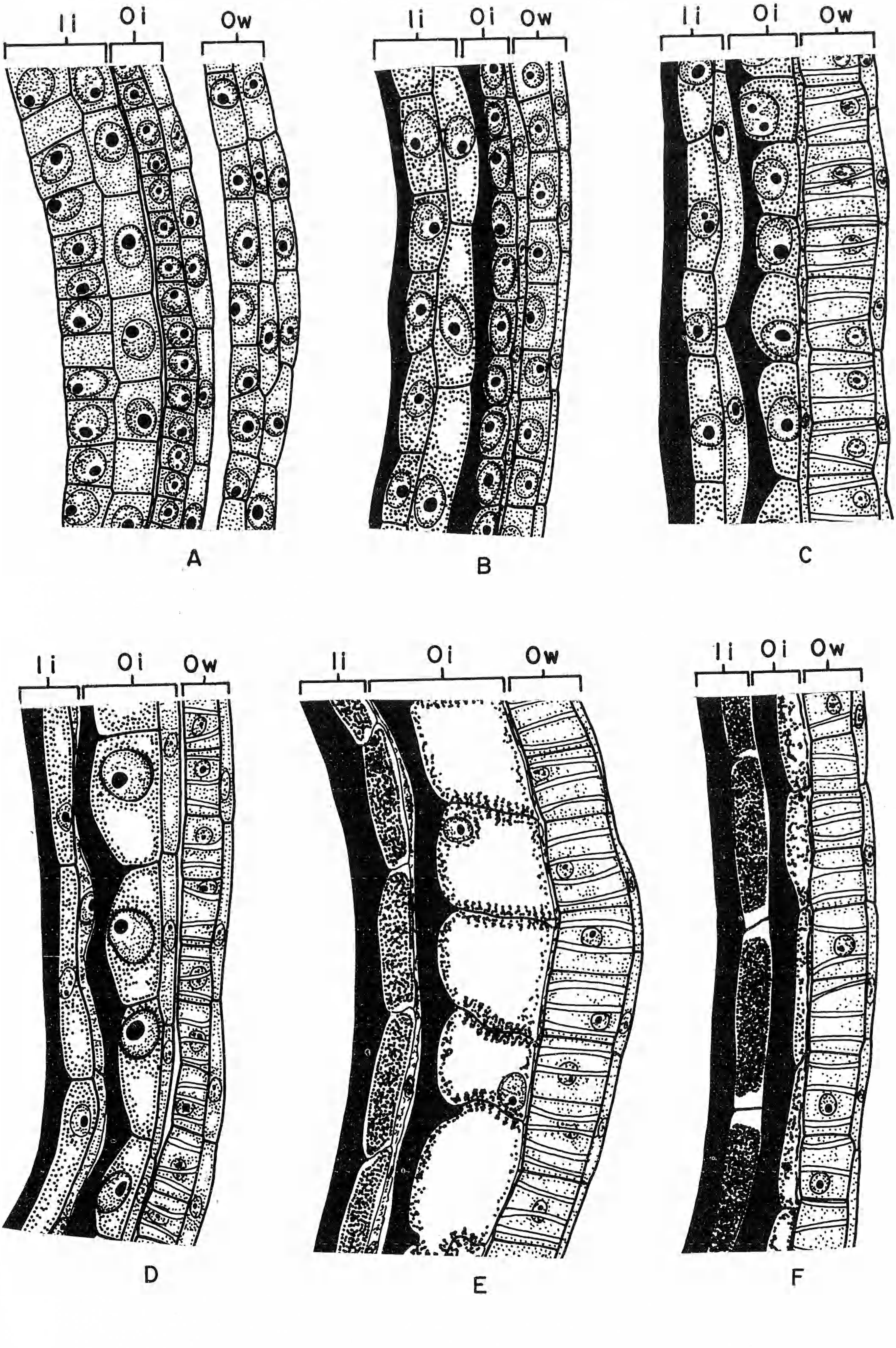
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archesporial cells engendering the primary perietal and primary sporogenous layers noted in *E. cinereum* (Patel & Patel 1964) and *E. quinquangulare* (Begum 1966) has also been observed in the present study. The subsequent development of the microsporangium wall in *E. hookerianum* follows the typical Monocotyledonous type (Davis 1966), in which the middle and tapetal layers are sisters. Although Smith (1910) and Begum (1966, 1968) did not follow the developmental sequence of the microsporangium wall in *E. septangulare* and *E. quinquangulare*, respectively, Patel & Patel (1964), contrary to the present observation, have described a Dicotyledonous type (Davis 1966) of the wall development in *E. cinereum*. However, Figs. 8 and 9 cited in support of their conclusion (Patel & Patel 1964) do not show the critical divisional stages of cells in the microsporangium wall. A careful reinvestigation of *E. cinereum* would probably reveal the Monocot type of wall development in that taxon as well.

The consistent occurrence of uninucleate cells in the glandular tapetum such as noted in *E. hookerianum* has also been recorded for *E. septangulare* (Smith 1910) and *E. cinereum* (Patel & Patel 1964). On the other hand, Begum (1966, 1968) recorded the organization of binucleate cells in the tapetum of *E. quinquangulare*. A reinvestigation of the same (Ramaswamy 1975), however, has revealed the absence of nuclear division and consequently the tapetal cells remain uninucleate throughout.

The microspore mother cells undergo the usual successive type of meiotic divisions and produce the isobilateral microspore tetrads. Nevertheless, the occasional production of decussate microspore tetrads has been noted in *E. quinquangulare* (Begum 1968). The account of simultaneous quadripartition of microspore mother cells given for Eriocaulaceae by Davis (1966) appears to be an oversight, as no worker has so far reported its occurrence in any member of the family.

The pollen grains of the present study are spherical and 3-celled at shedding with a thin intine and a thick, finely-sculptured spiraperturate exine. Although a similar condition has been recorded in *E. septangulare* (Smith 1910) and *E. cinereum* (Patel & Patel 1964), Begum (1968) reported the occurrence of triporate pollen in *E. quinquangulare*. Thanikaimoni (1965) and Sharma (1965) who independently examined the pollen of *E. quinquangulare*, however, noted a spiraperturate grain in the species. This feature was confirmed in the reinvestigation of the taxon (Ramaswamy 1975). The organization of a regular stomium in the anther wall between adjacent microsporangia, before the pollen release, and the subsequent discharge of pollen of both sporangia through a common opening observed in *E. hookerianum* has also been noted in *E. quinquangulare* (Begum 1968).

The organization of a hypodermal archesporial cell and its direct development into a megaspore mother cell in the ovular primordium such as noted in the present taxon, has also been reported in other investigated species of the family. As in *E. septangulare* (Smith 1910), *E. cinereum* (Patel & Patel 1964) and *E. quinquangulare* (Begum 1968), after normal meiotic divisions, both linear and obliquely T-shaped megaspore tetrads are formed in *E. hookerianum*. Though normally the lowermost megaspore of the tetrad is functional in *E. hookerianum*, as in other species of the family studied (Smith 1910, Patel & Patel 1964, Begum 1966, 1968), two megaspores of a tetrad rarely show signs of further development. The occasional functioning of all the megaspores of a tetral reported in *E. septangulare* by Smith (1910) appears to be a misinterpretation. A critical perusal of his (Smith 1910) Fig. 12 reveals that it does not represent ''germination of all the 4 megaspores'' but actually refers to an organised 8-nucleate embryo sac. His report concerning the presence of 5–6 nuclei belonging to sterile megaspores in Fig. 13, also appears to be a misinterpretation.

The mode of embryo sac development in the present study conforms to the Polygonum type (Maheshwari 1950 b), as in other investigated species of *Eriocaulon* (Smith 1910, Patel & Patel 1964, Begum 1966, 1968).

The antipodal cyst. The most noteworthy feature of the embryo sac of *E. hookerianum*, probably peculiar to Eriocaulaceae, is the behaviour of the antipodal cells. The disorganization of the walls of the antipodal cells and the subsequent fusion of the three uninucleate protoplasts to organize an extremely conspicuous antipodal cyst such as noted in the present study, has also been noted in 8 other species of *Eriocaulon* and two more of Brazilian taxa, viz. *Paepalanthus bifidus* and

Syngonanthus nitens (Ramaswamy 1975). However, according to Smith (1910), the antipodal cells are very inconspicuous in *E. septangulare*. But a reassessment of Smith's (1910) diagrams 12, 13 and 14 clearly reveals the organization of an antipodal cyst which has been overlooked. Furthermore, in all three of his (Smith 1910) illustrations the egg apparatus has been mislabelled as the nucellus while he referred to the antipodal region in Fig. 12 as "germinating megaspores". It is surprising how Smith (1910) was led to labelling this stage as the "germination of megaspores" although the egg apparatus can be seen in the micropylar side and the two polar nuclei in the centre of the embryo sac. It is quite possible that he (Smith 1910) missed the earlier stages of the embryo sac development including the organization of the antipodal cells. This is also true for the studies on *E. cinereum* by Patel & Patel (1964). Their Figs. 39–40 show the degenerating antipodal cyst in which they have tried to discern imaginary superposed antipodal cells. Begum (1968) who reported three conspicuous superposed antipodal cells in *E. quinquangulare* mentioned their subsequent fusion. It is strange to note that she (Begum 1968) showed 3 antipodal cells arranged in a vertical row in an embryo sac in which the polar nuclei have already fused forming the seccondary nucleus (cf. Fig. 20), while the fusion of antipodal cells has been depicted in an embryo sac in which the polar nuclei have not yet fused (cf. Fig. 21). In the light of the present study, it could be pointed out that transverse walls shown between the nuclei depicting the superposed antipodal cells (cf. Fig. 21) could also be imaginary, as at that stage of the embryo sac the antipodal cyst begins to degenerate. Apparently, Begum (1986) has not noted stages of the early organization of the 8-nucleate embryo sac. A similar existence of superposed antipodal cells has been depicted by Swamy & Krishnamurthy (1970) in *E. sexangulare*.

The secondary nucleus in the mature embryo sac is always located at the chalazal end in *Eriocaulon hookerianum*, a feature which has also been observed in the other investigated Eriocaulaceae (Smith 1910, Patel & Patel 1964, Begum 1968).

The existence of an endothelium in the ovules of *E. quinquangulare* has been recorded by Begum (1966, 1968). The investigations of Swamy & Krishnamurthy (1970) regarding a species of *Eriocaulon* have shown that an endothelium similar in histology and function such as seen in the dicots does not exist in Eriocaulaceae. The present study supports the results of Swamy & Krishnamurthy (1970).

The endosperm in the present species is *ab initio* nuclear as in the other taxa examined in the family (Smith 1910, Patel & Patel 1964, Begum 1968). Accumulation of a large number of nuclei in the chalazal part during the development of the endosperm noted in the present study has also been observed in *E. quinquangulare* (Begum 1968). However, a uniform distribution of endosperm nuclei in the peripheral part of embryo sac is recorded in *E. cinereum* (Patel & Patel 1964).

In *E. hookerianum*, cell wall formation in the developing endosperm starts from the chalazal end and gradually extends to the micropylar part. Its subsequent centripetal growth ultimately replaces the central vacuole. In *E. septangulare* (Smith 1910) wall formation starts from both the chalazal and micropylar ends.

The fully developed endosperm in the present study forms three distinct regions, a feature that has also been noted by Smith (1910) in *E. septangulare*.

The first division of the zygote is transverse and the proembryonal tetrad is of the A_1 category (Souèges 1948) in all the investigated Eriocaulaceae (Smith 1910, Patel & Patel 1964, Begum 1968). The elimination of a typical octant stage before the production of dermatogen in the developing embryo such as noted in *E. hookerianum* is also recorded in the other investigated Eriocaulaceae. The tardy segmentation of cells in the lower region of the developing embryo recorded in the present study is similar to the condition observed in *Eriocaulon septangulare* (Smith 1910). Although the early sequence of divisions follow the Penaea variation of the Asterad type (Johanson 1950) in *E. hookerianum*, the embryo of a ripe seed is bell-shaped and undifferentiated. The cells belonging to deflexed flaring edges shown in the embryos of ripe seeds of *E. cinereum* (Patel & Patel 1964), *E. quinquangulare* (Begum 1968) actually belong to the persistent endosperm tissue around the embryo. This has been established by critical studies of embryos in a number of species of *Eriocaulon* (Ramaswamy 1975).

Each of the two integuments is two-layered in

E. hookerianum as in the other investigated species (Patel & Patel 1964, Begum 1968, Swamy & Krishnamurthy 1970). Both integuments contribute to the seedcoat, but the principal contribution is by the inner layers of the two integuments. Marked histological changes take place in the cells of these layers during the development of the seedcoat. They elongate along their vertical axes and their inner tangential walls become very thick. Contrary to the present observations in *E. quinquangulare* Begum (1968) has reported the lignification of outer tangential walls of cells of the outer layer of the inner integument. A reinvestigation of the same (Ramaswamy 1975) has revealed a type of thickening such as the one noted in *E. hookerianum*.

The middle layer of the fruit wall becomes crushed during the development of the fruit wall. The cells of the inner layer increase in size and develop band-like thickenings on the inner side of their tangential walls which help in the dehiscence of the fruit, a feature also recorded for *Eriocaulon quinquangulare* (Begum 1968).

Systematic position of the family

As far as the systematic position of Eriocaulaceae is concerned, the arrangement of Cronquist (1968) appears to be more appropriate. The present embryological studies support Cronquist (1968), in elevating the family to a separate order as it is one of the most evolved families under Commelinideae in having the highly derived pseudanthial involucrate heads pollinated by insects. Thier morphological individuality and distinctiveness are also apparent in their embryology, especially in their 3-celled spiraperturate pollen, tenuinucellate ovules, a micropyle organized by the inner integument alone, the organization of a unique antipodal cyst in the embryo sac, and a nuclear endosperm associated with the chalazal location of the primary endosperm nucleus. Nowhere else in the Commelinideae do we find these embryological features (Davis 1966). The family Eriocaulaceae, therefore, deserves to be placed under a separate order under Commelinideae. It appears to be related to Xyridaceae which in turn is perhaps related to the Commelinaceae.

However, so far, the embryology of only a few genera of Commelinaceae, of only one genus in Xyridaceae (Davis 1966) and of three genera of Eriocaulaceae (Ramaswamy 1975) has been worked out. Amongst the Englerian Farinosae which comprise more than 5,000 species distributed in about 180 genera, embryological information is available on 25 genera only (Davis 1966), and often only for a single species in each genus (see also Hamann 1964). Therefore, a better and firmer foundation for the phylogeny and systematic position of Eriocaulaceae can be laid down only after a detailed study of the embryology of many more taxa of Eriocaulaceae, Xyridaceae and Commelinaceae in particular and the related Farinosae in general.

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Floral anatomy of Nelsonieae (Acanthaceae) with a note on its taxonomic status

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The floral anatomy of *Elytraria crenata* Vahl. and *Nelsonia campestris* R. Br. has been studied. The flower is tetracyclic and pentamerous except the gynoecium. The bract is 3-traced. The bracteoles in *E. crenata* are 1-traced, while in *N. campestris*, the bracteoles and their traces have suffered complete reduction. Anatomy shows that the calyx in *N. campestris* is basically pentamerous though there are only four sepals externally. The sepals are 3-traced. The petals are single traced. In *E. crenata* the free limbs of the anterior corolla lobe fuse by their margins resulting in the formation of three successive tubes. The androecium in *E. crenata* consists of two anterolateral epipetalous stamens and three filiform staminodes, while in *N. campestris* two epipetalous fertile stamens are posterolateral in position and the staminodes are absent. The stamens are 1-traced. The carpels are 7-traced in *E. crenata* and 3-traced in *N. campestris*. Judging from the position of the ventral bundles, the placentation is described as parietal. A residual stele is noticed in *E. crenata*. It is tentatively suggested that Nelsonieae be retained in Acanthaceae.

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The Acanthaceae have received considerable attention from the point of floral anatomy (Rao 1953, De 1967, Dutta & Maithi 1969). But the tribe Nelsoniae of doubtful systematic position remains uninvestigated from this angle. The present study on the floral anatomy of *Elytraria crenata* and *Nelsonia campestris* has been undertaken to see how far the data from floral anatomy together with the data from other disciplines could help in assessing the systematic position of these taxa.

Material and methods

Flower buds of different sizes and small bits of inflorescences of *Elytraria crenata* Vahl. and *Nelsonia campestris* R. Br. were fixed in F.A.A. and processed following the standard procedures of dehydration, infiltration and embedding. Sections cut at a thickness of 8–12 μm were stained with crystal violet, using erythrosin as counter stain.

Observations

Flower

The flower is bracteate, tetracyclic, zygomorphic, heterochlamydeous, bisexual and hypogynous (Figs. 1 A, 2 A). It is bracteolate in *E. crenata* and ebracteolate in *N. campestris*. The pentamerous calyx, with unequal sepals is basally connate and the free limbs show quincuncial aestivation in *E. crenata* (Fig. 1 H–N). The calyx is tetramerous with basal connation in *N. campestris*. It exhibits imbricate aestivation (Fig. 2 E–G). The free limbs of the bilabiate corolla in both the taxa show inbricate aestivation (Figs. 1 R, S, 2 N, O). The androecium consists of three epipetalous filiform staminodes and two fertile anterolateral stamens in *E. crenata* (Fig. 1 Q) and only two epipetalous postero-lateral fertile stamens in *N. campestris* (Fig. 2 L–N). The bicarpellary syncarpous ovary is bilocular at the base and unilocular from the ovule-bearing region upwards (Figs. 1 N, O, 2 H–K). The style is single, solid and terminates in a bilobed stigma (Figs. 1 A, 2 A).

Floral anatomy

The peduncle shows a ring of vascular tissue. It extends in the direction of origin of the bract. An arc-like portion from the distal extended part of the stele becomes separated and this constitutes the bract supply (Figs. 1 C, 2 B). It soon trifurcates into one median and two lateral traces (Fig. 1 D). Further division of these bundles takes place after their entry into the bract (Figs. 1 E, F, 2 C). The outer epidermal cells of the bract in *E. crenata* are radially elongated with greatly thickened walls and narrow lumena (Fig. 1 B). In both the taxa after the demarcation of the bract supply, the extended stele becomes constricted proximally from the stele of the peduncle resulting in two arcs of vascular tissue which unite to form a ring of vascular tissue and this constitutes the stele of the pedicel. In *E. crenata* at about the level of separation of the bract, two bracteole traces are organized from the stele of the pedicel (Fig. 1 E), while in *N. campestris* the bracteoles as well as their vascular supply are completely suppressed.

The ring-like stele expands in the thalamus, where five sepal traces are organized (Figs. 1 F, 2 C). In *E. crenata* each sepal trace divides into a median and two lateral branches in the receptacular cortex itself (Fig. 1 G). Deep staining cells are noticed at the junction of sepal margins. These glandular cells continue along the margins for some height after the separation of the limbs (Fig. 1 J–L). In *N. campestris* five sepal traces are organized (Fig. 2 C), though externally there are only four sepals (Fig. 2 E–G). The "anterior sepal" receives two traces while the other three receive one each (Fig. 2 D–G). The lateral traces arise conjointly with the midrib (Fig. 2 D).

In *E. crenata* after the organization of the sepal supply the main stele closes to form a ring of vascular tissue from which traces for the five petals, three staminodes along the posterior sector of the flower and two fertile stamens along the anterior sector are demarcated in close succession (Fig. 1 H, I), and all the ten traces enter the base of the corolla tube (Fig. 1 J–O). The bundles of the fertile stamens are more prominent and staminodal bundles are weaker (Fig. 1 O). The latter extend only half-way into the staminodal filaments and terminate blindly in them (Fig. 1 P, Q). In *N. campestris*, the sepal traces are followed by five petal traces and two traces for the two fertile posterolateral stamens (Fig. 2 E) and all the seven traces enter the corolla tube (Fig. 2 F).

While the bundles of the perianth divide to form smaller bundles, the staminal and staminodal bundles remain undivided (Figs. 1 P–V, 2 E–O).

A little above the separation of fertile stamens, the two lobes of the bilabiate corolla become free. In both taxa the vasculature shows that the upper lobe is a composite structure of two petals and the lower lobe is composed of three petals (Figs. 1 R, 2 N). In *E. crenata* a little above this level, there appear in the inner and outer sides of one antero-lateral petal and on the inner side of the second antero-lateral petal, small flattened filaments traversed by small vascular bundles (Fig. 1 T). The free limbs of the anterior petals fuse by their margins gradually at higher levels (Fig. 1 U). As a consequence of this three successive "tubes" are formed; the innermost formed by the fusion of the margins of the anterior petal and the two successive outer ones by the fusion of the margins of the antero-lateral petals (Fig. 1 V). It is the uneven lower ends of these three "tubes" that are cut transversely at lower levels appearing as flattened filaments.

After the organization of perianth and androecial supply the stele is in the form of a ring of vascular tissue (Figs. 1 J, 2 F). In *E. crenata* it breaks into two median bundles which function as the dorsal bundles and two lateral bands of vascular tissue (Fig. 1 K). Each lateral band of vascular tissue divides into a median and two lateral bundles (Fig. 1 L); the latter function as median lateral bundles, while the median bundle divides tangentially demarcating a common median lateral bundle to the exterior and common ventral bundle towards the centre (Fig. 1 M, N). The common median lateral bundles give off branches into the wall of the ovary (Fig. 1 M, N). In *N. campestris* from the ring of vascular tissue a pair of dorsal carpellary traces and a pair of common ventral traces are organized and the remaining stele expands and emerges out in the form of a number of traces which supply the wall of the ovary (Fig. 2 F–H).

The ovary is bilocular below and the common

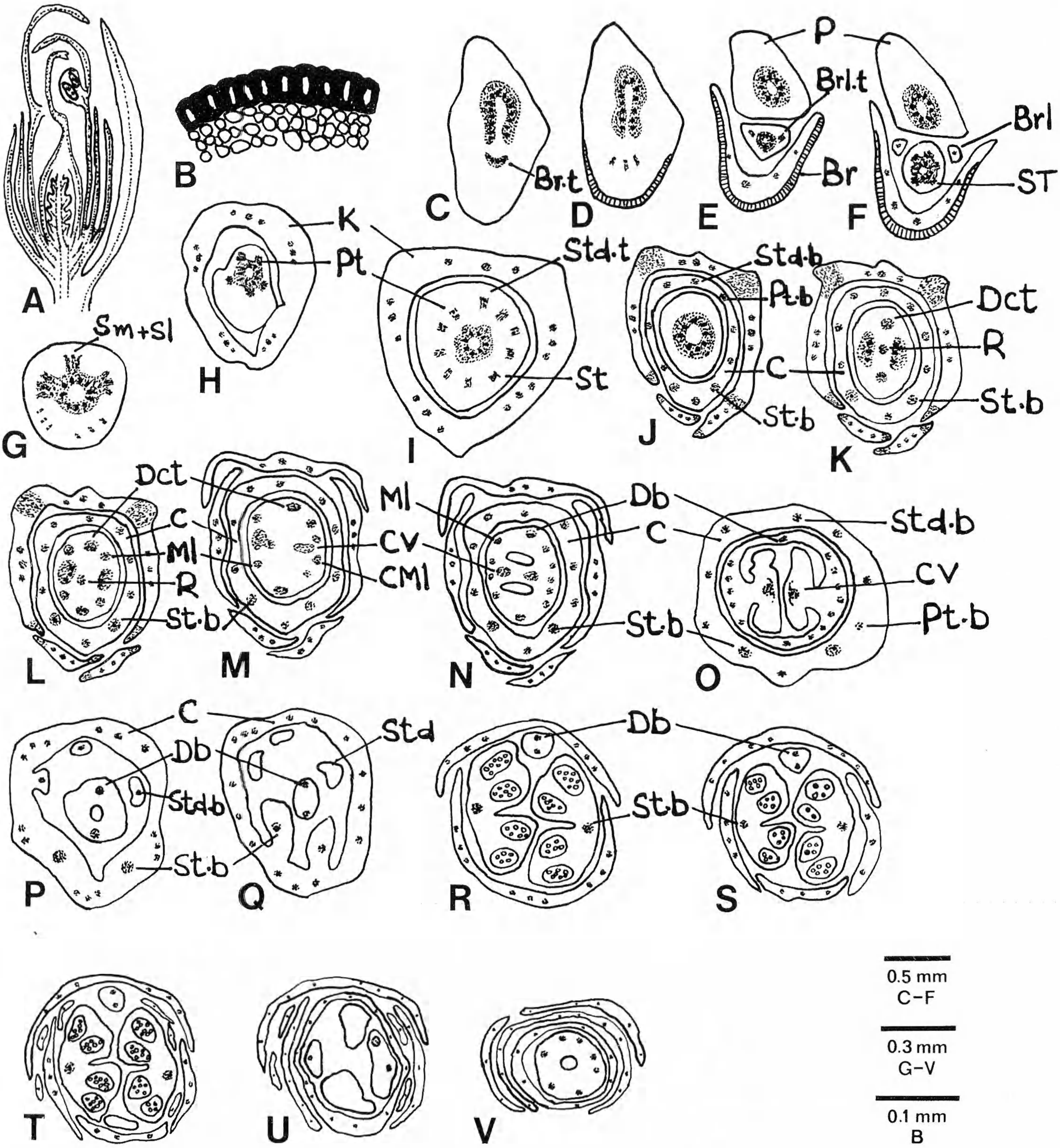

Fig. 1. *Elytraria crenata*. — A: Diagrammatic longitudinal section of flower showing the course of vascular bundles in different floral parts. — B: Transverse section of bract showing the outer epidermal cells radially elongated with greatly thickened walls and narrow lumina. — C–V: Serial transverse sections of flower showing the origin and distribution of traces to the different floral parts. — Abbreviations in Figs. 1 and 2: Br Bract, Brl Bracteole, Brl.t Bracteole trace, Br.t Bract trace, C Corolla tube, CMl Common Median lateral, CV Common Ventral, Db Dorsal bundle, Dct Dorsal carpellary trace, K Calyx tube, Ml Median lateral, P Peduncle, Pt Petal trace, Pt.b Petal bundle, R Residual stele, Sl Sepal lateral trace, Sm Sepal median trace, Sm+Sl Sepal median trace + Sepal lateral trace, ST Sepal trace, St Staminal trace, St.b Staminal bundle, Std. Staminode, Std.b Staminodal bundle, Std.t Staminodal trace, Wb Wall bundle.

ventral bundles lie in the septum (Figs. 1 N, 2 I, J), which breaks down in the middle making the ovary unilocular in the ovule bearing region (Figs. 1 O, 2 K). The common ventral bundles are completely utilized in the ovular supply. The solid style is vascularized by the dorsal bundles alone (Figs. 1 Q–T, 2 M), while other bundles traversing the ovary wall terminate towards the apex of the ovary.

In *E. crenata* after the organization of the carpellary supply, a small amount of receptacular vascular tissue is left over as the residual stele (Fig. 1 K, L).

Discussion

A study of the floral anatomy of *Elytraria crenata* and *Nelsonia campestris* shows that the Nelsonieae is not basically different from the rest of the tribes of Acanthaceae in floral anatomical characters.

The tetracyclic flower is basically pentamerous except the gynoecium with a tendency towards reduction in the number of parts of calyx, corolla and androecium through fusion or suppression.

In both the taxa the bracts subtending the flowers are 3-traced, the lateral traces arising conjointly with the midrib and these three bundled traces arise from a single gap. The bracteoles in *E. crenata* are 1-traced presumably due to suppression of lateral traces. However, according to Johri & Singh (1959) the bracts as well as bracteoles are 3-traced in *E. acaulis*. In *N. campestris* there is not only external suppression of bracteoles but also their vasculature. It may be pointed out that according to De (1967) the bracts and bracteoles in Acanthaceae are generally single traced, except in *Gendarussa vulgaris* Nees, *Strobilanthus glomeratus* Nees and *Crossandra infundibuliformis* (L) Nees, where a 3-traced condition is present. Rao (1953) in his study on the floral anatomy of Acanthaceae involving all the tribes, except Nelsonieae, did not mention bract and bracteole supply.

The calyx in Acanthaceae is basically pentamerous and shows quincuncial or imbricate aestivation (Rao 1953, De 1967, present study). In *E. crenata* it is described as four-partite by Gamble (1967) and Cooke (1967). But the present study clearly shows that in the calyx of this taxon all the five sepals are present. Therefore, the statements of Gamble (1967) and Cooke (1967) need revision. Pentamerous condition of calyx were reported by Rao (1953) and De (1967) in some of the taxa studied by them. Another unrecorded feature of interest about the calyx of *E. crenata* is the presence of localized glandular cells along the radii of the fused sepal margins and these continue along the margins for some height even after the separation of the limbs. A tendency towards reduction in the number of sepals through fusion of parts is noticed in this family (Rao 1953, present study). In *N. campestris* (present study) the calyx shows only four parts; one posterior, one anterior and two lateral. A similar condition was reported in a few taxa of Acanthaceae by Rao (1953).

The sepals in *E. crenata* and *N. campestris* (present study) as in many taxa of angiosperms are 3-traced. Two types of connation of sepal traces is noticed in the Acanthaceae. The lateral traces of sepals arise conjointly with sepal medians as in *E. crenata, N. campestris* (present study) *Sanchezia nobilis* Hook. fil., *Eranthemum capense* Linn., *E. roseum* (Vahl) R. Br., *E. nervosum* (Vahl) R. Br. and *Rungia parviflora* Nees var. *pectinata* C. B. Clarke (Rao 1953). In the second type the lateral traces of adjacent sepals arise conjointly (Rao 1953, De 1967, Dutta & Maithi 1969).

There is a reduction in the number of sepals to four as in *N. campestris* (present study) and certain other taxa of Acanthaceae (Rao 1953, De 1967). In such cases one of the four sepals, generally the anterior receives two traces indicating that it is a composite structure formed by fusion two antero-lateral sepals. Thus the reduction is due to fusion and not due to suppression.

The corolla in *E. crenata* and *N. campestris* is zygomorphic, gamopetalous and 2-lipped and the limbs show imbricate aestivation. The petals are 1-traced and the traces arise in one whorl.

The behaviour of the lobes of the anterior corolla segment in *E. crenata* is noteworthy. As a result of fusion of the margin of lobes, three lobes are formed. The innermost is formed by the anterior petal and the other two by two antero-lateral petals. No mention of this situation is made in the description of Gamble (1967) and Cooke (1967). Thus *E. crenata* stands distinct from *N. campestris* (present study) and other investigated taxa of Acanthaceae (Rao 1953, De 1967, Dutta & Maithi 1969).

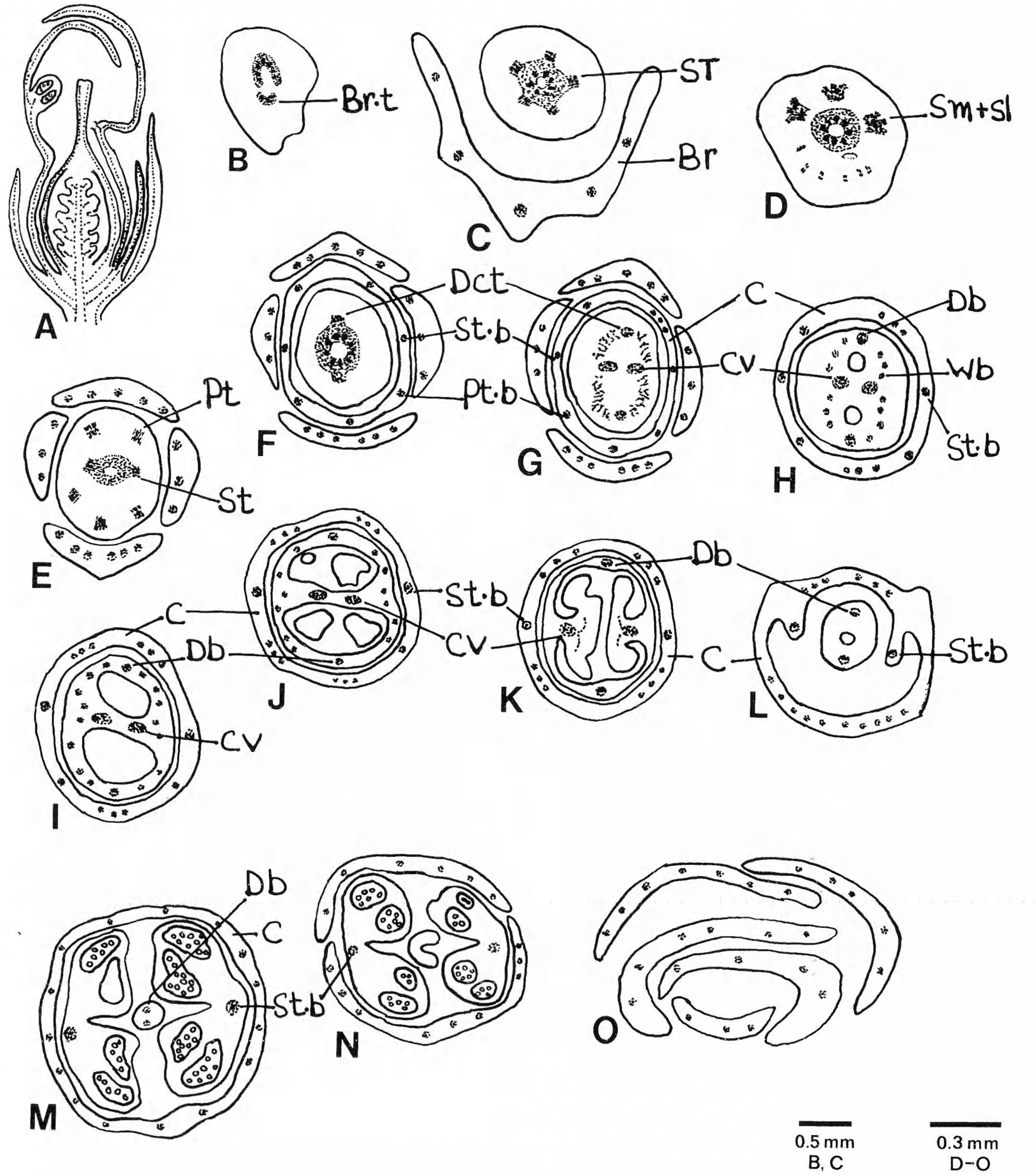

Fig. 2. *Nelsonia campestris*. — A: Diagrammatic longitudinal section of flower showing the course of vascular bundles in different floral parts. — B–O: Serial transverse sections of flower showing the origin and distribution of traces to the different floral parts. — Abbreviations see Fig. 1.

The androecium is basically pentamerous with reduction of stamens to two in *E. crenata*, *N. campestris* (present study) and a few others (Rao 1953, De 1967). The fertile stamens are antero-lateral in *E. crenata* and postero-lateral in *N. campestris*. The stamens are 1-traced. A trend towards elimination of staminodes and their vascular supply is noticed in different taxa of the family. In *Thunbergia, Blepharis,* and *Crossandra* (Rao 1953) there are four fertile stamens and one staminode, and the solitary staminode ratains the vascular supply. In *E. crenata* (present study) the three staminodes in the posterior sector of the flower show feebly developed vascular supply extending only half-way. In *Sanchezia nobilis* though a staminode is present externally its vascular supply has suffered complete reduction (Rao 1953). In *N. campestris* (present study) there is no external or anatomical evidence for suppressed staminodes.

E. crenata and *N. campestris* differ from the rest of the taxa of Acanthaceae in the absence of a hypogynous nectariferous disc.

The gynoecium in Acanthaceae is uniformly bicarpellary syncarpous (Rao 1953, De 1967, Dutta & Maithi 1969, present study). The carpels are 3-traced in *N. campestris* (present study), *Andrographis paniculata* (Burm.) Wall ex Nees, *Ecbolium linneanum* Kurz (Dutta & Maithi 1969), *Eranthemum capense* and *E. roseum* (Rao 1953). *Elytraria crenata* stands apart from others regarding the 7-traced condition of the carpels. Judging from the position of the common ventral bundles the placentation in the light of Puri's (1952) view can be interpreted as parietal. In the vascularization of the style by dorsal bundles *E. crenata* and *N. campestris* resemble the taxa studied by Rao (1953).

A residual stele is present in *E. crenata* and this supports the classical view of the carpel. So far this is the only record in this family.

The systematic position of Nelsonieae is controversial. It was kept in Acanthaceae by Bentham & Hooker (1862–1883), Lindau (1895) and Leonard (1951). Bremekamp (1953) after a careful study of Acanthaceae and related families, arrived at the conclusion that Acanthaceae is a heterogenous group and transferred Nelsonieae to the vicinity of Rhinantheae of Scrophulariaceae on the basis of endospermic seeds, placentation and dehiscence of fruit.

Johri & Singh (1959) on the basis of their study on the embryology of *Elytraria acaulis* favoured its retention in Acanthaceae. Mohan Ram (1960), Mohan Ram & Masand (1962), Phatak & Ambegaokar (1961) pointed out that endospermic seeds are not exclusive to Nelsonioideae, but are also present in other acanthaceous taxa. Mohan Ram & Masand (1963 p. 90) observed: "It is thus obvious that Acanthaceae and Rhinantheae have a close resemblance in several important features. However, the asymmetrical growth of endosperm in Nelsonioideae in contrast to the symmetrical type in Rhinantheae is an exclusively acanthaceous feature. The presence of rudimentary and nonfunctional jaculator in *Elytraria* and *Nelsonia* and its absence in the Rhinanthaeae mark a strong point of difference." Bremekamp (1965) pointed out certain inaccuracies in the table given by Johri & Singh (1959) and claimed that their findings actually supported his own contention favouring the transfer of Nelsonieae to the vicinity of Rhinantheae. According to Mohan Ram & Wadhi (1965), the resemblances of Nelsonieae with Rhinantheae are due to parallel evolution and therefore do not indicate close relationship to keep them together. Foliar anatomical studies by Nafday (1965), Paliwal (1966, 1967, 1969) and Ahmad (1974, 1978) also do not support the transfer of Nelsonieae to Scrophulariaceae. Shashikumar & Paliwal (1975 p. 30) observed: "There is no doubt that the morphological characters of Nelsoniaea are in conformity to those of the other tribes of Acanthaceae and a single character of absence of hydathodes does not warrant its placement in the Rhinantheae". The present study on the floral anatomy also does not warrant such a transfer since Nelsonieae is not basically different from the other tribes of Acanthaceae in floral anatomical characters. As there is no information on the floral anatomy of Rhinantheae a comparison with Nelsonieae has not been possible. Bhaduri (1944) on palynological grounds favoured the retention of Nelsonieae in Acanthaceae though Raj (1961) and Chaubal (1966) on the same grounds supported Bremekamp (1953, 1965). Cytological evidence of Grant (1955) also does not support Bremekamp's (1953, 1965) view.

Thus the data from the present study and the available data from other disciplines like embryology, foliar anatomy, and cytology do not lend support to the transfer of Nelsonieae to Rhinantheae of Scrophulariaceae.

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A new species of Thecotheus (Pezizales) from the Western Himalayas

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Kaushal, S. C. 1980 09 18: A new species of Thecotheus (Pezizales) from the Western Himalayas. *Bot. Notiser 133:* 319–321. Stockholm. ISSN 0006-8195.

A new species, *Thecotheus himalayensis* Kaushal, is described. It is characterized by additional interascal elements in the hymenium and minutely warted ascospores. Anatomical features of *T. cinereus* (Cr. & Cr.) Chen., based on Indian collections are given. Ascospores of *T. pelletieri* (Cr. & Cr.) Boud. are found to be smaller than in American and Canadian collections.

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I agree with Korf (1972) in including *Thecotheus* Boud. in the tribe Iodophaneae of the family Ascobolaceae. In my opinion, the presence of amyloid asci, the simple excipular structure and small apothecia in *Thecotheus* point to its close relationship with Ascobolaceae and justify its inclusion in this family.

Three species, *T. himalayensis* Kaushal, *T. cinereus* (Cr. & Cr.) Chen. and *T. pelletieri* (Cr. & Cr.) Boud. were examined during the course of the present investigations.

T. cinereus was listed by Batra & Batra (1963) in their checklist of Indian Discomycetes as *Ascophanus holmskjoldii* Hans. The Indian collections of this species by Batra (PAN s.n.) and Waraitch (PAN 2094) contain clearly warted and prominently apiculate ascospores. According to Eckblad (1968), these collections should be treated under *Thecotheus holmskjoldii* (Hans.) Eckbl. As Brummelen (1967) found the spores of *T. cinereus* to be completely smooth, Eckblad (1968) accepted it as a species distinct from *T. holmskjoldii*. However, studies by Le Gal (1960, 1963) and Kimbrough (1969) amply indicate that *T. holmskjoldii* is conspecific with *A. cinereus*. This view is accepted in this work and the Indian collections are placed accordingly under *T. cinereus*.

Observations regarding anatomical features of the Indian collections of *T. cinercus* are added here (Fig. 1 A): ectal excipulum up to 85 μm thick, a textura angularis, cells up to 25 × 16μm, with their longitudinal axis somewhat perpendicular to the surface, outer few layers with smaller cells; medullary excipulum 100–125 μm thick, a textura globulosa-angularis, cells often hyphoid, up to 8 μm wide; hypothecium very much reduced, textura intricata.

T. pelletieri is a rare species in India. Two collections from the Western Himalayas (Batra s.n. and Waraitch 2166 at PAN) have greyish apothecia and smaller ascospores (28–32 × 14–17 μm) than those reported from the American and Canadian collections (32–40 × 20–24 μm) by Kimbrough (1969).

T. himalayensis was collected in the late autumn of 1971 and 1974. Usual fungal stain have been used to study the microfeatures in the field and in the laboratory. The collections are deposited at PAN.

Thecotheus himalayensis Kaushal sp. nov., Fig. 1 B–D

Holotypus: India, Dalhousie, Panjpula, in stercore caprarum, 28.8.1974, S. C. Kaushal 2625 (PAN). Paratypi: Dalhousie, Jandri Ghat, in stercore caprarum, 29.8.74, S. C. Kaushal 2632 (PAN) — Simla, Narkanda, 18.8.71, S. C. Kaushal 2412 (PAN).

Apothecia ad 2,5 mm diam., solitaria vel aggregata, sessilia vel brevistipitata, cupulata vel turbinata et raro

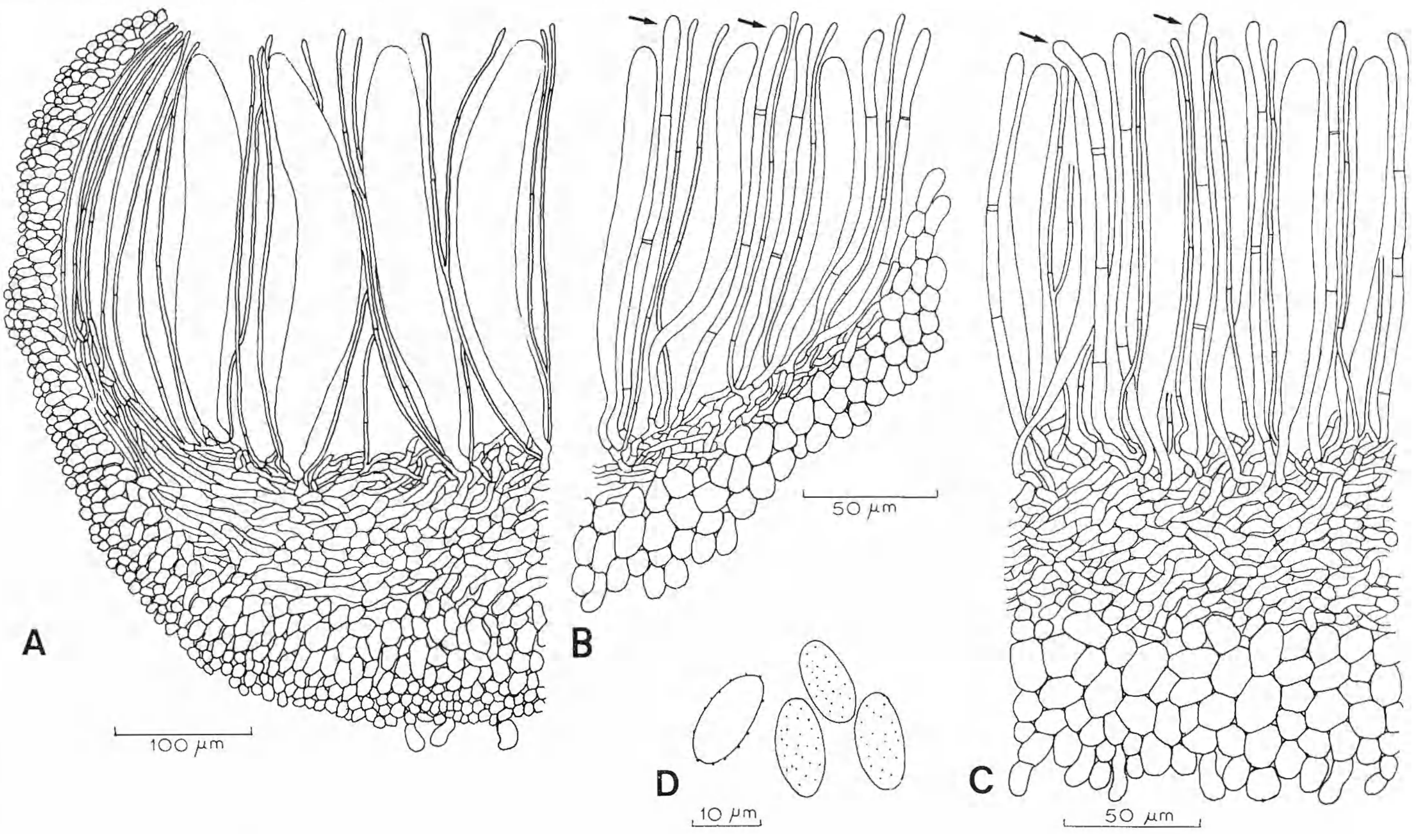

Fig. 1. A: *Thecotheus cinereus.* — B–D: *T. himalayensis.* — A, B: V.S. of the apothecium passing through its margin. — C: V.S. of the apothecium passing through its centre. — D: Ascospores. — Arrows in B and C show additional interascal elements.

conoidea, carnosa, alba, margine integro; hymenium album, asperum propter apices prominentes ascorum. Excipulum externum e textura angulari, ad 65 µm crassum, cellulis ad 24 × 17 µm, parum crassitunicatis; excipulum medullosum e textura intricata densa, ad 85 µm crassum, tenuis ad marginem, hyphis ad 6 µm latis; hypothecium indistinctum. Asci (120–)160–175(–186) × 11–14 µm, octospori, cylindrici, apice rotundo, longe stipitati, J +. Ascosporae 12,0–15,5 × 6–7 µm, uniseriatae, aliquando ad apicem congestae, ellipsoideae, subhyalinae, verruculosae. Paraphyses filiformes, septatae, ramosae, ± rectae, deorsum ad 1,5 µm crassae. Filamenta simplicia, robusta, ± recta vel sursum paullo curvata, subhyalina, ad 5 µm crassa ascis et paraphysibus immixta.

Apothecia up to 2.5 mm in diameter, gregarious, single to crowded (only 2–3 cups placed together), sessile or with a short thick stipe, shallow, cupulate to turbinate or rarely obconical, regular, fleshy; external surface white, smooth; margin entire; hymenium white, somewhat roughened by protruding ascal tips. Ectal excipulum a textura angularis, up to 65 µm thick, with cells up to 24 × 17 µm, usually more or less hyphoid at margin with clavate tips, slightly thick-walled; medullary excipulum a dense textura intricata, up to 85 µm thick in the middle, gradually reduced towards margin, with up to 6 µm broad hyphae; hypothecium indistinct. Asci (120–)160–175(–186) × 11–14 µm, 8-spored, cylindrical, apex rounded, base long and narrow, intensely J+ in fresh material (specially the young asci), slightly less in dry material. Ascospores 12.0–15.5 × 6–7 µm, uniseriate, sometimes a few spores crowded near apex, ellipsoid, subhyaline, verruculose. Paraphyses up to 1.5 µm wide below, very slightly enlarged above or not at all, thin-walled, filiform, septate, freely branched at various levels, straight or slightly bent. Interspersed between asci and paraphyses are additional interascal elements which are erect, paraphyses-like, up to 5 µm broad, slightly narrow below, subhyaline, simple, stout, septate (septa at irregular intervals), straight or slightly bent at top.

The additional interascal elements described for the present species are not known anywhere else in operculates except in *Iodophanus kimbroughii* Thind & Kaushal (Thind & Kaushal 1978). However, such elements have been reported amongst inoperculates for *Lambertella acuminata* and *L. phaeoparaphysata* by Dumont

(1971). *T. himalayensis* is distantly related to *T. apiculatus* Kimbr. but the latter has larger asci and ascospores with very conspicuous apiculi.

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Chlorophyll in embryos of angiosperm seeds, a review

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The occurrence of chlorophyll in embryos is known from 428 species of angiosperms (224 genera, 72 families); 1,094 species (666 genera and 182 families) have been investigated. Species of the same genus do not differ, and several families and even orders also seem homogeneous. A list of species investigated is presented. In investigations of the chlorophyll content in embryos several developmental stages must be investigated, as the chlorophyll sometimes disappears in the mature seed.

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The occurrence of green pigments in the embryo, and sometimes in the endosperm and seed coat of some angiosperms has been known since Hofmeister (1859). We have given an account of the phenomenon in a paper written in Russian (Yakovlev & Zhukova 1973). In the present paper we attempt to review the presence of chlorophyll in the embryo and its structural basis. A list of genera investigated up to now is included.

In our own investigations of this feature we have tried to include various stages of embryogenesis, as the chlorophyll in some taxa disappears when the seed matures. Such a species is considered to have chlorophyllous embryos, irrespective of whether it is present in mature seeds or during some developmental stages only; and also irrespective of whether it is present in the whole embryo or only in part of it.

Green pigments in seeds

Lubimenko (1906) discovered that the absorption spectra of green pigments from the embryo and the seed coat of some species of Cucurbitaceae were different. Later Monteverde & Lubimenko (1909) showed that there were no significant differences between leaf and embryo chlorophyll, but that the green pigments of the seed coat differed and were similar to the protochlorophyll of etiolated plants. The seed coat pigments did not, however, change into chlorophyll with increased light exposure. The presence of protochlorophyll in seed coat does not, however, seem to be universal in Cucurbitaceae, since Seybold (1948) failed to detect it in two species of *Trichosanthes,* although their seeds were examined at various stages of development; the seed coats contained chlorophyll a and b and (unidentified) carotenoids instead. Rothemund (1935) found protochlorophyll in the seed coat of *Cannabis* (Cannabinaceae).

Later, as the result of studies with the Mg test, chromatographic analysis and spectrophotometric analysis, it was shown that the seeds of some angiosperms contain chlorophyll rather than protochlorophyll (Kantor 1955, Toyoda 1959, 1961, Meeuse & Ott 1962, Negbi & Tamari 1964, Orsenigo 1964, Dovbish 1965, Ionesova 1968, Marin & Dengler 1972, Ryczkowski & Szewczyk 1972).

Zhukova (1963, 1965, 1967), using spectrophotometry of pigments isolated by paper chromatography of extracts of isolated embryos, investigated the green pigments of 9 species, viz. *Acer platanoides* L., *Alcea rosea* L., *Geranium ruprechtii* Woron. ex Grosch., *Iberis gibraltarica* L., *I. umbellata* DC., *Linum alpinum* (L.) Jacq., *Nelumbo nucifera* Gaertn., *Raphanus sativus* L. and *Vicia faba* L. The green pigments of the embryos proved to be chlorophylls a and b. Neither chromatographic nor spectrophotometric analysis indicated any differences from the leaf chlorophylls of these species. This is also valid for *Nelumbo,* and we cannot support Toyoda's (1959) view that seed chlorophylls seem to "differ slightly from those in the normal leaves, especially in *Nelumbo* and *Cucurbita*". Chlorophylls from embryos and leaves of *Nelumbo* have the same absorption maxima.

The chlorophyll in *Nelumbo nucifera* embryos is restricted to the plumule. The species has a woody pericarp and therefore the chlorophyll must be synthesized in darkness, a notable feature.

In 8 of the species the embryo invariably contained the following carotenoids: carotene, lutein, violaxantin, neoxantin and probably lutein-epoxide, viz. the same pigments as in the leaves. Again *Nelumbo nucifera* showed an unusual feature as the plumule did not contain carotene. The embryo of *N. lutea* also lacks carotene (Meeuse & Ott 1962).

Plastid structure

The ultrastructure of plastids in green embryos have been studied by Orsenigo (1964), Rezende-Pinto (1964), Bain & Mercer (1966), Zhukova & Yakovlev (1966), Klein & Pollock (1968), Öpik (1968), Marin & Dengler (1972), Zhukova (1972, 1975), Pinfield et al. (1973) and Yakovlev & Zhukova (1973).

These plastids are not inert during embryogenesis, as previously supposed by some authors. They are distinctly differentiated and active, with a well-developed inner membrane system. The studies have shown that in reality they are chloroplasts, in spite of a number of features distinguishing them from mesophyll chloroplasts. The most conspicuous difference is the irregularly amoeboid form of the embryo chloroplasts. The numerous invaginations and evaginations enlarge the outer surface. The inner envelope membranes are also invaginated (Zhukova 1972, 1975).

The embryo chloroplasts differ considerably between different taxa. Variation can be seen in all the structural elements, viz. in the subdivision of the inner membrane system into the central and peripheral parts, in the formation of giant grana, in the occurrence of strictly orientated tubules, in the formation of large peristrome evaginations free from the membrane systems, and in the size and contents of the vesicles. Contact between chloroplasts and the membranes of the ER is typical for many species (Zhukova 1975).

We thus conclude that the capacity for chlorophyll accumulation underlies the embryo greening, and that the embryo chlorophyll does not differ from the leaf chlorophyll. Consequently the concept of 'chlorophyllous embryos' seems appropriate.

Occurrence within angiosperms

Chlorophyllous embryos have been found in 428 species, belonging to 224 genera of 72 families. Information has been available for 1,094 species, belonging to 666 genera from 182 families; literature reports are included. A list of the investigated plants are given at the end of this paper.

Species of the same genus do not differ, and in many cases the character is constant in whole families and even in orders. Thus, for example, all the investigated representatives of Brassicaceae, Convolvulaceae, Dipsacaceae, Rhamnaceae, Tiliaceae, Fabales and Plumbaginales have chlorophyllous embryos, (they are chloroembryophytes; Yakovlev 1969, Yakovlev & Zhukova 1973), while e.g. Boraginaceae, Caprifoliaceae, Oleaceae, Ranunculaceae, Solanaceae, Betulales and Fagales lack chlorophyll in the embryos (their representatives being leucoembryophytes).

Some families, such as Araceae, Chenopodiaceae, Meliaceae, Myrtaceae, Polemoniaceae, Scrophulariaceae, are heterogeneous regarding this character and it may be useful for the intrafamilial taxonomy.

We have analysed 31 genera and 65 species of Rosaceae and found no case of embryo greening. Yet Toyoda (1961) reported chlorophyllous embryos in *Rhaphiolepis umbellata*. In Malvaceae embryos are chlorophyllous in 9 species in 7 genera (the embryo of *Thespesia lampas* has only been studied in mature seeds). However, in *Gossypium hirsutum* the embryo remains colourless during the entire embryogenesis (Engleman 1966). Finally, Netolitzky (1926) noted green embryos in Caryophyllaceae but none of the 18 species studied (14 genera) showed this feature.

In our previous publications (Yakovlev & Zhukova 1973, 1975) we demonstrated that the character can be used in the analysis of relationships within and between families. A closer examination of the distribution of this character among the angiosperms as a whole is given by Dahlgren (1980). Clearly, further work on screening various families for this character seems worthwhile.

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Appendix

Chlorophyllous (+) and achlorophyllous (–) embryos in angiosperm seeds. Alphabetic list of families, genera and species investigated. In the species indicated with an asterisk the embryos were investigated in mature seeds only. (E. N.) refers to unpublished material by E. Nikolayeva.

DICOTYLEDONEAE

Acanthaceae	
**Acanthus mollis* L.	–
spinosus L. (Lubbock 1892)	–
Crossandra nilotica Oliver	–
Ruellia formosa Andr.	–
Aceraceae	
Acer campestre L.	+
insigne Boiss. et Buhse	+
macrophyllim Pursh (Flahault 1879)	+
negundo L. (E. N.)	+
palmatum Thunb.	+
platanoides L.	+
pseudoplatanus L. (Flahault 1879)	+
f. *bicolor* Dieck	+
tataricum L. (E. N.)	+
Actinidiaceae	
Actinidia arguta (Sieb. et Zucc.) Miq.	–
kolomikta Maxim.	–
Aizoaceae (=Ficoidaceae)	
Delosperma ecklonis Schwantes	–
Mesembryanthemum criniflorum L. fil.	–
**Tetragonia expansa* Murr. (Lubbock 1892)	–
Alangiaceae	
Alangium ridleyi King	+
Amaranthaceae	
Amaranthus retroflexus L. (E. N.)	–
Amygdalaceae see Rosaceae	
Anacardiaceae	
**Anacardium occidentale* L.	–
Buchanania latifolia Roxb. (Lubbock 1892)	+
Cotinus coggygria Scop. (E. N.)	+
Mangifera indica L.	–
Parishia sp.	+
Schinus terebinthifolius Raddi (Lubbock 1892)	+
Annonaceae	
Asimina triloba (L.) Dunal	–
Cyathocalys sp.	–
Mitrephora celebica Scheff.	–
polypyrena Miq.	–
Polyalthia littoralis Boerl.	–
Apiaceae	
Aegopodium podagraria L.	–
Archangelica decurrens Ledeb.	–
Bupleurum fruticosum L.	–
Caropodium platycarpum (Boiss. et Hausskn.) Schischk.	–
Carum carvi L.	–
Eryngium aquaticum L.	–
Heracleum sibiricum L. (E. N.)	–
Libanotis sp.	–
**Ptychotis ajowan* DC. (Lubbock 1892)	–
Sium latifolium L. (E. N.)	–
Apocynaceae	
Apocynum androsaemifolium L.	–

**Kopsia albiflora* Boerl.	–
**arborea* Blume	–
**Nerium oleander* L.	–
Ochrosia glomerata Val.	–
Rauwolfia serpentina Benth. et Kurz	–
sumatrana Jack	–
Rejoua aurantiaca Gaudich.	–
Tabernaemontana sp.	–
**Thevetia nereifolia* Juss.	–
**Vinca herbacea* Waldst. et Kit. (E. N.)	–
Voacanga grandiflora Rolfe	–
Aquifoliaceae	
**Ilex aquifolium* L.	–
latifolia Thunb.	–
Araliaceae	
Acanthopanax trifoliatus Voss	–
**Aralia chinensis* L.	–
racemosa L.	–
Aristolochiaceae	
**Aristolochia clematitis* L. (E. N.)	–
**Asarum europaeum* L. (E. N.)	–
sieboldii Miq.	–
Asclepiadaceae	
Antitoxicum medium Pobed.	+
officinale (Moench) Pobed.	+
rossicum (Kleop.) Pobed.	+
scandens (Somm. et Lev.) Pobed.	+
Asclepias incarnata L.	+
Cynanchum purpurascens E. Morr. et Decne.	+
Stapelia gigantea N. E. Brown	+
Asteraceae	
Artemisia sp.	–
**Baccharis halimifolia* L.	–
Bidens tripartita L.	–
Calendula officinalis L.	–
Carthamus tinctorius L.	–
Centaurea huettii Boiss.	–
orientalis L. (E. N.)	–
Cichorium sp.	–
Cirsium arvense (L.) Scop.	–
Crepis tectorum L.	–
Helianthus annuus L.	–
Lapsana communis L.	–
Rhagadiolus edulis Willd.	–
Senecio vulgaris L.	–
Taraxacum hybernum Stev. (Poddubnaya-Arnoldi 1952)	–
kok-saghyz Rodin (Poddubnaya-Arnoldi 1952)	–*
officinale Weber	–
Tragopogon dubius Scop.	–
majus Jacq. (E. N.)	–
Xanthium strumarium L. (E. N.)	–
**Zinnia elegans* Jacq.	–
Averrhoaceae see Oxalidaceae	
Balsaminaceae	
Impatiens balsamina L.	–
**noli-tangere* L. (E. N.)	–
Basellaceae (Netolitzky 1926)	+
Berberidaceae	
Berberis francisci-ferdinandii Schneid.	–
gagnepainii Schneid.	–
jamesiana Forr. et Wirm.	–
pruinosa Franch.	–
Berberis saulieana Schneid.	–
sieboldii Miq.	–
vulgaris L. (E. N.)	–
Mahonia aquifolium (Pursh) Nutt. (E. N.)	–
Betulaceae	
Alnus glutinosa Willd.	–
Betula pubescens Ehrh. (E. N.)	–
verrucosa Ehrh.	–
Bignoniaceae	
Catalpa bignonioides Walt.	–
Chilopsis linearis (Cav.) Sweet	–
**Incarvillea delavayi* Bur. et Franch.	–
Markhamia stipulata Seem.	–
Bixaceae	
Bixa orellana L.	–
Bombacaceae	
Ceiba sp.	+
Durio sp.	+
Pachira affinis Decne	+
Boraginaceae	
**Alkanna orientalis* L.	–
Anchusa officinalis L.	–
Cerinthe minor L. (E. N.)	–
Cynoglossum officinale L. (E. N.)	–
Echium vulgare Lam. (E. N.)	–
Lappula echinata Gilib. (E. N.)	–
**Lithospermum multiflorum* S. Wats.	–
Lycopsis arvensis L. (E. N.)	–
**Macrotomia echioides* (L.) Boiss.	–
**Mertensia primuloides* Clarke	–
Myosotis palustris (L.) Nath. (E. N.)	–
sylvatica Ehrh. et Hoffm.	–
Nonea lutea (DC.) Reichenb. (E. N.)	–
pulla Lam. et DC. (E. N.)	–
Symphytum asperum Lepech.	–
officinale L. (E. N.)	–
**Tournefortia sibirica* L. (E. N.)	–
Brassicaceae	
Alliaria officinalis Andrz. (Chernoyarov 1962)	+
Alyssum cretaceum Kotov (E. N.)	+
minutum Schlecht. (E. N.)	+
Arabis alpina L.	+
aubrietioides Boiss.	+
caucasica Willd.	+
rhaetica Bruegg.	+
Aubrietia cultorum Bergm.	+
olympica Boiss.	+
Barbarea vulgaris R. Br. (E. N.)	+
Berteroa incana (L.) DC. (E. N.)	+
Brassica campestris L.	+
elongata Ehrh. (E. N.)	+
juncea (L.) Coss. (Yoffe 1952)	+
nigra (L.) Koch (Lubbock 1892)	+
Bunias orientalis L.	+
Camelina glabrata (DC.) Fritsch (E. N.)	+
sativa (L.) Crantz (E. N.)	+
Capsella bursa-pastoris (L.) Medik.	+
Chorispora tenella (Pall.) DC. (E. N.)	+
Conringia orientalis (L.) Dumort. (E. N.)	+
Crambe abyssinica Hochst. (Belyajeva 1965)	+
maritima L.	+
Descurainia sophia (L.) Webb (E. N.)	+
Diplotaxis tenuifolia (L.) DC. (E. N.)	+
Draba lasiocarpa Rochel	+
verna L. (E. N.)	+
Eruca sativa Mill.	+
Erysimum canescens Roth	+

cheiranthoides L.	+
Erophila verna E. Mey. (E. N.)	+
Hesperis matronalis L. (Chernoyarov 1962)	+
Hutchinsia alpina (L.) R. Br.	+
Iberis amara L.	+
gibraltarica L.	+
umbellata DC.	+
Isatis tinctoria L. (E. N.)	+
Lepidium campestre (L.) R. Br.	+
draba L. (E. N.)	+
perfoliatum L. (E. N.)	+
ruderale L.	+
Lobularia maritima Desv.	+
Lunaria annua L.	+
Matthiola annua Sweet (Yoffe 1952)	+
incana R. Br. (E. N.)	+
Raphanus sativus L. var. _radicula_ Pers. (Yoffe 1957)	+
Sinapis alba L. (Yoffe 1952)	+
arvensis L.	+
Sisymbrium Irio L. (E. N.)	+
loeselii Jusl. (E. N.)	+
Syrenia siliculosa (M. B.) Andrz. (E. N.)	+
Thlaspi arvense L.	+
Buddlejaceae	
Buddleja alternifolia Maxim.	−
davidii Franch. var. _magnifica_ (Wils.) Rehd. et Wils.	−
lindleyana Fost.	−
Burseraceae	
Pachylobus sp. (Netolitzky 1926)	+
Santiria sp. (Netolitzky 1926)	+
Buxaceae	
Sarcococca humilis Stapf	−
ruscifolia Stapf	−
Cactaceae	
*_Cereus napoleonis_ (Lubbock 1892)	−
*_Opuntia dillenii_ (Ker-Gawl.) Haw. (Lubbock 1892)	−
humifusa Rafin.	−
Phyllocactus crenatus Walp.	−
Rhipsalis virgata Web.	−
Caesalpiniaceae	
Bauhinia sp.	+
Brownea ariza Benth.	+
hybrida hort.	+
Cassia spectabilis DC.	+
Cercis siliquastrum L. (E. N.)	+
Gleditsia triacanthos L. (E. N.)	+
Gymnocladus dioica (L.) C. Koch	+
Calycanthaceae	
Calycanthus sp.	−
Campanulaceae	
Adenophora sp.	−
Campanula collina Bieb.	−
*_sibirica_ L. (E. N.)	−
*_trachelium_ L. (E. N.)	−
Codonopsis clematidea Clarke	−
Jasione humilis Lois.	−
Capparidaceae (incl. Cleomaceae)	
Cleome spinosa L.	+
Caprifoliaceae incl. Sambucaceae	
Leycesteria formosa Wall.	−
Lonicera alpigena L.	−
henryi Hemsl.	−
involucrata (Richards.) Banks ex Spreng.	
olgae Regel et Schmalh.	−
pileata Oliver	−
tatarica L.	−
Sambucus nigra L. (E. N.)	−
racemosa L.	−
Symphoricarpus occidentalis Hook.	−
orbiculatus Moench.	−
racemosus Richt. (E. N.)	−
Triosteum rosthornii Diels	−
Viburnum cotinifolium D. Don	−
odoratissimum Ker-Gawl.	−
opulus L.	−
rhytidophyllum Hemsl.	−
tinus L.	−
Caricaceae	
Carica papaya L.	−
Caryophyllaceae (see also Illecebraceae)	
Arenaria polaris Schischk.	−
Cerastium purpurascens Adams	−
Cucubalus baccifer L. (E. N.)	−
Dianthus gratianopolitanus Vill.	−
Gypsophila paniculata L. (E. N.)	−
Lychnis chalcedonica L. (E. N.)	−
Melandrium album L. (E. N.)	−
elisabethae (Jan.) Rohrb.	−
rubrum (Weig.) Garcke	−
Minuartia laricifolia (L.) Schinz et Thell.	−
Saponaria officinalis L.	−
Silene venosa Aschers. et Graebn.	−
wallichiana Klotzsch	−
Spergula arvensis L.	−
Stellaria media L.	−
Vaccaria pyramidata Medik.	−
segetalis (Neck.) Garcke	−
Viscaria viscosa (Scop.) Aschers. (E. N.)	−
Celastraceae	
Celastrus sp.	+
Euonymus alata (Thunb.) Sieb.	+
bungeana Maxim.	+
europaeus L. (Lubbock 1892)	+
hamiltoniana Wall.	+
japonicus Thunb. (Toyoda 1961)	+
latifolia Mill	+
leiophloea Stev.	+
maackii Rupr.	+
macroptera Rupr.	+
maximowicziana Prokh.	+
pauciflora Maxim.	+
planipes Koehne	+
sachalinensis (F. Schmidt) Maxim.	+
sacrosancta Koidz.	+
semenovii Regel et Herd.	+
verrucosa Scop. (E. N.)	+
yedoensis Koidz.	+
Tripterygium wilfordii Hook. fil.	+
Ceratophyllaceae (Netolitzky 1926)	+
Cercidiphyllaceae	
Cercidiphyllum magnificum Nakai	−
Chenopodiaceae	
Aellenia autranii (Post) Zohary (Negbi & Tamari 1964)	+
subaphylla C. A. Mey. (Ionesova 1968)	+
*_Atriplex hortensis_ L.	−
*_Beta vulgaris_ L. (E. N.)	−

Chenopodium album L.	–
anthelminticum L.	–
bonus-henricus L.	–
Haloxylon aphyllum (Minkw.) Iljin	+
Kochia indica Wight (Negbi & Tamari 1964)	+
prostrata (L.) Schrad. (Ionesova 1968)	+
Salicornia sp. (Vassilczenko 1936)	+
Salsola arbuscula Pall. (Ionesova 1968)	+
inermis Forsk. (Negbi & Tamari 1964)	+
rigida Pall. (Ionesova 1968)	+
ruthenica Iljin (E. N.)	+
volkensii Schweinf. et Aschers. (Negbi & Tamari 1964)	+
Cistaceae	
Helianthemum grandiflorum DC.	+
Clusiaceae see Guttiferae	
Cneoraceae	
Cneorum tricoccum L.	–
Combretaceae	
*_Combretum grandiflorum_ G. Don	–
*_Laguncularia_ sp. (Netolitzky 1926)	+
*_Terminalia_ sp.	–
Compositae see Asteraceae	
Convolvulaceae	
Calystegia sepium (L.) R. Br. (E. N.)	+
Convolvulus arvensis L.	+
lineatus L. (E. N.)	+
scammonia L.	+
sepium L. (Lubbock 1892)	+
tricolor L. (Lubbock 1892)	+
Ipomoea pes-caprae (L.) Roth	+
purpurea (L.) Roth (E. N.)	+
roxburghii Steud.	+
Merremia dissecta (Jacq.) Hall. fil. (Sankhla et al. 1966)	+
Pharbitis purpurea (L.) Voigt	+
Cornaceae	
Cornus femina Mill.	+
Cornus sp. (Netolitzky 1926)	+
Cynoxylon japonicum Nakai	+
Thelycrania sanguinea (L.) Fourr.	+
Corylaceae	
Corylus avellana L.	–
Crassulaceae (Netolitzky 1926)	+
Rhodiola rosea L.	–
*_Sedum acre_ L. (E. N.)	–
aizoon L.	–
hybridum L.	–
Cruciferae see Brassicaceae	
Cucurbitaceae	
*_Alsomitra macrocarpa_ (Bl.) Roem.	–
*_Benincasa hispida_ (Thunb.) Cogn.	–
*_Bryonia alba_ L.	–
Citrullus lanatus (Thunb.) Mansf.	–
vulgaris Schrad. (E. N.)	–
Cucumis melo L.	–
sativus L. (E. N.)	–
Cucurbita pepo L. (E. N.)	–
Ecballium elaterium (L.) A. Rich.	–
*_Momordica_ sp.	–
*_Sicyos angulatus_ L. (E. N.)	–
Cuscutaceae	
Cuscuta campestris Junck. (E. N.)	+
europaea L. (E. N.)	+
lupuliformis Krock.	+
Cuscuta sp. (Netolitzky 1926)	+
Dilleniaceae	
Dillenia indica L.	–
Dipsacaceae	
Cephalaria brevipalea (Somm. et Levier) Litv.	+
gigantea (Ledeb.) Bohr.	+
tatarica Gmel. (Lubimenko 1906)	+
uralensis Schrad. (E. N.)	+
Dipsacus azureus Schrenk	+
fullonum L.	+
laciniatus L.	+
Knautia arvensis (L.) Coult. (E. N.)	+
macedonica Griseb.	+
montana (Bieb.) DC.	+
Scabiosa bipinnata C. Koch	+
caucasica Bieb.	+
lucida Vill.	+
ochroleuca L. (E. N.)	+
olivieri Coult.	+
soongorica Schrenk	+
Dipterocarpaceae	
Anisoptera marginata Korth.	+
Dipterocarpus turbinata Gaertn.	+
Dryobalanops aromatica Gaertn.	+
lanceolata Burck	+
Shorea palembanica Miq.	+
Vatica bancana Scheff.	+
Ebenaceae	
Diospyros discolor Willd.	–
frutescens Blume	–
kaki L. fil.	–
Ehretiaceae	
Ehretia acuminata R. Br.	–
macrophylla Wall.	–
Elaeagnaceae	
Elaeagnus angustifolia L. (E. N.)	–
argentea Pursh	–
latifolia L.	–
umbellata Thunb.	–
Hippophaë rhamnoides L.	–
Elaeocarpaceae	
Elaeocarpus sp.	+
Ericaceae (see also Vacciniaceae)	
Arbutus andrachne L.	–
unedo L.	–
Pieris floribunda Benth.	–
*_japonica_ (Thunb.) D. Don	–
Erythroxylaceae	
Erythroxylum coca Lam. (Monteverde & Lubimenko 1909)	+
Euphorbiaceae	
Aleurites cordata R. Br.	–
fordii Hemsl.	–
Baccaurea javanica Muell. Arg.	+
Bridelia monoica Merr.	+
Drypetes macrostigma J. J. S.	–
Euphorbia lamprocarpa Prokh.	–
petrophila C. A. Mey (E. N.)	+
soongorica Boiss.	–
Euphorbia sp. (E. N.)	+
virgata Waldst. et Kit. (E. N.)	+
Glochidion cyrtostylum Miq.	–
Jatropha curcas L.	–
Joannesia princeps Vell.	–
*_Mallotus japonicus_ (Thunb.) Muell. Arg.	–

**Ricinus communis* L. (E. N.)	–
Securinega suffruticosa (Pall.) Rehd.	+
Fabaceae	
Amorpha fruticosa L. (E. N.)	+
Astragalus cicer L. (E. N.)	+
glycyphyllus L. (E. N.)	+
hamosus L.	+
Astragalus sp. (Flahault 1879)	+
Baptisia australis (L.) R. Br.	+
Caragana arborescens Lam.	+
frutex (L.) C. Koch (E. N.)	+
Cicer arietinum L. (E. N.)	+
Clitoria ternata (L.) Baker (Lubbock 1892)	+
Colutea arborescens L.	+
Coronilla varia L. (E. N.)	+
Cytisus ruthenicus Fisch. (E. N.)	+
Dolichos lablab L.	+
Galega officinalis L. (E. N.)	+
Genista tinctoria L. (E. N.)	+
Glycine max (L.) Merr. (Toyoda 1959)	+
Glycyrrhiza echinata L. (E. N.)	+
Hedysarum coronarium L. (Lubbock 1892)	+
grandiflorum Pall. (E. N.)	+
Indigofera gerardiana (Wall.) Baker	+
Laburnum anagyroides Medik.	+
Lathyrus pratensis L. (E. N.)	+
tuberosus L. (E. N.)	+
Lespedeza bicolor Turcz.	+
Lupinus barkeri Lindl. (E. N.)	+
luteus L. (Poddubnaya-Arnoldi 1952)	+
polyphyllus Lindl. (E. N.)	+
Maackia amurensis Rupr. et Maxim.	+
Medicago arabica All.	+
arborea L.	+
denticulata Willd.	+
falcata L. (E. N.)	+
lupulina L.	+
minima (L.) Grufb. (E. N.)	+
orbicularis (L.) Bart.	+
Melilotus alba Medik. (E. N.)	+
officinalis (L.) Pall. (E. N.)	+
Onobrychis viciifolia Scop. (E. N.)	+
Ononis arvensis L.	+
spinosa L.	+
Phaseolus coccineus L.	+
lunatus L. (Klein & Pollock 1968)	+
multiflorus Willd. (Rezende-Pinto 1964)	+
vulgaris L. (E. N.)	+
Pisum sativum L.	+
Pterocarpus echinatus Pers.	+
Robinia pseudacacia L. (E. N.)	+
Sophora flavescens Ait.	+
japonica L.	+
Thermopsis fabacea (Pall.) DC.	+
Trifolium campestre Schreb.	+
hybridum L.	+
pratense L. (E. N.)	+
repens L.	+
strepens Crantz (E. N.)	+
Vicia bithynica L.	+
cracca L. (E. N.)	+
elegans Guss. (E. N.)	+
faba var. *major* Harz (Yoffe 1957)	+
grandiflora Scop. (E. N.)	+
incisa Bieb.	+
sativa L. (Poddubnaya-Arnoldi 1952)	+
sepium L.	+
tenuifolia Roth (E. N.)	+
Wisteria sinensis Rehd. et Wilson	+
Fagaceae	
Castanea vulgaris Lam. (Lubbock 1892)	–
Fagus silvatica L. (Lubbock 1892)	–
Quercus coccifera L.	–
**grosseserrata* Blume	–
**ilex* L.	–
**occidentalis* J. Gay	–
**serrata* Thunb.	–
**suber* L.	–
Ficoidaceae see Aizoaceae	
Flacourtiaceae	
Hydnocarpus alpina Wight	–
polypetala (Sloot.) Sleum.	–
Fumariaceae	
Dicentra formosa Walp	–
Fumaria officinalis L.	–
Gentianaceae	
Centaurium confertum Druce	–
Gentiana lutea L.	–
Swertia iberica Fisch. et Mey.	+
Geraniaceae	
Erodium ciconium (L.) Ait.	+
cicutarium (L.) L'Hérit.	+
Geranium columbinum L. (Lubimenko 1906)	+
divaricatum Ehrh.	+
gracile Ledeb.	+
lucidum L. (Flahault 1879)	+
palustre L. (Lubimenko 1906)	+
pratense L. (Lubimenko 1906)	+
pusillum Burm. (E. N.)	+
rotundifolium L.	+
ruprechtii Woron. ex Grossh.	+
sanguineum L. (Lubbock 1892)	+
sylvaticum L. (E. N.)	+
Pelargonium zonale Ait. (E. N.)	+
Gesneriaceae	
Ramondia pyrenaica Pers.	–
Grossulariaceae	
Grossularia reclinata Mill.	–
Ribes nigrum L.	–
vulgare Lam.	–
Guttiferae (Clusiaceae)	
Garcinia echinocarpa Thw.	+
loureiri Pierre	+
picrorhiza Miq.	+
xanthochymus Hook. fil.	+
Haloragaceae	
Myriophyllum spicatum L.	–
Helleboraceae	
Aconitum napellus L.	–
Actaea rubra (Ait.) Willd.	–
Aquilegia ottonis Orph.	–
Cimicifuga foetida L.	–
Trollius altaicus C. A. Mey.	–
asiaticus L.	–
dschungaricus Regel	–
europaeus L.	–
Hippocastanaceae	
Aesculus hippocastanum L.	+
Hydrangeaceae	
Hydrangea petiolaris Sieb. et Zucc.	–

Hydrastidaceae	
Hydrastis canadensis L.	–
Hydrophyllaceae	
Hydrophyllum fendleri (A. Gray) Heller	–
occidentale (Wats.) A. Gray	–
Phacelia tanacetifolia Benth.	+
Hypericaceae	
Hypericum elegans Steph. (E. N.)	+
perforatum L.	+
Icacinaceae	
Gonocaryum fuscum Hochr.	+
Illecebraceae (Caryophyllaceae)	
Herniaria besseri Fisch. (E. N.)	–
polygama J. Gay (E. N.)	–
Illiciaceae	
*_Illicium floridanum_ Ellis	–
Juglandaceae	
Carya cordiformis C. Koch	–
Juglans mandschurica Maxim.	–
nigra L.	–
regia L.	–
Labiatae see Lamiaceae	
Lamiaceae	
Betonica foliosa Rupr.	–
grandiflora Benth.	–
Coleus sp. (E. N.)	–
Dracocephalum ruyschianum L.	–
Lamium purpureum L. (E. N.)	–
Lavandula spica DC.	–
Leonurus cardiaca L. (E. N.)	–
villosus Desf.	–
Marrubium praecox Janka (E. N.)	–
Melissa officinalis L.	–
Mentha canadensis L.	–
piperita L.	–
Phlomis pungens Willd. (E. N.)	–
tuberosa L. (E. N.)	–
Prunella vulgaris L. (E. N.)	–
Salvia aethiopis L. (E. N.)	–
nutans L. (E. N.)	–
Scutellaria galericulata L. (E. N.)	–
Sideritis montana var. *comosa* Rochel (E. N.)	–
Stachys palustris L. (E. N.)	–
recta L. (E. N.)	–
sylvatica L. (E. N.)	–
Ziziphora capitata L.	–
Lauraceae	
Beilschmiedia roxburghiana Nees	–
Cinnamomum sp.	–
*_camphora_ T. Nees et Eberm.	–
Cryptocaria sp.	–
*_Laurus nobilis_ L.	–
Persea gratissima Gaertn. fil.	–
Lentibulariaceae	
Utricularia emarginata Benj. (Netolitzky 1926)	+
Linaceae	
Linum alpinum (L.) Jacq.	+
angustifolium Huds. (Kantor 1959)	+
austriacum L. (Schimper 1885)	+
flavum L. (E. N.)	+
grandiflorum Desf. f. *flora rubro* hort.	+
hirsutum L. (E. N.)	+
humile Mill. (E. N.)	+
pallasianum Schult. (E. N.)	+

perenne L.	+
tenuifolium L. (E. N.)	+
usitatissimum L. (Poddubnaya-Arnoldi 1952)	+
Loasaceae	
Loasa vulcanica André	–
Lobeliaceae	
Lobelia sessilifolia Lamb.	–
urens L.	–
Loranthaceae incl. Viscaceae	
Lepidoceras kingii Hook fil. (Hofmeister 1859)	+
Loranthus europaeus L. (Hofmeister 1859)	+
Phrygilanthus aphyllus Eichl. (Netolitzky 1926)	+
Viscum album L. (Flahault 1879)	+
Lythraceae	
Lagerstroemia indica L. f. *rosea* hort.	–
Lythrum salicaria L.	–
virgatum L. (E. N.)	–
Magnoliaceae	
*_Magnolia kobus_ DC.	–
Talauma sp.	–
Maloideae see Rosaceae	
Malvaceae	
Alcea rosea L.	+
Althaea officinalis L.	+
Gossypium hirsutum L. (Engleman 1966)	–
Hibiscus syriacus L.	+
Kitaibelia vitifolia Willd.	+
Lavatera thuringiaca L.	+
trimestris L. (E. N.)	+
Malope trifida Cav.	+
Malva neglecta Wallr. (E. N.)	+
pusilla Smith	+
*_Thespesia lampas_ Dalz.	–
Melastomataceae	
Clidemia hirta D. Don	–
Meliaceae	
Aglaia rufa Miq.	+
Cedrela odorata L.	–
Cipadessa baccifera Miq.	+
Dysoxylum acutangulum Miq.	+
Melia azadirachta L.	+
toosendan Sieb. et Zucc.	+
Sandoricum koetjape (Burm. fil.) Merr.	–
Swietenia macrophylla King	–
mahagoni L.	–
Turraea billardieri Benn.	+
Memecylaceae	
Memecylon myrsinoides Blume	+
nudum Blume	+
Mimosaceae	
Acacia auriculiformis A. Cunn.	+
biuncifera Benth.	+
dealbata Link	+
melanoxylon Roxb.	+
neriifolia A. Cunn.	+
Adenanthera pavonina L.	+
Albizia julibrissin (Willd.) Durazz.	+
lophantha Benth.	+
saponaria Blume	+
Neptunia plena (L.) Benth.	+
Molluginaceae	
Mollugo cerviana (L.) Ser. (E. N.)	–

Monimiaceae	
Matthaea calophylla Perkins	–
Monotropaceae	
Monotropa sp.	–
Moraceae	
Antiaria toxicaria Lesch.	–
Artocarpus integra Merr.	–
Artocarpus sp.	–
Dorstenia contrajerva L.	–
**Ficus carica* L. (E. N.)	–
peltata Blume	–
Maclura pomifera (Rafin.) C. B. Rob.	–
Morus alba L.	–
Streblus asper Lour.	+
Moringaceae	
Moringa oleifera Lam.	+
Myristicaceae	
Horsfieldia batjanica Warb.	–
glabra Warb.	–
Myristica ferruginea Wall.	–
macrothyrsa Miq.	–
Myrsinaceae	
Ardisia crenata Roxb.	–
japonica (Thunb.) Blume	–
tuberculata Wall.	–
Myrtaceae	
Eugenia aquea Burm. fil.	+
brasiliensis Lam. (Monteverde & Lubimenko 1909)	+
paucipunctata Koord. et Valet.	+
Leptospermum scoparium Forst.	–
Melaleuca hypericifolia Smith	–
Myrtus communis L.	–
Psidium littorale Raddi	–
Myzodendraceae	
Myzodendron linearifolium DC.	+
Nelumbonaceae	
Nelumbo lutea (Willd.) Pers. (Meeuse & Ott 1962)	+
nucifera Gaertn.	+
Nyctaginaceae	
Allionia ovata Pursh	+
**Mirabilis jalapa* L.	+
Nymphaeaceae	
Nuphar luteum (L.) Smith	+
Nymphaea alba L.	+
caerulea Sav.	+
**Victoria amazonica* (Poepp.) Sow.	–
Olacaceae	
Strombosia zeylanica Card. var. *sessilis* Hochr.	+
Oleaceae	
Fraxinus excelsior L. (E. N.)	–
oxycarpa Willd. (E. N.)	–
**viridis* Michx.	–
Jasminum humile L.	–
officinale L.	–
Ligustrum compactum Hook. fil. et Thoms.	–
henryi Hemsl.	–
lucidum Ait.	–
ovalifolium Hassk.	–
vulgare var. *sempervirens* Loud.	–
Phillyrea angustifolia L.	–
Syringa vulgaris L.	–
Onagraceae	
Chamaenerium angustissimum (Hausskn.) Sosn.	–
Clarkia elegans Dougl.	–
Epilobium tetragonum L.	–
Fuchsia sp. (E. N.)	–
Onagra biennis L.	–
Orobanchaceae	
Orobanche sp. (E. N.)	–
Oxalidaceae	
Averrhoa bilimbi L.	+
carambola L.	+
Oxalis acetosella L.	+
corniculata L. (E. N.)	+
hirta L. (Netolitzky 1926)	+
Paeoniaceae	
Paeonia anomala L.	–
lactiflora Pall.	–
suffruticosa Andr.	–
tenuifolia L.	–
Papaveraceae	
Chelidonium majus L.	–
Corydalis cava (Mill.) Schweigg. et Koerte (E. N.)	–
Eschscholtzia sp.	–
Glaucium corniculatum (L.) J. Rudolf. (E. N.)	–
Meconopsis cambrica (L.) Vig.	–
Papaver rhoeas L. (E. N.)	–
somniferum L.	–
Sanguinaria canadensis L.	–
Passifloraceae	
**Passiflora edulis* Sims	–
Peganaceae see Zygophyllaceae	
Petiveriaceae	
Rivina humilis L.	–
Philadelphaceae	
Deutzia scabra Thunb.	–
Philadelphus coronarius L.	–
falconeri Sarg.	–
latifolius Schrad. ex DC.	–
mexicanus Rehd.	–
sericanthus Koehne	–
tenuifolius Rupr. et Maxim.	–
Phytolaccaceae	
Phytolacca esculenta Van Houtte	–
Pistaciaceae	
Pistacia lentiscus L.	+
mutica Fisch. et Mey.	+
**Pistacia* sp. (Lubimenko 1916)	+
vera L. (Vassilczenko 1936)	+
Pittosporaceae	
Pittosporum crassifolium A. Cunn.	–
tobira Ait.	–
Plantaginaceae	
Plantago indica L. (E. N.)	–
lanceolata L. (E. N.)	–
major L. (E. N.)	–
media L. (E. N.)	–
ovata Forsk.	–
psyllium L.	–
Plumbaginaceae	
Armeria maritima (Mill.) Willd.	+
pseudarmeria (Murr.) Mansf.	+
Goniolimon tataricum (L.) Boiss. (E. N.)	+
Limonium gmelinii Willd. (E. N.)	+
Plumbago scandens L.	+

Podophyllaceae	
Podophyllum emodi Wall.	–
Polemoniaceae	
Cobaea scandens Cav. (Lubbock 1892)	–
Cobaea sp. (Netolitzky 1926)	–
Collomia coccinea Lehm. (Lubbock 1892)	+
Phlox drummondii Hock	+
paniculata L. (E. N.)	+
Polemonium caucasicum N. Busch	–
coeruleum L.	–
occidentale Greene	–
Polygalaceae	
Polygala comosa Schkuhr	+
vulgaris L. (E. N.)	+
Polygonaceae	
Fagopyrum esculentum Moench (Poddubnaya-Arnoldi 1952)	–
sagittatum Gilib. (E. N.)	–
Oxyria digyna (L.) Hill	–
Polygonum amphibium L. (E. N.)	–
convolvulus L. (E. N.)	–
coriarium Grig.	–
cuspidatum Sieb. et Zucc.	–
nitens V. Petr.	–
perfoliatum L.	–
Rheum tataricum L. (E. N.)	–
undulatum L.	–
Rumex acetosa L. (E. N.)	–
acetosella L.	–
confertus Willd.	–
Portulacaceae	
Portulaca grandiflora Hook.	–
oleracea L. (E. N.)	–
Primulaceae	
Anagallis arvensis L.	–
Dodecatheon sp.	–
Hottonia palustris L. (E. N.)	–
Lysimachia nummularia L. (E. N.)	–
punctata L.	–
verticillaris Spreng.	–
vulgaris L. (E. N.)	–
Primula auricula L.	–
bulleyana G. Forrest	–
macrocalyx Bunge	–
Proteaceae	
**Hakea pubescens* Schrad.	–
Punicaceae	
**Punica granatum* L. (E. N.)	–
Pyrolaceae	
Pyrola sp.	–
Ranunculaceae (see also Helleboraceae and Hydrastidaceae)	
Adonis vernalis L. (E. N.)	–
Anemone crinita Juz.	–
sylvestris L. (E. N.)	–
Ceratocephalus orthoceras DC. (E. N.)	–
Clematis campaniflora Brot.	–
paniculata Thunb.	–
Delphinium consolida L. (=*Consolida arvensis*) (E. N.)	–
Pulsatilla patens (L.) Mill. (E. N.)	–
vulgaris Mill.	–
Ranunculus acer L. (E. N.)	–
lateriflorus DC. (E. N.)	–
lingua L. (E. N.)	–

muricatus L.	–
polyphyllus Kit. (E. N.)	–
Thalictrum minus L. (E. N.)	–
Resedaceae	
Reseda lutea L. (E. N.)	+
odorata L.	+
Rhamnaceae	
Ceanothus thyrsiflorus Eschsch.	+
Frangula alnus Mill. (E. N.)	+
Hovenia dulcis Thunb.	+
Rhamnus catharticus L.	+
dahurica Pall.	+
pallasii Fisch. et Mey.	+
Rosaceae incl. Amygdalaceae and Malaceae	
Agrimonia eupatoria L. (E. N.)	–
Alchemilla sp.	–
Amelanchier sp. (E. N.)	–
Amygdalus nana L. (E. N.)	–
Armeniaca vulgaris Lam. (E. N.)	–
Cerasus fruticosa Pall. (E. N.)	–
vulgaris Mill. (E. N.)	–
Chaenomeles japonica (Thunb.) Lindl.	–
chinensis Koehne	–
Cotoneaster dammeri C. K. Schneid.	–
franchetii Bois	–
glaucophylla Franch.	–
henryana Rehd. et Wils.	–
integerrima Medik.	–
pannosa Franch.	–
salicifolia Franch.	–
thymifolia (Baker) Koehne	–
tomentosa (Ait.) Lindl.	–
Crataegus crus-galli L.	–
macracantha Lodd.	–
monogyna Jacq.	–
prunifolia (Marsh.) Pers.	–
Cydonia oblonga Mill.	–
Exochorda albertii Regel	–
racemosa (Lindl.) Rehd.	–
Geum strictum Ait.	–
virginianum L.	–
urbanum L.	–
Laurocerasus lusitanica (L.) Roem.	–
officinalis Roem.	–
Malus domestica Borkh. (E. N.)	–
floribunda Sieb.	–
scheideckeri (Spaeth) Zabel	–
toringo Sieb.	–
Mespilus sp.	–
Moquilia tomentosa Benth.	–
Osteomeles schwerinae C. K. Schneid.	–
Padus racemosa (Lam.) Gilib.	–
virginiana (L.) Mill. (E. N.)	–
Photinia serrulata Lindl.	–
Physocarpus amurensis Maxim.	–
Potentilla reptans L. (E. N.)	–
Prunus divaricata Ledeb. (E. N.)	–
domestica L. (E. N.)	–
spinosa L. (E. N.)	–
Pyracantha crenulata (D. Don) Roem.	–
gibbsii A. Jacks.	–
pauciflora Roem.	–
Pyrus communis L.	–
Rhaphiolepis umbellata Makino (Toyoda 1961)	+
Rosa canina L.	–

rugosa Thunb.	–
Rubus caesius L. (E. N.)	–
idaeus L. (E. N.)	–
Sanguisorba officinalis L.	–
Sorbaria grandiflora Maxim.	–
lindleyana Maxim.	–
sorbifolia (L.) A. Br.	–
Sorbus aucuparia L. (E. N.)	–
Spiraea bella Sims	–
blumei G. Don	–
media Schmidt (E. N.)	–
opulifolia (L.) Maxim. (E. N.)	–
vanhouttei (Briot) Zabel	–
Stranvaesia nussia Decne.	–
Rubiaceae	
*_Alberta magna_ E. Mey. (Lubbock 1892)	–
Asperula humifusa (Bieb.) Bess. (E. N.)	–
Galium aparine L. (E. N.)	–
boreale L. (E. N.)	–
Gardenia jasminoides Ellis	–
*_thunbergia_ L. fil. (Lubbock 1892)	–
*_Genipa clusiifolia_ Griseb.	–
Ixora sp.	–
Psychotria maingayi Hook. fil.	–
viridiflora Reinw.	–
Randia tomentosa Hook. fil.	–
Rutaceae	
Citrus depressa Hayata (Toyoda 1959)	+
erythrosa hort. ex Tanaka (Toyoda 1961)	+
keraji hort. ex Tanaka (Toyoda 1959)	+
kinokuni hort. ex Tanaka (Toyoda 1961)	+
*_limon_ (L.) Burm. fil. (E. N.)	+
nobilis Lour. (Toyoda 1959)	+
oto hort. ex Tanaka (Toyoda 1959)	+
sinensis Osbeck (Toyoda 1959)	+
tachibana (Nak.) Tanaka (Toyoda 1959)	+
*_unshiu_ Marcovicz (E. N.)	+
Dictamnus albus L.	–
Euodia daniellii (Benn.) Hemsl.	+
Fortunella margarita (Lour.) Swingle (Toyoda 1959)	+
Poncirus trifoliata (L.) Rafin.	+
Ptelea trifoliata L.	–
Ruta bracteosa DC.	+
graveolens L.	+
macrophylla Soland.	+
Skimmia repens Nakai	+
*_Zanthoxylum alatum_ Roxb. var. *planispinum* Rehd. et Wils.	–
*_bungei_ Planch.	–
*_longipes_ Rose	–
*_piperitum_ L.	–
*_simulans_ Hance	–
Salicaceae	
Populus alba L. (Zonova 1953)	+
balsamifera L. (Nikolayeva 1964)	+
hybrida Bieb. (Zonova 1953)	+
nigra L. (E. N.)	+
Salix acutifolia Vill. (E. N.)	+
caprea L. (Nikolayeva 1958)	+
fragilis L. (E. N.)	+
pentandra L. (Zonova 1953)	+
Sambucaceae see Caprifoliaceae	
Santalaceae	
*_Thesium linifolium_ Schrank (E. N.)	–

Sapindaceae	
Allophylus fulvinervis Blume	+
Aphania boerlagei Valefon	+
Harpullia arborea Radik.	+
cupanoides Roxb. (Monteverde & Lubimenko 1909)	+
thanatophora Blume	+
Hebecoccus ferrugineus Radik.	–
*_Nephelium lappaceum_ L.	–
Paranephelium macrophyllum King	–
*_Sapindus drummondii_ Hook. et Arn.	+
Ungnadia speciosa Endl.	–
Sapotaceae	
Achras zapota L.	–
*_Lucuma campechiana_ H. B. K.	–
Mimusops elengi L.	–
Palaquium gutta Baill.	–
Saxifragaceae	
Mitella caulescens Nutt.	–
Saxifraga caespitosa L.	–
volenatiana Ryl.	–
Tellima grandiflora (Pursh) R. Br.	–
Scrophulariaceae	
Antirrhinum majus L.	–
Collinsia heterophylla Buist	+
Digitalis grandiflora Mill.	–
Gratiola officinalis L. (E. N.)	–
Limosella sp. (Netolitzky 1926)	+
Linaria odorata Chav. (E. N.)	–
vulgaris (L.) Mill. (E. N.)	–
Melanpyrum arvense L. (E. N.)	–
Mimulus luteus L.	–
Nemesia floribunda Lehm.	–
Paulownia imperialis Sieb. et Succ.	–
Penstemon humilis Nutt.	+
Rhinanthus sp.	–
Scrophularia nodosa L. (E. N.)	–
Tetranema mexicanum Benth.	–
Verbascum blattaria L. (E. N.)	–
lychnitis L. (E. N.)	–
phlomoides L.	–
thapsiforme Schrad. (E. N.)	–
thapsus L. (E. N.)	–
Veronica anagallis-aquatica L. (E. N.)	–
andersonii Lindl.	–
incana L. (E. N.)	–
longifolia L. (E. N.)	–
persica Poir.	–
prostrata L.	–
sibirica L.	–
spicata L. (E. N.)	–
urticifolia Jacq.	–
Simaroubaceae	
Ailanthus grandis Prain	+
Brucea amarissima Desv.	+
Harrisonia brownii Juss.	+
Solanaceae	
Atropa belladonna L.	–
Brunfelsia sieberi Regel	–
Capsicum annuum L. (E. N.)	–
Datura metel L.	–
stramonium L. (E. N.)	–
Hyoscyamus niger L. (E. N.)	–
Lycium barbatum L. (E. N.)	–
chinense Mill.	–

Lycopersicum esculentum Mill. (E. N.)	–
Nicotiana alata Link et Otto	–
glauca Graham	–
tabacum L. (Poddubnaya-Arnoldi 1952)	–
Petunia hybrida hort. (E. N.)	–
Physalis alkekengi L. (E. N.)	–
Physochlaina orientalis (Bieb.) G. Don	–
Scopolia carniolica Jacq.	–
stramonifolia (Wall.) Semenova	–
Solanum dulcamara L. (E. N.)	–
nigrum L. (E. N.)	–
persicum Willd. ex Roem. et Schult.	–
pseudocapsicum L.	–
Sonneratiaceae	
Sonneratia caseolaris (L.) Engl.	+
Staphyleaceae	
Staphylea pinnata L. (Lubbock 1892)	+
Sterculiaceae	
Cola acuminata Schott et Endl.	+
Firmiana malayana Kosterm.	+
Pterocymbium tinctorium (Blanco) Merr. var. *javanicum* (R. Br.) Kosterm.	+
Sterculia sp.	+
Styracaceae	
Styrax benzoin Dryand.	–
obassia Sieb. et Zucc.	–
Theaceae	
Camellia japonica L.	–
**Thea sinensis* L.	–
Thymelaeaceae	
Daphne mezereum L.	–
Phaleria macrocarpa (Scheff.) Boerl.	–
Phaleria sp.	–
Tiliaceae	
Clappertonia ficifolia Decne.	+
Colona scabra Burr.	+
Grewia acuminata Juss.	+
Tilia cordata Mill. (E. N.)	+
petiolaris DC. (Lubbock 1892)	+
platyphyllos Scop. f. *praecox* (A. Br.) Ig. Vassil.	+
rubra Rupr.	+
tomentosa Moench	+
Trochodendraceae	
Trochodendron aralioides Sieb. et Zucc.	–
Tropaeolaceae	
Tropaeolum majus L.	+
Ulmaceae	
Celtis australis L.	–
glabrata Stev. (E. N.)	–
**occidentalis* L.	–
Ulmus laevis Pall. (E. N.)	–
scabra Mill. (E. N.)	–
Umbelliferae see Apiaceae	
Urticaceae	
Parietaria officinalis L.	–
Urtica cannabina L.	–
Vacciniaceae	
Oxycoccus palustris Pers.	–
Vaccinium arctostaphylos L.	–
myrtillus L.	–
vitis-idaea L.	–
Valerianaceae	
Centranthus ruber (L.) DC.	+
Valeriana nitida Kreyer (E. N.)	+
officinalis L.	+
Verbenaceae	
Callicarpa giraldiana Hesse	–
Clerodendrum thomosonae Balf.	–
**Lantana camara* L.	–
Verbena hybrida hort.	–
Vitex incisa Bunge	–
Violaceae	
Viola altaica Ker-Gawl.	+
ambigua Waldst. et Kit. (E. N.)	+
declinata Waldst. et Kit. (E. N.)	+
elatior Fries (E. N.)	+
epipsila Ledeb. (E. N.)	+
rugulosa Greene	+
Viola sp.	+
tricolor L. (Flahault 1879)	+
Viscaceae see Loranthaceae	
Vitaceae	
Vitis vinifera L.	–
Zygophyllaceae	
Nitraria sibirica Pall.	+
Peganum harmala L. (Netolitzky 1926)	+
Tribulus terrestris L. (E. N.)	+

MONOCOTYLEDONEAE

Agavaceae	
Agave sp.	–
**Phormium tenax* J. R. et G. Forst.	–
**Yucca aloifolia* L.	–
Alismataceae	
Alisma lanceolatum With. (E. N.)	–
plantago-aquatica L.	–
Echinodorus sp.	–
Sagittaria sagittifolia L.	–
Alliaceae	
**Agapanthus umbellatus* L'Hérit.	–
Allium oleraceum L. (E. N.)	–
pulchellum G. Don (E. N.)	–
rotundum L. (E. N.)	–
stipitatum Regel	–
Amaryllidaceae	
Amaryllis (=*Hippeastrum*) sp. (E. N.)	–
Clivia cyrtanthiflora Van Houtte	–
Eucharis amazonica hort. (E. N.)	–
Galanthus nivalis L. (E. N.)	–
Haemanthus albiflorus Jacq. (E. N.)	+
katherinae Baker (E. N.)	+
Hymenocallis occidentalis (Le Conte) Kunth (Flint & Moreland 1943)	–
Anthericaceae	
Anthericum ramosum L.	–
Paradisia liliastrum Bert.	–
Aponogetonaceae (Netolitzky 1926)	+
Araceae	
Acorus sp. (Netolitzky 1926)	+
Aglaonema sp. (Netolitzky 1926)	+
Arisaema amurense Maxim.	–
Calla palustris L.	+
Nephthytis sp. (Netolitzky 1926)	+
Pothos scandens L. (Monteverde & Lubimenko 1909)	+
Zantedeschia aethiopica Spreng. (E. N.)	+
Arecaceae see Palmae	
Asparagaceae	

Asparagus verticillatus L. (E. N.)	–
Asphodelaceae	
Eremurus sp.	–
Bromeliaceae	
Pitcairnia xanthifolia	–
Butomaceae	
Butomus umbellatus L. (E. N.)	–
Commelinaceae	
Tradescantia virginiana L.	–
Convallariaceae	
Convallaria majalis L.	–
Majanthemum dilatatum (Wood) Nels. et Macbr.	–
Polygonatum multiflorum (L.) All. (E. N.)	–
officinale All.	–
Smilacina stellata (L.) Desf.	–
Cyperaceae	
**Bulboschoenus maritimus* (L.) Palla (E. N.)	–
**Carex* sp. (E. N.)	–
Dianellaceae	
Dianella coerulea Sims	–
Dioscoreaceae	
Dioscorea caucasica Lipsky	–
Hemerocallidaceae	
Hemerocallis flava L.	–
Hyacinthaceae	
Bellevalia sarmatica (Pall.) Woron.	–
Chionodoxa gigantea Whitt.	–
Muscari racemosum (L.) Mill.	–
Ornithogalum caudatum Jacq.	–
umbellatum L. (E. N.)	–
Scilla sibirica Haw.	–
Hydrocharitaceae	
Stratiotes aloides L. (E. N.)	–
Iridaceae	
**Gladiolus imbricatus* L. (E. N.)	–
Iris pseudacorus L.	–
pumila L. (E. N.)	–
sogdiana Bunge	–
Sisyrinchium angustifolium Mill.	–
Tritonia crocosmifolia (Hont.) Bak.	+
Juncaceae	
Juncus bufonius L. (E. N.)	–
filiformis L.	–
lamprocarpus Ehrh. (E. N.)	–
Luzula pedemontana Boiss. et Reut.	–
Liliaceae s. lat. see Anthericaceae, Asphodelaceae, Convallariaceae, Dianellaceae, Hemerocallidaceae, Hyacinthaceae and Liliaceae s. str.	
Liliaceae s. str.	
Fritillaria ruthenica Wikstr. (E. N.)	–
Tulipa iliensis Regel	–
Marantaceae	
Donax canniformis K. Schum.	–
Najadaceae (Netolitzky 1926)	+
Orchidaceae	
Calanthe veitchii hort. (Poddubnaya-Arnoldi 1952)	+
Coelogyne cristata Lindl. (Burgeff 1932)	+
flaccida Lindl. (Burgeff 1932)	+
Cypripedium sp. (Poddubnaya-Arnoldi 1956)	–
Dendrobium nobile Lindl. (Poddubnaya-Arnoldi 1952)	+
Dendrochilum sp. (Pfitzer 1899, Netolitzky 1926)	+
Orchis latifolia L. (Pfeitzner 1880)	+
Platyclinis sp. (Rendle 1930)	+
Palmae (=Arecaceae)	
Archontophoenix cunninghamianus D. Don	–
Areca catechu L.	–
Arenga pinnata Merr.	–
Phoenix roebelenii O'Brien	–
Sabal sp.	–
Socratea durissima H. Wendl.	–
Trachycarpus excelsus H. Wendl.	–
Veitchia joannis H. Wendl.	–
Zalacca edulis Blume	–
Poaceae	
Agropyrum elongatum (Host) Beauv. (Poddubnaya-Arnoldi 1952)	–
intermedium (Host) Beauv. (Poddubnaya-Arnoldi 1952)	–
repens (L.) Beauv. (E. N.)	–
sativa L. (E. N.)	–
Briza maxima L.	–
Clinelymus sibiricus (L.) Nevski	–
Cynodon dactylon (L.) Pers. (E. N.)	–
Dactylis glomerata L.	–
Melica nutans L. (E. N.)	–
Paspalum sp.	–
Sorghum sp.	–
Triticum aestivum L. (Poddubnaya-Arnoldi 1952)	–
durum Desf. (Poddubnaya-Arnoldi 1952)	–
Potamogetonaceae incl. Zannichelliaceae	
Potamogeton crispus L.	–
nutans L. (E. N.)	–
Zannichellia palustris L.	–
Ruscaceae	
Danaë racemosa (L.) Moench	–
Ruscus aculeatus L.	–
ponticus Woron. (E. N.)	–
Scheuchzeriaceae	
Scheuchzeria sp. (Netolitzky 1926)	+
Sparganiaceae	
Sparganium polyedrum Aschers. et Graebn. E. N.)	–
Trilliaceae	
Paris sp.	–
Typhaceae	
Typha angustifolia L. (E. N.)	–
latifolia L. (E. N.)	–
Zannichelliaceae see Potamogetonaceae	
Zingiberaceae	
Zingiber sp.	–

The taxonomic significance of chlorophyllous embryos in angiosperm seeds

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Evidence presented by Yakovlev & Zhukova 1980 in the article "Chlorophyll in embryos of angiosperm seeds, a review" is discussed. The data are illustrated in the angiosperm diagram from Dahlgren 1975.

A clear tendency of chlorophyllous embryos to occur in non-endospermous seeds is pointed out. This may be related to the fact that chlorophyll production is at least normally dependant on a certain amount of light, and consequently chlorophyllous embryos would be exposed to light at least for some period of their development. A chlorophyllous embryo is found more or less regularly in seeds of the orders Fabales, Geraniales, Capparales, Malvales, Cistales, Plumbaginales and Salicales (Dicotyledons) and in Orchidales, Arales and Najadales (Monocotyledons). This is also the case in a certain proportion of the taxa of Rutales, Sapindales, Polygalales, Santalales, Celastrales, Rhamnales, Dipsacales and Cornales but less frequently in Solanales, Myrtales, Theales and Caryophyllales. Certain pairs of allied orders and families are pointed out which differ from each other in this attribute. Thus the investigated taxa of Fabales have chlorophyllous embryos but not those of Rosales, even when these are endospermless. Similar differences are found between Plumbaginales and Polygonales, Convolvulaceae and Solanaceae, Asclepiadaceae and Apocynaceae, Cistaceae and Dilleniaceae, Valerianaceae and Caprifoliaceae, etc. In some cases the difference is related to the amount of endosperm in the seeds but this is not always the case.

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This brief account is based on information presented in the preceding article by Yakovlev & Zhukova (1980).

These authors have asked me to illustrate the occurrence of chlorophyllous embryos using the diagram presented by me (Dahlgren 1975 a) with a note on the possible taxonomic significance of the character, and I gratefully comply. Consequently the present article serves as a contribution to the series of articles entitled: "The distribution of characters within an angiosperm system" (see Dahlgren 1975 b, Jensen & al. 1975, Behnke & Dahlgren 1976, Dahlgren 1977, etc.).

Yakovlev & Zhukova (1980) present information on embryos from 1,094 species distributed among 666 genera in 188 families. The embryos of 428 species of 224 genera in 72 families proved to contain chlorophyll.

In spite of the extent of the material there are still, however, important gaps in our knowledge and this character has not yet been studied in orders such as Casuarinales, Droserales, Gunnerales, Myricales, Podostemales and Sarraceniales. They have therefore been left blank but with question-marks in the diagram (Fig. 1). The diagram should preferably be studied in conjunction with the Table in Yakovlev and Zhukova's article.

The over-all pattern of distribution seen in Fig. 1 indicates that seeds with chlorophyllous embryo are scattered throughout the angiosperms and have evolved in many unrelated groups.

Dicotyledons

Looking at the distribution of seeds with a chlorophyllous embryo (Fig. 1) the immediate impression is that they are concentrated to a great extent on groups without endosperm, e.g. Fabales, Capparales and Geraniales, although this is not always the case. They are also largely absent in groups with copious endosperm and/or a massive nucellar cap, such as in Magnolianae and Ranunculanae. This raises the question as to the conditions for chlorophyll synthesis in the embryo of an angiosperm seed. Exposure of the embryo to a certain amount of light during the development should be one of the decisive, maybe the essential, requirement for the formation of chlorophyll, although there are certain cases where Yakovlev and Zhukova suspect that chlorophyll can be formed without light, as in *Nelumbo*. It should be stressed here that these authors have studied the embryos in the course of their development and have not only recorded the presence of chlorophyll in the embryo in mature seeds. Actually chlorophyll can be formed but disappear when the seeds ripen; such embryos are recorded as being chlorophyllous.

If light is normally of decisive importance for chlorophyll synthesis in embryos, then the expected consequence would be that a chlorophyllous embryo had not been permanently enclosed either by a thick ovary wall (pericarp) or by a compact endosperm or perisperm developed ahead of the embryos or by thick integument(s) or nucellus tissue which could absorb the light. Pigment in the protecting envelopes would also be important. Moreover, all stages from the few-celled embryos to the mature seed should be taken into consideration. Whether access to light can account for the phenomenon at large is uncertain and makes a more thorough experimental investigation particularly urgent (see Yakovlev & Zhukova 1980).

Considering the above, I will proceed to describe the distribution of seeds with a chlorophyllous embryo. This was observed in some (but not all) species of Nymphaeales, which is indeed worth noting as it is enclosed by a certain amount of endosperm (the even more extensive perisperm, however, does not cover the embryo but is located below it).

Consequently among the ‘primitive’ superorders Magnolianae, Ranunculanae and Nymphaeanae, chlorophyllous embryos are rare. This is also the case in other large complexes, e.g. most or all Hamamelidanae, including orders such as Hamamelidales and Fagales, the latter mostly with the endosperm wholly consumed in the mature seed, which is notable and in conflict with the above remarks.

Seeds almost constantly with non-chlorophyllous embryo also occur in Dilleniales (incl. *Paeonia*) (endosperm-rich) and Rosales (where the ripe seeds are generally endospermless). The difference between Rosales and Fabales the latter of which has a chlorophyllous embryo is conspicuous and possibly indicates that the affinities are not as close as is often presumed.

In the Dillenianae the families of Malvales more or less consistently have chlorophyllous seeds. Their seeds mostly have a thin testa and although endosperm is often present this tends to be fairly thin in the ripe seeds. Cistaceae agrees with the families of Malvales and is probably best placed in this order. While the embryo may be chlorophyllous or not in Euphorbiales, it generally lacks chlorophyll in Urticales (an exception noted is *Streblus* of Moraceae). The embryo in the few seeds studied of Thymelaeaceae (Thymelaeales) were white in spite of the fact that the seeds are almost or completely endospermless.

In all the families of Violales, which generally have endospermous seeds the embryo lacks chlorophyll with the exception of some species of Violaceae. This is a notable difference from the Malvales, the importance of which cannot yet be evaluated. In Cucurbitaceae, the endospermless seeds have a chlorophyll-free embryo, which might be explained by the fact that they are embedded in a carnose, mostly indehiscent fruit. Salicaceae, with endospermless hairy seeds in small capsules, have a chlorophyllous embryo.

All taxa of Capparales investigated (incl. Tropaeolaceae) are characterized by seeds having a chlorophyllous embryo. The blank patches in this order represent families not yet investigated. It is probably no mere chance that the seeds in most Capparales are endospermless. Balsaminaceae, which is often considered to be closely allied to Tropaeolaceae as well as to the families here placed in the order Geraniales, has a non-chlorophyllous embryo in spite of the fact that the fruits are carnose, green and sometimes semitransparent and the seeds lack endosperm, while in Tropaeolaceae and Geraniales the embryo is chlorophyllous.

In the superorder Rutanae (Rutales, Polygalales, Geraniales, Sapindales, etc.) the embryo is frequently chlorophyllous (the blank parts of Polygalales representing families that have not yet been investigated). All taxa investigated in Geraniales have a chlorophyllous embryo, while

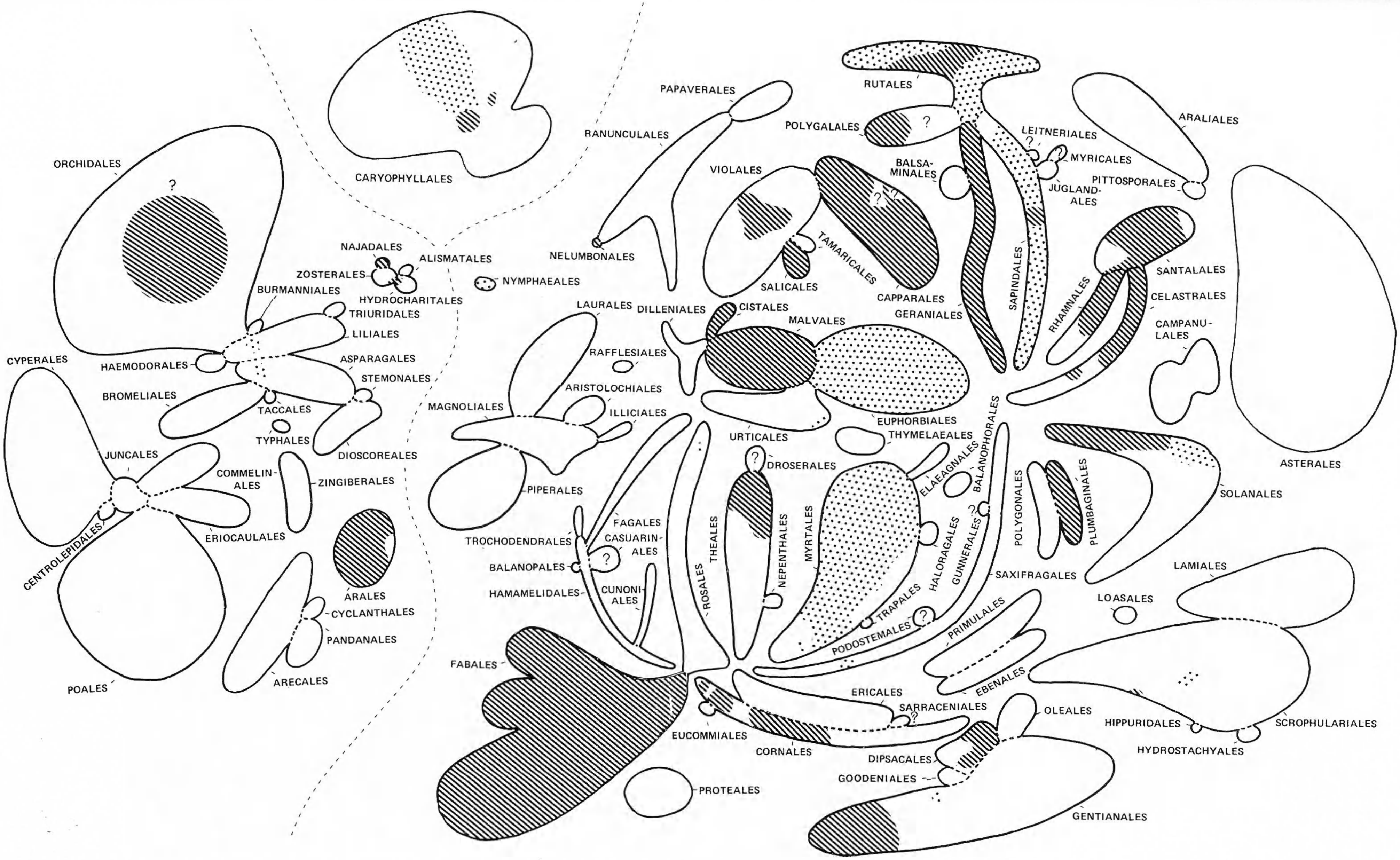

Fig. 1. Distribution of seeds with chlorophyllous embryo in the angiosperms. In this diagram each family has its specific position. Those families where chlorophyllous embryos have been recorded in all the species investigated are hatched. Those in which the embryo is sometimes chlorophyllous sometimes not, are dotted. Families which have not been investigated and those with a non-chlorophyllous embryo have been left blank. All the data on which the diagram is based have been taken from the preceding article (Yakovlev & Zhukova 1980) and this diagram should be interpreted in conjunction with the Table in this article.

in Sapindales and Rutales the embryo may or may not contain chlorophyll, such as in Anacardiaceae and Sapindaceae. Chlorophyll is lacking in the embryo of the juglandaceous seed, which is enclosed by a thick pericarp. Myricaceae has not yet been investigated.

Celastrales is no doubt a heterogeneous order in its present circumscription. Of the two large families Celastraceae has seeds with thin or hardly any endosperm and a chlorophyllous embryo, while Vitaceae has seeds with copious endosperm and a non-chlorophyllous embryo.

The investigated taxa of the orders Polygonales, Primulales and Ebenales (the last two often being regarded as related to each other) have seeds with a non-chlorophyllous embryo while those in Plumbaginales have an embryo with chlorophyll. In most of these groups the seeds have copious endosperm. This is also the case in Plumbaginaceae, where the endosperm is starchy. In spite of this the embryo is reported to be chlorophyllous.

The families of Myrtales vary somewhat in the presence or absence of chlorophyll in the embryo; in Lythraceae and Onagraceae it is completely lacking in the seeds investigated. Elaeagnaceae (Elaeagnales) agrees with these two families, and with Thymelaeaceae and Proteaceae, in lacking chlorophyll which is also the case concerning the embryo of *Myriophyllum* in Haloragaceae.

Apart from a single unspecified statement by Netolitzky (1926) for Crassulaceae, the order Saxifragales is reported to have seeds with a non-chlorophyllous embryo. Notably, the saxifragalean seeds are endosperm-rich with the exception of Crassulaceae.

In Theales, the families of which have a very variable amount of endosperm in the seed, the embryo is mostly non-chlorophyllous, an exception being the (endospermless) seed of Clusiaceae (= Hypericaceae).

Some large and probably related complexes in which all taxa seem to have seeds with a non-chlorophyllous embryo are Araliales and Pittosporales s.str., Campanulales and Asterales, the last-mentioned order having endosperm-less seeds. These orders seem to be closely related to each other for several reasons. In Solanales the seeds vary with regard to chlorophyll in the embryo. It is present in taxa of Convolvulaceae, Cuscutaceae and part of Polemoniaceae, otherwise absent.

In Santalales, the embryo which is generally embedded in endosperm and enclosed by the pericarp, with testa lacking, is still chlorophyllous, which is notable.

In the natural series of orders of Cornanae the seeds generally have non-chlorophyllous embryos embedded in copious endosperm, but in Cornales there are some families, e.g. Icacinaceae, which form notable exceptions. The seeds may or may not contain endosperm.

In the Gentiananae Dipsacales is heterogeneous, the seeds of Dipsacaceae and Valerianaceae (with and without endosperm respectively) having a chlorophyllous embryo and those of Caprifoliaceae and Morinaceae (with endosperm) having a non-chlorophyllous embryo. Likewise, in Gentianales the seeds normally have a non-chlorophyllous embryo, the exception being Asclepiadaceae, precisely that family in the order where endosperm is more or less absent in the seed.

Caryophyllales is a heterogeneous order regarding this character. Whereas in most families (incl. Phytolaccaceae) the embryo in the seeds is white, it is green in the (few) investigated taxa of Basellaceae and Nyctaginaceae and in most members of Chenopodiaceae.

Monocotyledons

In the Monocotyledons, chlorophyllous embryos are known in a few taxa of Alismatanae (*Aponogeton, Scheuchzeria, Najas*), in some of Aranae, viz. in six genera of Araceae, and in several orchids (Orchidaceae) of the Lilianae. It is notable that these are precisely those groups which have no endosperm in the mature seeds. Besides, there are a couple of other (puzzling) taxa, viz. *Haemanthus* (Amaryllidaceae) and *Tritonia* (Iridaceae) which are reported to have seeds with chlorophyllous embryo. The seeds have been studied in many taxa with copious endosperm, all except the two mentioned genera having non-chlorophyllous embryo.

Conclusion

It is obvious from the above that there is a certain but incomplete correlation between chlorophyllous embryos and lack of endosperm. Quite a number of groups having seeds with more or less endosperm do have a chlorophyllous embryo and there are also conspicuously large groups, such as Asterales, where non-endospermous seeds have a non-chlorophyllous embryo. Obviously other conditions are important for the chlorophyll formation. Whether these all influence the access of light to the embryo or not is not completely clear.

Besides the probable conclusion that various conditions influence the transmission of light to the embryo the great constancy of this character in many large groups indicates that this may reflect phylogenetic relationships to a certian degree within each of these complexes. Detailed investigations including experimental methods are highly desirable in order to elucidate these conditions

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Cyathus griseocarpus, a new bird's nest fungus from India

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Brodie, H. J. & Sharma, B. M. 1980 09 18: Cyathus griseocarpus, a new bird's nest fungus from India. *Bot. Notiser 133:* 343–345. Stockholm. ISSN 0006-8195.

Cyathus griseocarpus Brodie & Sharma from India is a rather large faintly plicate species of pale ivory to pale pink colour. A tunica and a one-layered cortex are both present. The peridioles are strongly ellipsoidal and possess a metallic grey sheen. The emplacement is broad and byssoid. The new species is believed to be most closely related to *C. bulleri* Brodie and may be the Eastern Hemisphere equivalent of the latter.

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Among collections of Nidulariaceae from the eastern Himalayan region of India, made by the junior author in 1978 and including possibly eight species of *Cyathus*, one collection consisting of thirteen fresh specimens in excellent condition appears to be a species not described heretofore. The unusual fungus is described, illustrated and named in this communication.

Cyathus griseocarpus Brodie & Sharma sp. nov., Fig. 1 A–D

Holotype: India, Ukhrul, Manipur State, on twigs and soil in mixed forest, Aug. 29, 1978, B. M. Sharma 23123 (Herbarium of H. J. Brodie, No. 78104. *Isotype*: ibid. 23123 (Herbarium of B. M. Sharma, PAN).

Cyathus griseocarpus sp. nov. Peridium pallide eburneum vel pallide incarnatum, obconicum, parietibus leviter curvatis, ore 6–8 mm latum, 8–9 mm altum basem globosam excludens; extus leviter plicatum sed non perspicue; ore non abrupte expansum; extus pilis longis retrorsis obtectum; labium minute fimbriatum et intus pallidum. Peridium intus leviter sed non distincte striatum, eburneum pallidum colore. Epiphragma eburnea, pilis longis obtecta. Basis globosa lata, byssoidea. Peridiola valde ellipsoidea, 2,5 mm longa, 1,50–1,75 lata, valde nitida grisea, tunicam ferentia. Tunica distincte visibilis sed tenua, 10–15 µm crassitie. Cortex simplex, densus, 30–40 µm crassitie. Sporae multae, parvae, pariete crassitie, subglobosae, 5,0–6,0 µm × 7,5–9,0 µm.

Habitat: in caulibus mortuis in silva; Ukhrul, India.

Peridium ivory coloured to pale pinkish buff, obconic with slightly curved sides, 6–8 mm wide at mouth, 8–9 mm high exclusive of emplacement; somewhat folded but not distinctly plicate; mouth not flaring; externally composed of a very fine-textured tomentum overlaid by conspicuous shiny golden conical tufts of down-pointing hairs, the tufts 0.50–0,75 mm wide at the base and up to 1.5 mm long. *Mouth* of peridium beset with short blunt tufts of hyphae and light coloured on the inside of lip. Peridium internally lightly but not markedly fluted, shiny ivory to silvery. Epiphragm pale ivory, beset with long tufted hairs. *Emplacement* broad, byssoid, fragile. *Peridioles* strikingly ellipsoidal in outline (2.5 mm long × 1.50–1.75 mm wide), distinctly shiny grey in colour (That of aluminium metal), provided with tunica. *Tunica* distinct but thin and easily broken, 10–15 µm thick. Cortex a single dense layer 30–40 µm thick. *Spores* abundant, small, thick walled (1.5 µm), broad ellipsoid and mostly 5.0–6.0 µm × 7.5–9.0 µm.

The specific name is given in allusion to the shiny grey metallic-coloured peridioles.

Discussion

Until tests for possible mycelial compatibility between *C. griseocarpus* and other species can be made, its relationship to them is problematic. If any one characteristic be chosen as suggesting relationship to another species, it immediately

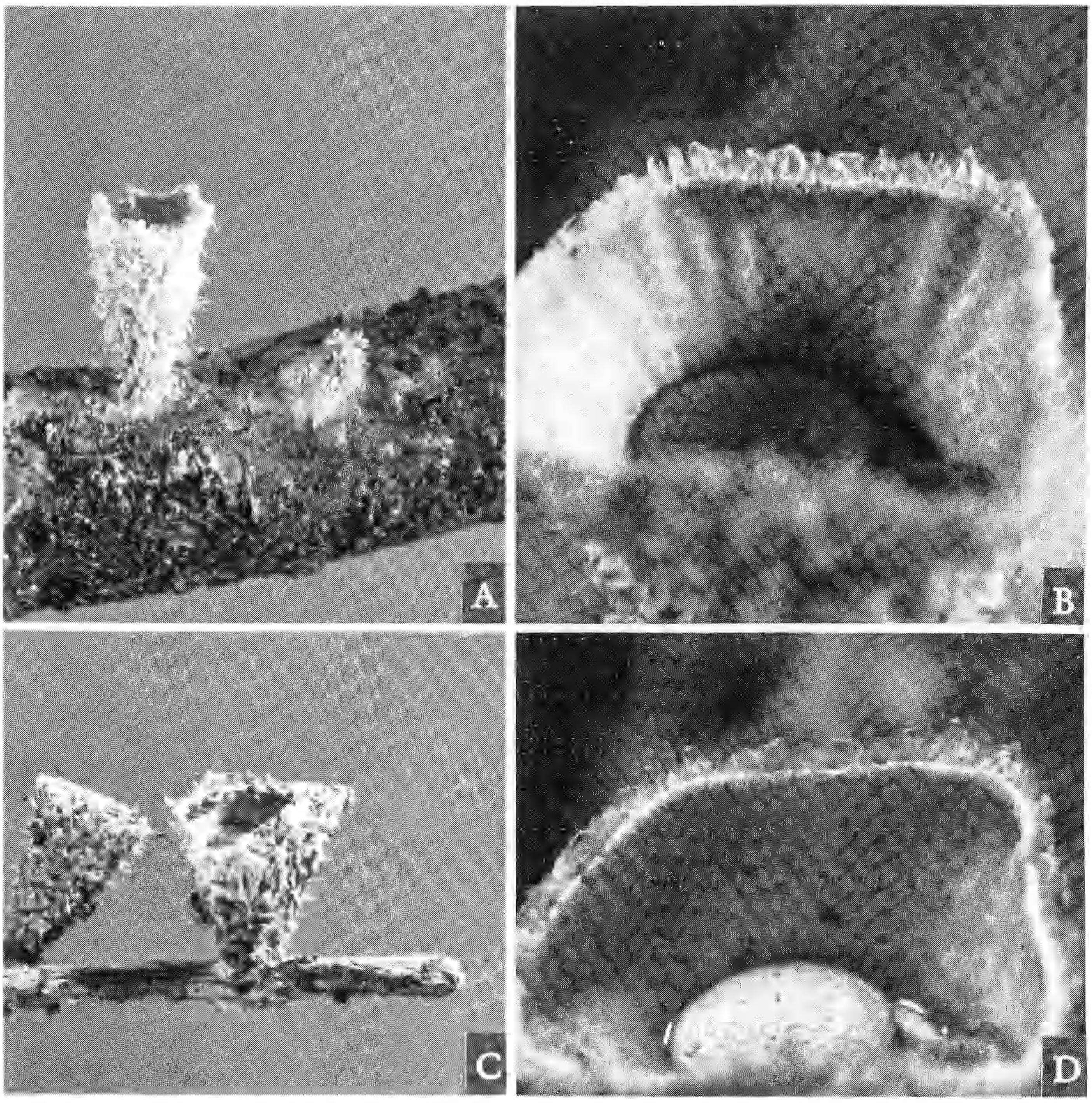

Fig. 1. *Cyathus griseocarpus* Brodie; all material from the holotype. — A: Mature and young fruit bodies on dead twig showing hairiness of peridium and loose cottony emplacement, × 2. — B: Mouth and inner surface of peridium showing light-coloured margin of lip and faint inner plication, × 10. — C: Mature peridia showing tufted hairs and unflared apex, × 2. — D: Peridium with light on a single ellipsoidal peridiole with metallic sheen, × 10.

becomes evident that the putative relatives differ strikingly from *C. griseocarpus* in some other characteristic. Take, for example, the strongly ellipsoidal peridioles (Fig. 1 D). The senior author has described (Brodie 1974) another species, namely *C. ellipsoideus*, from India, the peridioles of which are also strongly ellipsoidal. The significance of this similarity as indicating relationship is, however, made extremely doubtful when one considers that *C. ellipsoideus* has strongly plicate peridia and large ellipsoidal spores whereas *C. griseocarpus* has scarcely plicate peridia (Fig. 1 B) and small subglobose spores.

The off-white colour, curving peridium wall and long hairs (Fig. 1 A, C) of *C. griseocarpus* might suggest relationship with *C. pallidus* Berk. & Curt.; however, the latter species has much smaller and strictly non-plicate peridia. *Cyathus*

Table 1. A comparison of *Cyathus griseocarpus* and *C. bulleri*. Both descriptions from the type material in Herbarium of H. J. Brodie.

	C. griseocarpus	*C. bulleri*
Size	8–9 mm high, 6–8 mm wide	5–9 mm high, 5–8 mm wide
Shape	obconic with curved sides (Fig. 1 C, left)	obconic with curved sides
Colour	ivory to pale pinkish buff	pale grey to linen colour
Emplacement	broad, byssoid, fragile (Fig. 1, A)	small or lacking
Exterior	only faintly fluted, long down-pointing hairs (Fig. 1 A, C)	strongly plicate, long down-pointing hairs
Interior	faintly fluted (Fig. 1 B) ivory to silvery	plicate, silvery
Lip	with short blunt tufts of hyphae (Fig. 1 B)	smooth or minutely fimbriate
Peridiole	strikingly elliptical, 2.5 mm × 1.50–1.75 mm (Fig. 1 D)	some slightly elliptical, 2.0–2.5 mm
Tunica	thin, shiny, metallic grey	thick, silvery
Cortex	single	single
Spores	broad ellipsoid, thick walled, 5.0–6.0 μm × 7.5–9.0 μm	spherical to subglobose, thick walled, variable 5.0–8.5 μm

bulleri Brodie (1967) is another almost white species, but has strongly plicate peridia. Despite this difference in plication, when all the commonly-used morphological features are considered, it appears that the highest degree of concordance of several features is between *C. griseocarpus* and *C. bulleri*, the latter being a species at present known to occur only in the American tropics (Brodie 1967). *C. bulleri*, is considered to be most closely related to *C. berkeleyanus* (Tul.) Lloyd.

Table 1 presents a point-by-point comparison of *C. griseocarpus* and *C. bulleri*. Although it has many characteristics in common with *C. bulleri, C. griseocarpus* differs clearly from *C. bulleri* in being somewhat larger, in its very pale ivory to pale pinkish colour, in having a broad byssoid emplacement, in being only faintly plicate, in having strongly ellipsoidal metallic-gray peridioles and in having conspicuous, glossy, conically-tufted peridium hairs.

It may well be that *C. griseocarpus* is the Eastern Hemisphere equivalent of *C. bulleri*.

Acknowledgement. The photographs reproduced herein were taken by Mr. H. F. Dietrich, Department of Biology, University of Victoria, to whom the authors express their thanks.

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The identity of the Ethiopian monotypic genus Tzellemtinia Chiov.

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Friis, I. & Vollesen, K. 1980 09 18: The identity of the Ethiopian monotypic genus Tzellemtinia Chiov. *Bot. Notiser 133:* 347–349. Stockholm. ISSN 0006-8195.

The monotypic genus *Tzellemtinia* Chiov. was described from material collected in the Begemder Province of Ethiopia, and has hitherto been referred to Rhamnaceae. The type material of the only species, *T. nervosa* Chiov., has been examined and found to belong to the widespread African species *Bridelia scleroneura* Muell. Arg. (Euphorbiaceae). The generic name *Tzellemtinia* Chiov. must therefore be treated as a synonym of *Bridelia* Willd. *Bridelia scleroneura* Muell. Arg. is shown to be widespread on the western escarpment and in the deep valleys of the Ethiopian plateau.

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Chiovenda described the new genus *Tzellemtinia,* together with its only species *T. nervosa,* whilst working on his own collections made during a trip to N Ethiopia in 1909 (Chiovenda 1911 pp. 55–56). The new taxon was published with detailed descriptions indicating that the plant was a small tree with alternate leaves and minute flowers in the leaf axils. The specific epithet referred to the marked reticulate nervation on the underside of the leaves. The flowers were said to be hermaphroditic with a short, five lobed calyx and very small subspathulate petals of the same length as the five stamens. The ovary was embedded in the disc and had two short entire styles. The fruit was a drupe with two pyrenes. Chiovenda suggested that the genus was closest to *Scutia* in the tribe Rhamneae of Rhamnaceae, differing from that genus in having alternate leaves of thick texture and reticulate nervation, and by the non undulate disc.

The genus *Tzellemtinia* was accepted by Pilger and Krause for the fourth 'Nachträge' of Engler and Prantl's 'Natürlichen Pflanzenfamilien' (Pilger & Krause 1915 p. 192), and by Süssenguth for the second edition of that work (Süssenguth 1953 p. 85). It has been included in the latest edition of Willis' Dictionary of Flowering Plants and Ferns (Airy Shaw 1973), and by Cufodontis in his enumeration of Ethiopian plants (Cufodontis 1958 p. 502). In an article on S Ethiopian plants collected by a German anthropological expedition Cufodontis referred a collection made by Kuls (Kuls 570; FR) in Sidamo Province to the species *Tzellemtinia nervosa* Chiov. (Cufodontis 1960 p. 374).

The type material of *Tzellemtinia nervosa* Chiov. has been examined by the present authors and found to be identical with material of *Bridelia scleroneura* Muell. Arg. (Euphorbiaceae), particularly specimens from C Kenya.

A close study of the diagnoses of *Tzellemtinia* and its only species shows how the misunderstanding may have come about: male flowers are much more numerous in *Bridelia* than female ones, and Chiovenda must have mistaken the male flowers for being bisexual. The male flowers do, when thus misinterpreted, show a certain similarity with the flowers of Rhamnaceae. The styles of the female flowers of *Bridelia scleroneura* are bifid, as is normal in Euphorbiaceae, while the rudimentary ovary of the male flowers has simple styles as in Rhamnaceae. The very short spathulate petals and the flat, prominent disc are also characters which the male flowers of *Bridelia* share with Rhamnaceae, while the very large conical disc and the almost completely immersed ovary of the female flowers of *Bridelia* are totally unlike anything found in Rhmanaceae. A further reason for confusion could be that the androphore of *Bridelia scleroneura* is very short (about 1 mm long) and has obviously been overlooked by Chiovenda.

The new synonymy of the genus *Bridelia* and the species *B. scleroneura* can be summarized in the following way:

Bridelia Willd.
Willdenow 1806 p. 978.

Types: *Bridelia montana* (Roxb.) Willd., *Bridelia scandens* (Roxb.) Willd. (=*B. stipularis* (L.) Blume), *Bridelia spinosa* (Roxb.) Willd. (=*B. retusa* (L.) Spreng.); syntype species.

Syn. nov.: *Tzellemtinia* Chiovenda 1911 p. 55. Type: *Tzellemtinia nervosa* Chiov.; holotype species.

Bridelia scleroneura Muell. Arg.
Müller 1864 p. 515.

Orig. mat.: Nigeria; Onitsha, Barter 577 (K, syntype); Nupe, Barter 908 (K, syntype).

Syn.: *Bridelia scleroneuroides* Pax 1893 p. 532. Orig. mat.: Sudan, Jur, Seriba Ghattas, Schweinfurth 1496, 1536 & 1844 (B, syntypes ?†, K, isosyntypes).

Syn. nov.: *Tzellemtinia nervosa* Chiovenda 1911 p. 56. Orig. mat.: Ethiopia, N Begemder Prov.; Mai Aini, Chiovenda 633, Mai Taclit, Chiovenda 721; Ceu Berr, Chiovenda 3187; Giamma River, Chiovenda 3227 (FI, syntypes).

Habitat and distribition. Bridelia scleroneura has only recently been noted from Ethiopia by Chaffey (1978), who records it from Kaffa Province and W Illubabor Province. Kuls' collection originates from Omo Valley in W Sidamo Province. Also collections from Didessa Valley in Wollega Province (de Wilde 8927; C, WAG) and from the W slope of Rift Valley above Arba Minch in Gamu-Gofa Province (Gilbert, Thulin & Aweke 382; ETH, K, MO, UPS, WAG) have been seen by us. The de Wilde collection agrees well with the collections made by Chiovenda, while the collection made by Gilbert, Thulin and Aweke has less pronounced reticulate nervation and more scarce indumentum on the underside of the leaves.

The Chiovenda collections were all made in river valleys in Tzelemti District (hence the generic name) on the N flank of Semien Mts. This district is in Begemder Province. *Bridelia scleroneura* is thus distributed in a large section of the W Ethiopian provinces (Fig. 1), either on the W escarpment or in the deep valleys. According to the collectors' field notes the species occur in dry scrub or in deciduous woodland between 800 and 1650 m.

The general distribution of *Bridelia scleroneura* ranges from the Guinean Republic in W Africa (Keay 1958 p. 370) to C and S Sudan (Andrews 1952 p. 56; Wickens 1976 p. 104), and from W Ethiopia southwards to Kenya, N Tanzania and the Shaba Province of Zaire (Léonard 1962 p. 32). Throughout its range the species is associated with the Sudanian type of savanna and deciduous woodland. Its distribution agrees well with the Sudanian domain of the Sudano-Zambezian region, as these are defined by Wickens (1976 p. 42, Fig. 18), although transgressing marginally into other phytochoria.

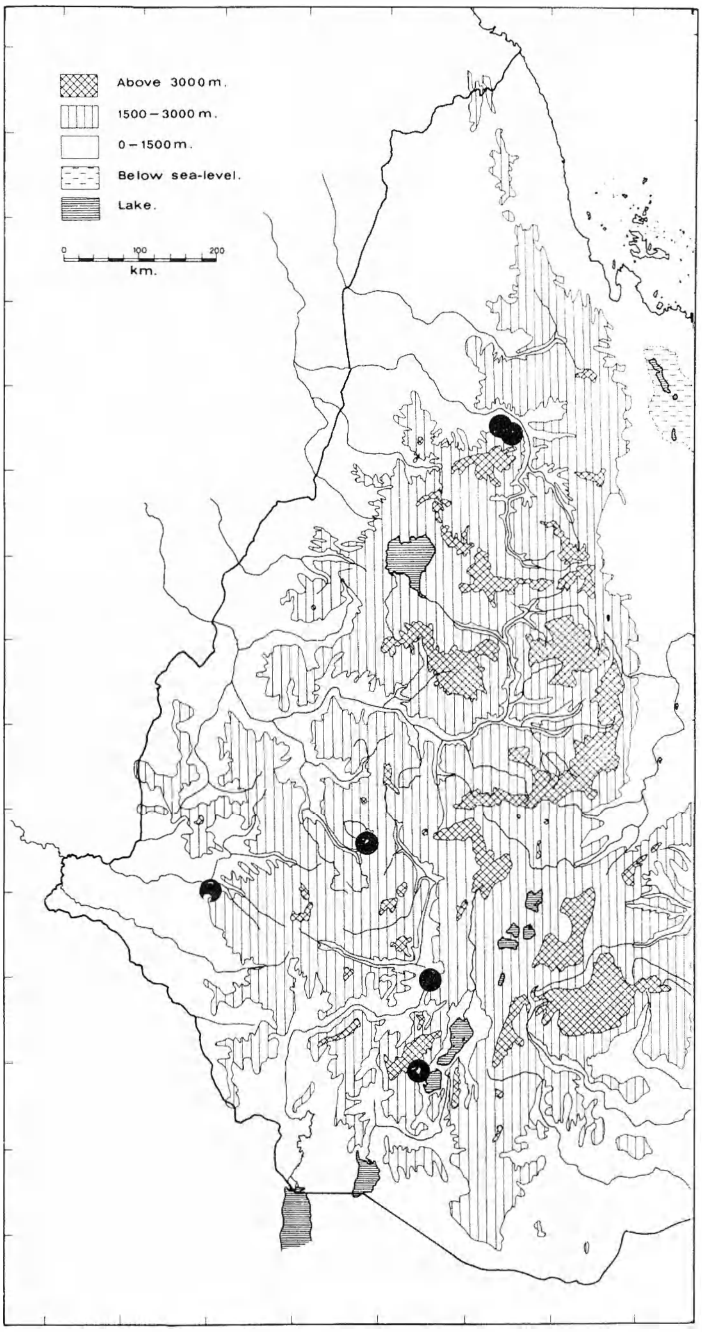

Fig. 1. Map of W Ethiopia, showing the known distribution of *Bridelia scleroneura*. — Based on the records mentioned in the text.

The occurrence of such a widely distributed

Sudanian species in the deep valleys of the Ethiopian plateau is in accordance with the observations of Thulin (1978) and lends further support to his conclusion that the large river valleys have served as migration routes far into the Ethiopian highlands for a large number of W African deciduous woodland species.

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External structure of peridium, pseudocapillitium and spores in the myxomycete genus Lycogala Adans.

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Eliasson, U. & Sunhede, S. 1980 09 18: External structure of peridium, pseudocapillitium and spores in the myxomycete genus Lycogala Adans. *Bot. Notiser 133:* 351–361. Stockholm. ISSN 0006-8195.

The results of a SEM-study indicate that the peridium ornamentation in species of *Lycogala* is due to foldings of the outermost peridial layer. This layer is identical with the slime sheath produced by and enclosing the living protoplast. A comparative study of peridium, pseudocapillitium and spores of different species sets apart *L. flavofuscum* and *L. fuscoviolaceum* as well distinguished species, while *L. conicum, L. epidendrum* and *L. exiguum* are more closely allied.

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Lycogala Adans. is a myxomycete genus with aethalioid fructifications, a pseudocapillitium of irregular, often branched tubes, and reticulate-ornamented spores. The fructifications generally have a constricted base and vary from more or less globose or conical to pulvinate. The size ranges from 1 or 2 mm in *L. conicum* and *L. exiguum* to 4 or 5 cm in *L. flavofuscum*. Five or six species are known. A doubtful species is *L. mysorensis* (Agnihothrudu 1966). It was originally described as a *Licea* (Agnihothrudu 1965). If it is really a *Lycogala*, it is unique in having (ex char.) the spore wall sculptured with blunt warts. Unfortunately it has not been possible to study the type material as requests for loan forwarded to the Mycological Herbarium of the State Agricultural College, Hebbal, Bangalore, India, have not been answered. *Lycogala* is closely related to *Reticularia* Bull., which, however, normally has pulvinate fructifications on a broad base and a more or less membranous pseudocapillitium, often frayed out into threads. Most species of *Reticularia* resemble *Lycogala* in having the spores reticulate-ornamented.

The aim of the present study is to clarify the surface structure of peridium, pseudocapillitium and spores in different species of *Lycogala*, and to determine whether possible differences might throw light upon interrelationships among, and justification of the intrageneric taxa. This is the first comprehensive SEM-study carried out in the genus. A few scattered SEM-pictures have been published previously, however. Schoknecht & Small (1972) illustrated spores and pseudocapillitium of *L. conicum, L. epidendrum* and *L. flavofuscum,* Onsberg (1972) spores of *L. fuscoviolaceum*, and Gaither (1976) spores and pseudocapillitium of *L. epidendrum*.

It should be emphasized that the present paper deals merely with surface structures. Structures within the peridium, below the outer surface of the slime layer, are not discussed.

Material and methods

The investigation was based on the following specimens:

Lycogala conicum, Sweden, Sunhede 4853 (GB) (Figs. 2 C–E, 4 D–F, 6 D);

L. epidendrum, Sweden, Sunhede 3211 (GB) (Figs. 2 F–H, 4 G–I, 5 A–C, 6 E, F);

L. exiguum, USA, New York, Long Island, Aug. 1924 (ex herb. Howard) (K) (Figs. 1 D, 3 A–H, 5 D, E, 6 G);

L. cf. *exiguum*, Sweden, 1946-08-20, Nathorst-Windahl s. n. (GB) (Fig. 5 F, G);

L. flavofuscum, Finland, Sunhede 7412 (GB) (Figs. 1 E, 3 I–K, 5 H–J, 6 H);

L. fuscoviolaceum, Nepal, Søchting 165 (holotypus, C) (Figs. 2 A, B, 4 A–C, 6 A–C, I, J).

Air dried specimens were mounted with glue and sputtered with gold-palladium. The SEM-study was performed with a JEOL JSM-1. We are grateful to Dr Leif Ryvarden, Oslo, for making it possible for us to use this instrument. All pictures were taken by Stellan Sunhede. Measurements on spore ornamentation and papillae of the pseudocapillitium are based on the SEM-pictures obtained from the above-mentioned specimens. Because of the limited material involved, the results have as far as possible been checked by light microscope studies of additional material, mainly in *L. conicum* and *L. epidendrum*. The limitation of the material has been considered upon drawing conclusions from the results obtained. Since a part of the spore wall often collapses inward in dry spores and dry spores are generally smaller than those studied in a liquid under the light microscope, it has not been regarded as meaningful to base measurements of spore diameters on the SEM-pictures. Instead the size range given for spores and pseudocapillitium is that found in the literature for determination of myxomycetes. The figures on spore size include the ornamentation.

Observations

Lycogala conicum Pers., Figs. 1 A, 2 C–E, 4 D–F, 6 D

A small species, forming conical to subglobose fructifications (Fig. 1 A) up to 2 mm broad and mostly 2–3 mm tall. The peridium generally exhibits a dark subreticulate pattern in the upper part. When typically developed it is a characteristic species.

The surface of the peridium (Fig. 2 C–E) is wrinkled, forming up to 20 μm high ridges which border fields 30–70(–100) μm across. The ridges may be intermingled and heaped into more complex patterns. The surface may bear numerous irregular pores (Fig. 2 E) 1–3 μm across.

The pseudocapillitium (Fig. 4 D–F) consists of a system of branched threads 3–8 μm thick with expansions at the ramifications. The threads appear rather smooth in the light microscope, but a system of ridges or interconnected papillae c. 0.1 μm high is revealed at higher magnification (Fig. 4 F).

The spores (Fig. 6 D) are 5–7 μm in diameter and have an ornamentation of about 0.3 μm tall ridges. The ridges form a network with quadrangular to septangular meshes averaging c. 0.7 μm across. The ridges appear thin, not exceeding 0.05 μm in thickness.

Lycogala epidendrum (L.) Fries, Figs. 1 B, C, 2 F–H, 4 G–I, 5 A–C, 6 E, F

A common and well-known species (Fig. 1 B, C). The fructifications are more or less globose or when closely massed angular from mutual pressure. They are normally 5–10 mm in diameter, but aethalia 2 mm or 15 mm or more in diameter occur. The peridium, when seen through a lens, often bears yellowish or brownish warts, but often it is almost smooth or with only diffuse thickenings.

The dark pattern of the peridium is at higher magnifications revealed to be made up by wrinkled or irregular warts (Fig. 2 G) or appressed ridges forming an inconspicuous network (Fig. 2 F). The warts are mostly 100–150 μm wide. The appressed ridges border fields mostly 50–100 μm across. A fine subreticulate pattern with meshes 2–6 μm wide may appear on the peridium (Fig. 2 H).

The pseudocapillitium (Figs. 4 G–I, 5 A–C) consists of a system of branched threads varying in thickness from 12–25 μm near the peridium down to c. 6 μm. Free tips (Fig. 4 H) are rounded and may be slightly swollen. The threads often bear transverse constrictions (Fig. 5 B, C), which may occasionally tend to form a spiral. Small rounded papillae 0.1–0.3 μm wide and sometimes interconnected by low ridges are common on the threads (Figs. 4 H, I, 5 B, C).

The spores (Fig. 6 E, F) are 6.0–7.5 μm in diameter and have a reticulate ornamentation similar to that in *L. conicum*. The ridges are 0.25–0.30 μm high and the meshes average something between 0.7 and 0.9 μm across. Like in *L. conicum* the ridges do not exceed 0.05 μm in thickness (Fig. 6 E). This figure is in accordance with the TEM-picture published by Gaither (1976) in which the ridges appear c. 0.03 μm thick.

Lycogala exiguum Morgan, Figs. 1 D, 3 A–H, 5 D–G, 6 G

An inconspicuous species, forming dark subglobose or globose fructifications mostly 2–4 mm wide (Fig. 1 D). A dark pattern normally appears at least in the upper part of the fructification (Fig. 1 D). The species is closely allied to *L. epidendrum* and has often been treated as a variety of the latter. The distinction between the two taxa is not altogether satisfactory. There have been different opinions about the identity of *L. epidendrum* var. *tesselatum* G. Lister (cf. Nannenga-Bremekamp 1962, 1974), but today it is generally agreed to be a synonym of *L. exiguum* (Martin & Alexopoulos 1969, Nannenga-Bremekamp pers. comm.).

The surface of the peridium (Fig. 3 A–H) bears numerous protuberances (Fig. 3 G) and low

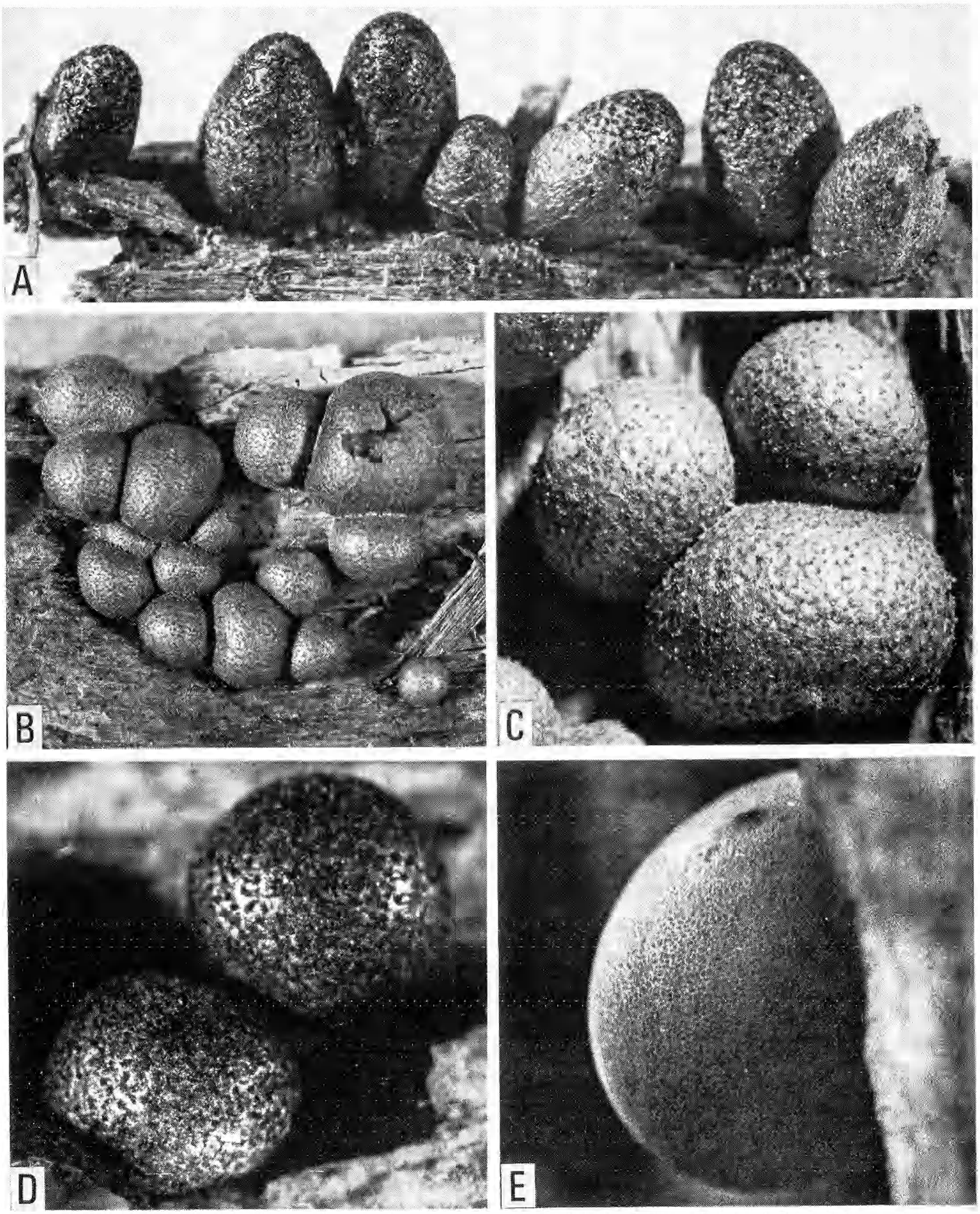

Fig. 1. Habit of different species of *Lycogala*. — A: *L. conicum* (Martinsson 1979-08-11, herb. GB) × 11. — B, C: *L. epidendrum* (Sunhede 3211, GB), B × 2.7, C × 8. — D: *L. exiguum* (USA, New York, Long Island, ex herb. Howard, K) × 18. — E: *L. flavofuscum*, fructification on wood of living *Acer*, × 2.3 (Finland, Nylandia, Fagervik, field picture by S. Sunhede 1978-08-24).

wart-like structures with folded, irregular surfaces (Fig. 3 C, D). The warts are mostly 40–70 μm wide, they are 40–80(–100) μm apart and may be interconnected by ridges (Fig. 3 A–C). The ridges may be twisted in various ways (Fig. 3 E, F).

The pseudocapillitium (Fig. 5 D–G) consists of a system of branched threads mostly 2–10 μm thick. Free ends are generally rounded and often dilated (Fig. 5 D). When seen in the light microscope the threads often appear smooth, but in the SEM-pictures an ornamentation made up by a dense network is revealed (Fig. 5 D, E). The network consists of ridges c. 0.15 μm thick. The ornamentation may be confluent so that the network is obscured (Fig. 5 F, G).

The spores (Fig. 6 G) are generally 4.5–5.5 μm in diameter and have an ornamentation of c. 0.2 μm high ridges forming a network with pentangular to septangular meshes averaging c. 0.5 μm across. The thickness of the ridges is about 0.05 μm.

Lycogala flavofuscum (Ehrenb.) Rost., Figs. 1 E, 3 I–K, 5 H–J, 6 H

This species forms the largest fructifications in the genus (Fig. 1 E). The aethalia are pulvinate to semiglobose and normally reach 2–4 cm in extent. When seen under some magnification the peridium bears a faint, whitish, reticulate pattern.

The peridium (Fig. 3 I–K) is wrinkled with numerous, regularly distributed low folds. No wart-like structures of the type observed in the preceding species have been seen.

The pseudocapillitium (Fig. 5 H–J) is much thicker and more robust than in other species of the genus. It consists of a system of branched, often irregularly expanded tubes, varying from 25–60 μm in some parts, down to c. 10 μm. Free ends are generally strongly swollen, rounded and club-shaped (Fig. 5 H, I). Papillae c. 1 μm high and sometimes interconnected are rather evenly distributed over the surface of the pseudocapillitium (Fig. 5 I, J).

The spores (Fig. 6 H) are generally 5–6 μm in diameter and bear a network of c. 0.3 μm high ridges forming pentangular to septangular meshes averaging c. 0.7 μm across. The ridges appear to be c. 0.05 μm thick.

Lycogala fuscoviolaceum Onsberg, Figs. 2 A, B, 4 A–C, 6 A–C, I, J

A species forming clustered aethalia (Fig. 2 A, B) which are subglobose and up to 10 mm in diameter. It differs from other species in the genus in its dark brown spore mass. So far it is known only from the type collection from Nepal (Onsberg 1972).

The dark brown peridium appears smooth with no conspicuous ornamentation. The SEM-pictures (Fig. 4 A–C) reveal a slightly wrinkled surface, but no big warts of the type seen in e.g. *L. exiguum* have been observed.

The pseudocapillitium (Fig. 6 A–C) consists of branched, irregular, often angular threads 10–35 μm thick. The surface bears only faint wrinkles (Fig. 6 B, C), there are no papillae or other protuberances.

The spores (Fig. 6 A, B, I, J) are generally 7–8 μm in diameter and have a rather regular reticulation with meshes averaging 0.4 or 0.5 μm across. The meshes give the impression of being more rounded than in the other species. The ridges of the reticulation are c. 0.2 μm high. On our pictures the ridges appear thicker (c. 0.08 μm thick) than in the other species studied. Since we are not sure, however, to what extent the gold-palladium sputtering may have influenced the thickness, we refrain from giving too much weight to this difference.

Taxa not included in the present study

Lycogala conicum var. *pustulatum* Thind. Known only from the type collection from W Bengal, India. Said to differ from typical *L. conicum* in "lacking reticulate marking on the cortex and in the possession of brown pseudocapillitial threads marked by faint wrinkles" (Thind 1977). Appears from the description to be close to typical *L. conicum*. Not seen by us.

L. mysorensis (Agnihothr.) Agnihothrudu. Known only from two collections from the Hassan district of Mysore State, India (Agnihothrudu 1965). As mentioned previously deviating (ex char.) from all other *Lycogala* species in having the spores sculptured with warts. A species of doubtful identity. Not seen by us.

Discussion

When seen through a dissecting microscope the peridium of *L. conicum* and *L. exiguum* normally exhibits a dark, dotted or subreticulate ornamentation. The pattern is often restricted to, or at least more prominent in the upper part of the fructification. At higher magnification the pat-

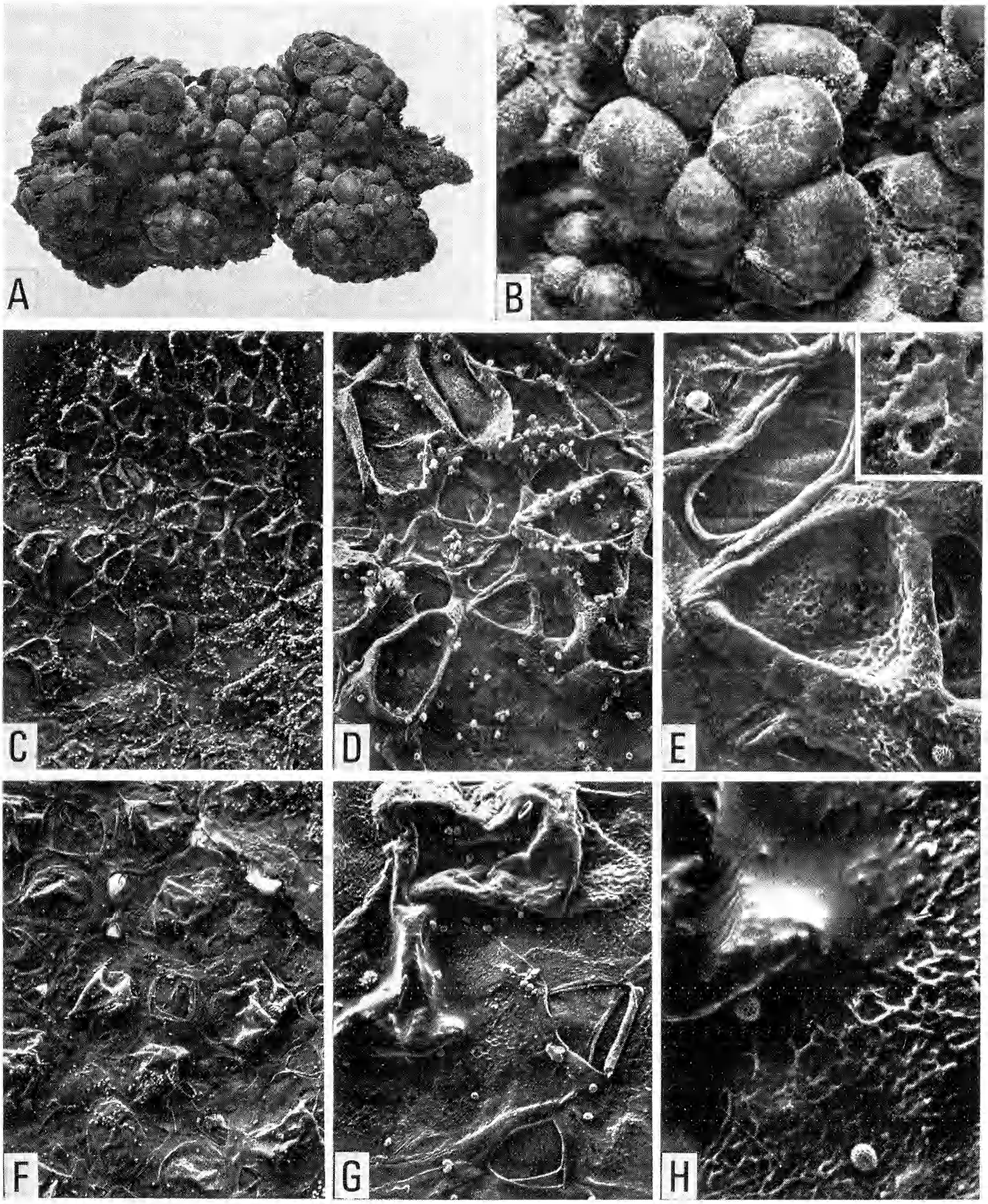

Fig. 2. A, B: Habit of *L. fuscoviolaceum* (holotype), A × 0.9, B × 3.2. — C–H: SEM-pictures of peridium of *L. conicum* (C–E) and *L. epidendrum* (F–H). — C, F, × 70; D, G, × 210; E, H × 700, E insert × 2100. — See further text.

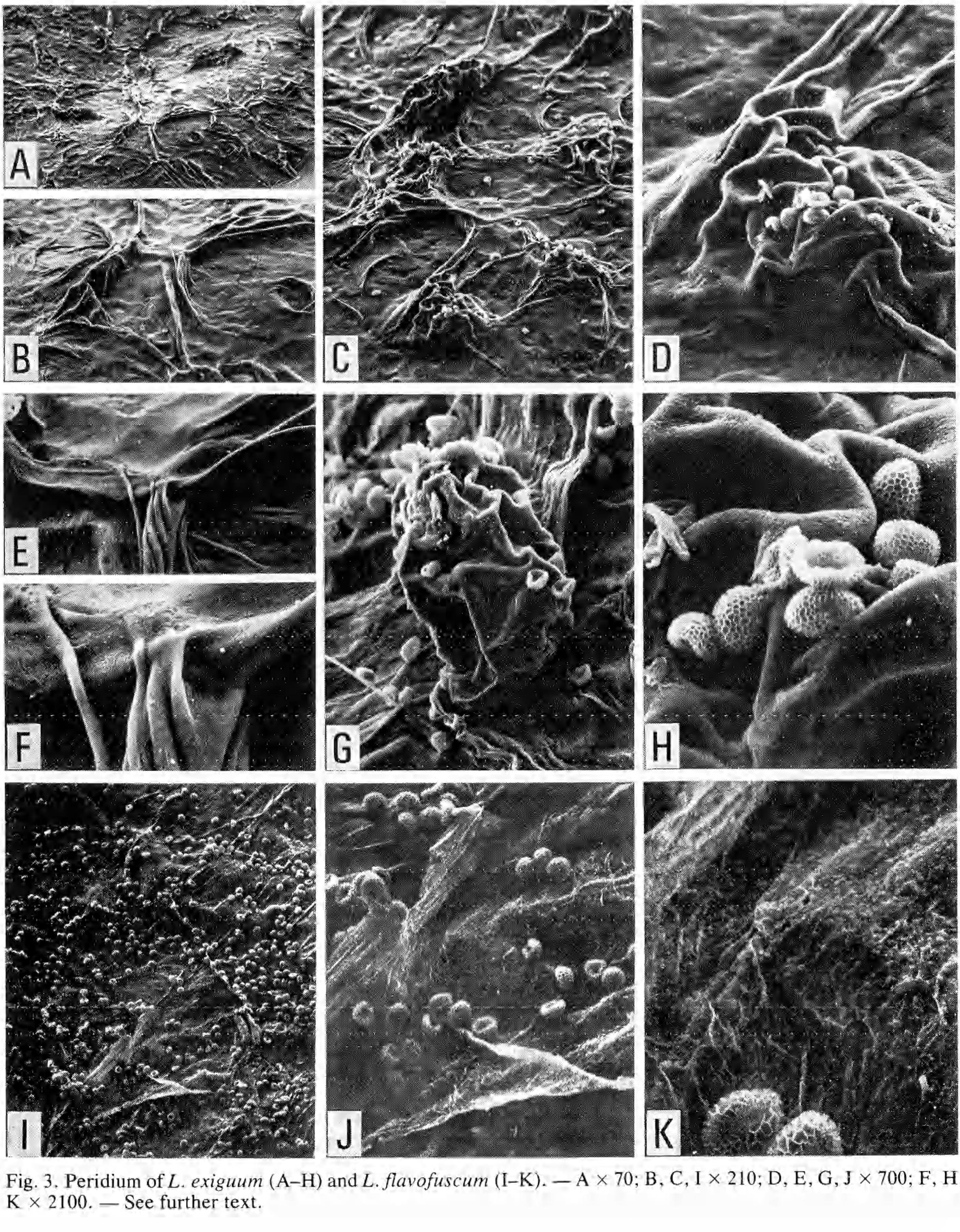

Fig. 3. Peridium of *L. exiguum* (A–H) and *L. flavofuscum* (I–K). — A × 70; B, C, I × 210; D, E, G, J × 700; F, H, K × 2100. — See further text.

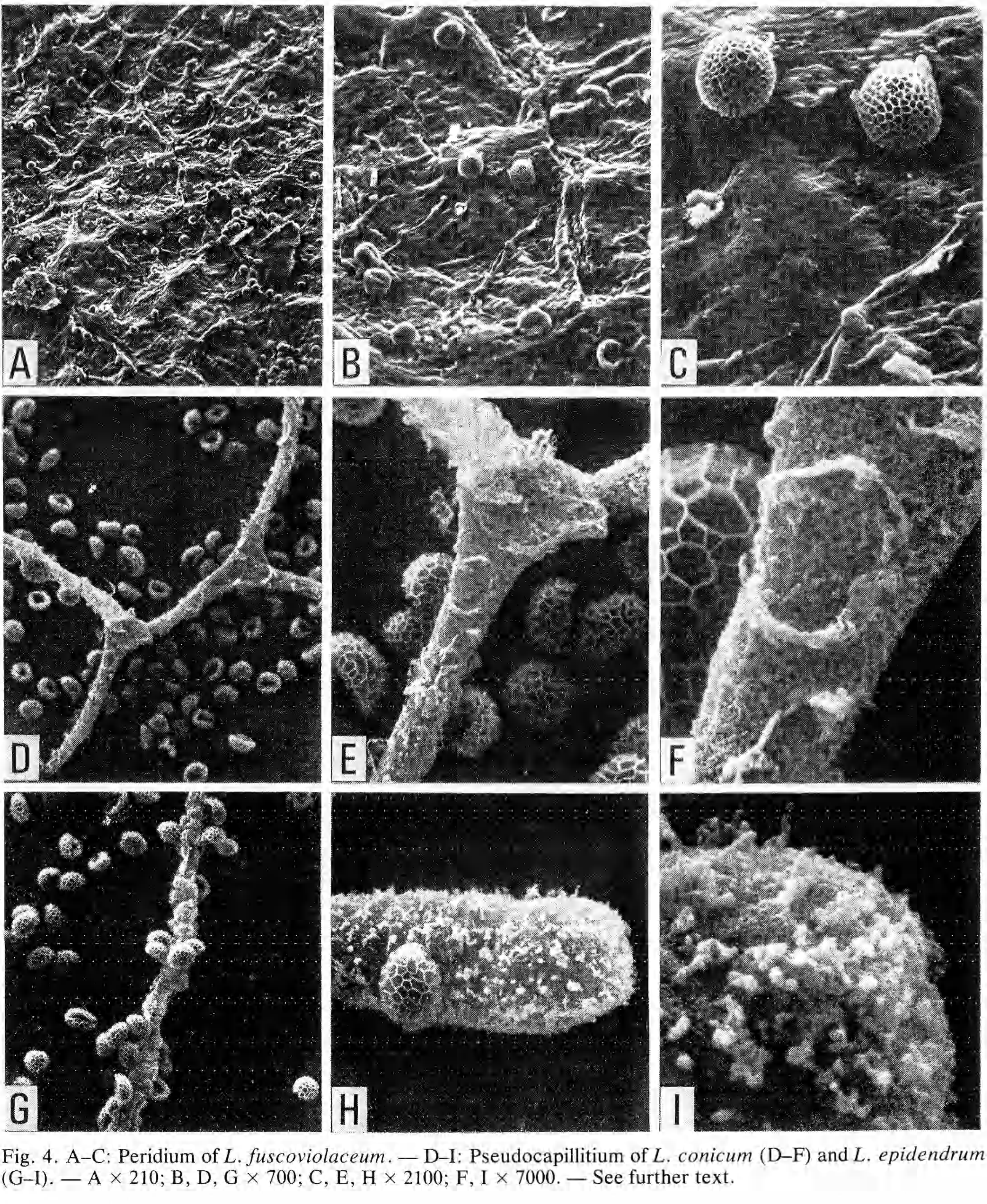

Fig. 4. A–C: Peridium of *L. fuscoviolaceum*. — D–I: Pseudocapillitium of *L. conicum* (D–F) and *L. epidendrum* (G–I). — A × 210; B, D, G × 700; C, E, H × 2100; F, I × 7000. — See further text.

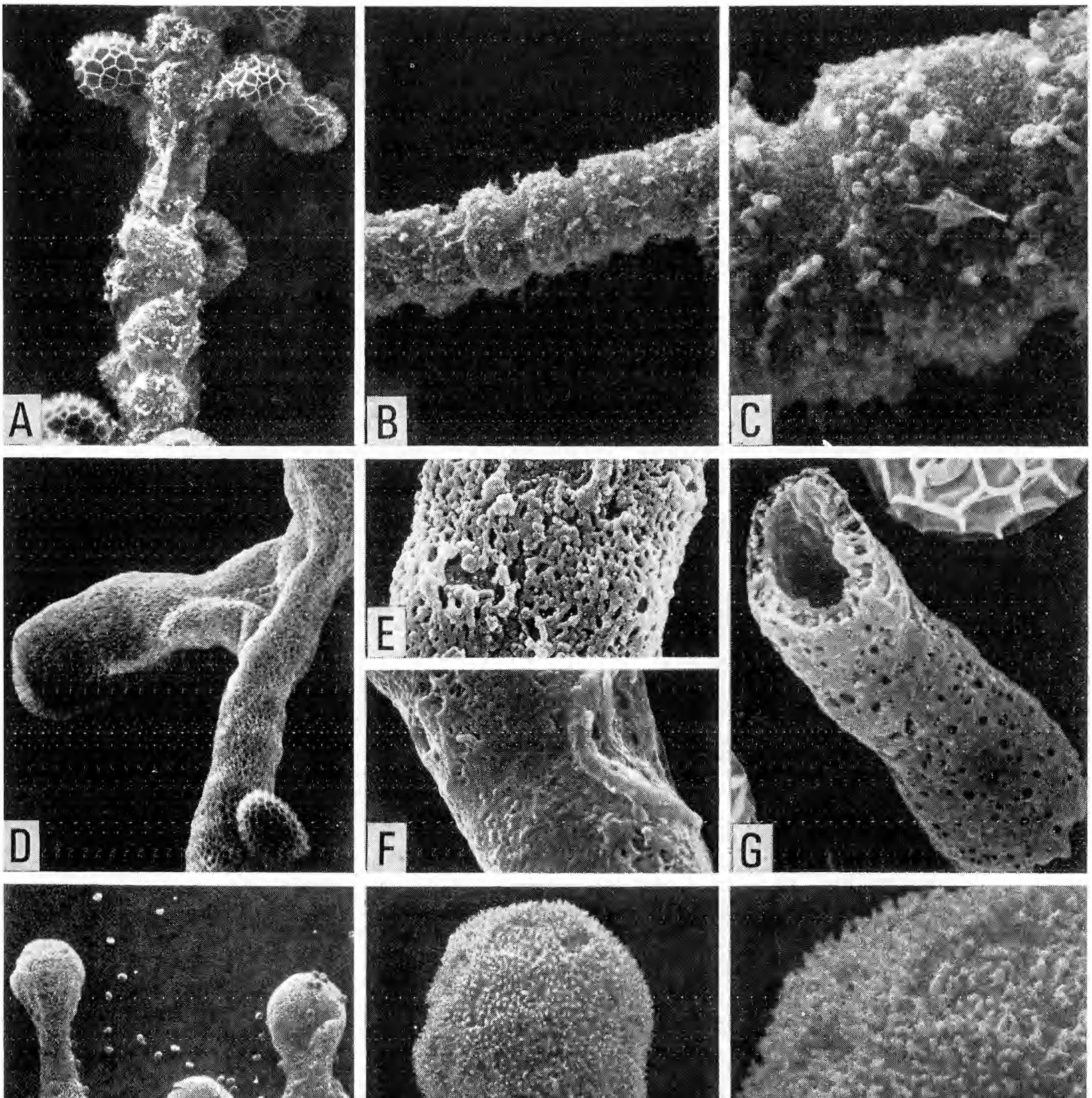

Fig. 5. Pseudocapillitium of *L. epidendrum* (A–C), *L. exiguum* (D, E), *L.* cf. *exiguum* (F, G), and *L. flavofuscum* (H–J). — A, B, D, J × 2100; C, E, F, G × 7000; H × 210; I × 700. — See further text.

tern dissolves into small protuberances, generally called warts or scales in keys and descriptions. In the SEM-microscope the protuberances are revealed to have arisen through foldings of the outermost peridial layer and their surface is confluent with that of the peridium. The protuberances may have the shape of warts or papillae which, however, are often irregularly wrinkled or folded. If a fold is so thin that the inner opposite surfaces touch each other, a structure arises that has generally been called a scale. This is attached at base and may be erect or appressed. It is thicker and appears darker near the periphery. Taken together the folds with their darker margins give the dark ornamentation to the peridium. Scales in the sense of loose flakes do not occur.

The layer forming the foldings and papillae is identical with the slime layer enclosing the living plasmodium. This layer is produced by the living protoplast and encloses it like a sheath. The protoplast moves within the sheath, continuously producing sheath material at its anterior end and leaving the empty sheath behind as it moves. When the plasmodium stops and rounds up in order to fructificate it is still enclosed in its sheath. The maturation involves loss of water and a decrease in size of the young fructification. If the slime sheath has such a composition that it cannot decrease its volume in accordance with the drying protoplast, the result will be a wrinkled and folded sheath; that is, a structure of the type seen in *Lycogala*. In *L. epidendrum* the ornamentation, if obvious at all, mostly consists of yellowish or brownish warts when seen through a dissecting microscope. However, in the SEM-microscope the warts are found to be folded and irregular and intermixed with more or less appressed foldings. Obviously these structures are homologous with the surface structures in *L. conicum* and *L. exiguum* and made up by the sheath originally surrounding the living protoplast. Due to the pattern formed by the dried slime layer the peridium may vary in appearance from warty to almost smooth, which in the latter case means with low appressed folds. In *L. flavofuscum* a reticulate whitish ornamentation is often seen. Also this pattern is the result of foldings of the slime sheath, although it seems to be more regular than in the previous species. Also in *L. fuscoviolaceum* foldings of the slime sheath occur, but they are generally too low to form a pattern detectable with a dissecting microscope. A microstructure of irregular pores or a faint reticulation has, as noted above, been observed in *L. conicum* (Fig. 2 E) and *L. epidendrum* (Fig. 2 H), respectively. However, no taxonomic conclusions should be drawn from this, since the investigation is based on very limited material and such structures may be dependent upon the conditions under which the fructification has matured and dried.

Martin (1967), in a light microscope study of the peridium ornamentation in *L. exiguum*, found that the "warts" begin as pustular bodies with homogeneous contents. The contents gradually break up into smaller units so that a tesselate stage is attained. Such "tesselated warts" were illustrated by Martin and have been found to be beautifully developed in the fructification included in this study. The tesselation, however, is an internal structure, easily seen in the light microscope but not resulting in any external pattern detectable in the SEM. The tesselation gives rise to internal chambers or vesicles about 25 μm in diameter. As expressed by Martin (1967) their appearance gives the impression of that of "a viscous semiliquid substance dividing into segments as it dries, with each segment forming a hyaline sheath surrounding the thickened contents". Martin found a continuous series from specimens with warts with homogeneous contents to specimens with tesselate warts. He also found that spore maturity and dehiscense of the fructification could occur at any stage of development of the warts. This supports our view that the vesicles are structures formed within the slime sheath surrounding the fructification.

The structure of the pseudocapillitium has for most species of *Lycogala* been described as "wrinkled, papillose or nearly smooth". Transverse thickenings or wrinkles may be noted in most species but are most prominent in *L. epidendrum*, where they occasionally may tend to form a spiral (Fig. 5 B). Papillae have been noted in all species studied, except in *L. fuscoviolaceum* where the surface is devoid of protuberances when seen in SEM (Fig. 6 A–C). The papillae seen in *L. epidendrum* are in the range of 0.1–0.3 μm high. They are unevenly distributed and sometimes closely grouped but also uneven in shape and often forming ridges rather than papillae (Figs. 4 I, 5 C). The papillae observed in *L. conicum* are smaller than those seen in *L.*

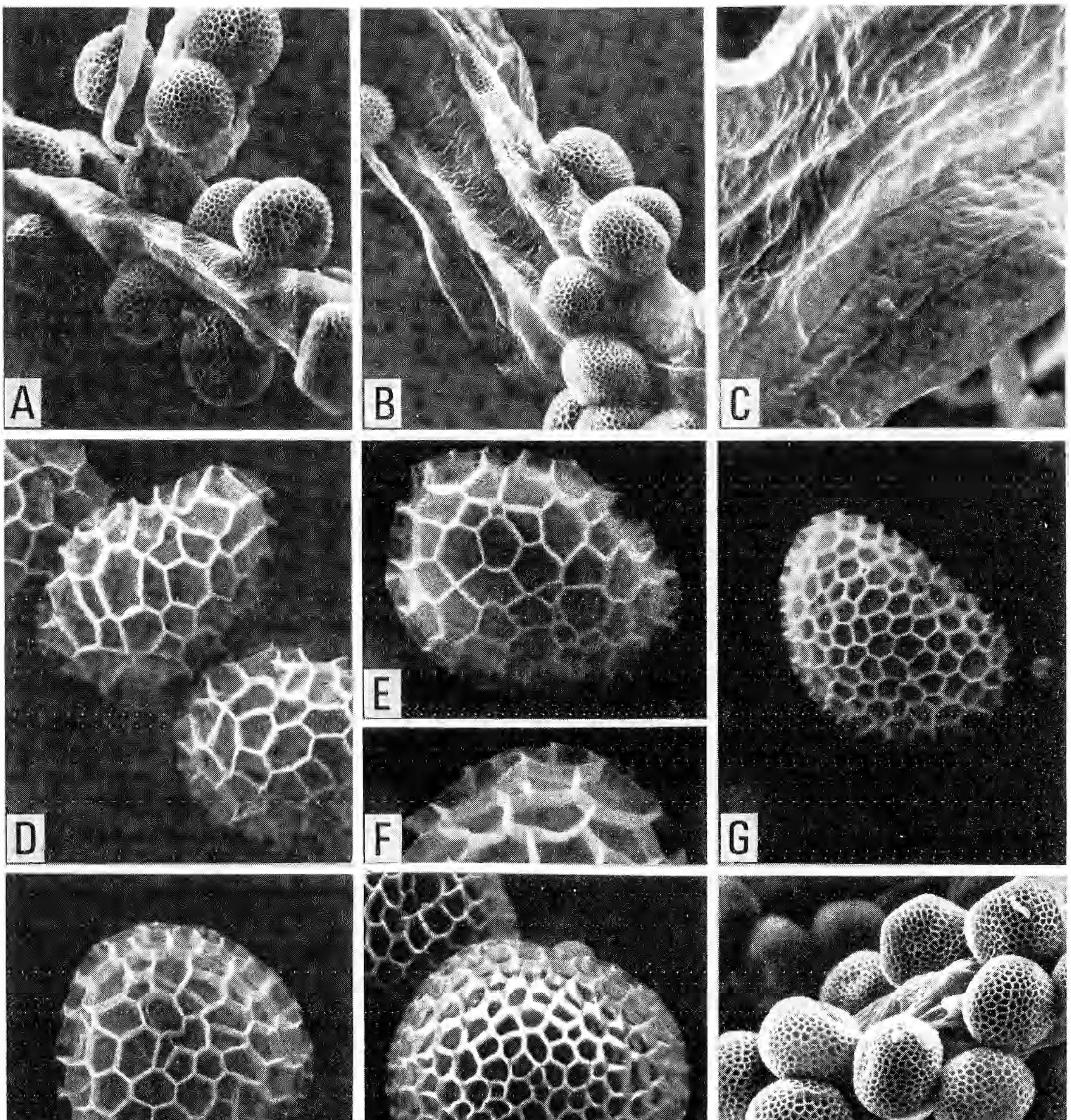

Fig. 6. A–C: Pseudocapillitium and spores of *L. fuscoviolaceum*. — D–J: Spores of *L. conicum* (D), *L. epidendrum* (E, F), *L. exiguum* (G), *L. flavofuscum* (H), and *L. fuscoviolaceum* (I, J). — A, B, J × 2100; C–E, G–I × 7000; F × 10500. — See further text.

epidendrum and do not exceed 0.1 μm. In *L. exiguum* the pseudocapillitium has often been described as almost smooth. The SEM-pictures reveal a reticulate ornamentation (Fig. 5 D–G) about 0.15 μm high. Thus the ornamentation has about the same height as that of *L. conicum* and *L. epidendrum*. Apparently the structures are homologous. The papillae may be regarded as remnants of a network or the network as a result of coalescence of papillae. The papillae may be interconnected or confluent in their apical parts, so that the outer part of the pseudocapillitial wall appears bilayered in transection, with trabeculae connecting the layers (Fig. 5 G). Also in *L. flavofuscum* papillae occur and are relatively evenly distributed (Fig. 5 I, J). However, these papillae are large, reaching about 1 μm in height (Fig. 5 J; note the different magnification as compared to e.g. 5 C, F, G). On the whole the pseudocapillitium is much coarser in *L. flavofuscum* than in the other species of the genus.

The fructifications of *Lycogala* are generally interpreted as aethalia, a type of fructification believed to have arisen phylogenetically through coalescence of sporangia. The capillitium is accordingly regarded as a pseudocapillitium, which means that it is regarded as phylogenetically homologous with sporangial walls. Although cases exist among the myxomycetes where such an interpretation is reasonable and likely, many cases are dubious, and the correctness of applying the terms "aethalium" and "pseudocapillitium" is often far from obvious. The terms have been used here in accordance with common custom in the genus. Capillitial structures are very variable in myxomycetes, and the results obtained in this SEM-study hardly permit conclusions about the phylogenetic origin of the fructifications.

With the exception of the dubious *Lycogala mysorensis*, all species in the genus have reticulate-ornamented spores (Fig. 6 D–J). As concerns ornamentation, spores of *L. conicum* (Fig. 6 D), *L. epidendrum* (Fig. 6 E, F) and *L. flavofuscum* (Fig. 6 H) are rather similar. All have meshes averaging 0.7–0.8 μm, the ridges are 0.25–0.30 μm high and do not exceed 0.05 μm in thickness. Spores of *L. exiguum* (Fig. 6 G) are, as observed also in the light microscope, generally smaller with smaller meshes. In the specimen studied here the meshes average c. 0.5 μm, the ridges are c. 0.2 μ high and do not exceed 0.05 μm in thickness. The most deviant species concerning spore ornamentation is *L. fuscoviolaceum* (Fig. 6 A, B, I, J). The meshes are small, on an average 0.4 or 0.5 μm across, and give the impression of being more rounded than in the other species. The height of the ridges is c. 0.2 μm.

From a taxonomic point of view this SEM-study sets apart *L. fuscoviolaceum* as a very distinct species. The peridium lacks warts and high ridges, the pseudocapillitium is devoid of ornamentation, and the spores are characteristic with small, somewhat rounded meshes. *L. conicum* and *L. epidendrum* are mutually rather similar in peridium, pseudocapillitium, and spore ornamentation. *L. exiguum* is allied to them in the structure of the peridium; differences have been recorded in the ornamentation of the pseudocapillitium and in the size of the spore meshes, but these differences might have been obscured if a larger amount of material of *L. exiguum* had been at hand. *L. flavofuscum* has a relatively smooth peridium without warts and high ridges. The spores are similar to those of *L. conicum* and *L. epidendrum*, but its pseudocapillitium is different, being coarser and provided with much larger papillae than in the other species.

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The genus Calceolaria in NW South America

V. New taxa in the sections Lehmannina and Dermatophylla

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Two taxa of *Calceolaria* (Scrophulariaceae) from Ecuador are described as new, viz. *C. cataractarum* (sect. *Lehmannina*), and *C. pedunculata* Molau subsp. *sumacensis* (sect. *Dermatophylla*). The pollination ecology of the species of sect. *Lehmannina* is discussed. The chromosome number 2n=36 is reported for *C. cataractarum, C. lehmanniana* Kränzlin, and both subspecies of *C. pedunculata.*

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During an expedition to Ecuador in 1979, in which the author participated, the genus *Calceolaria* was extensively collected. Within the rich material (more than 200 collections of the genus) two collections turned out to represent new taxa belonging to sections earlier revised in this series. On the other hand it is noteworthy that, although several botanically very poorly known areas were visited, no other new species were found. Thus, the present revision of *Calceolaria* in NW South America probably comprises most of the species actually growing in Ecuador. Narrow endemics in botanically unexplored areas may, however, still be found in the future.

Calceolaria cataractarum Molau spec. nov. (sect. Lehmannina)

Orig. coll.: Løjtnant, Molau & Madison 12316 (GB holotype, AAU; cultivated at GB).

Illustrations. Fig. 1.

Differt a Calceolaria lehmanniana pedunculis et pedicellis flavo-virentibus, et corolla lutea cum elaeophoro.

Robust, ascending, perennial *subshrub,* 0.5–1.0 m high, with the flowering branches herbaceous. Inflorescence and younger stems velutinous with brownish hairs. *Leaves* sessile, decussate; blades lanceolate or elliptic, 7.2–9.3×1.9–2.5 cm (up to 17×7 cm in culture), acute, cuneate at base; yellow-green above, velutinous; brownish to yellowish green beneath, reticulate-venose, velutinous on the major veins, interspaces pilose to villous with gland-tipped hairs; margins serrate, revolute and appearing crenate. *Inflorescence* distal, comprising 1(–2) pairs of 12–62-flowered cymes on greenish-yellow primary peduncles 8.5–17.0 cm long. Cyme bracts present. Pedicels 0.5–1.8 cm. *Sepals* greenish-yellow (turning brown with age), triangular or lanceate, acute and slightly caudate, 5.3–6.2×2.5–3.2 mm at anthesis, externally glandular-pilose, internally glandular-puberulous. *Corolla* deep yellow, externally minutely glandular-puberulous; upper lip arched, 5–7×8–10 mm; lower lip somewhat pendent to almost projecting, 10–14×8–11 mm, saccate in c. 1/3 of its length, internally possessing a well-developed elaiophor (= an oil-producing tissue on the infolded lobe at the distal end of the orifice, consisting of a dense tuft of pluricellular gland-hairs; see Vogel 1974), orifice exposed. *Anthers* brown, glabrous, 2.8–3.0 mm, opening throughout; thecae divaricate, elliptic, equal. *Filaments* c. 0.8 mm. *Style* 2.0–2.5 mm, straight or slightly curved. *Capsule* subglobose, 5–7 mm long, glandular-tomentose.

Chromosome number. 2n=36. Voucher: Løjtnant, Molau & Madison 12316 (AAU, GB).

Habitat. Seasonally inundated cliffs along stream at waterfall, in cloud forest; altitude c. 2600 m.

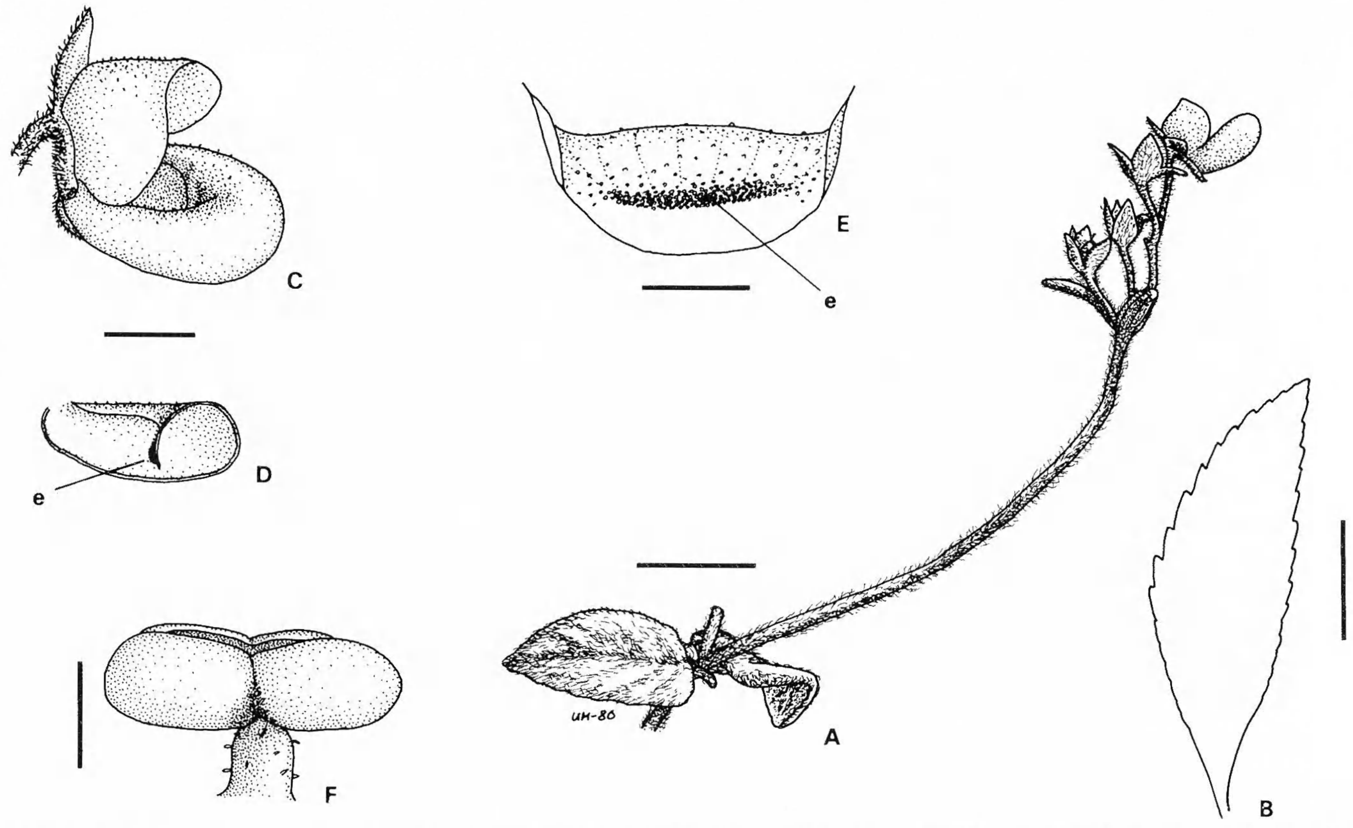

Fig. 1. Calceolaria cataractarum (Løjtnant, Molau & Madison 12316). — A: Flowering branch. — B: Outline of leaf. — C: Flower. — D: Lower corolla lip, length section. — E: Infolded lobe of lower corolla lip with a distinct elaiophor, ventral view. — F: Stamen. — Symbol: e elaiophor. — A drawn from photograph, B drawn from herbarium material, C–F drawn from fixed material. — Scales: A, B 2 cm, C, D 5 mm, E 3 mm, F 1 mm.

Distribution. Fig. 2. Known only from two collections from the same locality, viz. in the Santa Bárbara Valley, E slopes of Cordillera Oriental, Andes of N Ecuador at the border with Colombia.

Remarks. Calceolaria cataractarum is very closely related to *C. lehmanniana* Kränzlin (see Molau 1978). The species agree in general growth habit and vegetative morphology. In a previous paper in this series (Molau 1978 p. 315) it was mentioned as a yellow-flowered form of *C. lehmanniana*. With the present knowledge, however, based upon field studies and cultivated material, *C. cataractarum* must be regarded as a distinct species.

The same chromosome number as in *C. cataractarum,* 2n=36, has also been found in *C. lehmanniana* (voucher: Løjtnant, Molau & Madison 11714 (GB); not previously reported).

Calceolaria cataractarum and *C. lehmanniana* differ in deep yellow vs. white corolla and presence vs. absence of elaiophor (definition given above). Thus, these two sympatric species are separated only by floral characters, but the characters referred to are taxonomically very important in *Calceolaria*.

The presence/absence of elaiophor can be used as a taxonomic character at the species level in *Calceolaria*. In NW South America 16 or 17 out of the approximately 60 species, distributed in 8 out of the 15 sections, do not possess an elaiophor, i.e. the infolded lobe of the lower corolla lip is naked (or, rarely, with a few irregularly dispersed glandular hairs). A review of this matter, comprising all the sections in NW South America, will be given in the final paper of this series.

In the absence of elaiophor as well as in other qualitative characters *C. lehmanniana* is constant throughout its distribution area. No intermediates between *C. cataractarum* and *C. lehmanniana* were seen in the Santa Bárbara Valley, even though we worked in the field there for two weeks.

The other *Calceolaria* species known to lack an elaiophor are all highly specialized (cf. Vogel 1974), more advanced than their probable relatives. When correlated with the degree of

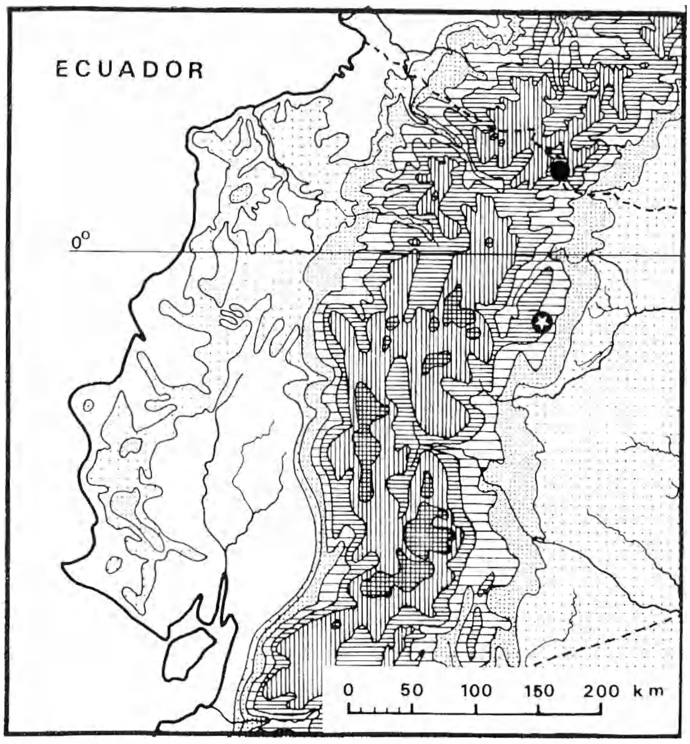

Fig. 2. Type localities of *Calceolaria cataractarum* (●) and *C. pedunculata* subsp. *sumacensis* (✪).

specialization in other characters (e.g. inflorescence structure) the presence of an elaiophor seems to be the basic condition in *Calceolaria*. Thus, *C. lehmanniana* is obviously derived from *C. cataractarum.*

C. lehmanniana seems to have a competitive advantage over *C. cataractarum;* it is today an abundant plant in the cloud forest areas of N Ecuador and adjacent Colombia, while *C. cataractarum* is known only from a single locality.

The change of corolla colour and the loss of the elaiophor must have altered the pollination ecology of *C. lehmanniana*. The flowers of *C. cataractarum* are typical *Calceolaria* flowers, producing fatty oil instead of nectar, and are pollinated by oil-gathering bees. Judging from the size of the orifice of the corolla and the position of anthers and stigma, the efficient pollinator in *C. cataractarum* is probably a species of *Centris* (tribus *Centridini,* subfam. *Anthophorinae;* cf. Vogel 1974). *C. lehmanniana,* on the other hand, has true pollen-flowers: the anthers are (as in *C. cataractarum*) relatively big, rigid, well-exposed and richly pollen producing; neither nectar nor oil is produced. The pollinator is here probably a pollen-gathering bee, but pollination was not observed in either of the two species. (The weather during our stay in the Santa Bárbara Valley was cold and rainy most of the time.) In a mixed population of *C. filicaulis* Clos. (yellow flowers, elaiophor present) and *C. tenella* Poepp. & Endl. (yellow flowers, elaiophor absent) in the Andes of Argentina, Vogel (1974) observed that the oil-gathering bees regularly visiting *C. filicaulis* paid no attention to *C. tenella.* The latter was supposed to act as a pollen-flower, and to be facultatively autogamous. However, the flowers of the oil-producing *Calceolaria* species also serve as pollen source for the oil-gathering bees. In some cases both pollen and oil are collected actively in the same flower (Vogel 1974 p. 131). The *Centris* species, however, usually do most of their pollen collecting in richly pollen producing flowers of other plant groups, e.g. *Cassia* and *Solanum* (Vogel 1974 pp. 217, 221). In the present case, it is not likely that an oil-gathering bee visiting *C. cataractarum* also would visit *C. lehmanniana* for collecting pollen, since the individual bees usually are very true to flower colour.

The two species of sect. *Lehmannina* represent a very obvious case of sympatric speciation, where reproductive isolation has originated as a by-product of evolutionary divergence (cf. Grant 1971 p. 122). The genus *Calceolaria* is remarkable in that there are usually no sterility barriers between species of the same section; sympatric species are isolated primarily by pollination ecology and habitat. On the other hand strong incompability barriers exist between the sections. The general pattern in *Calceolaria* thus approaches the 'Aquilegia pattern' (Grant 1971 p. 100). Consequently, the species concept in *Calceolaria* must be based on external barriers (e.g. pollination syndrome) rather than internal ones.

Specimens studied. Ecuador. Napo: Road from El Carmelo (El Pun) towards La Bonita, SE of Santa Bárbara, km 53 from El Carmelo, c. 2600 m, 5.III.1974, Harling & Andersson 12507 (GB); 13.IV.1979, Løjtnant, Molau & Madison 12316 (AAU, GB).

Calceolaria pedunculata Molau subsp. **sumacensis** Molau subsp. nov. (sect. Dermatophylla)

Orig. coll.: Løjtnant & Molau 12855 (GB holotype, AAU; cultivated at GB).

Differt a subspecie pedunculata foliis infra pallide viridibus, siccatis in colorem flavo-virentem non conversis, pedunculis et pedicellis et sepalis purpuraceis, corolla alba vel eburnea.

Differing from subsp. *pedunculata* (see Molau

1979) in the following characters: lower leaf surfaces pale green, not turning yellow-green when dried; peduncles, pedicels and sepals purplish (green to yellow-green in subsp. *pedunculata*); corolla white to cream-white (deep to bright yellow in subsp. *pedunculata*).

Chromosome number. 2n=36. Voucher: Løjtnant & Molau 12855 (AAU, GB). The same chromosome number has also been found in subsp. *pedunculata* (vouchers: Løjtnant & Molau 11031 (AAU, GB) and 11389 (AAU, GB); not previously reported).

Habitat. Rocky streambanks in virgin cloud forest, altitude c. 3100 m.

Distribution. Fig. 2. Known only from the type, collected on the NE slopes of Volcán Sumaco, prov. Napo, Ecuador.

Remarks. During the first biological expedition to Volcán Sumaco ever carried out (1979), in which I participated, we found white-flowered specimens of *C. pedunculata* in an absolutely virgin area. Volcán Sumaco in situated far from the distribution area of subsp. *pedunculata,* viz. the W slopes of Cordillera Occidental, Andes of N Ecuador (Molau 1979). There is also a single record of subsp. *pedunculata* from Cordillera Oriental (Papallacta, prov. Napo, Løjtnant & Molau 11389), but this specimen we found along the roadside, and it was probably spread by man.

White-flowered forms are rare within the genus *Calceolaria.* No such cases are previously known from the section *Dermatophylla.* The white-flowered population of *C. pedunculata* is furthermore geographically widely separated from the typical, yellow-flowered form, and hence recognized as a subspecies.

Specimens studied. Ecuador. Napo: NE slopes of Volcán Sumaco, c. 3100 m, Løjtnant & Molau 12855 (AAU, GB).

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The pollination ecology of Dactylorhiza sambucina (Orchidaceae)

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Interactions between anthophilous insects and *Dactylorhiza sambucina* L.) Soó were studied in three Swedish populations. Queens of *Bombus* Latr. (Hymenoptera, Apidae) dominated as visitors and transported about 90 % of the pollinaria. The species acts by deceit and obviously exploits a short stage of the queens' lives when they are newly emerged after hibernation and have not established foraging routes and are inexperienced on food-flowers. Unconditioned scouring queens are induced to visit the gregarious *D. sambucina* due to its comparative superiority in floral display and perhaps its strong floral terpene emission. *D. sambucina* seems not to mimic concurrently flowering bumble-bee-plants. After a few exploratory non-rewarding visits predominantly to the lowermost flowers in a very few inflorescences, queens hurriedly leave the place in renewed scouring and searching. Their behavioural response on deception produces a characteristic decline in fruit-setting within inflorescences. Interactive floral and insect morphologies indicate optimal adaptation to queens of species having medium-long probosces, median-broad faces and bare centre of the clypeus. The legitimate pollinators in the study areas are queens of *Bombus lapidarius* (L.) and *B. sylvarum* (L.).

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Sprengel (1793) introduced the concept of "Scheinsaftblume" when he discovered that some species of the genus *Orchis* s.l. lack nectar secretion and act by deceiving their pollinators. Darwin (1862) rejected this principle— "we can hardly believe in so gigantic an imposture"—and believed that flower-visitors regularly suck concealed juices by piercing the spur-tissues, a theory which later became commonly accepted (e.g. Müller 1869, Knuth 1899, Ziegenspeck 1936). However, Delpino (1873–74), who like Müller had made field observations on spring flowering species, supported and concretized Sprengel's deception hypothesis. He argued that these orchids are visited only during the first two or three days of flowering when bumble-bees have newly emerged and are inexperienced on flowers and that they soon realize the trick and learn to avoid the flowers. Since Daumann (1941) finally disproved Darwin's theory, the interpretation made by Delpino has been revived (e.g. van der Pijl 1966, van der Pijl & Dodson 1966). Vogel (1972) observed that pollination in *Orchis papilionacea* L. is positively influenced by the repetitive flight pattern (patrolling) performed by males of solitary bees i.e. *Eucera* (Hymenoptera, Anthophoridae) and proposed that the absence of nectar secretion might be an evolutionary response to the incorporation of orchids in the swarming routes. Whilst the majority of *Orchis* (s.l.) species act by deceit, at least three species are nectariferous and obviously act as true food-plants viz. *Galearis (Orchis) spectabilis* (L.) Raf. (Robertson 1893), *Orchis coriophora* L. (Eberle 1974) and *O. sancta* L. (Dafni & Ivri 1979). However, although the genus displays spectacular and popular elements in the European flora, the anthecological specializations have largely remained an enigma (cf. Dafni & Ivri 1979).

The purpose of the present study was to reveal details in the interaction between pollinators and *Dactylorhiza sambucina,* a species of the nectarless *Orchis*-type. This gregarious spring flowering species is distributed from Iran to NW Europe, including SE Sweden (Sundermann 1975). Strangely enough, it occurs in two colour morphs, red and yellow, which normally coexist on the same localities although their proportions vary considerably (see Pettersson 1958). Its general floral morphology agrees with the ordinary *Orchis*-type (cf. Darwin 1862, Ziegenspeck 1936, Faegri & van der Pijl 1971). Flower-visitors observed are "bumble-bees" (Delpino 1873–74), queens of the bumble-bee *Bombus wurfleini mastrucatus* Gerst. (Hoffer 1883) and the butterfly *Leptidea sinapis* (L.) (Pieridae) (Wiklund 1977). Hitherto, however, no insect carrying the pollinaria seems to have been identified.

Material and methods

Three populations of *Dactylorhiza sambucina* were studied during May–June 1974–79, two on Öland (A and B) and one in Uppland (C). The very rich population A grows near the northern border of the Alvar S of Ölands Skogsby. Population B is much more limited and grows in a 50 m broad and 400 m long area on the old beach 2 km W of Vickleby. Population C occurs on Häverö, Hallstavik, on the east coast of Uppland.

More or less concurrently blooming entomophilous plants in the same association as *D. sambucina* of importance for Hymenoptera Apoidea are in the population A *Taraxacum* spp., *Salix repens* L., *Pulsatilla pratensis* (L.) Mill., *Primula veris* L., *Saxifraga granulata* L., *Potentilla tabernaemontani* Asch., *Anthyllis vulneraria* L., *Oxytropis campestris* L., *Geum rivale* L., *Lotus corniculatus* L. and *Allium schoenoprasum* L. In addition two other very common orchids which both act by deceit (lack nectar) are in flower viz. *Orchis mascula* L. and *O. morio* L. *Orchis militaris* L. which is less frequent begins to flower in early June. Along borders near fields *Lamium purpureum* L. is often frequent. Higher trees and bushes occur here and there in the open landscape viz. *Prunus spinosa* L. and *Malus sylvestris* Mill. and when in flower attract bees.

Population B grows between fields and deciduous trees. Most of the concurrently flowering species are the same as in A. Differences are the absence, or practically so, of *S. repens, O. campestris, A schoenoprasum. O. morio* and *O. militaris* whilst *Pulsatilla vulgaris* Mill. is very common.

Population C occurs mainly along cliffs about 50 m from the sea shore but some scattered individuals are also present further up in meadows. Important for Apoidea are especially *Primula veris, Lathyrus vernus* (L.) Bernh., *Saxifraga granulata, Polygonatum odoratum* (Mill.) Druce, *Glechoma hederacea* L., *Taraxacum* spp. and in shady places *Polygonatum multiflorum* (L.) All. and a few late *Pulmonaria officinalis* L. *Corydalis* spp. which are adapted bumble-bee-plants occur at B and C but are practically finished before *D. sambucina* flowers. During the actual period flowering *Viola hirta* L. is present, scattered on all three localities.

The behaviour of flower-visitors was observed. Pollen vectors were collected in connection with their visits to *D. sambucina* but also when they frequented other plants or when they were flying about in the area. To distinguish the pollinaria of *D. sambucina* on collected insects from those of the three frequent *Orchis* species in the same areas on Öland, morphometric measurements were made of the pollinaria in all four species. As a complement to field observation, interactive morphologies were investigated in experiments with newly killed but relaxed bumble-bee queens whose mouthparts and heads were inserted into or pressed against spur-mouths of fresh flowers.

Scent emitted from inflorescences of *D. sambucina* and from flowers of some of the concurrently flowering plants, was analysed as far as possible by gas chromatography—mass spectrometry (GC–MS) with the method described previously (Nilsson 1978). Experiments on self- and cross-pollination were carried out using isolated racemes. The presence of embryos was checked (under magnification) by spreading capsule contents on a glass plate. Fruit sets in the two colour morphs was compared in one population (C) by marking all representatives of one morph within a restricted area. Unfortunately, three further similar experiments in 1977 became destroyed by exceptionally fast decomposition of withered racemes (A and B) or by grazing cattle (C).

Flowering phenology

The 3–4 week flowering period of *D. sambucina* on Öland normally starts around May 10 and proceeds into the first week of June (Fig. 1 B). Minor yearly deviations occur due to the spring weather. During anthesis the maximum day temperature rises from about 14° to 19°C (Fig. 1 A). The most expansive stage of anthesis occurs between May 13 and 20 when the maximum day temperature normally is 15–16°C. The maximum number of open flowers occurs during May 20–28. In Uppland (population C) the period occurs only a little later. In certain shady subhabitats fresh flowers can some times be found until the middle of June.

The first (lowermost) flowers open when the stalks are still very short, sometimes only a few centimeters high. Very early in 1978 it was noted in population B that such flowers often were non-resupinate which means that the labellum was directed towards the axis of the inflorescence and the spur-mouth was turned upwards. When the stalks later grew higher these flowers soon (in a day or so) rotated and became resupinate. Later, flowers higher up in the inflorescence were resupinate when they opened. In the same year much of the population became damaged by cold and by a snowfall which temporarily covered the shooting inflorescences. Many stopped growing and approximately 56 % of the buds (n=2617) never opened but withered. In

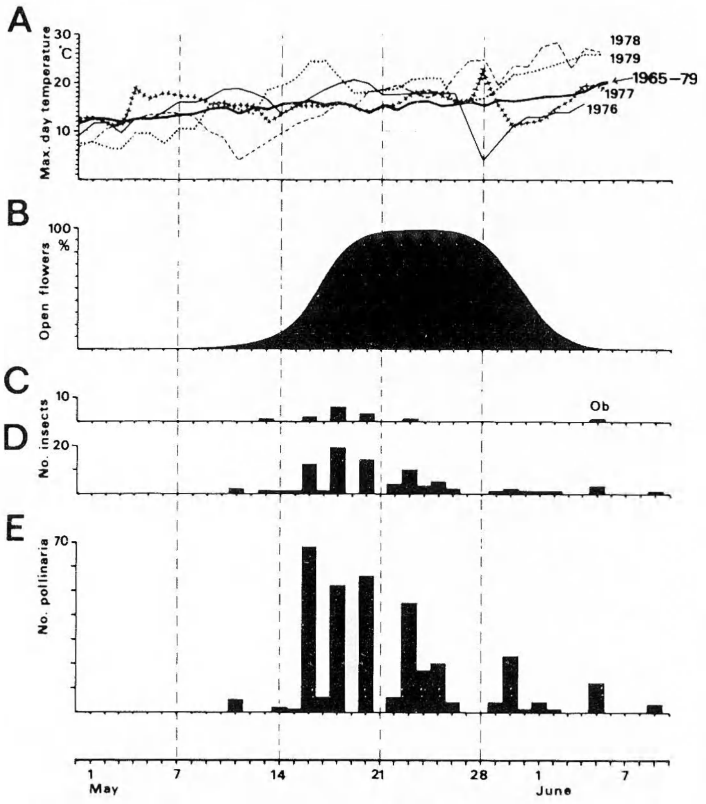


Fig. 1. Spring temperatures, flowering of *Dactylorhiza sambucina* and the activity of pollen vectors on Öland. — A: Maximum day temperatures at A (The Ecological Station) for the years 1976–79 and during the period 1965–79. — B: Average flowering period during the years 1974–79. — C: No. of visitors of Hymenoptera seen on the flowers. All except Ob (*Osmia bicolor* ♀) were bumble-bees. — D: No. of recorded pollen vectors. — E: No. of pollinaria of *D. sambucina* on pollen vectors.

1979 a considerably smaller number of flowering individuals were produced in the area indicating that many plants had not restored vigour.

The flowering phenologies of concurrently blooming food-plants on Öland important to Hymenoptera Apoidea during the anthesis of *D. sambucina*, indicate that a comparatively limited number of species are present (Fig. 2). Only 7 species regularly frequented by bumble-bees cover most of the actual time period, viz. *Primula veris, Pulsatilla* spp., *Taraxacum* spp., *Lamium purpureum* and *Salix repens*. The last species, however, is mainly visited by solitary bees.

Visitors and pollinators

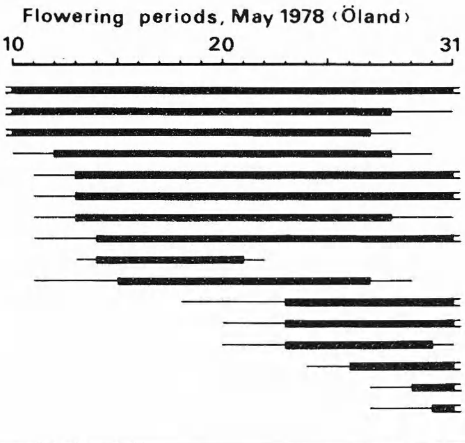
Notwithstanding 134 hours of observation, rather few visitors were seen on *D. sambucina*. On the other hand quite a number of insects bearing witness of visitation (i.e. pollinaria) were captured on other flowers or when they flew about. Normally the pollinaria of *D. sambucina* were easily identified due to their long caudicles in combination with rather weak pigmentation and not very compressed massulae. In doubtful cases the caudicles were also morphometrically compared with the different orchids present (Fig. 3). In exceptional cases it was even possible to distinguish between deposited pollinaria of the two colour morphs on vectors because those from the red usually have comparatively darker pigmented massulae, sometimes distinctly so (Fig. 5 C). In A, 21 % of the pollen vectors (n=33) carried also pollinaria from either *Orchis mascula* or *O. morio*.

The flower-visitors of *D. sambucina* found consisted of Hymenoptera Apoidea (14 species) and of Lepidoptera (2 species) (Table 1). In quantity, queens of 9 species of *Bombus* strongly dominated (Fig. 4, left bars). The species *B. lapidarius* and *B. sylvarum* were clearly most frequent and together with *B. lucorum* and *B. terrestris* they were recorded in all populations. Cuckoo bumble-bees (*Psithyrus* spp.) and solitary bees were seldom found as visitors, with the exception of *Osmia bicolor* (Megachilidae), which was recorded in all populations. Once also a female of *Andrena*, probably *A. tibialis* (K.), was seen crawling on one inflorescence but it did not try to enter the flowers and it carried no pollinaria. Honeybees (*Apis mellifera*) were only found as visitors in B. The average time for observing visitation by one bumble-bee queen was 6.4 hours but under certain circumstances the frequency was clearly higher (see below).

Pollinaria were exclusively transported by Hymenoptera (Fig. 4, right bars). The genus *Bombus* carried 86 % and the two species *B. lapidarius* and *B. sylvarum* alone no less than 65 % of all pollinaria (Table 1). If the expected numbers carried by observed visitors to *D. sambucina* which were not captured are added also (as an estimation of the mean number carried by captured insects of the same species) the outstanding importance of *Bombus* is even more pronounced viz. 89 % transportation.

Phenology of pollen vectors

Hibernated bumble-bee queens are occasionally seen on various early spring flowers (e.g. *Salix* spp.) as early as in the middle of April but since



Species	Bombus lapidarius	B. sylvarum	B. lucorum	B. terrestris	B. pascuorum	B. hypnorum	B. hortorum	B. soroeensis	B. muscorum	Psithyrus bohemicus	P. barbutellus	Apis mellifera	Osmia bicolor	No. with pollinaria of D. sambucina	No. of pollinaria of D. sambucina
	Pollen vectors of D. sambucina found														
Primula veris	·	+	·	·	+	·	1(>1)	·	·	·	·	·	·	1	**>1**
Pulsatilla vulgaris	3(>5)	2(>2)	1(>1)	+	·	·	·	·	·	·	·	4(15)	+	10	**>23**
Potentilla tabernaemontani*	1(>1)	+	1(>1)	·	1(11)	·	·	·	·	·	·	+	1(2)	4	**>15**
Dactylorhiza sambucina	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Taraxacum Sect. Erythrosperma	5(>16)	·	+	·	·	·	·	1(4)	·	+	·	+	1(1)	7	**>21**
T. Sect. Taraxacum	1(2)	·	+	+	1(4)	1(14)	·	+	1(2)	1(2)	·	2(5)	·	7	**29**
Pulsatilla pratensis	+	3(>20)	1(>1)	1(1)	·	·	1(1)	·	·	·	·	·	+	6	**>23**
Lamium purpureum	1(6)	+	+	·	+	·	1(2)	·	·	·	·	·	·	2	**8**
Salix repens	·	·	2(5)	1(9)	+	·	·	·	·	·	·	+	+	3	**14**
Saxifraga granulata*	+	·	·	·	·	·	·	·	·	·	·	1(2)	·	1	**2**
Anthyllis vulneraria	1(7)	1(6)	·	·	·	·	1(4)	·	·	·	·	·	·	3	**17**
Oxytropis campestris	+	·	·	·	+	·	·	·	·	·	·	·	·	·	·
Prunus spinosa	1(>1)	·	+	+	+	+	·	·	·	1(7)	·	+	·	2	**>8**
Malus sylvestris	1(12)	3(3)	·	+	·	·	·	·	·	·	·	+	+	4	**15**
Geum rivale	+	+	+	·	+	·	·	·	·	·	1(3)	·	·	1	**3**
Lotus corniculatus	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·
Allium schoenoprasum	2(10)	·	·	·	·	·	·	·	·	·	·	+	·	2	**10**

Fig. 2. Important food-plants for bees during the flowering period of *Dactylorhiza sambucina* and in the same biotope on Öland. The flowering periods illustrated refer to the situation in 1978. Presence of a few open flowers in a species is marked with a thin line and frequent flowering with a heavy line. Pollen vectors and their number of pollinaria (in parenthesis) of *D. sambucina* found on the different flowering plants 1974–79 are given to the right. Crosses mark that the insect species in question has been recorded as visitor to the respective plant species in the same association during the present investigation but hitherto, during these visits, not observed as carrying the pollinaria of *D. sambucina*. — * Species only occasionally visited by bumble-bees.

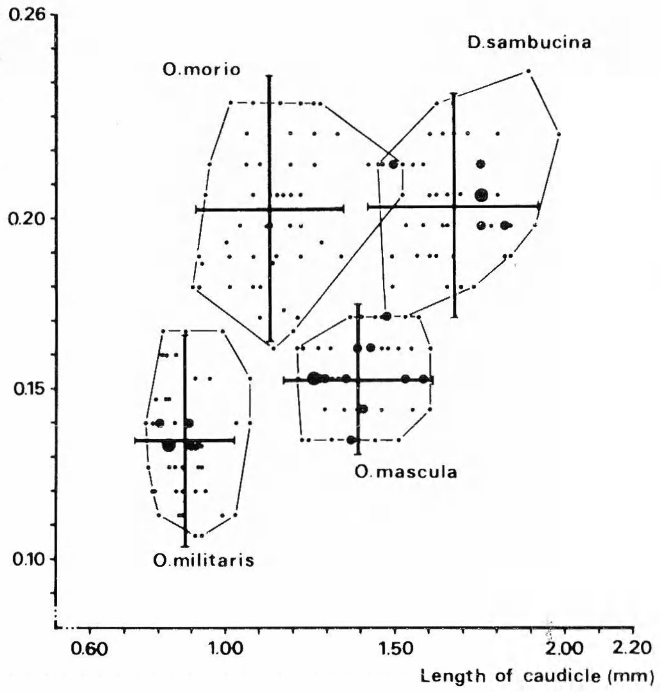


Fig. 3. Morphometry of the caudicles of the pollinia in *Dactylorhiza sambucina* and in three species of *Orchis* at Skogsby, Öland (each species n=50). The three categories of dots represent one, two and three specimens, respectively and the sizes of the crosses illustrate the 95 % confidence interval.

spring weather undulates, flights are possible only on certain favourable days. During the first active period (1–2 weeks), queens feed on pollen and nectar to restore vigour and to make ovary development possible (Richards 1977). Then, gradually, nest-seeking is induced and individuals showing this characteristic behaviour are seen on Öland from late April to June.

Queens which have found a nest site, construct their first brood cell and a honey pot which are provisioned with pollen and nectar respectively. The food is obtained by regular foraging flights to areas with food-flowers. Conditions for high bumble-bee flight activity occur when air temperatures are 12.5–14.9°C (Teräs 1976). On Öland the maximum day temperatures (1.5 m above ground) usually reach this level during the first week of May (Fig. 1 A). Such temperatures of longer duration normally prevail some days later i. e. about the time that *D. sambucina* comes into flower. During the middle of May a number of queens have already established nests and are beginning to explore the surroundings for clusters of food-flowers to

Table 1. Insects recorded as flower-visitors to *Dactylorhiza sambucina* and the occurrence of pollinaria on different species. — * Including the expected number of pollinaria on observed visitors which were not captured, estimated from the mean number carried by captured insects of the same species. — ** Observed but not collected.

Species	Localities	No. observed on *D. sambucina*	No. of visitors to *D. sambucina* found on other flowers	No. of visitors to *D. sambucina* captured but not on flowers	Total no. recorded as visitors to *D. sambucina*	No. on which the pollinaria were counted	Total no. of carried pollinaria of *D. sambucina*	Expected load of pollinaria per species* (%)
Bombus lapidarius (L.) ♀♀	A B C	7	18	7	28	21	123	39
B. sylvarum (L.) ♀♀	A B C	2	9	16	25	23	96	25
B. lucorum (L.) ♀♀	A B C	4	5	2	9	4	14	7.4
B. terrestris (L.) ♀♀	A B C	6	3	2	8	4	15	7.1
B. pascuorum (Scop.) ♀♀	B	·	2	·	2	2	15	3.5
B. hypnorum (L.) ♀	A	·	1	·	1	1	14	3.3
B. hortorum (L.) ♀♀	B C	1	4	·	4	3	7	2.2
B. soroeensis (F.) ♀	B	·	1	·	1	1	4	0.9
B. muscorum (L.) ♀	B	·	1	·	1	1	2	0.5
Psithyrus bohemicus (Seidl.) ♀♀	B	·	2	1	3	3	13	3.1
P. barbutellus (K.) ♀	A	·	1	·	1	1	3	0.7
Apis mellifera L. ☿☿	B	·	7	·	7	7	22	5.2
Osmia bicolor (Schr.) ♂, ♀♀	A B C	2	2	3	7	6	10	2.8
Halictus s. l. ♀**	A	1	·	·	1	1	0	0
Pyrgus malvae (L.) ♂♂, ♀♀	A C	6	·	·	6	6	0	0
Gonepteryx rhamni (L.) ♀♀**	B	2	·	·	2	2	0	0

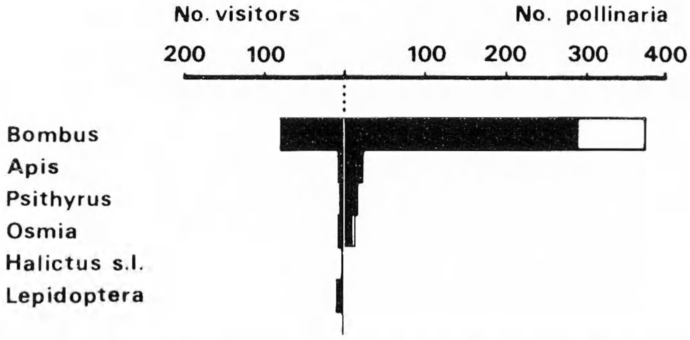


Fig. 4. The recorded number of different visitors (left bars) and the transported pollinaria of *Dactylorhiza sambucina* (right filled bars). Unfilled portions added to the right bars represent the expected number of pollinaria carried by those visitors which were not captured (estimated from the mean number carried by captured insects of the same species).

which repetitive foraging flights are made. However, many queens still have not established nests but fly about, roaming, especially the somewhat later emerging species e.g. *Bombus sylvarum*. In the case of queens carrying pollinaria of *D. sambucina*, 91 % (n=58) had no traces of collected pollen in their corbiculae. In *B. sylvarum* none of 23 queens and only 3 of 20 in *B. lapidarius* had ever collected pollen.

After foraging to their first brood, queens usually sit in their nests and remain there when the workers have emerged. On Öland, the first workers of the common species (e.g. *Bombus lapidarius*) are regularly observed during the first or second week of June. Since brood development takes 3–4 weeks e.g. about 21 days in *B. lapidarius* (Valle 1955), the emergence of workers reflects the queens' busy foraging during the middle of May.

A number of queens, however, keep on flying about but never establish nests due to nematode infection which prevents the ovaries from developing (Palm 1948). Such queens make up an increasing percentage among the late-flying individuals. On Öland this is most obvious from the end of May and onwards (B. Cederberg, pers. comm.).

Psithyrus queens appear somewhat later than their hosts (*Bombus* spp.) and are present on various flowers from about the middle of May. The solitary bee, *Osmia bicolor*, inhabits old shells of snails often in the same biotope where *D. sambucina* grows and at least the females are present throughout anthesis. The males are early and at maximum in May and perform repetitive patrolling flights in certain subhabitats where *D. sambucina* and *Orchis* spp. often are abundant.

Behaviour of flower-visitors

Visits of bumble-bees to *D. sambucina* were seen only during the first half of flowering (Fig. 1 C). Also the numbers of recorded visitors and their attached pollinaria indicate that maximum of visitation occurred during the most expansive stage of anthesis (Fig. 1 D, E). Various observations and smaller notes all suggest that the behaviour pattern of queens mainly was exploited by *D. sambucina* during a period of perhaps 5–6 days only in the middle of May when they were in a certain mood favourable for deception. For example, in B on May 16 and 18 1977, 5 queens were seen on inflorescences but none on May 20. At the same place on May 18 1978, 4 queens were observed as visitors but none on the next day. In C on May 22 1977, 6 queens visited flowers but 4 days later only one. In B on May 20 1979, only a single queen made visits but 9 further vectors carrying pollinaria were captured nearby. Observations however, on May 22 and 24 were all negative except two pollen vectors found on other plants. Later this year a remarkably high fruit set showed that a very high visiting frequency must have occurred before May 20 i.e. during the first few days with really warm and sunny weather (Fig. 1 A).

To 75 % (n=20), the queens' visits occurred between 10.30 and 12.30. Generally they came scouring into the area in fast flight and suddenly descended when approaching an inflorescence. In these cases, even if the orchids grew among food-flowers, inflorescences of *D. sambucina* were usually the first showy objects to become approached and visited. The behaviour of the queens always indicated optical far attraction i.e. direct approach. Either a single or up to 5 racemes in sequence were visited, whereafter the queens hurriedly left the place (Table 2, Nos. 1–12) or directed their attention to food-flowers on which constancy became established (Table 2, No. 16). Four queens which showed constancy or had just visited food-flowers approached *D. sambucina* only (Table 2, Nos. 16, 18, 20, 21) while two queens alternated between food-flowers and the orchids (Nos. 19, 22). Occasionally queens were seen to interrupt nest-seeking to make a visit (No. 17) or to visit an orchid after a rest on the ground (No. 14). Once a *Bombus hortorum* approached a yellow inflorescence and touched two flowers with its front tarsi but did not alight although having constancy on the yellow flowered *Primula veris* (No. 23). Later after many visits to *P. veris,* if flew away approximately 7 meters and then suddenly visited a red inflorescence. *Osmia bicolor* females, as well as the lepidopterans, became attracted as they came scouring (Nos. 24–28). In single cases bumble-bees approached leaves or made visits to inflorescences in bud which emphasizes the seeking character of their behaviour (Nos. 3, 22).

Inflorescences develop between 4 and 37 flowers (Fig. 12A). The left side of the histogram slopes more strongly which perhaps suggests that individuals with few flowers have selective disadvantages. Moreover, there exists a positive correlation between the number of flowers and the fruit set (Fig. 12 B). Reasonably this simply reflects the increasing ability to influence pollinator behaviour i.e. superiority of floral display.

In inflorescences on developed stalks, bumble-bee queens alighted on one of the lowermost flowers and then grasped with the front legs behind the 5 upstanding perianth leaves. They supported themselves on the labellum and sometimes on adjacent flowers by the claws (Fig. 5 B). They pressed their heads as far as possible into the spur-mouth while the stretched mouthparts explored the inner of the spur, sometimes making small scratches or slits in the wall. Queens were also seen to creep behind the front and bite holes in the spur from the outside by using the mandibles (as they often do on many food-flowers, e.g. *Corydalis* spp.). Also ovaries and buds were attacked by biting. In 1977 in B, 18 % (n=262) of pollinated flowers showed minor perforations made in one way or another by bumble-bees. Butterflies probed into spurs with their probosces. The labellum and the spur-entrance have pigmented spots which form a false nectar guide (Fig. 5 A, 7 A, fng). On both sides in the stigmatic surface, red pigments also line the bottom of small tubes (Fig. 7 A, B, fng). The tubes are in the positions to stimulate the eyes of the advancing visitors at a close distance. The deceptive nectar guide is also red in the yellow morph.

After the first flower, the queens crept upwards and visited *a very limited number of further flowers* in the inflorescences, normally only 1–3 flowers. The maximum number of flowers visited within the same inflorescence observed was 7. Thus negative experience caused by the (repeated) lack of food-stimulation soon released renewed seeking flight (constancy was not in-

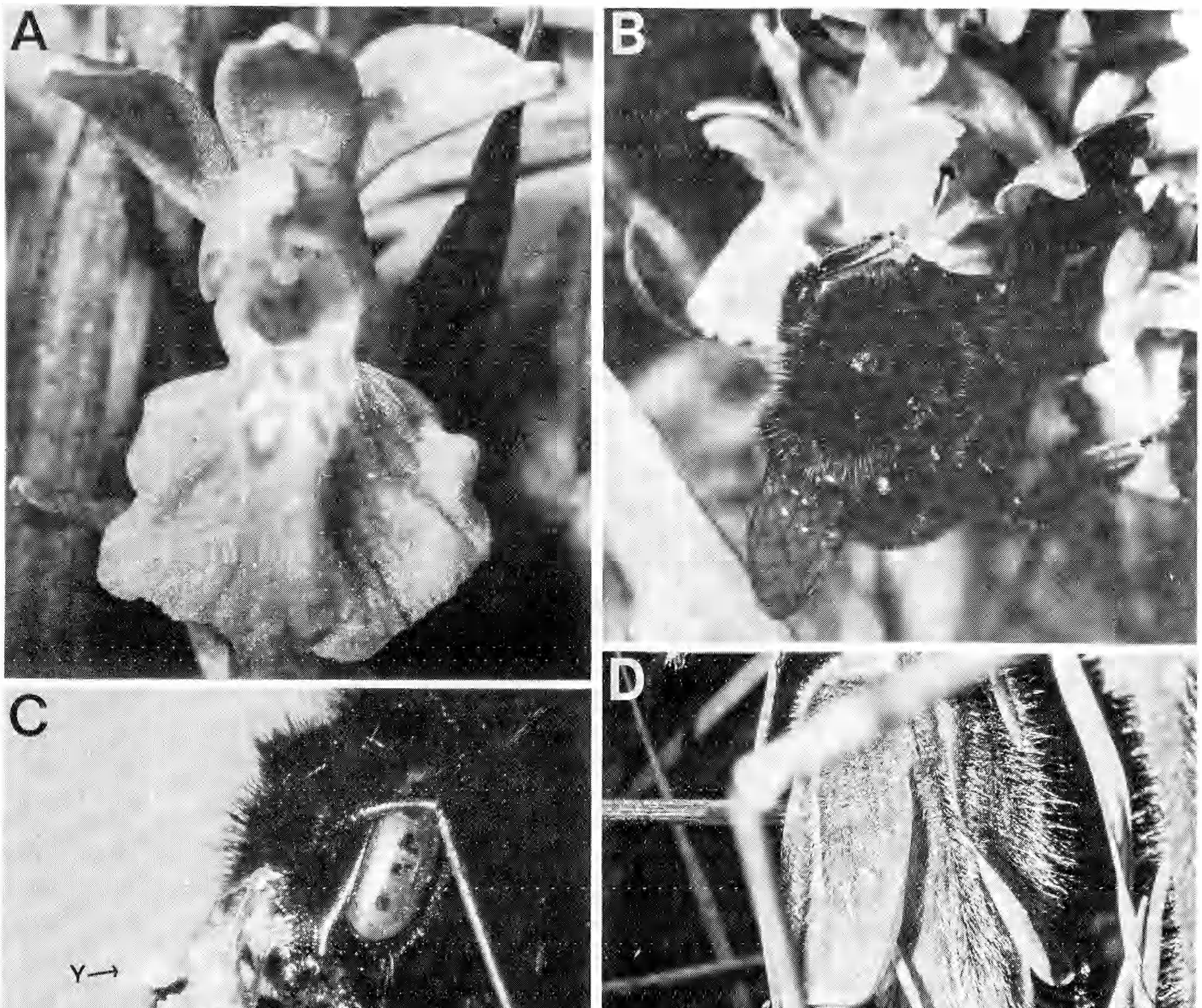
Table 2. Behavioural responses of individual insects on *Dactylorhiza sambucina*. — Explanations: a arrives to the place, ap approaches, const. constancy, 1 leaves the place, *P. prat. Pulsatilla pratensis*, *P. tab. Potentilla tabernaemontani*, *P. veris Primula veris*, *P. vulg. Pulsatilla vulgaris*, **R** red inflorescence of *D. sambucina*, *T. eryth. Taraxacum* Sect. *Erythrosperma*, **Y** yellow inflorescence of *D. sambucina*. Arrows indicate flights between individual inflorescences (*Dactylorhiza, Orchis, Taraxacum, Primula*) or between individual flowers (*Pulsatilla, Potentilla*). Numeral before abbreviation of plant species indicates the number of plants visited in sequence while numeral behind and in parenthesis indicates the number of individual flowers visited.

No. Species	Behaviour
1. *Bombus lapidarius* ♀	a→**R**(>3)→1
2. *B. lapidarius* ♀	a→**Y**(>1)→1
3. *B. lapidarius* ♀	a→4**R**(>1)→ap leaves of *P. vulg.*→1
4. *B. sylvarum* ♀	a→3**Y**(>1)→2**R**(>1)→1
5. *B. terrestris* ♀	a→**R**(1)→1
6. *B. terrestris* ♀	a→**R**(>2)→1
7. *B. terrestris* ♀	a→**R**(>1)→**Y**(>3)→**R**(>1)—5m→*P. vulg.*(1)→1
8. *B. terrestris* ♀	a→2**R**(>1)→1
9. *B. terrestris* ♀	a→2**R**(>1)→1
10. *B. lucorum* ♀	a→3**Y**(>1)→ap**R**→**Y**(>1)→1
11. *B. lucorum* ♀	a→2**R**(>1)→1
12. *B. lucorum* ♀	a→3**R**(>1)→1
13. *B. lapidarius* ♀	a→**R**(2), grooms→netted
14. *B. lapidarius* ♀	rests on the ground→**R**(>7)→*Orchis mascula* (>3)→netted
15. *B. lapidarius* ♀	*Orchis morio*(>1)→**R**(2)→1
16. *B. lapidarius* ♀	a→ap**R**→**R**(>2)→*T. eryth.*(1)→*P. tab*(2)→ap**R**→ap**R**→7*T. eryth.*→ap**R**→3*T. eryth.* →ap**R**→*T. eryth.* const.
17. *B. terrestris* ♀	nest seeking→**R**(>2)→nest seeking
18. *B. lapidarius* ♀	*P. vulg.* const.→ap**R**→ap**R**→*P. prat.*(1)→ap**R**→1
19. *B. sylvarum* ♀	apR→2*P. prat.*→*P. vulg.*(1)→2*P. prat.*→*P. vulg.*(1)→*P. prat.*(1)→**R**(1)→2*P. vulg.* →**R**(>1)→*P. prat.*(1)→**R**(>1), grooms→*P. prat.*(1)→**R**(2)→ap**Y**—8m→**R**(2)→**R**(2) →ap**R**→**R**(>1)→1
20. *B. terrestris* ♀	*P. prat.* const.→ap**R**→ap**R**→1
21. *B. lucorum* ♀	*P. prat.* const.→ap**Y**→ap**Y**→ap**R**→ap**R**→*P. vulg.*(1)→1
22. *B. lucorum* ♀	*P. vulg.* const.→2**R**(>1)→3*P. vulg.*→3*P. prat.*→ap**R** buds→*P. prat.*(1)→ap**R** buds →ap**R** buds→**R**(>2)→*P. prat.*(1)→**Y** bites buds→ap**R** buds→2*P. prat.*→**R**(>1) →2*P. prat.*→ap**R** buds→2*P. prat.*→*P. prat.* bud→ap*P. prat.*→ap*P. prat.* →ap*P. prat.*→*P. prat.*(1)→ap**R**→*P. prat.*(1)→6*P. vulg.*→5*P. prat.*→1
23. *B. hortorum* ♀	*P. veris* const.→ap**Y**, touches two flowers with its front tarsi→*P. veris* const.—7m →**R**, slides to the ground, returns and visits two flowers→*P. veris* const.
24. *Osmia bicolor* ♀	a→3**R**→1
25. *O. bicolor* ♀	a→**Y**(1)→netted
26. *Pyrgus malvae* ♀	a→**R**(>1)→oviposits on a leaf of *Filipendula vulgaris*
27. *Gonepteryx rhamni* ♀	a→2**R**(>1)→1
28. *G. rhamni* ♀	a→2**R**(>1)→**Y**(>1)→**R**(>1)→1

duced). This behaviour strongly contributes to a characteristic distribution of pollination and fruit set within inflorescences viz. fruits are produced mainly in the lower flower positions (see below). The time spent per inflorescence was generally only a few seconds and never more than 20 seconds. Queens repeatedly groomed in order to get rid of attached pollinaria. The fore legs were then moved over the face from the sides (Fig. 5 E). Similar grooming has been observed in pollen vectors on *Orchis* (Müller 1869, Malan 1885, Vogel 1972).

In B very early in 1978 another type of visiting behaviour was practised by queens on plants still very short and with non-resupinate flowers. Queens alighted on the top and then turned around and inserted the probosces from above into the flowers i.e. in the proper position for visiting non-resupinate flowers. Once a queen was seen to explore a damaged inflorescence which was lying on the ground.

In the case queens arrived to the place with the orchids, 80 % (n=15) first turned to the red morph and the rest to the yellow one. The three


A
B
C
Y
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butterflies all first approached the red one. In approaches made by bumble-bees, 19 % (n=72) occurred to the yellow morph and of their visits, 20 % (n=46) occurred to yellow inflorescences. Two queens and also one butterfly shifted between the two morphs (Table 2, Nos. 18, 20, 21). In the case of inter-spike flights made by queens from the red morph, 89 % (n=37) were directed to another red one, while of those made from the yellow morph, 45 % (n=11) were directed to a second yellow spike. On the localities studied, the yellow morph occurred in much lower frequency than the red morph e.g. on B, 10.7 % (n=2129) and on C, 15.8 % (n=3366) only were yellow.

Food-flowers visited by queens in direct connection with their observed visits to *D. sambucina* were *Pulsatilla vulgaris* and *P. pratensis* (Fig. 5 D), *Taraxacum* Sect. *Erythrosperma* (Fig. 5 F), *Potentilla tabernaemontani* and *Primula veris* (Table 2). Occasionally *Orchis mascula* or *O. morio* were visited before or after *D. sambucina*. Queens did not discriminate between the two species of *Pulsatilla*. Vectors carrying pollinaria were captured or observed on 14 different species of food flowers to which they evidently had shifted after negative experience on *D. sambucina* (Fig. 2). In A on May 10 1979, 8 of 9 queens that passed a landmark in the centre of the orchid-area, carried pollinaria but in an abandoned field 1 km NE of this site (about 300 m from the nearest *D. sambucina*), none of 8 queens that visited *Lamium purpureum* carried pollinaria.

According to some dissections made, queens parasitized by *Sphaerularia bombi* Duf. (Nematoda) often carry pollinaria (B. Cederberg, pers. comm). Parasitized queens gradually fall into a disrupted behaviour pattern including weakly maintained constancy, so that they sometimes frequent various strange and non-rewarding flowers (Lundberg & Svensson 1975). It is not known whether some of the queens in Table 2 were infected but according to their behaviour, Nos. 19 and 22 are suspected in this respect.

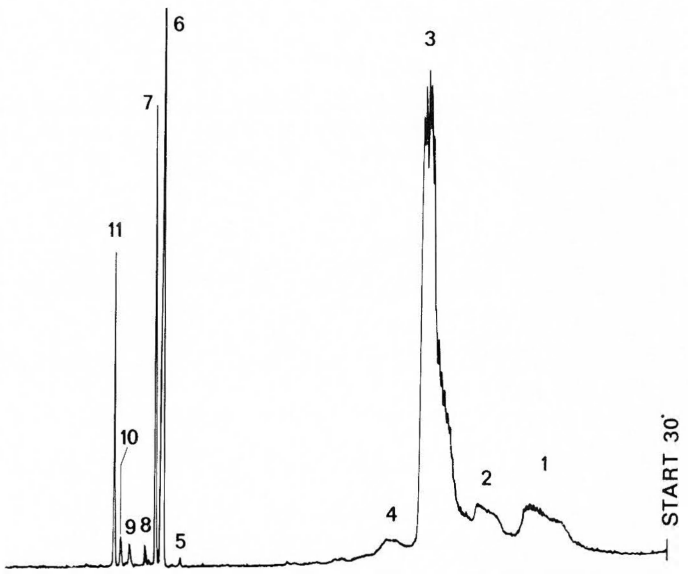

Fig. 6. Gas chromatogram showing the emission of terpenes from 8 inflorescences of *Dactylorhiza sambucina* with 132 open flowers. Collection was made during 9 hours with a pre-column filled with Porapak Q 50–80 M. GC conditions: LKB OV–101 25 m glass capillary column programmed from 30° to 220° at a rate of 8° per minute. Tentative identification: 1 α-pinene, 2 Probably myrcene, 3 Limonene, 4 Unknown, 5 Sesquiterpene, 6 Trans-caryophyllene, 7 α-bergamotene, 8 Probably β-selinene, 9 Sesquiterpene, 10 β-bisabolene, 11 Sesquiterpene.

Floral fragrance

Fragrance analyses revealed that inflorescences emit a blend of at least 3 mono- and 7 sesquiterpene hydrocarbons (Fig. 6). The first group is clearly dominated by limonene while trans-caryophyllene seems largest in the second group. No data suggested fragrance differences between the two morphs. The concentrated odour over enclosed inflorescences resembles that given off by ripe apples.

Fig. 5. *Dactylorhiza sambucina* and queens of *Bombus lapidarius*. — A: Close view of flower of red colour morph (5×). — B: Queen visiting flower. Note that support also is obtained by the claws on adjacent flowers. — C: Close view of face showing attached pollinaria from the red (R) and the yellow (Y) colour morphs on the clypeus. — D: Queen carrying pollinaria on clypeus and visiting a flower of *Pulsatilla pratensis*. The elastic and bendable caudicles of the pollinia have been forced backwards by the corolla and some of the pollinia (p) are visible from the outside. — E: Queen trying to scrape off the pollinaria with the front legs while gripping with mid and hind legs on a flower of *Pulsatilla vulgaris*. Note that the right front claw (cl) is grasping behind some of the pollinia whose caudicles (partly concealed by the straw of a grass) have been streched out about three times their original length. — F: Queen taking nectar from a head of *Taraxacum* Sect. *Erythrosperma*. The pollinaria (p) do not become forced down amongst the florets and worn due to the comparatively long mouthparts.

Floral fragrance of *Primula veris* (a species from which a queen once shifted to *D. sambucina*) run on GC–MS likewise gave a mixture of terpenes where limonene was present in rather large amounts. However, linalool was a larger constituent and dominates the quality of the scent. Only one sesquiterpene seems to be emitted in larger amounts viz. α-farnesene, thus there is no striking similarity with the emission of *D. sambucina*. The fragrances of further plants from which shifting was observed viz. *Pulsatilla* spp. and *Taraxacum* spp., were run on GC–MS or GC. Although similar or identical compounds (e.g. various monoterpenes) were present to some extent, the resemblances between the fragrances of *D. sambucina* and these plants seem trifling. For example the fragrance of *P. vulgaris* has ocimene as the largest monoterpene. Fragrance mimesis in *D. sambucina* is therefore unlikely.

Functional morphology

Most of the perianth, including outer parts of the labellum and the spur, is thin and soft but the spur entrance and the basal part of the labellum have a more rigid construction (Fig. 7 A, B). Therefore, a visiting large bumble-bee queen often supports herself on adjacent flowers in addition to the grip obtained by the front claws behind the sepals (Fig. 5 B). On one occasion, a queen of *Bombus hortorum* was observed to lose its grip and fall to the ground when the soft perianth suddenly gave way. The action of bumble-bee claws normally causes visible scratches on various floral parts, particularly on the labellum. Non-resupinate early flowers function morphologically because queens then adjust their visiting behaviour (see above).

When the proboscis is stretched into the comparatively long spur, the face simultaneously approaches the spur-mouth and strikes the bursicula: thereby the membrane ruptures along a weakened cell layer (Fig. 7 C, bp). Further pressing swings the bursicula backwards like a hinge and gradually exposes viscid matter which comes into contact with the dorsal surface of the advancing insect's head, where it acts as a glide-layer until no further advancement is possible. The bursicula is finally swung up into a space behind the projection to which it is hinged, just in front of the outer border of the stigma (Fig. 7 D). Under press, the somewhat rectangular outline of the spur entrance becomes slightly adjusted by extension so that the front part of the visitor's face is tightly enclosed laterally. At the same time the vertically narrow space below the rigid projection holding the bursicula becomes completely filled and tensed by the head. Gradually during advancement, viscid matter beneath the viscidia becomes swept off (in optimal cases) until finally, when further penetration is not possible, a very thin layer of viscid matter is left between the surface of the insect and the discs. In this position (Fig. 5 B) the mandibles, labrum and front parts of the clypeus have passed the viscidia and fill up the widened part of the spur-mouth formed by the lateral out-curvings (Fig. 7 A, c). The thin walls of the spur often become scratched or penetrated from the inside in various ways by the sclerous mouthparts.

When the insect retreats from the spur-mouth, the bursicula swings back to approximately its original position at the same time as the tightly adhered viscidia become withdrawn, together with the pollinia which slip through the protecting folds. In perfect cases (thin viscid layer under the discs), the caudicles undergo depression to almost 90° in about 20 seconds after removal. Since inflorescences normally are visited in a shorter time (see above), this favours cross-pollination. If the viscid layer underneath the discs has not become thin enough, no complete depression is possible because the discs curve within viscid matter when drying. On a legitimate pollinator, the depressed caudicles are directed forward–downward with the pollinia a little curved forward (Fig. 5 C).

Pollination occurs when such a visitor presses its face into the spur-mouth of a flower because the stigma covers 'the ceiling' at a distance behind the entrance corresponding to the depth reached by the protruding pollinia. The large stigmatic surface is slightly excavated along the middle (Fig. 7 B, s) which compensates for the somewhat rounded outline of the clypeus. As the pollinia normally are situated in front of the face, they neither become squeezed between the face and the stigma nor plunged into the surface. This is important since the stigmatic surface is covered by a thick layer of sticky mucilage which would destroy the delicate arrangement of massulae of the pollinia by cementing them into a

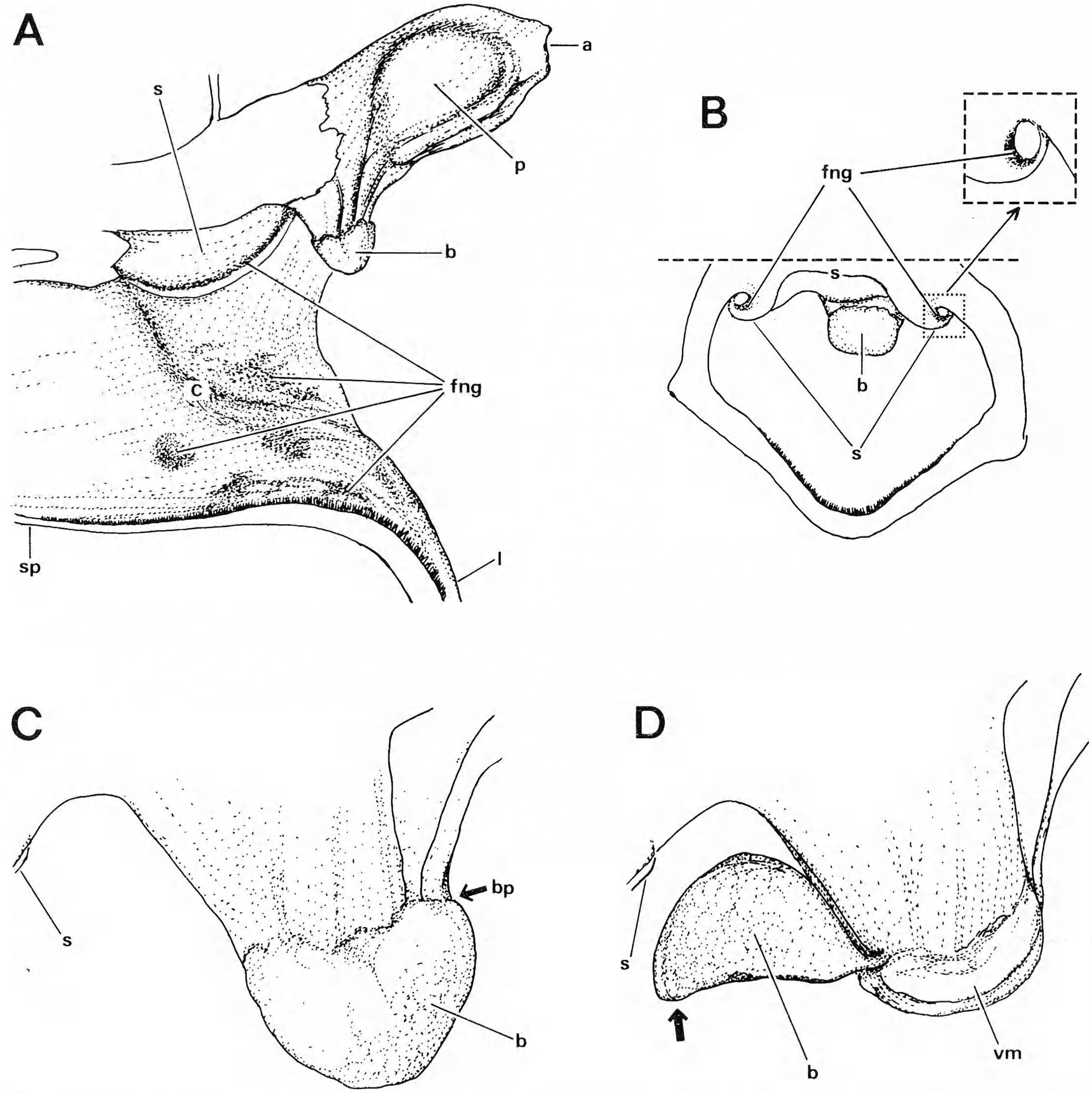

Fig. 7. Floral morphology in *Dactylorhiza sambucina* — A: Lateral view of column and spur-mouth (left part of flower removed) (12×). — B: Cross-section of spur-mouth (2.3 mm behind the bursicula) in posterior view (12×). Detail enlarged shows the incurved left border of the stigma and the false nectar guide running along the ventral side of the lateral canal. — C: Lateral view of bursicula and adjacent parts (50×). The point where the membrane ruptures by pressure is marked by an arrow. — D: Do. showing the action of the hinged bursicula which swings backwards into the groove in front of the stigmatic surface thus exposing viscid matter. Arrow indicates direction of pressure by the head of a pollinator. — Abbreviations: a anther, b bursicula, bp breaking-point, c curving (outwards), fng false nectar guides, l labellum, p enclosed pollinium, s stigma, sp spur, vm viscid matter.

compact and ineffective club after one flower-visit.

The mean value of the spur-length in population B was 15.3 mm (SD=1.6, n=200) and in C 16.1 mm (SD=1.7, n=200). In both populations the yellow colour morph had slightly shorter spur-length than the red one, viz. 15.1 (SD=1.6, n=100) and 15.5 mm (SD=1.5, n=100) in B and 15.6 (SD=1.5 n=100) and 16.5 mm (SD=1.7 n=100) in C. Extended probosces of dead bumble-bees of the four most important *Bombus* species, showed that the spurs normally are

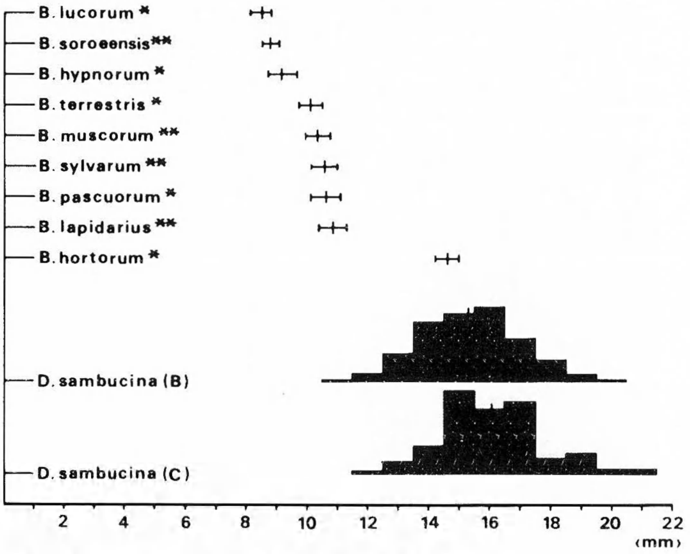

Fig. 8. The length of the spur in *Dactylorhiza sambucina* (n=200 on each locality) and the length of the proboscis (range and mean of prementum + glossa) in bumble-bee species occurring in southern Fennoscandia which were recorded as visitors. — * from Pekkarinen (1979) — ** from Medler (1962 a, b).

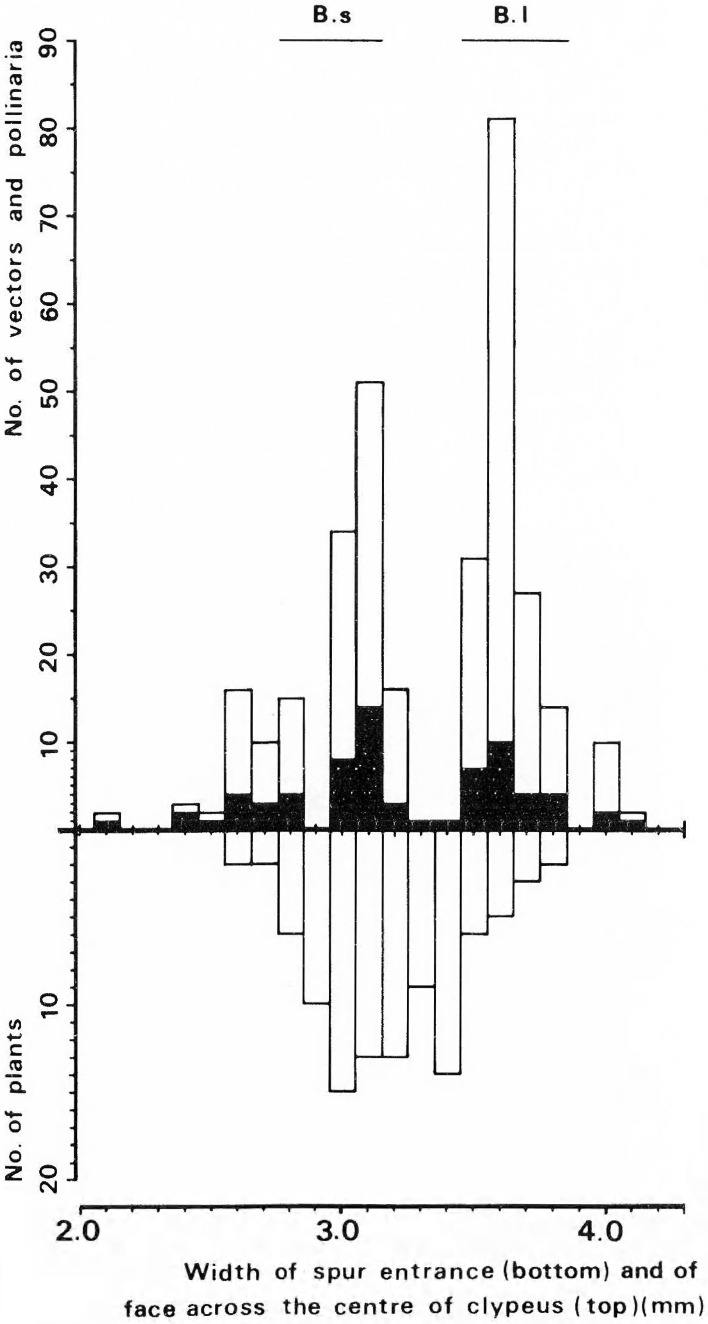

Fig. 9. Morphological adaptation of the flowers of *Dactylorhiza sambucina* on Öland to the head of the pollen vectors. Lower unfilled bars represent the width of the spur-entrance x̄=3.18, SD=0.27, n=100) and the upper filled bars the width of the face across the centre of clypeus of pollen vectors (x̄=3.22, SD=0.43, n=70). Upper unfilled bars from the base line illustrate the number of carried pollinaria on faces (x̄=3.31, SD=0.39, n=316). The two distinct peaks in the upper histograms are due to the frequency of *Bombus sylvarum* ♀♀ B. s, (x̄=3.0 mm) and *Bombus lapidarius* ♀♀ B. l, (x̄=3.6 mm).

longer than the depth which could be reached by the mouthparts. This ensures that the vectors advance underneath the column which favours effective removal of pollinaria and pollination. The length of the probosces in the visitor species indicates that queens of *B. hortorum* are not legitimate pollinators since their probosces are too long for a large portion of the plant populations (Fig. 8). Comparisons also indicate that *B. lucorum*, *B. soroeensis* and *B. hypnorum* are not legitimate pollinators as the spurs are much longer than 'necessary' (Fig. 8).

In Öland there exists a close adaptation of the inner width of the spur-mouth to the width of faces (across the centre of clypeus) in vectors. Both parameters have an approximate mean value of 3.2 mm (Fig. 9). Accordingly, optimal adaptation occurs with *Bombus* queens having not too broad faces. Two such species, i.e. *B. lapidarius* and *B. sylvarum,* have a face-width of about 3.6 (n=21) and 3.0 mm (n=23), respectively and appear as two distinct peaks in the histogram (Fig. 9).

Interactions between flower and vector morphologies give rise to differences in the deposition of viscidia (Fig. 10 A–I). Visitors having small heads (Fig. 10 A–C) receive deposition high up on the face as more of the head penetrates into the entrance. Since broad-faced species operate more outside the flower, they receive the viscidia on the front edge of clypeus or on labrum (Fig. 10 H, I) which is unfavourable because after depression the pollinia then easily become destroyed between the mandibles. Species having middle-sized faces receive viscidia on the centre of clypeus (e.g. Fig. 10 D, G and

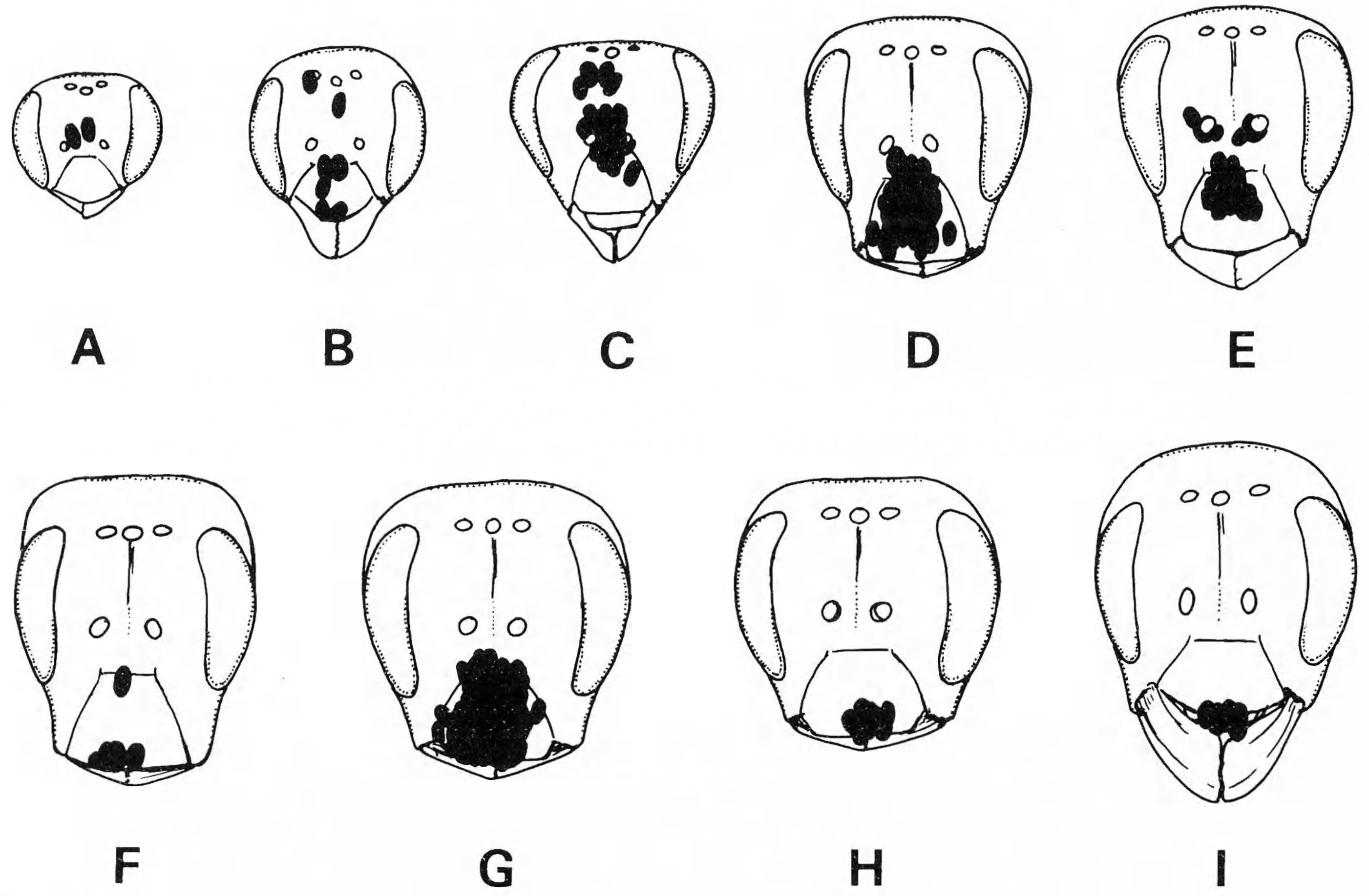

Fig. 10. The deposited pollinaria of *Dactylorhiza sambucina* on the heads of different visiting bees (5×). Viscidia have been filled black and represent a cumulative picture of the deposition on one or more specimens of the same bee species. — A: *Osmia bicolor* ♂ with two pollinaria. — B: Do. 4 ♀♀ with a total of 7 pollinaria. — C: *Apis mellifera* 7 ☿☿ with 22 pollinaria. — D: *Bombus sylvarum* 19 ♀♀ with 82 pollinaria. — E: *Bombus pascuorum* 2 ♀♀ with 15 pollinaria. — F: *Bombus hortorum* 3 ♀♀ with 7 pollinaria. — G: *Bombus lapidarius* 19 ♀♀ with 118 pollinaria. — H: *Bombus terrestris* 4 ♀♀ with 16 pollinaria. — I: *Psithyrus bohemicus* 2 ♀♀ with 9 pollinaria. — The heads A–I have been arranged in respect to increasing face-width across the centre of clypeus in the different species.

Fig. 5 C). This surface is most favourable for attachment due to the absence or relative sparseness of hairs. In *Bombus* queens, parts of the face near clypeus are densely hairy and not suitable for effective adherence of viscidia. In queens of *Psithyrus bohemicus,* clypeus is densely hairy also in the centre. Thus the pattern of deposition indicates floral adaptation to queens of a group of not too broad-faced *Bombus* species.

The number of attached pollinaria on vectors is generally quite low (Fig. 11): the largest number found on a single vector was 15. Many (47 %) carried only one or two pollinaria and 66 % carried 4 or less. About half of the vectors (53 %) had even numbers which suggests some interactive imperfectness. However, in B in 1978, examination showed that in flowers which had missing pollinaria 80 % (n =75) had both removed and 68 % had been pollinated. In the case of flowers with one pollinarium removed, 53 % had been pollinated (n=15) while of flowers with both pollinaria left, only 1.1 % (n=1119) had been pollinated. Thus it seems that both removal of pollinaria and cross-pollination efficiently take place during the same visit.

The elasticity of the caudicles allows them to be stretched to more than 5 times the original length before they break off. With optimal (thin layer) attachment on the clypeus of a legitimate vector, caudicles break off at their bases close to the discs rather than the discs becoming detached from the surface of the vector. Bumble-bees are hardly able to stretch caudicles more than 3 times the original length in attempts to get rid of the pollinaria (Fig. 5 E). During visits to other plants with deep flowers the caudicles easily bend backwards if the pollinia become run

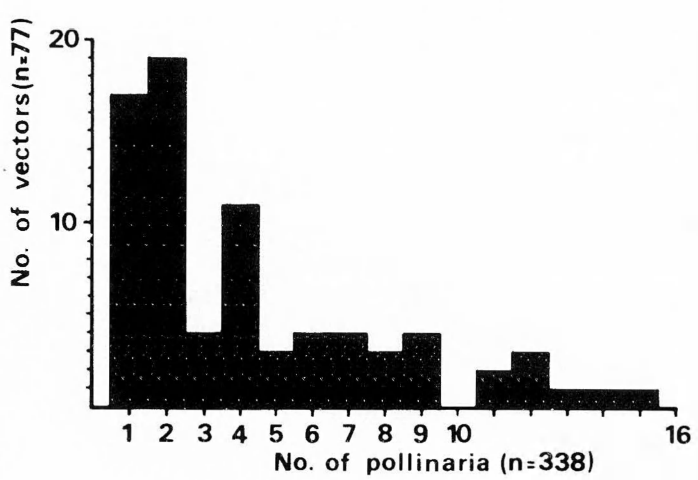

Fig. 11. The number of pollinaria on pollen vectors of *Dactylorhiza sambucina*.

into various floral parts which minimizes loss of massulae (Fig. 5 D). On more superficial food-flowers the pollinaria on bumble-bees do not touch floral parts at all due to the comparatively long probosces (Fig. 5 F). Within a few days after the beginning of anthesis, vectors were regularly found with only caudicles and discs left on their heads which suggests that the pollinia become worn out in one or maybe a few days due to the highly active, extremely anthophilous and powerful vectors.

Fruit set

Fruits are developed only after pollination (Table 3). Auto-pollination does not occur although sometimes the pollinia lean out of their pockets when the enclosing folds of the anther shrink during the final part of anthesis. Compared to conspecific crossing, selfing gives a lower percentage of seeds containing distinct embryos. Pollination with *O. mascula* and *O. morio* pollen produces no or practically no fruits and embryos. In a single specimen a very weak positive reaction for *O. mascula* pollen was noted. Obviously fruit set of *D. sambucina* found in mixed populations with these *Orchis* species can be regarded as a result of conspecific pollen transfer.

Fruit set of natural populations fluctuates considerably between different years but also between different populations (Table 4). Population A has constantly a very small success per individual while others may reach above 40 % fruit set. On one occasion in A 43 inflorescences on a small spot were examined but only 2 (0.3 %) of the 694 open, almost finished flowers had been pollinated which suggests rareness of visitors in certain subhabitats. The low fruit set in B in 1978 was mainly due to the damage caused by cold. Next year the fruit set was 15 times higher. In C the percentage was about 5 times higher in 1977 than in 1976. On Skabbholmen in Uppland, Skottsberg (1907) reported very low fruit sets for the years 1900 and 1901 viz. 2.2 and 3.1 % of the flowers respectively.

In C in 1977 the yellow morph had 5.6 % higher fruit set than the red morph. In B in 1977, 100 inflorescences of each morph in mid-anthesis were examined: on average, 0.9 and 1.8 flowers per plant were pollinated of the red and yellow morphs respectively. Additional scattered observations support that there is at least no drastic difference in fruit production between the morphs.

A slight, almost linear, correlation exists between the number of flowers in inflorescences and number of fruits produced (Fig. 12 B). For individuals with less than 10 flowers there seems to be a fast decline towards no fruit set at all. The

Table 3. Results of controlled pollination experiments with *Dactylorhiza sambucina*. — * on the same plant individual.

Conditions	No. of plants	No. of flowers	No. of strongly swollen ovaries	No. of slightly swollen ovaries	Seeds with embryos. Range (%)	Seeds with embryos. Mean (%)
Self-pollinated	15	30	29	0	4.5–88	43
Cross-pollinated	15	29	29	0	32–95	75
With *O. mascula* pollen	10	20	0	2*	1.7*	0.2*
With *O. morio* pollen	10	20	0	0	0	0
Untouched	15	160	0	0	0	0

Table 4. Fruit set of *Dactylorhiza sambucina*. — * This value is probably too high as only large fruiting individuals could be found this year due to exceptionally fast decomposition.

Locality	Year	No. of plants	No. of flowers	No. of fruits	Fruit set per specimen (%)
A	1976	135	2157	41	2.1
A	1977	30	595	54	8.2
A	1978	44	640	117	18.2*
A	1979	180	2588	219	9.3
B	1978	257	2617	65	2.8
B	1979	62	572	213	41.7
C	1976	68	1268	115	9.7
C	1977	62Y	845	417	48.5
C	1977	217R	3075	1341	42.9
C	1979	90	1305	255	20.6

phenomenon is probably a result of differences in attractive capacity (see above).

A very striking decrease in fruit production exists from the bottom to the top of inflorescences (Fig. 12 C, Ds). Compared to flowers in the lowermost position (No. 1) flowers in positions Nos. 26–37 have about 15 times less fruit set. If a curve is constructed for a non-deceptive nectar producing orchid which stimulates pollinator constancy, a completely different picture is obtained as showed with *Platanthera chlorantha* (Cust.) Rchb. (Fig. 12 C, Pc), a moth-pollinated species (see Nilsson 1978). The rapid decline of fruit set upwards in inflorescences of *D. sambucina* reflects the behaviour of deceived pollen vectors and the early visiting before all flowers are open.

Discussion

Phenologies, interactive morphologies, flower-visiting and occurrence of pollinaria on insects show that *D. sambucina* is almost exclusively pollinated by *Bombus* queens. In the study areas, species having middle-sized heads are the legitimate pollinators i.e. *B. lapidarius* and *B. sylvarum*. These two species are common in Fennoscandia also outside the distribution of *D. sambucina* (cf. Løken 1973 and Hultén 1971). Solitary bees seldom act as pollinators which is remarkable since many species (e.g. *Andrena*) are at maximum during the anthesis of *D. sambucina*. Even patrolling males of *Osmia bicolor*, which spend most of their lives among *D. sambucina*, contribute rarely to pollination. Floral allurement seems inefficient for solitary bees.

The pollination system based on deception functions optimally during the unconditioned stage in the *Bombus* populations that occurs shortly after their emergence from hibernation. This is in accordance with the preliminary observations made by Delpino (1873–74). Hoffer (1883) recorded visits on May 13 which thus points in the same direction. During this stage, which occurs in May for all *Bombus* species, queens have to make frequent exploratory visits to various supposed food-sources, which favours the system. Examination of the corbiculae clearly indicates that this occurs before the food for the first brood is collected. Since bumble-bees soon establish individual foraging routes to clusters of food-flowers (Manning 1956, Heinrich 1976), the system of deception reasonably functions mainly before such habits have been acquired. The general behaviour of bumble-bees in relation to *D. sambucina* seems similar to that observed on *Calopogon pulchellus* (Salisb.) R. Br., another orchid acting by deceit (Heinrich 1975 a). Later, obviously, only occasional visits take place in addition to those made by unhealthy queens. Delpino (1873–74) argued that bumble-bees soon learn to avoid *D. sambucina* and *Bombus* has been observed to avoid *Orchis* species when these are growing amongst other flowers (van der Pijl 1966). During constancy on food-flowers in mixed populations such reactions are to be expected (if not mimetic resemblance is involved). However, there is no evidence to suggest that the drop in visiting after the unconditioned stage, reflects anything but the queens' habits to keep to their daily foraging routes which certainly do not incorporate *D. sambucina*.

Inexperienced bumble-bees ("Neulinge") are attracted to their first flowers by optical cues after which they explore the floral construction for food (Kugler 1935). Thus, the colours in *D. sambucina* are probably adaptations for spontaneous far attraction of pollinators. In the case of *Calopogon pulchellus* Heinrich (1975 a) presented a theory that the ability to deceive is increased by its variability in colour as it should take pollinators longer time to avoid the species. The coexisting of colour morphs in *D. sambucina* might be such an adaptation. Further observations are needed, however, before any conclusions can be made. The colours of the morphs are expected to fall close to optical sen-

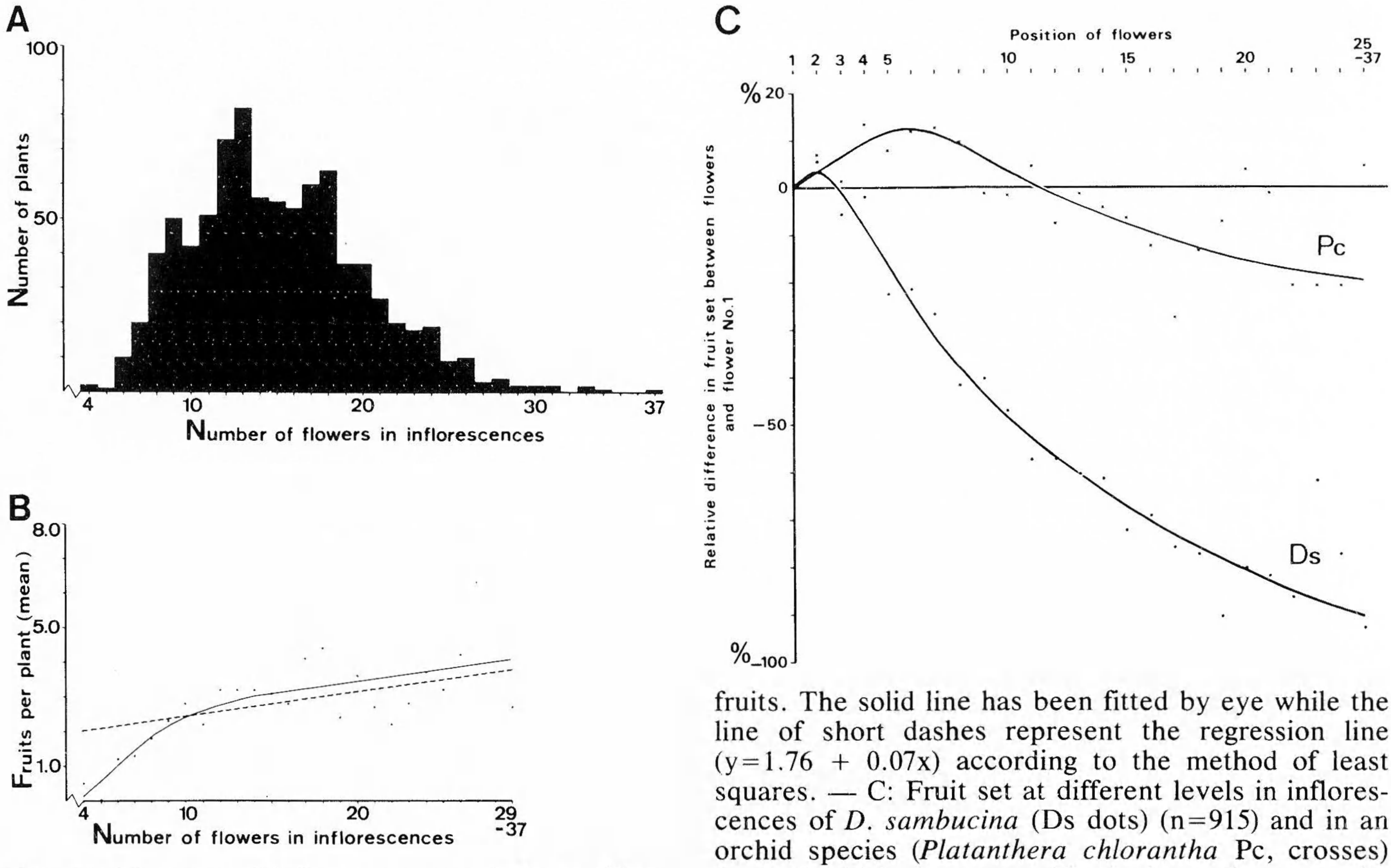

Fig. 12. The size of inflorescences and the positions and production of fruits in *Dactylorhiza sambucina*. Countings have been lumped from the three populations studied. — A: Histogram illustrating the number of flowers developed by inflorescences (n=853). — B: Relationship between the number of flowers in inflorescences (n=853) and the (mean) number of produced fruits. The solid line has been fitted by eye while the line of short dashes represent the regression line ($y=1.76 + 0.07x$) according to the method of least squares. — C: Fruit set at different levels in inflorescences of *D. sambucina* (Ds dots) (n=915) and in an orchid species (*Platanthera chlorantha* Pc, crosses) (n=296) which gives reward in the form of nectar to its visitors (moths). The positions of flowers have been numbered from below. Fruit set (mean) for each flower position is given as the relative difference in percent between the value for each position and the fruit set (mean) of flowers in the lowermost position (flower No. 1). The curves have been fitted by eye.

sitivity maxima in bumble-bees since many bumble-bee-adapted plants have either of these two ground colours e.g. *Corydalis* spp., *Lamium, Stachys, Galeopsis* etc. In contrast to the situation in the populations studied, the yellow morph dominates in frequency in Central Gotland and also further south in Europe (Pettersson 1958). In Norway only the yellow morph occurs (Robak 1940). Whereas the latter might reflect long distance dispersal of monotypic seed, regional and local morph ratios probably reflect adaptations to the diversity of concurrently flowering food-flowers and to the composition of bumble-bee faunas in different regions and ecological habitats. Existence of the two morphs seems advantageous as it should provide a sophisticated possibility for fast selection towards optimal utilization of the locally available potential for deception. The small differences in spur-lengths between the morphs found, are perhaps correlated to small differences in the composition of pollinators or in their behaviour vis-à-vis the morphs. A possible trend from the few data on comparative fruit set and "morph constancy" by queens might be that the yellow morph has a slight selective advantage and therefore slowly increases in percent in the populations studied.

However, the genetical system responsible for the colour variability is unknown. In addition to the distinct two colours, there also exist intermediate light red specimens at, normally, very low percentages in all populations. Since queens do not seldom shift between the morphs, the light red individuals cannot reflect a simple F_1 offspring but probably represent certain gene combinations which are produced in continuous introgressive hybridization between the two morphs.

The false red pigmented nectar guide pattern is obviously an adaptation to stimulate alighting and food searching reactions (cf. Kugler 1970). The impression of a deep spur also has this effect (Kugler 1970). That the spur is "apparently functionless" (van der Pijl & Dodson 1966) seems doubtful. In *Dactylorhiza incarnata* (L.) Soó Daumann (1941) found that 8.4 % of the visited flowers showed damages caused by probosces.

The non-resupination of early flowers might perhaps be interpreted as an adaptation to the behaviour of queens. However, Ziegenspeck (1936) noted that bumble-bees spontaneously turned the head down when confronted with non-resupinate flowers of *Dactylorhiza maculata* (L.) Soó. The floral terpene emission in *D. sambucina* probably stimulates the queens to alighting and food searching on the flowers.

Why is *D. sambucina* gregarious and why does it normally dominate the floral display on its localities? Since the species normally grows in the open, gregariousness probably attracts scouring queens very effectively. It also releases renewed scouring after a few exploratory visits. This might favour cross-pollination and perhaps minimizes the energetic costs of the pollination system (which is paid by other plants), in that queens soon become directed to clusters of food-flowers.

No evidence suggests that *D. sambucina* mimics either one or a group of food-plants utilized by the queens. Since the orchid is totally dependent on the energy produced by other plants to its pollinators, it seems improbable from an energetic point of view that selection towards such resemblance should be advantageous. Bumble-bee queens are highly energy-requiring pollinators (Heinrich 1975 b) and simply cannot spend much of their active time flying about and becoming deceived. Therefore selection probably acts in a way which, to a certain degree, makes *D. sambucina* distinguishable from the queens' food-plants as its deception system acts within the limits of the energy flow from these plants. This is supported also by the fact that food competition between pollinators is most severe in spring (Mosquin 1971). Thus colour and fragrance resemblances with food-plants are not necessarily of selective advantage for the pollination system in *D. sambucina*. The pollination system probably benefits from *Sphaerularia* infection of queens since no nesting, frequent scouring and disrupted constancy (Lundberg & Svensson 1975) produce more situations for deception. The spread of *Sphaerularia* within populations varies and sometimes reaches very high levels (Palm 1948). In contrast to healthy queens, infected individuals are expected to contribute to pollination now and then throughout anthesis.

The visitation which results in predominant fruit set in the lowermost flower positions, was already reported by Delpino (1873–74) but Ziegenspeck (1936) later denied the correctness of Delpino's conclusions. Only a few flowers in the inflorescence contribute directly to seed production whilst the majority functions only in attraction. Therefore few flowers in an inflorescence have a selective disadvantage. The number of flowers produced must be much higher than what is necessary for seed production alone. Apparently this is one of the costs of deception. On the other hand queens' short actions reasonably produce a prominent outcrossing breeding system which promotes high genetic variability in the species. It seems therefore that *D. sambucina* has an extraordinary potential for evolutionary response.

The inhibited development of fruits and embryos in crosses with *Orchis* pollen points to an existence of a strong genetic barrier in that direction. However, hybrid records indicate that the barrier is incomplete (Sundermann 1975). According to observations of pollinaria on queens, interspecific pollen transfer with *D. sambucina* as a mother plant, is frequent. Also the non-discriminating exploratory behaviour of queens points to a low degree of 'ethological' isolation between these orchids.

The strong multi-component terpene emission seems to render *D. sambucina* to an isolated position within *Dactylorhiza*. For instance, *D. incarnata* is practically scentless, only very small amounts of α-copaene are emitted, while *D. maculata* ssp. *fuchsii* Druce only produces small amounts of 4 sesquiterpenes (Nilsson unpubl.). *D. sambucina* is the only spring flowering member of *Dactylorhiza* in northern Europe (Sundermann 1975) and since the early *Orchis* species *O. mascula* and *O. morio* also have strong terpene emissions (Nilsson unpubl.), pollination of nectarless orchids in spring by bumble-bee queens seems to require strong fragrances. Thus, the statement that the nectarless *Orchis* species "are scentless or have faint fragrance" (Dafni & Ivri 1979) is contradicted by gas chromatographic evidence.

The pollination system based exclusively on deception of queens seems also isolated within *Dactylorhiza*. For example *D. incarnata* is pollinated by inexperienced bumble-bee workers (Daumann 1941) and since fresh workers emerge from nests all the time ('newcomers'), deception is working fully throughout anthesis, not only the first days of flowering as supposed by van der Pijl & Dodson (1966). A general pollination principle probably cannot be ascertained for either *Dactylorhiza* or *Orchis* but these species are anthecologically specialized to exploit more or less diverse deception situations. That any additional attractants are present (Faegri & van der Pijl 1971) in addition to colour and scent is not supported by any evidence (cf. Daumann 1971).

The early flowering makes *D. sambucina* exposed to hazard with unreliable factors such as spring weather and the hibernation success of *Bombus* queens. However, both flowering and emergence from hibernation are probably controlled by the same spring weather factors which ensure coexistence (cf. Siivonen 1942). Van der Pijl & Dodson (1966) suppose that the pollination system of *Orchis* spp. (s.l.) is "rather unbalanced and unsatisfactory" and "more or less unspecialized". This seems not to be the case in *D. sambucina*. On the contrary, the pollination system in this species is highly specialized not only to a certain congeneric group of available insect pollinators but also to a certain stage in their lives.

Acknowledgements. I wish to thank all friends at the Ecological Station of Uppsala University, Ölands Skogsby, for good working facilities. I am greatly indebted to Professors Olov Hedberg and Bertil Kullenberg, Mrs Anita Nilsson, Mr Björn Cederberg and Dr Bo G. Svensson for valuable suggestions on the manuscript in whole or in part. Special thanks are due to the two last mentioned persons for various information on bumble-bees. Finally I thank Mrs Ulla-Britt Sahlström for making the photographs and Mrs Linda Berry-Mennerdahl for the linguistic check of the text.

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Everniastrum andense sp. nov., a neotropical paramo lichen

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Kärnefelt, I. 1980 09 18: Everniastrum andense sp. nov., a neotropical paramo lichen. *Bot. Notiser 133:* 387–394. Stockholm. ISSN 0006-8195.

Brief introductory remarks on the genus are followed by a detailed description of the new species, *E. andense* Kärnef. The section on taxonomy deals mainly with the affinity of the new species with *E. ecuadoriense* (R. Sant.) Hale. *E. andense* appears to be endemic to the northern Andean region of Neotropis colonizing twigs of paramo shrubs. Illustrations of anatomical and morphological characteristics and a distribution map are included.

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The genus *Everniastrum* was established by Hale (1976 a) and comprised 21 species, several of which had earlier been included in *Parmelia* subgenus *Everniiformes* (Hale & Wirth 1971). Since then *E. mexicanum* has been discribed by Egan (1978) and *E. paramense* by Hale & Lopéz-Figueiras (1978).

The genus is mainly characterized by long more or less canaliculate lobes, with or without long marginal cilia. Further the thin epicortical layer is pored, and atranorin was found as cortical substance in all 23 species. Several medullary substances, including protolichesterinic acid, are also reported.

Everniastrum is a mainly neotropical genus, most of the species occurring in high mountain regions from Mexico to Chile and Argentina. Only four species occur in Asia and one, *E. africanum*, is described from a similar habitat in Tanzania.

Material and methods

I have examined the material of *Everniastrum* in LD and GB. The material of *E. andense* was borrowed from GB, M and S. In US I saw in addition material from the type locality.

Light and interference contrast microscopy was carried out on sections c. 10–15 μm thick, sectioned on a freezing microtome and stained in Lactic Blue. Scanning electron microscopy was carried out on one specimen each of *E. andense* and *E. ecuadoriense* according to the procedure described by Hale (1973, 1976 b). Thin layer chromatography was carried out according to the method described by Culberson (1972).

Everniastrum andense Kärnef., sp. nov.

Holotype: Venezuela, Merida State, Sierra de Santo Domingo, Páramo de Mucuchies, near Laguna Negra, alt. 3500–3750 m, on dead twigs of *Hypericum laricifolium*, 13.1 1979 Santesson 20418 (S).

E. ecuadoriensi simile a quo differt lobis magis canaliculatis brunneis apice non ramosis et ciliis marginalibus longioribus minus ramosis. Cortex et medulla K–, C–, KC–, PD–. Atranorinum deest in cortice; in medulla acidum lichesterinicum et acidum protolichesterinicum adsunt.

Thallus subfruticose, unbranched or sparsely dichotomously branched, apically always unbranched, forming rather open colonies. *Lobes* longish, linear, 0.3–0.5(–1.0) cm, suberect, 0.2–0.5(–1.0) mm broad. *Upper surface* slightly vaulted, pale brown to dark brown, sometimes with blackish portions, smooth and usually dull. *Lower surface* canaliculate, pale brown to brown, often with transverse ridges or smooth, usually dull. *Basal portions* of the lobes usually blackish. *Margins* usually thicker and darker than the middle portions of the lobes. *Cilia* abundant on the margins, (1–)2–3(–5) mm long, often singly branched, or sometimes several times, blackish. *Pseudocyphellae* and soralia not present.

Epicortical layer pored. *Pores* usually irregularly formed 10(–20) μm large, often assembled in smaller groups. *Upper cortex* 20–30 μm thick, prosoplectenchymatous, composed of more or less anticlinally oriented hyphae, peripherically with a brown pigmentation. Portions of the cor-

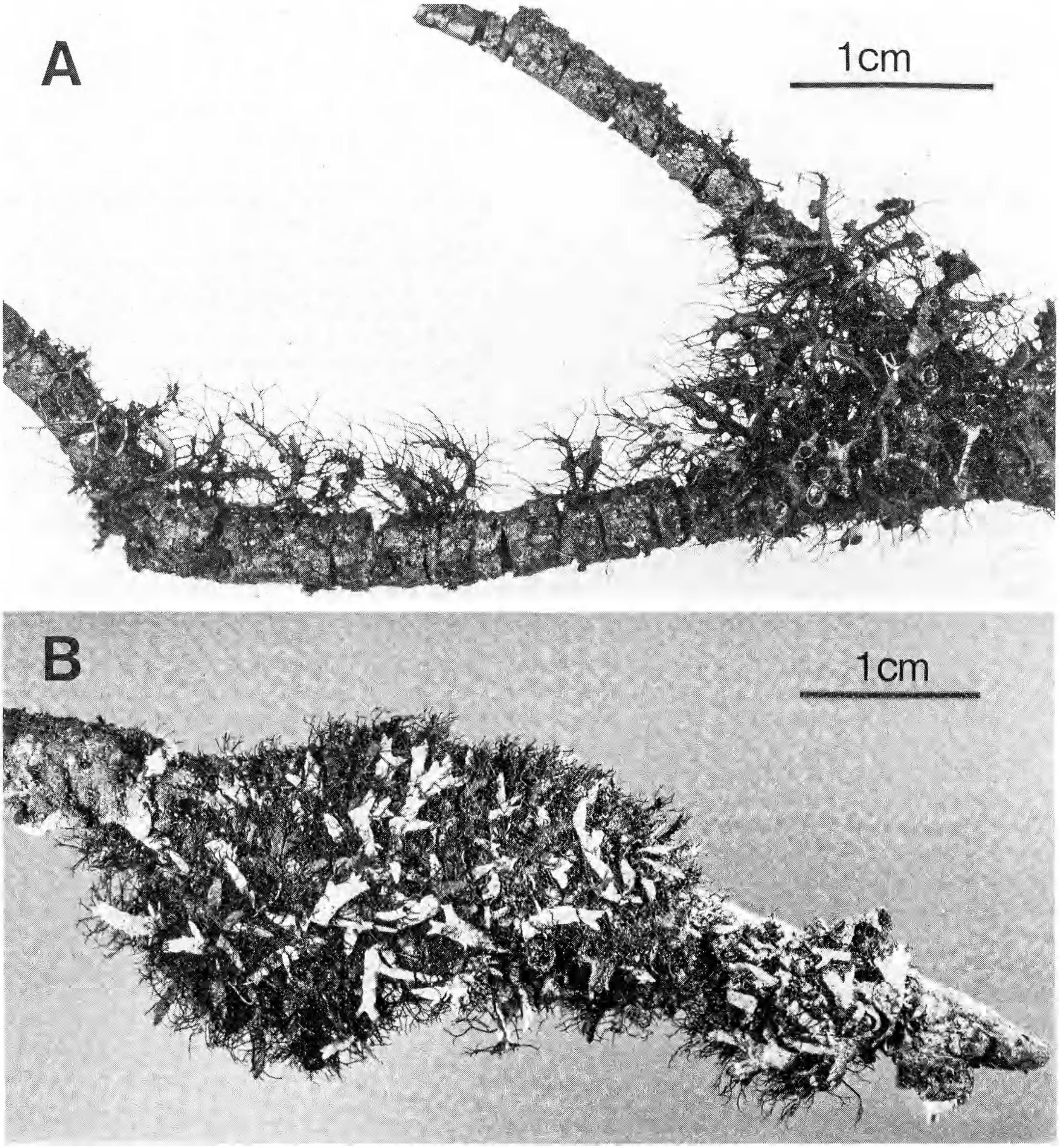
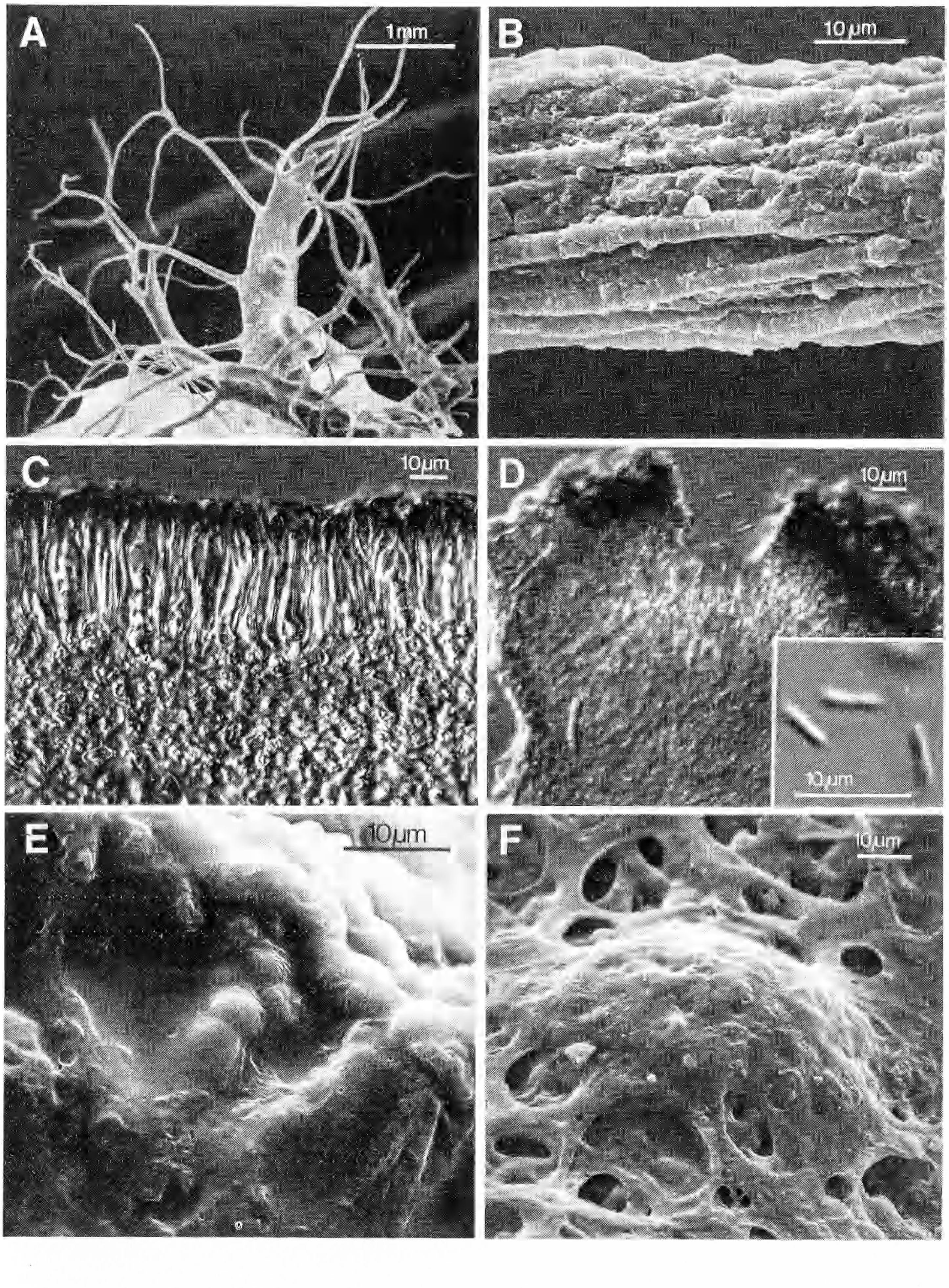


Fig. 1. A: *E. andense*. Venezuela, Anden, Estado Merida, Strasse Apartaderos–Valera, El Aguila, c. 3850 m, 1969 Oberwinkler 15158 c (M). — B: *E. ecuadoriense*. Ecuador, Pichincha, eastern slopes of Cerro Iliniza, alt. c. 4200 m.s.m., paramo, epiphyte on *Chuquiraga*, 1972 Arvidsson & Nilsson 903 (GB).

Fig. 2. Cilia, hymenium and pycnidium of *E. andense*. — A: SEM micrograph showing the simply branched marginal cilia. 1979 Santesson 29418 (S, holotype). — B: Close to the tip of a cilium showing the strongly conglutinated bundles of hyphae. 1979 Santesson 24418 (S, holotype). SEM. — C. Cross-section of hymenium with asci and ascospores. 1969 Hertel 10662 (M). Interference contrast micrograph. — D: Cross-section of pycnidium. Enlarged the slightly dumb-bell-shaped pycnoconidia. 1969 Hertel 10662 (M). Interference contrast micrograph. — E: Cross-section of hymenium with asci and ascospores. 1979 Santesson 24418 (S, holotype). SEM. — F: Immature pycnidium immersed in the pored surface. 1979 Santesson 24418 (S, holotype). SEM.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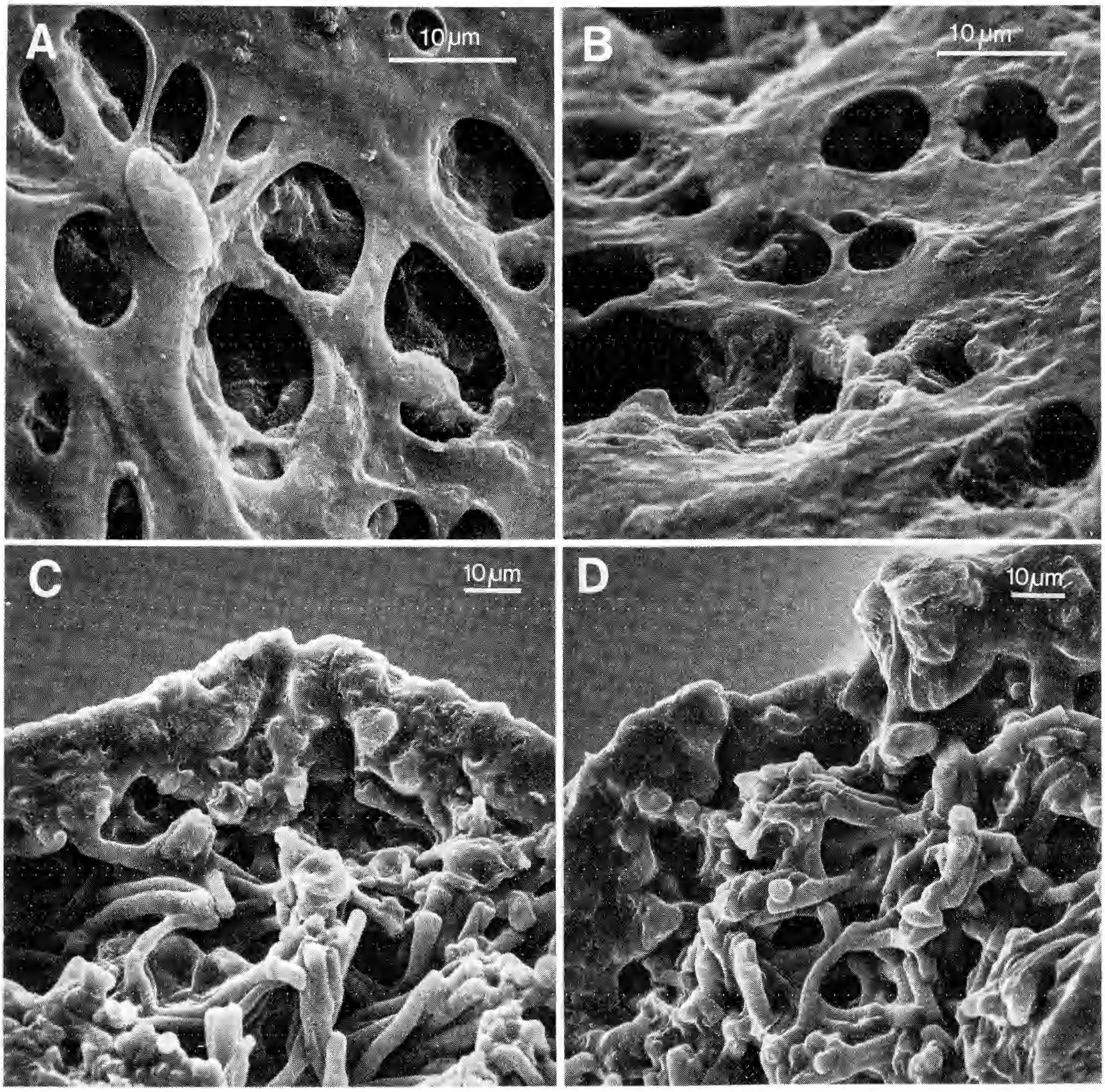

Fig. 3. Pored epicortical layer and cortex. — A. *E. andense.* 1979 Santesson 24418 (S, holotype). SEM. — B: *E. ecuadoriense.* Malme, Lich. austroamericani 356 (LD). — C: *E. andense.* Cross-section showing penetrated upper cortex. 1979 Santesson 24418 (S, holotype). SEM. — D. Another part of the same cortical section as in C showing a larger gap in the cortex.

tex perforated, in places broken under the pores. *Medulla* 60–220 µm thick, structure dense, hyphae 2.5–3.5 µm thick. *Algae* concentrated near the upper cortex in a layer 10–20 µm thick, individual cells green and spherical, 8–12 µm in diameter. *Lower cortex* 10–20 µm thick, prosoplectenchymatous, darker than the upper cortex.

Apothecia often abundant, developing on the upper surface, laminal. *Disc* (0.2–)0.5–2.0(–4.0) mm broad, usually darker brown than the thallus, glossy. *Thalline margin* with a pored epicortical layer, sometimes slightly crenulated and with short cilia, 0.2–0.5(–1.0) mm. *Hymenium* 40–50 µm thick. *Asci* cylindrical to clavate, 25–35×5–10 µm. *Spores* 8, hyaline, round to subglobose 4–6×4–5 µm. *Paraphyses* septated, c. 50×1.5 µm. *Hypothecium* 20–30 µm thick, colourless. *Pycnidia* scattered on the upper sur-

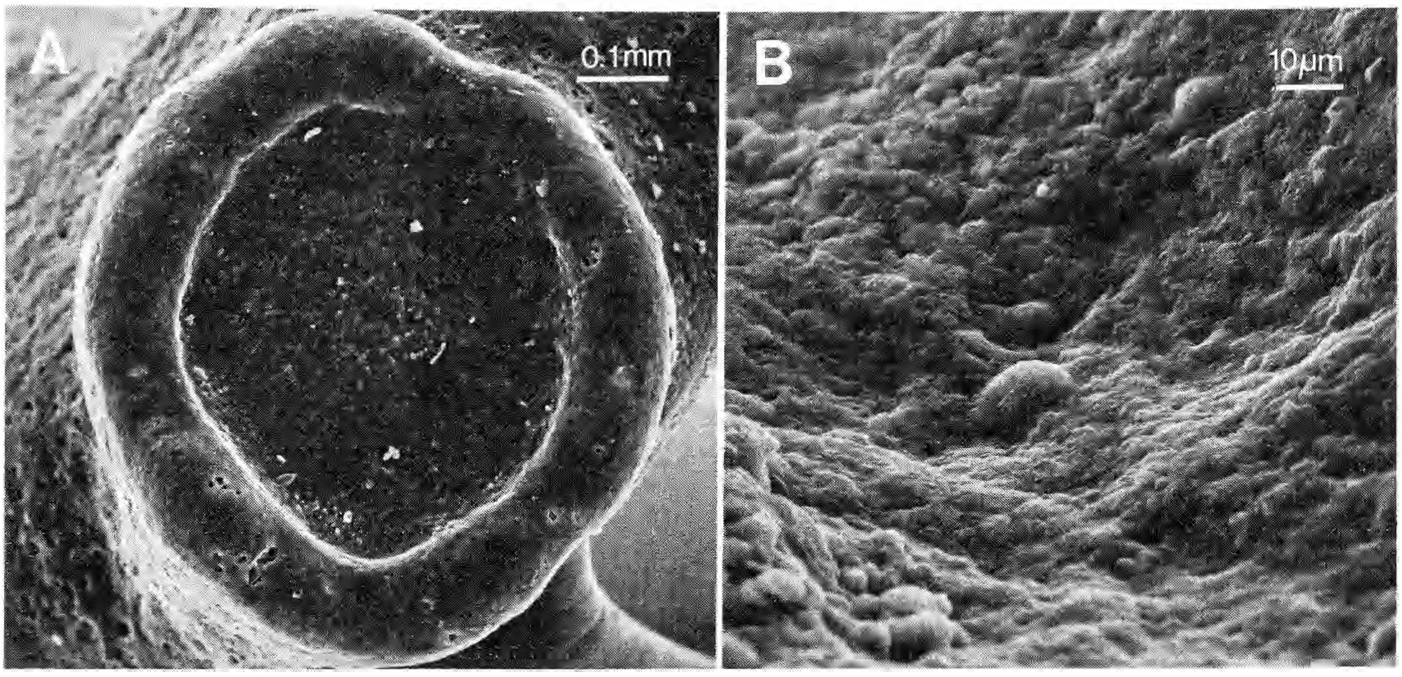

Fig. 4. *E. andense.* — A: Pored thalline margin of apothecium. 1979 Santesson 24418 (S, holotype). SEM. — B: Unpored lower surface. 1979 Santesson 24418 (S, holotype). SEM.

face, immersed, pyriform. *Conidiophores* about 30 µm thick in the mature pycnidial chamber. *Pycnoconidia* slightly dumb-bell-shaped, about 5.0×0.5 µm.

Chemistry

Cortex and medulla K–, C–, KC– and PD–. *E. andense* contains lichesterinic and protolichesterinic acids in the medulla. No cortical reactions or substances were detected, *E. andense* thus being the only species in the genus lacking atranorin in the cortex.

Taxonomy

Of the other 23 species included in the genus, *E. andense* appears to be closest to *E. ecuadoriense* (see Santesson 1942). The new species is distinguished on the linear brownish and canaliculate lobes with rather long blackish singly branched marginal cilia (Fig. 1 A, 2 A). *E. ecuadoriense* has slightly wider less canaliculate lobes, the upper surface being flatter. Further the branching of the lobes of *E. ecuadoriense* is different, apically usually dichotomously branched and with several lateral branches (Fig. 1 B). The cilia on *E. ecuadoriense* are usually more abundant but are shorter and the lateral branches often numerous. The ultrastructure of the cilia of both species is as described by Hale (1976 b), composed of strongly conglutinated bundles of hyphae (Fig. 2 B).

Because of the long marginal cilia and the linear canaliculate lobes *E. andense* have certain characteristics in common with *Anaptychia* and other members of the *Physciaceae*. The reproductive structures, however, are parmeliaceous (Fig. 2 C, D, E, F).

Further *E. andense* differs from *E. equadoriense* in the brown colour of the upper lobe surface, the upper surface of the lobes in *E. ecuadoriense* being more greyish. The lower surface of the two species also differs in structure, *E. andense* being ridged while in *E. ecuadoriense* it is rougher.

The pored epicortical layer is a generic character rather than a critical species character. When I first saw material of *E. andense* I believed it could be in the genus *Cetraria*. For practical purposes I also used a herbarium name which unfortunately has also become known outside Lund. However, after having studied the material in the SEM I realized the new taxon could not possibly belong to *Cetraria*. All species of *Cetraria* examined in the SEM have a non-pored epicortical layer. I therefore also decided not to use the unpublished specific epithet which had

Fig. 5. Habitat of *E. andense*, showing the site in Venezuela on the Paramo de Mucuchies at about 3500–3750 m.s.m. The vegetation is dominated by the large shrubby *Espeletia* (Asteraceae). The darker shrubs are *Hypericum laricifolium*, where the corticolous species is growing. January 1979, Rolf Santesson.

been intended to honour a *Cetraria* monographer (see López-Figueiras 1977).

According to Hale (1976 b) the epicortical pores are c. 10–30 µm in diameter. In *E. andense* the pores are usually about 10 µm in diameter, appearing in smaller groups as also stated by Hale (1973) (Fig. 3 A). The structure of the epicortical layer of *E. ecuadoriense* is the same as that in *E. andense* (Fig. 3 B).

The cortical layer is usually only broken by narrow passages penetrating to the algal and medullary layers (Fig. 3 C). Occasionally even larger parts of cortical tissue are lacking (Fig. 3 D). In addition scattered pores occur on the apothecial thalline margin (Fig. 4 A). The lower surface, however, is non-pored (Fig. 4 B).

The main function of the pores is presumably to allow gas exchange between the algae and the atmosphere. Hale (1976 b) concluded that a pored epicortex could be characteristic of lichen groups that have evolved or are centred in the tropics, giving examples from the genera *Coccocarpia* and *Hypotrachyna*. Species within ecologically corresponding lichen genera in boreal or arctic regions have non-pored epicortical layers. A pored epicortex would probably be an inadequate cover for the sensitive algal layer during the long period of frost.

Habitat

Subalpine habitats in the Andean region are locally characterized by giant shrubby *Espeletia* (Asteraceae) and other large shrubs. This unique type of vegetation is called paramo.

In Venezuela *E. andense* has been found at altitudes of c. 3500 m to 4250 m growing on twigs of *Hypericum laricifolium* (Fig. 5). According to Professor Santesson (in litt) the new species was locally abundant on dead shrubs 1–2 m high. In Ecuador it was found together with *E. ecuadoriense* at c. 4200 m growing on twigs of *Chuquiraga* (Asteraceae).

Hypericum laricifolium is the substrate also for other notable species, such as *Parmeliopsis angustior* Nyl. and an undescribed species of *Nephromopsis*.

Distribution

E. andense is so far only known from the northern neotropical Andean region (Fig. 6 A). The specific epithet refers to this region. Most collections have been made in a rather limited area south of Lago de Maracaibo in the paramo region of Cordillera de Mérida in Venezuela. In a lichen collection from Ecuador in the Pichincha Andean region east of the Cotopaxi massif I also discovered a small specimen of the species. *E. andense* probably occurs outside these two Andean areas. I assume the species to colonize similar Andean habitats from northern Venezuela to Colombia and Ecuador.

Two other species, *E. peruvianum* and *E. subnepalense*, have in addition been described from high elevations in Peru (Hale 1976 a), a probable southern limit for the species distribution. *E. ecuadoriense* is only known from a few localities in the central Andean region of Ecuador (Fig. 6 B). This species presumable has a somewhat wider Andean distribution.

A number of other lichens are also mainly distributed within the northern Andean region. *Hypotrachyna lopezii* (Hale 1975), *H. cendensis, H. meridensis, H. neoflavida, H. primitiva* (Hale & López-Figueiras 1978) and *Pseudoparmelia venezolana* (Hale 1976) are described from the Venezuelan paramo, and one crustose species, *Rhizocarpon oberwinkleri* (Hertel 1974). *Hypotrachyna andensis, H. chicitae, H. enderythraea, H. obscurella, H. osteoleuca, H. physodalica* and *H. protenta* are also centred in the region, some with extensions to the Caribbean region in the north and to the Amazon region in the south (Hale 1975). Also mainly endemic to

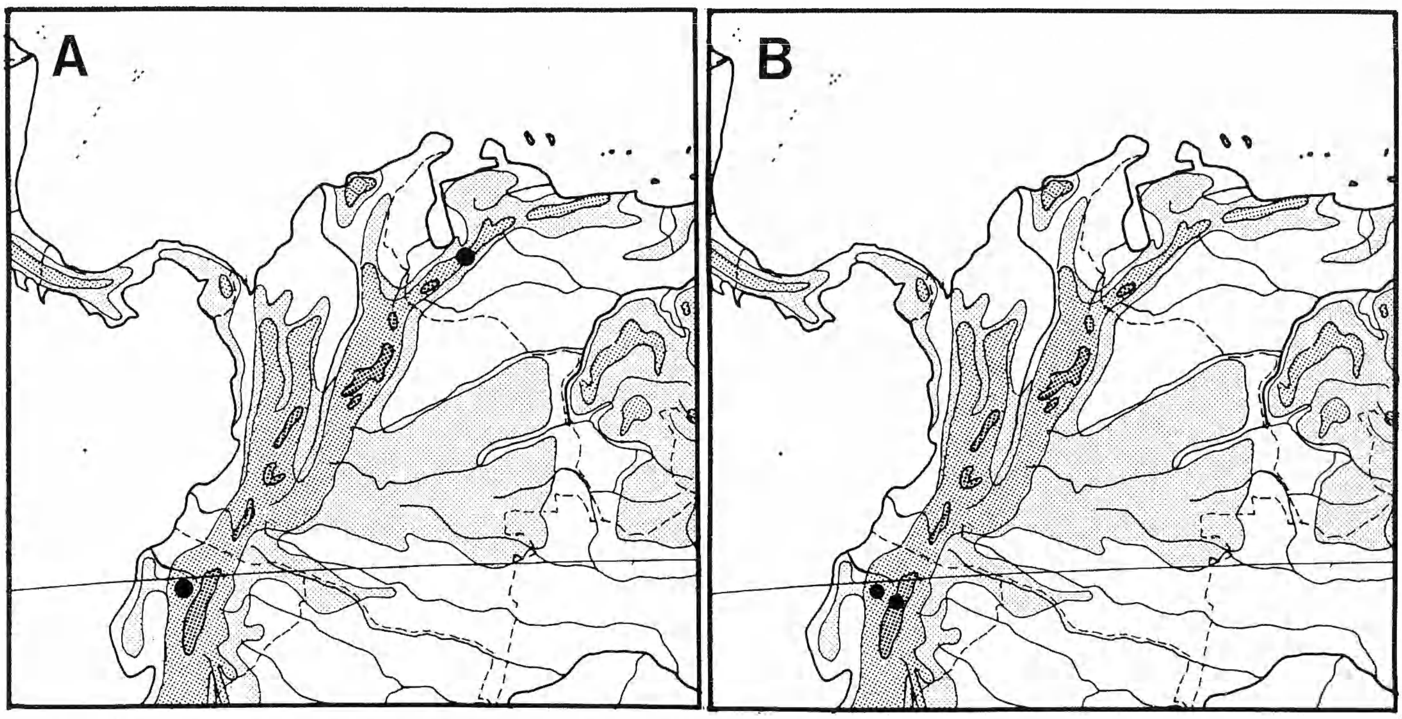

Fig. 6. A: The known distribution of *E. andense*. — B: The known distribution of *E. ecuadoriense*.

the northern Andean region are a few species of *Cladonia*, viz. *C. arcuata, C. bicolor, C. boliviana, C. polia* and *C. rotundata* (Ahti 1961).

However, the northern Andean region and the paramo type of vegetation are not wholly unique floristically. Hertel (1971) reported a number of common Holarctic crustose lichens from the Venezuelan paramo, i.e. *Candelariella vitellina, Lecanora atra, L. badia, L. polytropa, Lecidea atrata, L. crustulata, L. lapicida, L. tesselata, Lecidella elaeochroma, Rhizocarpon superficiale, Sarcogyne simplex* and *Trapelia coarctata*.

Localities. Ecuador. Pichincha: Eastern slopes of Cerro Iliniza, alt. ca 4200 m.s.m. Páramo, epihyte on *Chuquiraga*, 1972 Arvidsson & Nilsson 903 (GB) (small specimens on dominating *E. ecuadoriense* colony).

Venezuela. Anden, Estado Merida: Strasse Apartaderos-Valera, El Aquila, c. 3850 m, 1969 Oberwinkler 15158 c (M, two packets with same number). — Distri tio Rangel, Páramo de Mucuchies, Höhenrücken oberhalb der Strasse von der Passhöhe El Aguila nach Pinango, c. 1 km NW von El Aguila, alpine Stufe, c. 3900 m, 1969 Hertel & Oberwinkler 10662 (M). — Sierra de Santo Dominigo, Páramo de Mucuchies, near Laguna Negra, alt. 3500–3750 m, on dead twigs of *Hypericum laricifolium*, 1979 Rolf Santesson 29418 (S, holotype; LD, isotype); 29402 (S).

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Pezizella kashmirensis, a new discomycete from India

K. S. THIND and M. P. SHARMA

Thind, K. S. & Sharma, M. P. 1980 09 18: Pezizella kashmirensis, a new discomycete from India. *Bot. Notiser 133:* 395–396. Stockholm. ISSN 0006-8195.

A new species, *Pezizella kashmirensis* Thind & Sharma, is described and illustrated from the North-Western Himalayas, India, and a key is provided for the three known Indian species of the genus.

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The generic name *Pezizella* was proposed by Fuckel (1870), including species having small excipular cells, asci and ascospores. No sharp line exists between *Pezizella* Fuck. and *Hymenoscyphus* S. F. Gray but the former differs from the latter by the smaller cells of the ectal excipulum lying at low level to the surface, slightly narrower asci and smaller ascospores (Dennis 1968).

In India, the genus is previously known only by two species, *P. discreta* (Karst.) Dennis and *P. companuliformis* (Fuck.) Dennis, recorded by Thind and Singh (1970) and Singh (1974), respectively. In the present paper a new species is described and illustrated. Key to the three Indian species is provided.

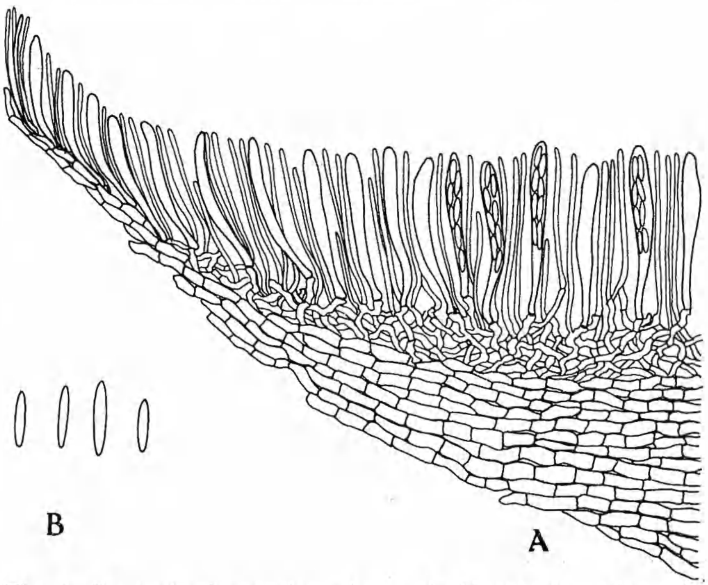

Fig. 1. *Pezizella kashmirensis*. — A: Vertical section of the apothecium showing excipulum and hymenium. × 320. — B: Ascospores. × 800.

Key to the Indian species of Pezizella

1. Ascocarps on fern rhizome *P. companuliformis*
– Ascocarps on other substrates 2
2. Ascocarps on *Salvia glutinosa* twigs; asci J+; ascospores 5.0–6.5×1.0–1.5 μm ...... *P. discreta*
– Ascocarps not on *Salvia*; asci J−; ascospores 6.5–9.0 × 1.0–1.5 .... *P. kashmirensis*

Pezizella kashmirensis Thind et Sharma sp. nov., Fig. 1 A–B

Orig. coll.: India, Jammu & Kashmir, on way to Pissu Ghati, Chandanwari (3,200 m), on dead herbaceous angiospermic stems, 29.8.1972. M. P. Sharma 3986 (PAN holotype; isotypes at TAA and with Dr. W. D. Graddon, Ross-on-Wye, England).

Ascocarpi ad 2,5 mm diametro, superficiales, sessiles ad subsessiles, dense gregarii, solitarii, nonnunquam confluentes, carnosi, discoidei vel haud profunde cupulati, regulares, in vivo cremicolorati ad pallide-flavi in sicco flavo-brunnei, glabri; hymenium concoloratum, concavum, leve; margo tenuis, integer in sicco incurvatus. Excipulum externum ad 95 μm crassitie, textura porrecta, hyphis ad angulam angustam superficiei; cellulae ad 8.0 × 5,5 μm , parietibus tenuibus; excipulum medullosum ad 33 μm crassitie, textura intricata densa; hyphae angustae, parietibus tenuibus ad 1,7 μm latae; hypothecium haud distinctum. Asci 50–57 × 3,5–6,5 μm, 8-spori, J−, clavato-cylindracei, apicibus angustis sed obtusis, deorsum brevistipitati. Ascosporae 6,5–9.0 × 1.0–1,5 μm, irregulariter biseriatae, anguste aciculares, rectae vel parum curvatae, hyalinae, parietibus tenuibus, leves, unicellulatae, haud guttulatae. Paraphyses ad 2,2 μm latae, filiformes, hyalinae, septatae, simplices vel ramosae, ascosporum superantes. In caulibus emortuis herbaceis Angiospermarum.

The specific epithet refers to the Kashmir Valley, where the material was collected.

Ascocarps up to 2.5 mm across, superficial, sessile to subsessile, highly gregarious, solitary, sometimes in confluent masses, fleshy, discoid or shallow-cupulate, regular; cream to light-yellow when fresh, becoming yellowish-brown on drying, smooth; hymenium concolorous, concave, smooth; margin thin, entire, incurved on drying. *Ectal excipulum* up to 95 μm thick, a textura porrecta with hyphae lying at low angle to the surface; hyphal cells small, up to 8.0×5.5 μm, thin-walled; *medullary excipulum* up to 33 μm thick, a compact textura intricata, with narrow, thin-walled, up to 1.7 μm wide hyphae; hypothecium indistinct. *Asci* 50–57 × 3.5–6.5 μm, 8-spored, J−, clavate-cylindrical, with narrowly obtuse apex, gradually tapering downwards into a small stipe. *Ascospores* 6.5–9.0 × 1.0–1.5 μm, irregularly biseriate, narrowly acicular, straight or slightly curved, hyaline, thin-walled, smooth, one-celled, aguttulate. *Paraphyses* up to 2.2 μm wide, filiform, hyaline, thin-walled, septate, simple or branched, slightly projecting beyond the tips of asci.

P. kashmirensis is recognised by cream-coloured sessile to subsessile shallow-cupulate ascocarps; small J− asci; and narrowly acicular ascospores. It differs from an allied *P. vulgaris* (Fr.) Höhn., in having larger asci and narrowly acicular, one-celled ascospores, and by its occurrence on herbaceous stems. *P. parile* (Karst.) Dennis is a similar fungus, but differs by its J+ asci, longer ascospores 6–14 × 1.5–2.0 μm (Dennis 1968), and occurrence on *Betula* stems.

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Foliar sclereids in Sri Lanka (Ceylonese) species of Memecylon (Melastomataceae)

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Rao, T. A., Bremer, K., & Chakraborti, S. 1980 09 18: Foliar sclereids in Sri Lanka (Ceylonese) species of Memecylon (Melastomataceae). *Bot. Notiser 133:* 397–401. Stockholm. ISSN 0006-8195.

The majority of Ceylonese *Memecylon* species have filiform foliar sclereids, whereas some species have variously shaped, ramiform sclereids. In the latter cases sclereids are useful diagnostically at the specific level. In one species the sclereids are aggregated to sclerocysts enclosing the veinlets and vein-endings.

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Recently Rao & Jacques-Félix (1978) surveyed foliar sclereids of African *Memecylon*. Bremer (1979) revised the taxonomy of *Memecylon* in Ceylon. In this paper we describe the sclereids of Ceylonese *Memecylon*, and discuss some pertinent taxonomic questions.

Material and methods

Herbarium specimens were kindly provided by the Museum of Natural History, Stockholm (S), and the Smithsonian Institution, Washington D.C. (US). The specimens are listed in Table 1. Leaves were cleared by the technique of Foster (1946) and unstained preparations were used for camera lucida drawings and photomicrography.

Sclereid morphology

The species and their sclereidal forms are summarized in Table 1. Studies of the cleared leaves, by hand sections and macerations (Figs. 1, 2), revealed the presence of sclereids in all 44 specimens of the 27 species investigated here. The leaf anatomy of the three Ceylonese species *M. gracillimum* Alst., *M. orbiculare* Thw. and *M. revolutum* Thw., known only from the type collections, is still unknown.

The sclereids are categorized into two main types, viz. filiform sclereids and ramiform sclereids. In addition, *M. parvifolium* has sclerocysts. The distributional pattern is distinctly terminal or subterminal at the vein-endings in the species with ramiform sclereids. In the species with filiform sclereids it is difficult to establish the relationship with the vein-endings because of their criss-cross pattern of distribution. The positional relationship with the vein-endings can be settled only by ontogenetic studies (Foster 1946, Rao 1951, 1957). The morphological details of the main forms are as follows.

Filiform sclereids. As already reported filiform sclereids predominate in *Memecylon* (Rao 1957, Rao & Bhupal 1974, Rao & Jacques-Félix 1978). The Ceylonese species of *Memecylon* are no exception and filiform sclereids are observed in 19 species. They form a tangled mass of thread-like forms, with or without branches. Their distribution over the lamina is not uniform and occasionally they form a loose strand at the margins. They have a thick secondary wall, a line-like lumen, and a smooth cell wall, rarely spiculated or undulating and often with acuminate endings. However, in *M. petiolatum* the filiform sclereids have a thin secondary wall and a comparatively large uniform lumen. Whether this is a developmental stage or a characteristic of the species is not clear.

The sclereids vary from being unbranched and relatively short to being extremely elongated, frequently branching to Y- or T-shape. Filiform but relatively stouter profusely branching sclereids with long drawn out branches occur in *M. varians*. Further characterization at specific

Table 1. Ceylonese species of *Memecylon*, investigated specimens or references to earlier investigations, and sclereid form, filiform (F), ramiform (R), or sclereids aggregated to sclerocysts (S).

M. angustifolium Wight	Fagerlind 2085 (S)	F
M. arnottianum Wight ex Thw., Fig. 2 D	Bremer 831, 1019 (S) Fagerlind 489 (S) Wambeek & Wanntorp 2887 (S)	R
M. capitellatum L., Fig. 1 D	Bremer 910 (S) Fagerlind 2066, 4575 (S)	F
M. clarkeanum Cogn. in DC., Fig. 1 A, B, 2 B	Waas 413, 423, 428 (US) Wambeek & Wanntorp 2908 (S)	R
M. sp. aff. *clarkeanum* Cogn. in DC.	Bremer 861 (S)	F
M. ellipticum Thw.	Bremer 900 (S)	F
M. fuscescens Thw., Fig. 21	Bremer 832 (S)	R
M. gardneri Thw., Fig. 2 G	Bremer 1003 (S) Fagerlind 4567 (S)	R
M. grande Retz.	Bremer (1979)	F
M. hookeri Thw.	Fagerlind 2084 (S)	F
M. leucanthemum Thw.	Kostermans 24493 (US)	F
M. macrocarpum Thw.	Rao (1957)	F
M. macrophyllum Thw., Fig. 2 E	Fagerlind 2076 (S)	R
M. ovoideum Thw., Fig. 2 F	Bremer 969 (S)	R
M. parvifolium Thw., Fig. 2 J	Klackenberg 436 (S)	S
M. sp. aff. *parvifolium* Thw., Fig. 2 K	Bremer 999, 1001, 1002 (S)	R
M. petiolatum Trim. ex Alst.	Jayasuriya 1711 (US)	F
M. phyllanthifolium Thw. ex Trim.	Bremer (1979) Rao (1957)	R
M. procerum Thw.	Jayasuriya & Bandaranayake 1801 (US)	F
M. sp. aff. *procerum* Thw., Fig. 2 C	Fagerlind 2081 (S) Waas 912 (US)	R
M. rhinophyllum Thw.	Sumithraarachchi DBS 622 (US)	F
M. rivulare Bremer	Fagerlind 4568 (S) Wambeek & Wanntorp 2883 (S)	F
M. rostratum Thw.	Wambeek & Wanntorp 2954 (S)	F
M. rotundatum (Thw.) Cogn. in DC., Fig. 2 A	Bremer 1044 (S)	R
M. royenii Bl.	Fagerlind 2077, 4571, 4577 (S)	F
M. sylvaticum Thw.	Fagerlind 487 (S)	F
M. umbellatum Burm. fil.	Fagerlind 2070 (S) Wanntorp 2584 (S)	F
M. urceolatum Cogn. in DC., Fig. 1 C	Fagerlind 4560 (S)	F
M. varians Thw., Fig. 2 H	Bremer 795, 881 (S)	F
M. wightii Thw.	Sumithraarachchi & Waas DBS 279 (US)	F

level would be difficult. However, this salient anatomical feature with a few internal characters of epidermal layers, palisade layers, crystals etc. may help in leaf identification of species with filiform sclereids.

Ramiform sclereids. This main form and its variants as recognized by Rao & Bhupal (1973) are found in 10 species. The simplest is the subspheroidal form with slightly or excessively drawn out arms with acuminate endings. There are many intergrading forms such as fusiform and rhizoform sclereids. Another significant form is represented by the columnar sclereids.

The species with ramiform sclereids fall into two groups. Columnar ramiform terminal sclereids oriented vertically in the mesophyll and sometimes touching the epidermis with or without flanges or forking arms occur in *M. clarkeanum, M. macrophyllum,* and *M. ovoideum*. There are subtle differences in the overall disposition, width of secondary wall and lumen, and outer surface of the sclereids in these species. Variously shaped short ramiform terminal sclereids oriented horizontally and/or vertically to the leaf surface occur in *M. arnottianum, M. fuscescens, M. gardneri,* and *M. rotundatum. M. phyllanthifolium* also belongs here (Bremer 1979, Rao 1957). The shape and orientation of the sclereids differ between the species. In *M. gardneri* the sclereids are distinctly vertically arranged.

Sclerocysts. Sclereids in aggregates or encasement of sclereids around the veins or vein-endings, which are thus often interrupted, occur in *M. parvifolium*. Parallel instances are found in *Hibbertia* (Rao & Das 1979), *Limonium* (Rao & Das 1968), and *Oryctanthus* (Kuijt 1961).

Taxonomic implications

Taxonomic problems alluded to by Bremer (1979) are here illuminated by sclereid morphology. In the three following cases the identity of the foreign entities cannot be confirmed before further flowering material is available, however.

M. clarkeanum. Among the five collections determined as *M. clarkeanum* the collections of Waas and Wambeek & Wanntorp show columnar ramiform sclereids, whereas Bremer's collection shows filiform sclereids. Apparently the

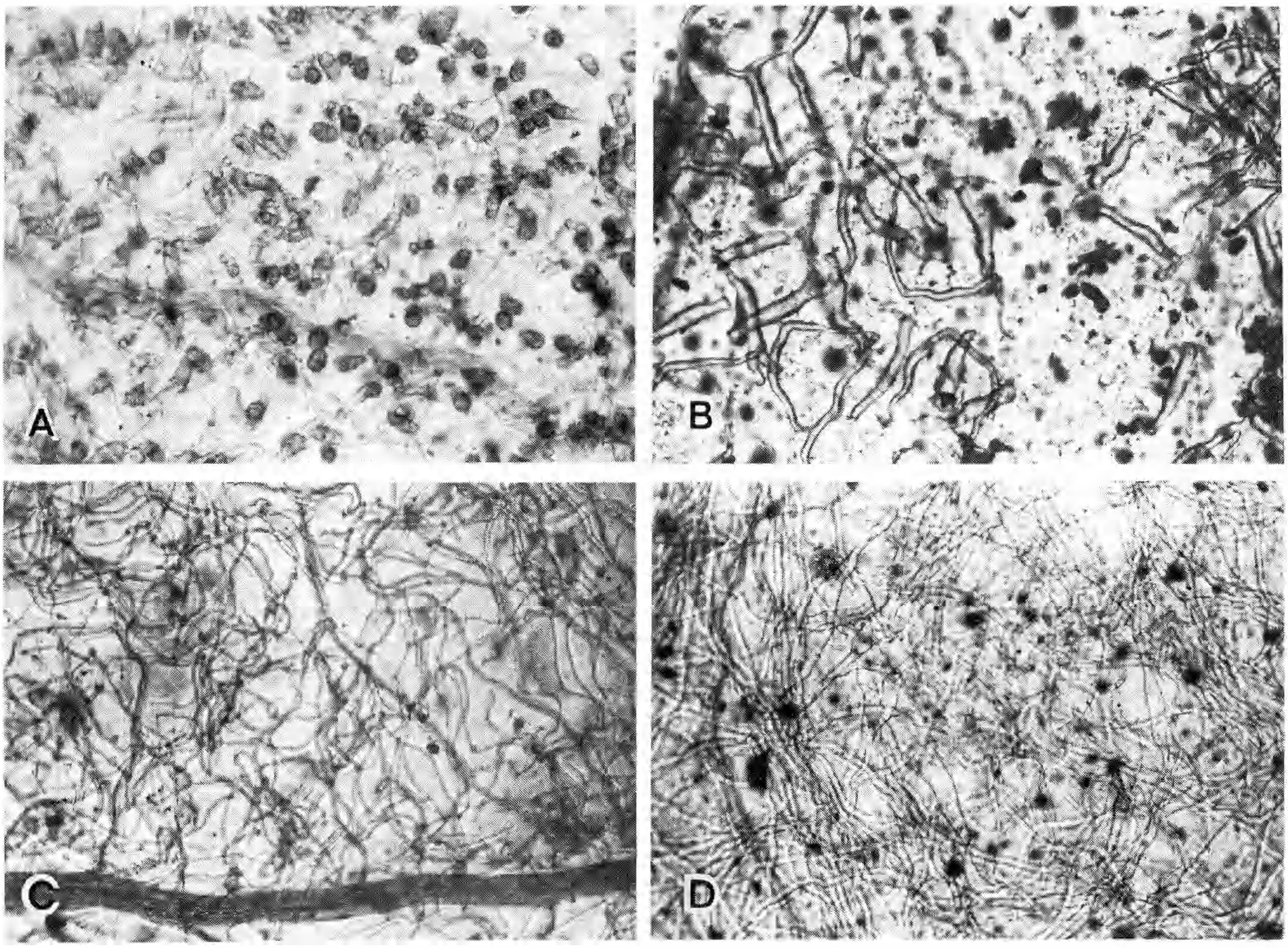

Fig. 1. Leaf clearings (A, C, D) and maceration (B) showing foliar sclereids, 50 ×. — A, B: *M. clarkeanum* with columnar ramiform sclereids (Waas 413). — C: *M. urceolatum* with filiform sclereids (Fagerlind 4560). — D: *M. capitellatum* with filiform sclereids (Fagerlind 2066).

latter collection represents another species. It could be the Indian species *M. heyneanum* or *M. jambosioides* or possibly a new species.

M. parvifolium. This species is characterized by sclerocysts, whereas the similar *M. cuneatum* has columnar sclereids (Rao 1957). Nevertheless, Bremer (1979) provisionally united the two species, pending a detailed study based on more material. Sclereid morphology indicates that Bremer's collections, provisionally identified as *M. parvifolium*, actually represent the little-known *M. cuneatum*.

M. procerum. Jayasuriya & Bandaranayake's collection of this species has filiform sclereids and rounded leaf bases, similar to those of the type collection, the sclereids of which are unknown. Waas' and Fagerlind's collections, determined as *M. procerum*, have columnar ramiform sclereids and cuneate leaf bases and apparently they represent another species, possibly *M. giganteum*, the sclereids of which are not known. This little-known species was provisionally united with *M. procerum* by Bremer (1979).

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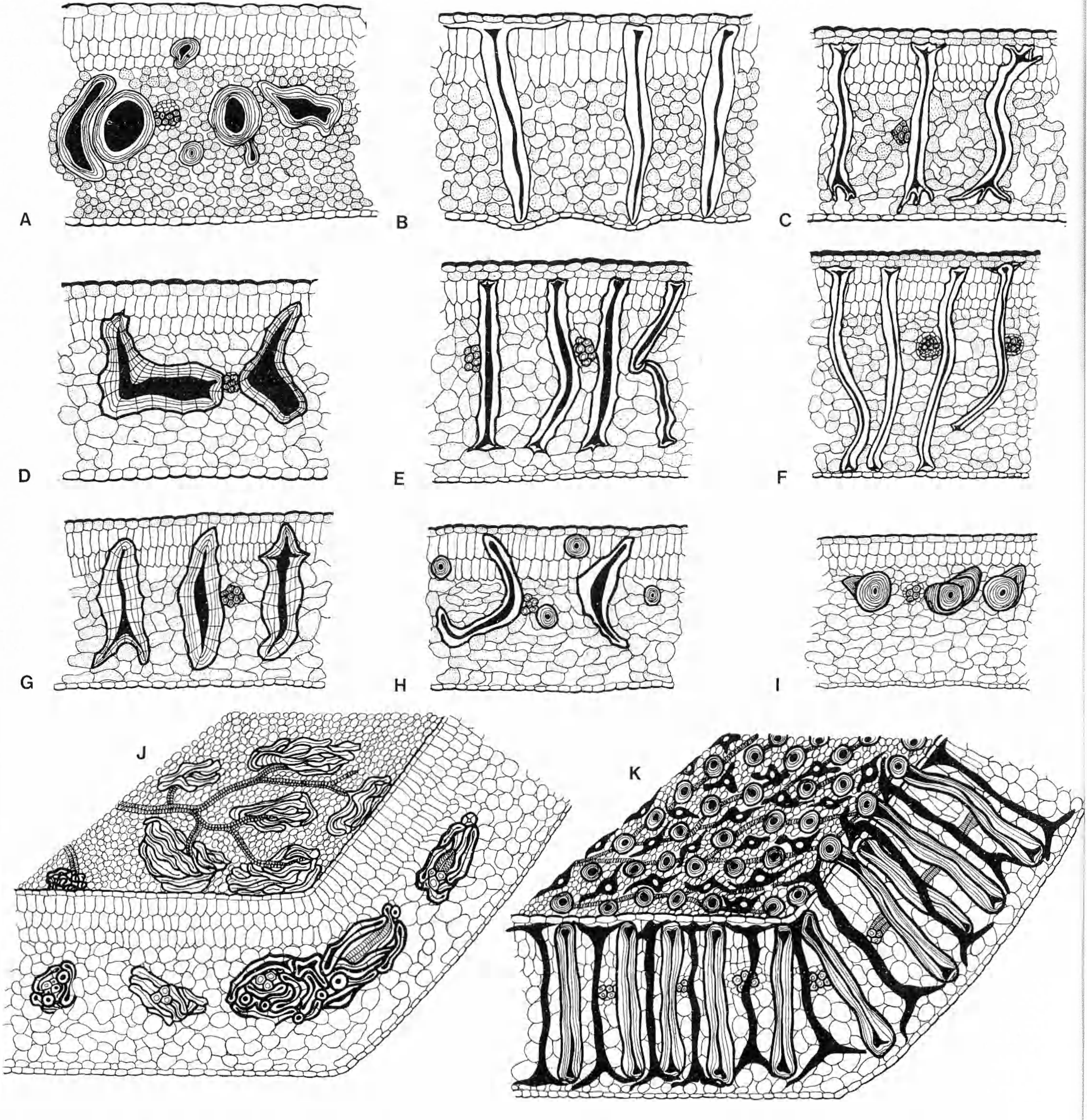

Fig. 2. Semi-diagrammatic sketches of leaf sections showing foliar sclereids, c. 75 ×. — A: *M. rotundatum* with subspheroidal-fusiform ramiform sclereids (Bremer 1044). — B: *M. clarkeanum* with columnar ramiform sclereids (Waas 413). — C: *M.* sp. aff. *procerum* with columnar ramiform sclereids (Waas 912). — D: *M. arnottianum* with ramiform sclereids (Wambeek & Wanntorp 2887). — E: *M. macrophyllum* with columnar ramiform sclereids (Fagerlind 2076). — F: *M. ovoideum* with columnar ramiform sclereids (Bremer 969). — G: *M. gardneri* with vertically arranged ramiform sclereids (Bremer 1003). — H: *M. varians* with comparatively stout filiform sclereids (Bremer 881). — I: *M. fuscescens* with subspheroidal-fusiform ramiform sclereids (Bremer 832). — J: *M. parvifolium* with sclereids aggregated to sclerocysts around the veins or vein-endings (Klackenberg 436). — K: *M.* sp. aff. *parvifolium* with columnar ramiform sclereids (Bremer 999).

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A new species of Polyalthia (Annonaceae) from Mozambique

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Vollesen, K. 1980 09 18: A new species of Polyalthia (Annonaceae) from Mozambique. *Bot. Notiser 133:* 403–404. Stockholm. ISSN 0006-8195.

Polyalthia mossambicensis Vollesen is described. The species is endemic in Mozambique and is phytogeographically restricted to the Zanzibar-Inhambane Regional Mosaic.

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In my paper on Annonaceae from Tanzania (Vollesen 1980 p. 56) a remark was made concerning an undescribed species of *Polyalthia* Blume from Mozambique. At that time the species was only known to me from a single fruiting specimen and was therefore left unnamed.

Excellent material of this species has now become available, showing without doubt that the species is new. Actually, the plant has previously been recorded from Mozambique (Paiva 1970 p. 370), but in that paper it was identified as *Polyalthia stuhlmannii* (Engl.) Verdc. The new species is undoubtedly related to *P. stuhlmannii* but the two taxa differ in a number of characters as shown in the key. As Paiva (1970) gives an adequate description in English, a good figure and precise localities for all known collections, I shall confine myself to adding a Latin diagnosis. A key to the species of *Polyalthia* now known from Africa is also included, slightly revised after Vollesen (1980 p. 59).

Polyalthia mossambicensis Vollesen, sp. nov.

Type: Mozambique, Zambezia, Maganja da Costa, Gombene Forest, January 10, 1968, Torre & Correia 17018 (LISC holotype; BR, COI, LMU, SRGH isotypes, not seen).

Polyalthia stuhlmannii auct. non (Engl.) Verdc., Paiva 1970, p. 370 & Tab. 1.

P. stuhlmanni (Engl.) Verdc. affinis, ramis juvenibus dense pilosis, bracteolis majoribus, sepalis inter se liberis, petalis longioribus, monocarpiis minoribus longius stipitatis ab ea diversa.

Habitat. The species has been recorded from coastal forest with *Hymenaea* (*Trachylobium*) *verrucosa* Gaertn., *Pteleopsis myrtifolia* (Laws.) Engl. & Diels, *Craibia, Cynometra, Albizzia, Mimusops*, at altitudes around 25 m a.s.l. The habitats of the species are very similar to those of *P. stuhlmanni* from the coastal forest in Kenya and Tanzania. The two other African species, although also endemic in the Zanzibar-Inhambane Regional Mosaic (White 1976), occur at somewhat higher altitudes: *P. tanganyikensis* Vollesen from 300–600 m a.s.l. and *P. verdcourtii* Vollesen around 250 m a.s.l.

Specimens studied. Torre & Correia 14564 (K, LISC), 14577 (LISC), 16201 (LISC), 17018 (LISC), 17062 (LISC).

Key to the species of Polyalthia in Africa, revised after Vollesen 1980 p. 59

1\. Stipes of monocarps 10–17 mm long, longer than monocarps 2
\- Stipes of monocarps 3–7 mm long, shorter than monocarps 3
2\. Stipes 10–12 mm long. Monocarps 9–10 mm long. Young branches with scattered adpressed hairs. Sepals united at base. Bracteoles c. 1 mm long, deciduous. Petals 10–17(–20) mm long .... *P. stuhlmannii*
\- Stipes 11–17 mm long. Monocarps 6–8(–9) mm long. Young branches densely pilose. Sepals free. Bracteoles 1.5–2.0(–3.0) mm long, persistent. Petals 15–28 mm long ... *P. mossambicensis*
3\. Petals 7–12 mm long and 3–4 mm wide. Leaves without domatia. Pedicels articulated. Sepals united at base .... *P. tanganyikensis*
\- Petals 23–35 mm long and 7–9 mm wide. Leaves with domatia. Pedicels not articulated. Sepals free .... *P. verdcourtii*

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Antler hyphae in the fungus genus Nidula (Nidulariaceae)

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Brodie, H. J. 1980 09 18: Antler hyphae in the fungus genus *Nidula* (Nidulariaceae). *Bot. Notiser 133:* 405–411. Stockholm. ISSN 0006-8195.

The peridiole walls of all four species of *Nidula* are composed chiefly of or include heavily-pigmented thick-walled hyphae having the form of antlers of a stag. The bases of these hyphae lie parallel to the peridiole outline and are interwoven; the branched portions tend to be radially arranged. The form of the hyphae is distinctive for each species and the species constitute a graded, taxonomically significant series from the most pigmented and most antler like to the least pigmented and least antler like. In two species of *Nidula (N. emodensis* and *N. niveotomentosa*) no tunica of thin-walled hyphae envelops the antler hyphae externally; and, for both species, it has been observed that the peridiole wall behaves in a strongly hydrophobic manner. In the other two species (*N. macrocarpa* and *N. candida*) antler hyphae are surrounded by a loosely-knit tunica and the peridiole wall as a whole exhibits hydrophilic behaviour. It is suggested that antler hyphae may play some important role in the dispersal of the peridioles of *Nidula* during the process of dissemination by rain splash.

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The presence of dark-brown, thick-walled branched hyphae in the peridiole wall of *Nidula emodensis* (Berk.) Lloyd was first commented upon by Lloyd (1906). In stating that he had "not met this structure in any other species of Nidulariaceae", Lloyd implied that the dark, branched hyphae constitute a highly specific character for the recognition of *N. emodensis*. However, the supposed restriction of such hyphae to *N. emodensis* was contradicted by Cunningham (1924) who reported that similar hyphae were to be found in the peridiole wall of specimens which he identified as *N. candida* (Peck) White (possibly an erroneous identification, as will be shown later).

In White's description of the genus *Nidula* (White 1902), there is no reference to the microscopic appearance and structure of the outermost bounding layer of the peridiole. This very distinctive genus was established to accommodate two fungi, *N. candida* and *N. microcarpa* Peck ex White (= *N. niveotomentosa* (Henn.) Lloyd), which had been described earlier but assigned to other genera. Some years later, Lloyd (1917) added one other species to *Nidula*, namely *N. macrocarpa* Lloyd from Chile, and again, no attention was given to the microscopic structure of the peridiole wall.

The four species named above were accepted as valid in my monograph of the Nidulariaceae (Brodie 1975). I believed that, because three of the four are easily recognized and separated from one another on the basis of gross morphology, several questions might be left unanswered temporarily. These questions are: (1) whether or not *N. emodensis* is separable from all other species of Nidulariaceae, as Lloyd believed, by means of the branched, thick-walled hyphae of the peridiole wall; (2) whether or not *N. emodensis* is a valid species; and (3) whether or not similar hyphae are present in the peridiole wall of other species of *Nidula*.

Only recently have I had the opportunity to reconsider these problems, the incentive being the receipt of a number of fresh collections (from India) of *N. emodensis*, a species which has heretofore been known to me from only a few scanty collections. This paper presents observations on the nature of the hyphae that compose the outer bounding layer of the peridioles of all four species of *Nidula*. The observations throw considerable light on the hitherto unsolved problems of taxonomy in this intriguing genus. In addition, some questions are raised as to the possible function of such highly modified hyphae.

Material and methods

The principal material studied consisted of specimens selected from my own herbarium, each chosen because it seemed to represent the species fully and 'typically', though the specimens were not the official types. Extra large, extra small and other deviant forms were avoided. Collection data and numbers of the material selected are as follows.

Nidula emodensis: Herb. H. J. Brodie No. 73022; I. P. S. Thind, Gulaba, Kula (H. P.), India, Sept. 25, 1971.

N. niveotomentosa: Herb. H. J. B. No. 68031; P. N. D. Seymour, Hope, British Columbia, Canada, Oct. 5, 1968.

N. macrocarpa: Herb. H. J. B. No. 71068; Roland Thaxter, Corral, Chile, Dec. 1905.

N. candida: Herb. H. J. B. No. 78007; Mrs. C. Scates, Post Falls, Idaho, U.S.A., July 9, 1978.

For each species, specimens from localities other than those given above were also examined; since no marked differences from the specimens listed were noted, the additional material is not cited, however.

After peridioles had been soaked for 24 hr. in water, portions of the outer peridiole wall were simply teased apart for microscopic examination. In addition, sections of peridioles were cut (10 μm) after being imbedded in paraffin in the usual way but not stained. It was much easier to discern the form and length of entire dark branched hyphae in teased-out bits of wall than in sections, where little of the branched hyphae appeared except as short sectioned pieces.

Observations

Description of antler hyphae

N. emodensis (Fig. 1 A, B, I). Undoubtedly the most impressive example of what I consider may appropriately be called antler hyphae is to be found in this species (Fig. 1 A, B). The antler hyphae are very dark brown in colour, very thick walled (3–4 μm) and branched in such a way as to suggest the antlers of a stag (Fig. 1 A, I). These hyphae are 8.5–10.0 μm in diameter at the widest portions and taper abruptly towards their apices, the narrow part often being somewhat prolonged as a peg. It is difficult to ascertain their length; many seem to be as much as 300 μm long and a few may exceed this. The walls of the hyphae are so thick (Fig. 1 A, I) that often no lumen is visible. They bear no recognizable clamp connections though occasionally a constriction of the lumen suggests a simple septum.

N. niveotomentosa (Fig. 1 C, D, I). Although the antler hyphae of this species (Fig. 1 C, D) bear considerable resemblance to those of *N. emodensis*, some distinct differences are to be noted. On the average, those of *N. niveotomentosa* are not quite as wide (6–9 μm); they taper towards the apices but less abruptly than in *N. emodensis*. Antler hyphae in this species are less heavily pigmented and less frequently branched than in *N. emodensis* and the branching is less suggestive of antlers (Fig. 1 C, D, I). Although a large portion of the antler hyphae in this species are thick walled many, with the same manner of branching, have walls of only moderate thickness. No clamp connections are evident though simple septa are present occasionally. As far as it is possible to trace individual hyphae in the tangle, many appear to be even longer than those of *N. emodensis*.

N. macrocarpa (Fig. 1 E, F, I). Antler hyphae are seldom over 3–5 μm wide (maximum measured, 7 μm). They are apparently rather short but they are so closely interwoven that it is difficult to be certain (Fig. 1 E, F). These hyphae are much less strongly coloured and much more frequently branched than in the two preceding species and usually (though not invariably) have quite blunt apices (Fig. 1 E).

N. candida (Fig. 1 G, H, I). Branched, coloured hyphae are present, but they are only slightly thicker walled than matrical hyphae, are not clearly branched antler fashion and seem differentiated from hyphae of the internally-located hyphal matrix chiefly by pigmentation (Fig. 1 G, H).

The antler hyphae, as described above, do not appear to project appreciably beyond the layer of mucilaginous material which coats the exterior of the peridioles: or, if they do, they are not recognizable under the stereomicroscope, even at a magnification of 30 ×; this is true whether dry or wetted peridioles are being examined.

Sections of peridiole wall

As noted above, sections of peridioles reveal next to nothing of the morphology of antler hyphae. Indeed, if one had recourse only to sections, it would be unlikely that the form of these structures would be revealed. In the photographs of sections of all four species illustrated in Fig. 2,

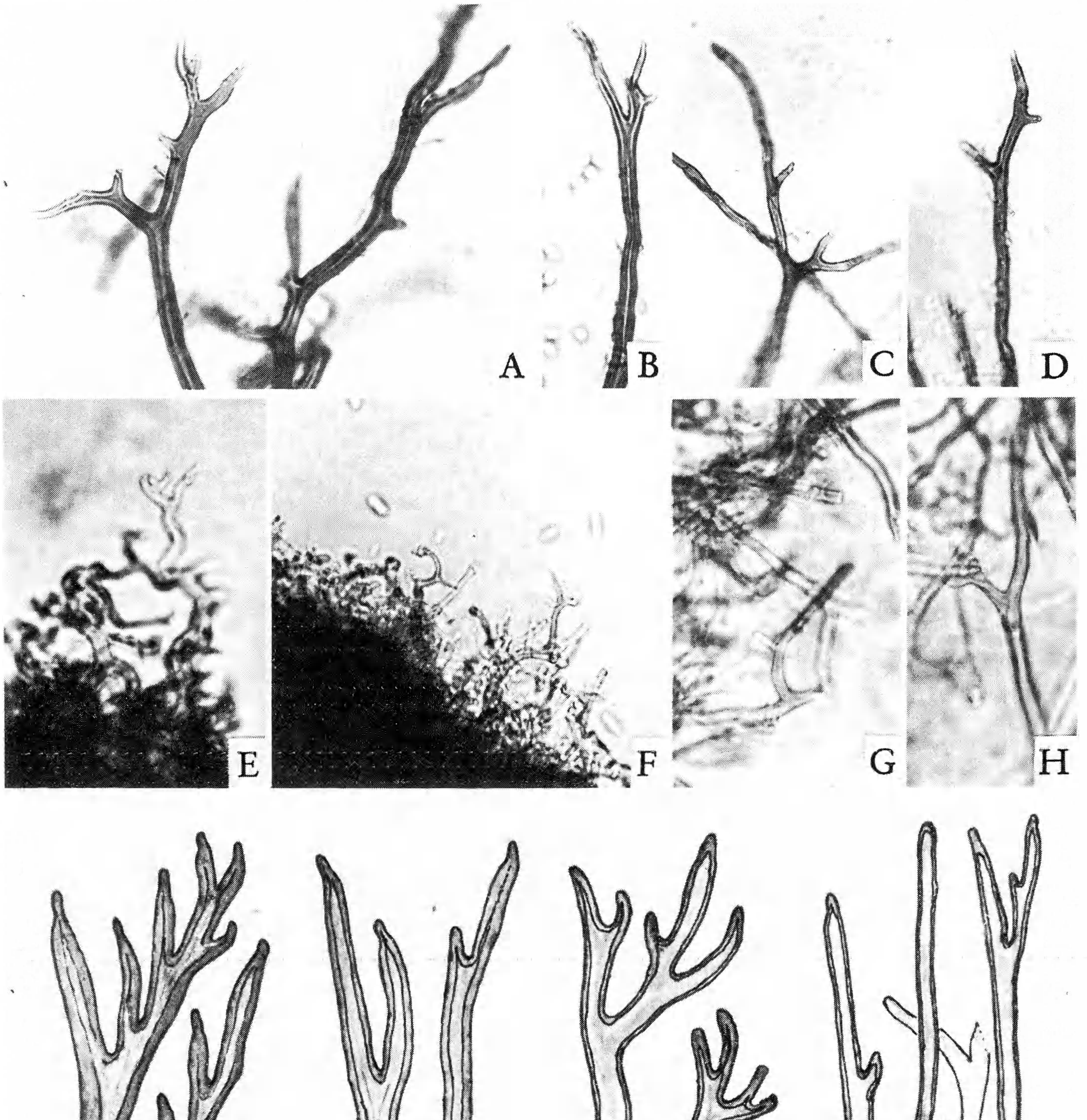

Fig. 1. A, B: *Nidula emodensis*; antler hyphae, showing thick walls, manner of branching and peg-like extensions of apices. × 300. — C, D: *N. niveotomentosa*; note sparse branching and blunt apices of antler hyphae. × 200. — E, F: *N. macrocarpa*; less strongly coloured sinuous antler hyphae showing tendency for more terminal branching (E); E × 250, F × 150. — G, H: *N. candida*; coloured hyphae among colourless matrical hyphae. × 200. — I: composite drawings of all four species of *Nidula*, based on camera lucida outlines, and emphasizing the differences in form among the four. × ca 600.

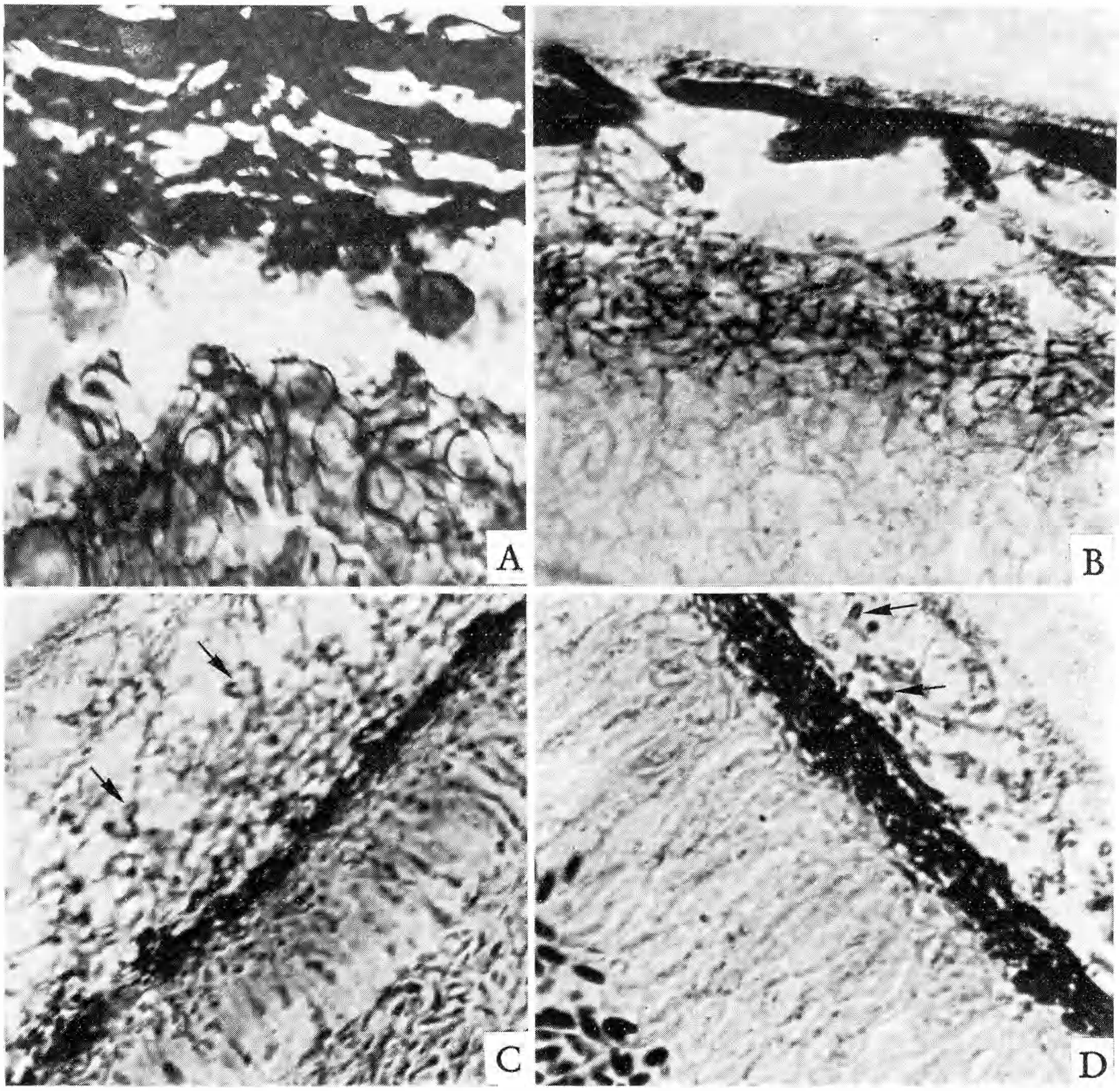

Fig. 2. A: Transverse section of peridiole wall of *Nidula emodensis*; bases of antler hyphae form the dark layer in the top half of photo. × 550. — B: *N. niveotomentosa*; bases of antler hyphae at top; below, inner portion of peridiole wall. × 450. — C: *N. macrocarpa*; section of peridiole wall showing wide, loose, outer layer (tunica); a few antler hyphae (arrows) are recognizable projecting from the dark compact layer below. × 450. — D: *N. candida*; peridiole wall composed of thin tunica; bases of antler hyphae form a dense lower layer from which some (upper center) project into tunica (arrows). × 450.

antler hyphae are clearly recognizable only in Fig. 2 C (compare Fig. 1 E and F). A strictly transverse section of the hyphae illustrated in Fig. 1 A, for example, would give no hint of their true form. Photographs of sections of the peridioles of all four species of *Nidula* are included in this communication because no such photographs have been published heretofore and because they do, very clearly, provide evidence regarding species differences in the genus *Nidula*. Comments on these sections, therefore, follow.

N. emodensis (Fig. 2 A). The outer boundary of the peridiole apparently consists almost entirely of antler hyphae, the horizontal basal parts of which form the large dark hyphae at the top of the photograph.

N. niveotomentosa (Fig. 2 B). The entire peridiole wall in section displays three regions. On the outside is a layer of almost amorphous hyphae which have given rise to the mucilage with which the peridioles are provided externally. Below this, the very dark antler hyphae are represented only by their horizontal basal parts. Internal to the antler hyphae is a layer of slightly darkened hyphae that are rather closely interwoven.

N. macrocarpa (Fig. 2 C). The outermost layer of the wall consists of a layer of rather loosely woven undifferentiated and unpigmented hyphae which probably corresponds to the 'tunica' in *Crucibulum* and some species of *Cyathus*. For a discussion of the use of the term tunica see Dring (1977) and Brodie (1977). Antler hyphae appear to project out into this tunica layer, and their basal horizontal elements form a single compact layer that is probably comparable to the cortex in *Cyathus*.

N. candida (Fig. 2 D). A loose outer covering or 'tunica' is present as in *N. macrocarpa* but is only about half as thick as in that species (compare Fig. 2 C and D). Antler hyphae probably project into this as is suggested by the dark blunt hyphal tips seen in the upper center of the photograph. The horizontal elements of antler hyphae are interwoven into a dense dark cortical layer as in *N. macrocarpa*.

Behaviour of peridiole wall toward water

That antler hyphae are strongly hydrophobic is readily observed by placing dry peridioles of either *N. emodensis* or *N. niveotomentosa* into contact with a droplet of water. Water drops about 4 mm in diameter were placed on a sheet of waxed paper where they assumed an almost spherical outline. A dry peridiole was placed close to the water drop and pushed slowly towards the drop using a needle, the operation being carried out under the stereomicroscope. Upon contact with the water sphere, a peridiole was seen to float on the surface; it could be pushed around with the needle but could not be forced into the inside of the water sphere. Only after a period of two hours on the water surface was it possible to immerse the peridiole. In contrast, peridioles of *N. macrocarpa* and *N. candida* were carried immediately to the inside of a water drop. It was also observed, for the two latter species, that the water drop quickly lost its spherical form and spread out widely, indicating a marked change in surface tension.

The difference in behaviour between the two groups of *Nidula* indicates clearly: (1) that the antler hyphae which form the outer boundary layer of the peridiole wall in *N. emodensis* and *N. niveotomentosa* confer a strong hydrophobic potential to the peridiole wall; (2) that the outer enveloping tunica sheath in *N. macrocarpa* and *N. candida* confers a strong hydrophilic potential to the peridiole wall.

Discussion

Taxonomic problems

The above observations give at least partial answers to the questions raised at the beginning of this communication. The structures which I have named antler hyphae occur in one form or another in all four species of *Nidula*. Lloyd's implication that *N. emodensis* can be recognized simply by the presence of antler hyphae is therefore not correct.

As to the validity of *N. emodensis*, the present study enables me to reaffirm the opinion given in my monograph (Brodie 1975) that *N. emodensis* is indeed a valid species. Although I have shown herein that antler hyphae occur also in *N. niveotomentosa*, the elements of the latter species are quite different from those of *N. emodensis* and provide an excellent character for the separation of these two species, additional to those which I recorded in my monograph (Brodie 1975 p. 144). A further point for species differentiation comes from examination of the sections of the peridioles, where *N. niveotomentosa* is characterized by the presence of a layer of somewhat coloured loosely-interwoven hyphae below the outermost layer (Fig. 2 B), a character not possessed by *N. emodensis* (Fig. 2 A).

As noted in the brief literature review given above, Cunningham (1924) reported the presence of antler hyphae in *N. candida* with the sentence "periodiola possess the peculiar stout, spiny, coloured fibrils so noticeable in the latter species" (referring to *N. emodensis*). I have shown (above) that antler hyphae are present in *N. candida* but they are very different from those of *N. emodensis* (cf. Fig. 1 A, B and G, H). Although I have been unable to examine Cunningham's material, several points in his description of *N. candida* lead one to believe that he was, in fact, dealing with a slightly atypical form of *N. emodensis*.

The 'tunica' of N. macrocarpa and N. candida

Both these species are separable from the other pair of *Nidula* species in possessing an external layer of unpigmented loosely-knit hyphae that comprise a 'tunica'; that of *N. candida* is thin (Fig. 2 D), while that of *N. macrocarpa* is twice as thick (Fig. 2 C). If this feature is taxonomically significant, one could assume that *N. macrocarpa* and *N. candida* are closer, taxonomically, to the next most 'advanced' genus, *Crucibulum* (with strongly developed tunica), than are *N. emodensis* and *N. niveotomentosa*, both of which lack any structure suggesting a tunica. On this point, it may be important to note that study of sections of entire fruit bodies of *N. macrocarpa* reveals the highly interesting fact that the peridioles of the latter species are 'connected' to one another and to the wall of the peridium by hyphae grouped into strong strands that are clearly revealed in sections (Overstreet 1955). The connecting hyphal strands to be seen in *N. macrocarpa* suggest that this species may be but little removed, in an evolutionary sense, from the status that characterizes the more advanced genus *Crucibulum* where the connecting hyphal strands are organized into the funicular cord (Brodie 1975).

Coloured, branched hyphae in other Nidulariaceae

The presence of coloured, thick-walled, branched hyphae was noted by R. E. Fries (1910) in the so-called "primary" wall of the fruit body of *Nidularia pisiformis* Tul. (= *N. farcta* (Roth. ex Pers.) Fr.). These hyphae are part of the peridium wall, however, and are not present in peridioles.

What appear to be the same kind of hyphae were recorded and illustrated by White (1902) as occurring in *Granularia pulvinata* (Schw.) Kuntze (= *Nidularia pulvinata* (Schw.) Fr.) though no detailed description was given.

The presence of spiny pigmented hyphae in the peridium wall of some species of the fungi formerly grouped together as the genus *Nidularia* and the absence of such hyphae in other species, led Palmer (1961) to establish a separate genus, *Mycocalia*, to include those species which do not possess spinose aseptate hypha in the peridium wall. Palmer also illustrated and described these "tinted, rigid, spinose, aseptate hyphae" (Palmer 1961 p. 56).

It is doubtful that the *Nidularia* hyphae are closely comparable to the antler hyphae of *Nidula*; the former are beset with short, broad, sharp spines entirely lacking in the latter. However, it is important to mention the *Nidularia* hyphae in the present context because I know of no other references to the presence of coloured branched hyphae of any comparable sort within the family Nidulariaceae.

Of other Gasteromycetes possessing dendritic hyphae, one in particular is especially worthy of attention in the present context, namely the genus *Limnoperdon*. This remarkable uniloculate gasteromycete (described by the authors as a floating "puffball") possesses a peridium composed of "clamped hyphae, interwined with dendrophyses" (Escobar et al. 1976). Although the dendrophyses of *Limnoperdon* are not closely comparable morphologically to the antler hyphae of *Nidula* (being much branched and only 1 μm in diameter) they are interestingly similar in being hydrophobic and contributing to the ability of the peridium of *Limnoperdon* to float upon water (McCabe 1979).

Possible phylogeny and function of antler hyphae

The form of the antler hyphae is sufficiently different among the four species of *Nidula* that the species may be arranged in a series (Fig. 1 I) ranging from the most highly specialized (left), or most extremely modified from vegetative hyphae, to the least specialized. Whether or not we are really dealing with a phylogenetic series is, at this point, problematic.

As for the possible function and adaptive value of such specialized structures as antler hyphae, again one can only speculate at present; however, I find it difficult to believe that the antler hyphae in *Nidula* do not have a function related to the process of spore dispersal by splash action. I therefore offer an hypothesis, hoping that it may stimulate efforts to establish its validity or to disprove it.

The peridioles of all species of *Nidula* are comparable to the shape of a somewhat flattened bun; i.e. circular in outline in one plane and ellipsoidal in in a plane at right angles. They are surrounded on the outside by a layer of gelatinous, adhesive material (presumably derived from the break-down of hyphae) which causes them to become securely attached to any vegetation which they may strike after being splashed out of their fruit bodies. I have often wondered why these peridioles do not become so firmly glued to one another, while still within the *Nidula* fruit body, that it would be improbable that they could be dispersed separately. It is now suggested that they are, so to say, kept discrete and separable by virtue of the stiff antler hyphae. It should be noted that these bear no hooks that might interlock; rather, they possess rigid, branched projections that, for adjacent peridioles, may prevent the agglutinating action of contiguous and continuous layers of mucilage.

Other considerations may complicate efforts to solve the problem of the function of the antler hyphae, the water relations of the peridiole wall for example. Dr. D. B. O. Savile (in litt. Oct. 1979) pointed out to me that, in the rusts and other fungi, depth of spore wall pigmentation is correlated well with resistance to penetration by water. It may be that the melanin which is (presumably) present in the dark-coloured antler hyphae has a profound effect upon the wettability or non wettability of the peridiole. Persuing this suggestion, I have found that the antler hyphae of two species of *Nidula* are hydrophobic; but whether or not this feature plays a significant role in the process of splash dispersal of peridioles is not yet clear. Investigations of such questions are in progress but the results are, as yet inconclusive.

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Dedication. It is a privilege to dedicate this communication to Dr C. J. Alexopoulos in recognition of his great contribution to mycology, both as a researcher and teacher.

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A new journal, Nordic Journal of Botany, and its supplementary series, Opera Botanica

Nordic Journal of Botany. From January 1981 the publication of four Scandinavian botanical journals will cease: *Botaniska Notiser* (Sweden), *Botanisk Tidsskrift* and *Friesia* (Denmark) and *Norwegian Journal of Botany* (Norway). A new joint Scandinavian journal, *Nordic Journal of Botany,* is to appear.

Nordic Journal of Botany is a new member of the family of journals supported by the Nordic Publishing Board in Science. The publication of the journal is a joint Scandinavian project with twenty-eight scientists from Denmark, Finland, Norway and Sweden as Editors in their special fields. Editor-in-Chief is Professor Morten Lange of the University of Copenhagen.

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