The species of Anthracoidea (Ustilaginales) on Carex subgen. Vignea with special regard to the Nordic species

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The taxonomic delimitation, position and structure of *Carex* subgen. *Vignea* is critically reviewed. The high number of intra- and inter-sectional, almost always sterile, hybrids is a characteristic feature. It is fundamental for an understanding of the host ranges of the smuts. The pattern of variation within *Anthracoidea* is also discussed. The Swedish (=Nordic) species on *Vignea* are *A. arenaria* (H. Syd.) Nannf. comb. nov., *A. aspera* (Liro) Kukk., *A. fischeri* (Karst.) Kukk., *A. karii* (Liro) Nannf. comb. nov., and *A. turfosa* (H. Syd.) Kukk. *Cintractia glareosa* Liro is found to be synonymous with *A. aspera*, *Ustilago caricis β leioderma* Lgh. with *A. arenaria*, and *Cintractia caricis-dioicae* Lehtola with *A. karii*. *A. vankyi* Nannf. sp. nov. from Central Europe, *A. douglasii* [Shear] Nannf. sp. nov. and *A. verrucosa* (Savile) Nannf. stat. nov. from North America, and *A. eleocharidis* Kukk. from North America and Asia are also dealt with.

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In two previous papers (Nannfeldt & Lindeberg 1957 and 1965) the echinosporous species and those infecting subgen. *Carex* sect. *Acutae* were dealt with in detail. Following Kukkonen's (1963) monographic studies the generic name *Anthracoidea* (instead of *Cintractia*) was adopted in 1965. The present paper deals with the smut species which attack *Carex* subgen. *Vignea* (Beauv.) Kük. and which were left aside by Kukkonen to avoid duplication of work. The late Mrs Brita Lindeberg had already made some preliminary studies on these smuts, but the main part of the work has fallen upon the present author, who regrets the long delay in its completion.

The fourth and concluding paper is in preparation, viz. a list of all the Swedish (=Nordic) species of *Anthracoidea* (some 30 in number), their hosts and distributions, together with keys and short descriptions.

The abbreviations of the names of the provinces of Sweden and Norway and the floristical districts of Finland follow Hylander (1953).

Sect. *Acutae* is a well-circumscribed group comprising a large number of critical, often highly polymorphous species, which as a rule hybridize freely and whose hybrids are often fertile to some extent and give rise to polymorphous hybrid swarms. No hybrids with any other section are known with certainty.

The subgen. *Vignea* also comprises a large number of hybridizing species, but the species are as a rule 'small' but distinct and their hybrids completely sterile (except in sect. *Arenariae?*). They often form groups of closely allied species, distinguished by minute but very constant characters, e.g. the species grouped around *C. canescens*.

As a background for a better understanding of the specialization and speciation within the smuts under consideration, some comments upon the current classification of *Carex*, with special regard to *Vignea*, will be given.

Features of Carex taxonomy

In Fennoscandia *Carex* has of old (following Fries 1845) been schematically divided into three groups *(Monostachyae, Homostachyae,* and *Heterostachyae).* These reappear almost unchanged in three of the four subgenera accepted by e.g. Kükenthal (1909) in his classical monograph and by most recent authors. Only their names have been changed, to *Primocarex, Vignea,* and *Eucarex (Carex)* respectively. The fourth subgenus *(Indocarex)* is mainly subtropical–tropical and is unrepresented in the North European flora.

These subgenera are of differing statuses. It has now become evident that *Primocarex* is by no means the primitive group which Kükenthal and others considered it to be. It has also turned out that the taxonomic limits towards *Kobresia, Schoenoxiphium* and *Uncinia,* as well as the phylogenetic connections between these genera, are highly debatable (cf. e.g. Krechetovitch 1936, Nelmes 1951, 1952, Savile & Calder 1953, and Kukkonen 1963).

The subgenus Indocarex

It seems fairly certain that *Indocarex,* characterized by bisexual 'spikes' and the presence of utriculiform cladoprophylls, is a natural group and also a relatively primitive one.

The female flower of *Carex* is borne laterally on a bracteolate branchlet which emerges from the axil of a glume, the bracteole being transformed into the utricle. A female spike (or the female part of a bisexual spike) is thus morphologically not a simple spike. However, the use of this term causes no misunderstanding.

The cladoprophyll is the bracteole ("prophyll") of the lateral spike. It may be ochreiform or utriculiform. Kukkonen's (1963 p. 30) definition is unsatisfactory.

Already Raunkiær (1899 p. 519) was inclined to regard the *"Carices homostachyae acroarrhenae tristigmaticae",* which roughly correspond to *Indocarex,* as the most primitive of all *Carices* and he coined the name *Protocarices* for them. All the other groups could be derived from the *Protocarices* through 'reductions' in various directions, e.g. in the number of spikes and stigmata and by the suppression of either sex in the individual spikes. Due to their publication in Danish and in a non-taxonomic monograph, Raunkiær's ideas remained practically unnoticed. Quite independently, Krechetovitch (1936) and Nelmes (1951) later put forward very similar ideas.

The few records of ovariicolous smuts on *Indocarex* are certainly – at least mainly – of *Farysia* species and Dr Kukkonen informs me (in litt. 28. XII. 1976) that all samples of smutted *Indocarices* seen by him were infected by *Farysia.* However, one of the two European species, viz. the Mediterranean *C. distachya* Desf. has been reported as infected by *Ustilago* (or *Anthracoidea) caricis* in Portugal (Lagerheim 1889 p. 127) and North Africa (Zambettakis 1970 p. 361). The description and drawings given by the latter author do not rule out *Anthracoidea,* but the spore drawings show very sparse, small warts, at least 5 μm apart. In this connection I cannot withhold the impression that *C. distachya* is far from being a typical *Indocarex.*

The subgenus Vignea

The diagnostic characters of *Vignea* are bisexual spikes and the lack of cladoprophylls. The bulk of the subgenus (sensu Kükenthal) forms a natural but certainly not primitive group, whose connections with the rest of the genus are obscure. Nelmes (1951) is inclined to derive also this subgenus from *Indocarex,* and Savile & Calder (1953) suggest that some relationship exists between it and that part of subgen. *Carex* which they include in their new subgenus *Kuekenthalia.*

It is evident that at least two of Kükenthal's sections should be excluded from *Vignea,* viz. *Baldenses* and *Curvulae,* both monotypical. They are tristigmatic and Kükenthal himself suggested affinities within subgen. *Carex,* for *C. curvula* with *Frigidae* and for *C. baldensis* in the vicinity of *Pallescentes.* A totally different disposition for *C. curvula* was proposed by Ivanova (1939), who transferred it to *Kobresia.* Kukkonen's (1963 p. 69) observation that the *curvula* smut is very close to *A. lindebergiae* Kukk. on *K. simpliciuscula* points in the same direction.

On the other hand, two sections which Kükenthal had placed in *Primocarex,* viz. *Dioicae* and *Ursinae,* should be added to *Vignea* and, following Mackenzie (1935), *Ursinae* might even be better included in *Heleonastes*.

Savile (1951 p. 326) and Savile & Calder (1953 p. 170) suggest that a tristigmatic species, *C. leiophylla* Mack., placed in the notoriously unnatural section *Atratae* (subgen. *Carex)* should have its position close to *C. maritima (Foetidae),* because of their general similarity and especially because they are the only known hosts for a most distinctive smut, *Planetella lironis* Savile, probably a close relative of *Anthracoidea*. This suggestion may be well-founded, but *C. leiophylla* seems to possess distinct ochreiform cladoprophylls. Raymond (1965 p. 27) found that *C. leiophylla* belongs to an otherwise Central-Asiatic complex grouped around *C. melanantha* C. A. Mey. and to be so close to *C. sabulosa* Turcz. that he regards them as conspecific. If Savile & Calder's suggestion gains support from future studies, this complex would occupy a key position phylogenetically.

The subgenus Primocarex

Primocarex sensu Kük. is a very heterogeneous assemblage of species having only one common character, viz. the single uni- or bisexual terminal spike. This is neither a proof of primitiveness nor one of monophyletic origin. On the contrary, the individual members have their "roots" in widely differing groups. It is true that a large percentage of the species show one character that undoubtedly is primitive, viz. a distinct rachilla. Nelmes (1952) and Savile & Calder (1953) have discussed these problems in detail and were able to find ± clear connections for more than half of the species with other groups, not only the subgenera *Vignea* (cf. above) and *Carex* but also *Kobresia, Schoenoxiphium* (?), and *Uncinia*.

Hylander (1966) is conservative, as is Chater (1977) in 'Flora Europaea', keeping *Primocarex* (sensu Kükenthal) almost intact and only transferring *Dioicae* to *Vignea*.

The subgenus Carex

The fourth subgenus (*Carex* or *Eucarex*) is characterized by possessing spikes of two kinds (both usually unisexual) and by ochreiform cladoprophylls. It is by far the largest of the subgenera, but is hardly monophyletic. It is divided into numerous sections, some of which (e.g. *Acutae*) are very natural, while others are obviously artificial. The relations between the sections have on the whole remained obscure.

Savile & Calder (1953), following up a suggestion by Mackenzie and taking also the smuts into consideration, tried to segregate a fifth subgenus (*Kuekenthalia*), which in their opinion represents a special line of evolution "governed largely by the development of seed dispersal mechanisms" and marked by "persistent styles and bladdery perigynia". The 'higher' links (*Collinsiae, Folliculatae, Lupulinae, Pseudocyperae, Squarrosae, Paludosae, Vesicariae,* and *Hirtae*) "certainly represent a natural entity" (Kukkonen 1963 p. 32). This has been known of old and is testified both by morphological features and the existence of numerous intersectional hybrids. Further proof is adduced by their smuts (cf. Nannfeldt & Lindeberg 1957 pp. 506–516, Kukkonen 1964 b). Kukkonen's results also suggest that *Granulares* belongs to the same natural group, although it does not possess persistent styles contiguous with the nuts. "Jointed" styles are also characteristic of *Hirtae,* whose affinity is testified beyond any doubt by intersectional hybrids. However, these sections cannot reasonably be treated as a subgenus coordinated with the rest of the subgenus *Carex,* and Hylander (1966) unites all the Nordic members into one section (*Paludosae*).

The 'lower' links in *Kuekenthalia* certainly have no connections at all with the 'higher' and probably have no close interconnections either. *Pauciflorae* may be close to *Uncinia* (cf. e.g. Nelmes 1952).

Taxonomic structure of Vignea

When the clearly misplaced species have been removed, the subgenus *Vignea* becomes a most natural and monophyletic assemblage. Very few (if any) primitive characters are to be found, unless the following feature of the utricle can be regarded as such, viz. "the orifice obliquely cleft dorsally and with dorsal suture more or less apparent" (Mackenzie 1935 p. 11). The number of stigmata is (almost always?) reduced to two, and the nuts are accordingly lenticular. No species has a rachilla. The lack of cladoprophylls is perhaps also a result of 'reduction'.

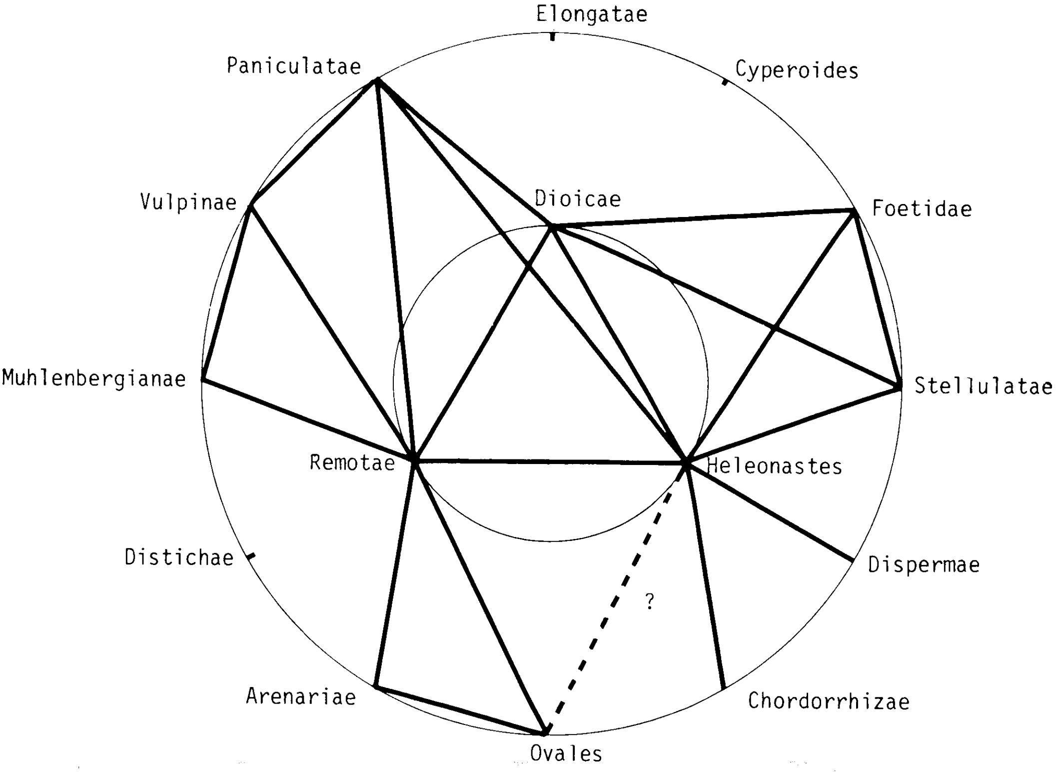


Fig. 1. Hybridization between the Nordic sections of *Carex* subgen. *Vignea*.

The members of *Vignea* are generally grouped into some 20 sections, most of which are natural. For the Nordic species I adopt Hylander's (1966) arrangement (cf. also Berggren 1969) with two exceptions. The most important differences from Kükenthal are that (1) *Dioicae* is transferred from *Primocarex* to *Vignea;* (2) *Canescentes* and *Tenuiflorae* are united into *Heleonastes;* (3) *Incurvae* (*C. maritima*) is included in *Foetidae* (Mackenzie 1935); and (4) *Remotae* (*C. remota*) and *Stellulatae* (*C. echinata*) are excluded from *Elongatae*.

In her treatment of *Vignea* in the Soviet Union Egorova (1966) includes some sections which are unrepresented in the Nordic countries, but otherwise the differences between her and Hylander's (1966) treatments are rather slight except for the sectional sequence and for the nomenclature. She retains *C. elongata* in *Canescentes* (=*Heleonastes*) and removes *C. disticha* from sect. *"Vignea"* (=*Arenariae*) placing it, together with some close allies, in a section of its own, *Holarrhenae*. Following Ohwi (1936), she excludes *C. disperma* from *Heleonastes* and treats it as a monotypical section, *Dispermae*.

Recent chromatographic and SEM studies by Toivonen (1974) and Toivonen & Timonen (1976) have confirmed the isolated position of *C. disperma*. In the ensueing pages it will thus be regarded as a separate section. In my opinion good reasons exist for separating *C. disticha* from *Arenariae*. This increases the number of Nordic sections to 15.

Chater's (1977) treatment in 'Flora Europaea' also deviates very little, except for nomenclature and sequence of sections.

Within certain sections the species are able to form sterile hybrids. Thus, in *Heleonastes*, with 9 Nordic species, 13 intrasectional hybrids are known within the area. In only one section (*Arenariae*) do ± fertile hybrids seem to occur (Sterner 1921). More remarkable is the occurrence of numerous intersectional hybrids, often between species of rather different morphology (Fig. 1). *C. dioica* and *C. remota,* especially, participate in such crosses. In the Nordic countries *C. dioica* is known to cross with *Foetidae* (*C. maritima*), *Heleonastes* (8 species), and *Stellulatae* (*C. echinata*). Although in the Nordic countries *C. remota* is only known to hybridize with *Heleonastes* (*C. canescens*) and *Paniculatae* (2 species), on the Continent it is also reported to cross with *Arenariae* (2 species), *Muhlenbergianae* (2 species), *Ovales* (*C. leporina*), *Stellulatae* (*C. echinata*), and *Vulpinae* (2 species).

Further Nordic intersectional hybrids are: *Chordorrhizae* × *Heleonastes* (*C. canescens* × *chordorrhiza,* Flatberg 1972), *Dispermae* × *Heleonastes* (3 hybrids), *Heleonastes* × *Ovales* (*C. lachenalii* × *macloviana,* Sylvén 1958; in my opinion very doubtful), *Heleonastes* × *Paniculatae* (C. *appropinquata* × *canescens*), *Heleonastes* × *Stellulatae* (*C. canescens* × *echinata*), and *Paniculatae* × *Vulpinae* (*C. otrubae* × *paniculata*).

It is only thanks to the activity of such eminent Nordic experts as e.g. H. Lindberg and J. Montell in Finland, J. Lid in Norway, and C. G. Alm, Otto R. Holmberg, and G. Samuelsson in Sweden, that it has been possible to study so many reliably-named hybrids and their smuts.

From other parts of the world many more hybrid combinations are recorded (e.g. Kükenthal 1909, Suessenguth 1939), but most of them seem dubious and in strong need of critical sifting. However, they do not influence the present discussion.

The main traits of importance for the evaluation of host-ranges and evolution of *Vignea* parasites are therefore as follows:

(1) The bulk of *Vignea* forms a very natural entity, whose connections with the other subgenera of *Carex* are remote and obscure. It is thus very unlikely that *Vignea* should have any *Anthracoidea* smut in common with any of the other subgenera.

(2) The species of *Vignea* are as a rule 'small' and clearly distinct from each other, even if the morphological differences may be minute.

(3) The species can be grouped into some 20 sections, mostly natural and well-defined.

(4) The species are to a great extent able to hybridize intra- and inter-sectionally. Both kinds of hybrids are sterile (except those within *Arenariae*?).

(5) The sections are to a remarkably high degree "chained" together by intersectional hybrids (Fig. 1).

Advances in the taxonomic treatment of the Vignea smuts

The gradual development of the taxonomy of the black ovariicolous smuts on Caricoideae has progressed from a single omnivorous species, characterized mainly by its symptoms, to a genus of its own, *Anthracoidea,* with several tens of species distinguishable by means of an everincreasing number of microscopical characters.

The first *Vignea* smut to be described as distinct from the collective *Ustilago caricis* (Pers.) Roussel was the echinosporous *Tilletia fischeri* Karsten (1878 p. 10) on *C. canescens.*

Lagerheim (1888 p. 3) described the smut on *C. brizoides* as *U. caricis β leioderma* with "membrana sporarum perfecte glabra", in contrast to the 'Hauptart' with "Membran der Sporen körnig punktiert", but it is impossible to be sure what he considered to be the 'Hauptart'.

Magnus (1895 pp. 78–79) pointed out that the size of the spores and the verrucosity of the spore walls vary from one host to another and suggested that continued studies might show these differences to be of taxonomic value. Two *Vignea* smuts were mentioned: one (now *A. fischeri*) on *C. vulpina* (spores M = 13.5 × 10.3 μm) and one (now *A. eleocharidis;* cf. Magnus 1896) on *C. stenophylla* Wg. (spores M = 15.7 × 11.6 μm).

When H. Sydow (1924) initiated a more systematic subdivision of the *Carex* smuts, he found two *Vignea* smuts to be worthy of specific rank, viz. *Cintractia turfosa* on *C. dioica* and *Ci. arenaria* on *C. arenaria* (and *C. ligerica*?). For a third species, *Ci. microsora,* the host was also given as a *Vignea* but belongs in fact to subgen. *Carex* (Nannfeldt & Lindeberg 1957 p. 495).

Liro (1938) described three more *Vignea* smuts, viz. *Ci. aspera* on *C. chordorrhiza, Ci. glareosa* on *C. glareosa,* and *Ci. karii* on *C. brunnescens* (and some hybrids). The very common smut on *C. echinata* was referred to

Lagerheim's taxon, which had meanwhile been raised to specific rank as *Ci. leioderma* (Lgh.) Ciferri (1931 p. 45). The smut on *C. lachenalii* was the only Finnish *Vignea* smut left in the still very collective *Ci. caricis.* Liro also observed that the spore size on some hosts, e.g. *C. dioica,* showed an extraordinarily large variation.

Lehtola (1940), a pupil of Liro's, studied variation in spore size and germination of some *Carex* smuts, including those growing on four species of *Vignea,* viz. *C. chordorrhiza, diandra, dioica,* and *echinata.* The spore size of the smut on *C. chordorrhiza* (7 samples) showed only a normal variation, as did that on *C. echinata* (91 samples). The single sample from *C. diandra* agreed with the *chordorrhiza* smut with regard to spore size, wall ornamentation, and germination. He accordingly referred it to *Ci. aspera.* On the other hand, two amply different smuts were found on *C. dioica,* one (8 samples) with large spores and long, rod-shaped sporidia (the true *Ci. turfosa*) and the other (5 samples) with small spores and small ovoid sporidia (*Ci. caricis-dioicae* sp. nov.).

Savile (1952) in his studies of the North American smuts on Caricoideae took into consideration a number of previously neglected morphological characters and definitively split up the old collective *Ci. caricis.* He recognized 17 smut taxa (10 species and 7 varieties) for at least 90 host species, amongst them 24 species of *Vignea* carrying 10 smut taxa. Only two of these taxa were confined to *Vignea,* viz. *Ci. aspera* to *C. chordorrhiza* and *Ci. carpophila* var. *verrucosa* to *Ovales.*

In four cases he found two different smuts present on the same host species, e.g. both *Ci. fischeri* and *aspera* on *C. chordorrhiza* and both *Ci. carpophila* and *limosa* var. *limosa* on *C. gynocrates* Wormskj. Nannfeldt & Lindeberg (1957 p. 504) critizied Savile's way of delimiting his taxa too schematically, without taking into consideration that the (relatively few) samples he studied might in fact be connected by a series of forms showing continuous variation. Kukkonen (1964 b p. 175) showed this to be the case for the *chordorrhiza* smuts and he referred them all to *A. aspera.* On the other hand, the two *gynocrates* smuts are the same as those which Lehtola had found on the closely allied *C. dioica.*

The echinosporous *Ci. fischeri* was treated by Nannfeldt & Lindeberg (1957) and found to occur not only on *C. canescens* but also on several other species (and hybrids) of *Vignea* whereas Savile's records of this smut on species of subgen. *Carex* were referable to the rather similar *Ci. americana* sp. nov.

Kukkonen (1961 etc.) was the first person to provide a reliable survey of the genus. Out of regard to the studies by B. L. and the present author, he excluded most of the *Vignea* smuts from his investigations, dealing only with the three echinosporous species *A. fischeri, aspera* and *eleocharidis* (sp. nov.).

Subgenera and sections of Anthracoidea

Kukkonen (1963, 1972) found that it was possible to divide *Anthracoidea* into two subgenera, *"Euanthracoidea"* (=*Anthracoidea,* including *A. caricis,* the generic type) and *Proceres* (with *A. limosa* as the type). The crucial character is the mode of germination: either with short (mostly 7–15, exceptionally up to 30 μm long), subglobose–ovate sporidia, two or more usually produced per promycelial cell; or with long (50–80 μm), rod-shaped sporidia and only one produced per promycelial cell, respectively. Kukkonen & Raudakoski (1964) soon showed that this distinction was connected with a fundamentally different behaviour of the nuclei. In subgen. *Proceres* both of the two nuclei of each promycelial cell enter the young sporidium. In subgen. *Anthracoidea,* on the contrary, only one of the nuclei enters the sporidium and the other divides; when the second sporidium is about to be formed, one of the daughter nuclei enters that sporidium and the other divides once again; this procedure may be repeated several times. It seems very unlikely that such a change, combined with the change in sporidium shape (and size), should have occurred more than once within *Anthracoidea.*

With regard to taxonomic structure, *Anthracoidea* clearly belongs to the kind of taxa which Munk (1962) recognized as groups "in active evolution" where it is impossible to establish a "tree of evolution". Instead, if the variation of each individual character is studied separately, the "lines of variation" will be found to be combined into what Munk aptly describes as a "lattice work of crossing lines" or a "multidimensional pattern of crossing lines". On the whole the "lines of variation" are the same in the two subgenera. As a rule, however, the individual characters vary within narrower limits within *Proceres* than within *Anthracoidea*.

There thus seems to be no truly echinosporous species amongst the *Proceres;* nor any species with very angular or irregular spores; nor any with very unevenly-thickened spore walls or light-refractive spots (cf. Kukkonen 1972 p. 1031). On the average the spores are larger than in subgenus *Anthracoidea,* and no really small-spored species is known. On the other hand, a species with very large spores belongs most probably to the *Proceres*. Nevertheless, because the sporidium (at least so far) provides the only reliable character, the assignment of a species to one or other of the subgenera, without knowing how it germinates, remains a ± qualified guess.

Subgenus *Anthracoidea* was divided by Kukkonen (1963) into three sections, based primarily on differences in spore shape and spore wall, viz. *"Angulosporae"* (= sect. *Anthracoidea;* including the generic type *A. caricis*), *Leiosporae* (type: *A. elynae* (H. Syd.) Kukk.), and *Echinosporae* (type: *A. subinclusa* (Koern.) Bref.). These sections may be useful for practical purposes but, as will be shown later, they are hardly monophyletic, nor are they sharply defined, since the diagnostic characters change gradually without sufficient discontinuities.

Sect. *Anthracoidea* is characterized by irregular–extremely irregular spores and unevenly thickened spore walls, the thickest points very often standing out as light-refractive spots. Sect. *Leiosporae* is characterized by regular, flattened spores and evenly or nearly evenly thickened, smooth or at the most very finely verrucose spore walls. An additional difference (Kukkonen 1963 pp. 25–26) is the size of the sporidia, which are slightly smaller in sect. *Anthracoidea* (M = 7–10 μm long) than in *Leiosporae* (M = 10–15(–20) μm long).

Nannfeldt & Lindeberg (1957) revised the five small-spored species with echinate spore walls known to them. Kukkonen (1963) added two species which have almost as high wall ornamentation but slightly larger spores, to form a third section, *Echinosporae,* characterized by "regular or, at most, slightly asymmetrical" spores and evenly thickened spore wall, covered with spines which are higher than broad. The only differences in the diagnosis from *Leiosporae* are therefore wall ornamentation and the lacking reference to sporidium size. (The sporidium lengths of these seven species are 6–15 μm.) One year later Kukkonen (1964 b; cf. 1969) treated the section monographically, adding another two species. He now allowed the spores to be also "moderately angular" and their walls "unevenly thickened, with light-refractive areas in the thickest places" or, in other words, of *"Angulosporae"* type.

The first five species dealt with were those with the highest wall ornamentation, reaching up to 2 μm. The emergences are usually called "spines" but this is rather inappropriate. They are best described as slender cylinders with very irregular sections, so slender that they are ± easily broken. They widen out and flatten apically and the tips may even tend to fuse. They parasitize sedges of the subgenera *Carex* (sects. *Paludosae* and *Acutae*) and *Vignea*. Their hosts are some ± exclusively hydrophilous species, as well as some less exacting ones, providing that they are growing close to open water. Savile (1954 pp. 742–743) suggested that the long "spines" are a habitat adaption, the spines serving to keep the spores afloat by means of trapped air bubbles, but Kukkonen (1964 b p. 176) showed that *Anthracoidea* spores remain afloat irrespective of the type of wall ornamentation.

The two additional species differ in several respects, both inter se and from the preceding ones. The wall ornamentation consists of ± conical spines with rounded tips, i.e. except in length they agree with the warts characteristic of so many members of the other sections and of *Proceres*. The ± arbitrary limit for inclusion in the *Echinosporae* is the possession of spines which are at least as high as broad.

One of these additional species (*A. aspera* on *C. chordorrhiza*) has medium-sized spores of the type characteristic for sect. *Anthracoidea,* with conical warts of rather unequal length, thus differing considerably from all the preceding species. Nevertheless, some North American samples of *C. chordorrhiza* have smuts so similar to *A. fischeri* that Savile (1952 p. 421) took them to be that species. Kukkonen (1964 b p. 173) has later shown that these samples are better placed under *A. aspera,* with which they are connected by intermediates. Whether this also implies that these two smut species are closely related is another problem. A second species (*A. eleocharidis*) is characterized by its peculiar mode of germination (see below). A third (*A. calderi* (Savile) Kukk. on *Phyllostachyae;* subgen. *Carex*) is the only truly large-spored species known to germinate in the manner of the species of subgen. *Anthracoidea.*

It is hard to believe that all these species belong to a common evolutionary line. A comparable examination of the species grouped into the sections *Leiosporae* and *Anthracoidea* leads to analogous results.

Pattern of variation

Even within a single sorus, the *Anthracoidea* spores on the whole vary widely both in size and shape. The specific criteria ought as a rule therefore to be expressed as means, ranges, and frequencies.

Spore size

After Lehtola's (1940) fundamental biometrical studies spore size variation has been studied and discussed by several authors, e.g. by Nannfeldt & Lindeberg (1957, 1965) and especially by Kukkonen (1963). Here it is sufficient to point out that such studies, when critically evaluated, are among the most valuable tools for delimiting and describing a species, but are fortunately not needed for routine determinations. Extraordinarily wide amplitudes of means would suggest that genetical differences may be involved. *A.* (*Proceres*) *limosa* (H. Syd.) Kukk. on *Limosae* (subgen. *Carex*) is a good example. Here the degree of ornamentation is more variable than usual and the largest spores concentrate upon some of the principal hosts (Kukkonen 1963 pp. 17–22, 91–95).

Spore shape

In the species with the smallest spores (M = up to c. 18 μm) the spores are mostly ± isodiametric and rounded, subglobose or only moderately flattened (e.g. *A. subinclusa* and *echinospora*), but they may also be strongly flattened ("biscuit-shaped"), e.g. *A. karii.* In species with larger spores these are as a rule distinctly flattened and in plan view not isodiametric, i.e. if rounded ± elliptic. They may also be ± angular and are then subrectangular in plan view (as often in *A. heterospora*), subpentagonal or more irregular. In several species the spore contour is very irregular, with rounded protuberances and concavities, e.g. *A. caricis-albae* Kukk. and *irregularis* (Liro) Boidol & Poelt.

Spore wall

The spore wall only reaches its definitive thickness and colour late in development, although different species behave differently. Thus the presence in every mount of spores in (seemingly?) different stages of maturity is a characteristic of *A. heterospora.*

If the spores are rounded, their wall is mostly rather even in thickness, except that in distinctly flattened spores the rim as a rule has somewhat thicker walls. In angular or irregular spores the wall thickness is as a rule very uneven, thickest at the angles and in the protuberances. The "light-refractive spots" often observed in such spores represent a ± obligatory consequence of extreme, local wall thickenings rather than being an independent character.

Internal swellings

The internal swellings, first described by Savile (1952 p. 416), are organelles within the spore wall, of doubtful origin and doubtful function. They certainly have some taxonomic value at species level, but seem to be of little use above it and must on the whole be used with the utmost caution.

Some species, e.g. *A. inclusa* and *subinclusa,* seem to be totally devoid of such swellings, whereas others (such as the closely allied *A. americana*) show 1–6 clear swellings in almost every spore. In still other species (the majority?) swellings are present, but only discernible at certain stages and/or under certain conditions and/or in certain spores. In such cases it is not even clear whether all the spores of a given species form incipient swellings, or whether certain sori or populations may be totally devoid of them, and in the latter case whether this is genetically based or due to external conditions. *A. aspera* is such a species, studied in some detail by Kukkonen (1964 b p. 173, 1969).

Wall ornamentation

The wall ornamentation provides some of the most valuable taxonomic characters. The species with the highest "spines" ("sect. *Echinosporae*") have already been discussed. The spores of most species have a verrucose–verruculose surface, but when the ornamentation is minute it is almost indiscernible by light microscopy without the use of oil-immersion. Lagerheim (1888) described *U. caricis β leioderma* as an extreme taxon with (supposedly) smooth spores. It is true that the rather young spores, which predominate in the type collection, look almost smooth, but on closer examination traces of granulosity can be discerned and riper spores (both in this and in other collections from the same host) show distinct warts (Fig. 2). As far as known, no *Anthracoidea* has spores which, at all stages, are totally devoid of warts.

Gelatinous coat and mode of dispersal

The spores of *Anthracoidea,* like those of *Ustilago,* form within hyphae and are thus covered by a gelatinous coat during maturation (cf. Kukkonen & Vaissalo 1964 p. 247). This coat smooths the spore surface and produces an even contour if the warts are not high enough. As a rule the coat is rather thin and soon disappears, but in a few species the coat is much thicker and more persistent. Such a smut is *A. externa* (Griff.) Kukk. on *C. filifolia* Nutt. (*Primocarex–Filifoliae*), discussed by Savile (1952 p. 422) and by Kukkonen (1963 p. 71), who suggests that "the gelatinous sheath is probably an adaption of the smut to the extreme drought in the prairies, and the sheath protects the spores very well". Another example is a smut growing on *C. pachystylis* J. Gay (*Vignea–Divisae*), for which Golovin (1952 pp. 108–109) even coined a new genus, *Cintractiomyxa* (cf. Nannfeldt & Lindeberg 1957 p. 503). *A. scirpi* (Kühn.) Kukk. is yet a third smut with a noteworthy thick and persistent coat (Kukkonen 1963 p. 69). A gelatinous coat has also been observed in a few collections of *A. scirpoideae* Kukk. on *C. scirpoidea* (Kukkonen 1963 p. 78).

The presence of a thick and persistent gelatinous coat leads to the formation of sori that are hard and compact (not dusting) when dry, but deliquescent when wet. This implies a radical change in the mode of dispersal, from dispersal by air currents to dispersal with water (rain drops) or, in other words, from xerospory to gloiospory. In *A. externa* Kukkonen (1963 p. 71) observed how part of the spore mass floated down from older sori to surround the axis of the spike.

Conidial state

A few species (of both subgenera) are known to possess a conidial state of the genus *Crotalia* Liro (cf. Kukkonen & Vatanen 1968), which infects and deforms the host utricles (sometimes also the ovaries). The morphological differences between these states of various *Anthracoidea* species are very small. The conidial state appears only rarely, but with differing frequency in different species. It is impossible as yet to decide if more (all?) species are able to form conidia; however, if they exist, they are formed so rarely (under so special conditions?) or so ephemerally that they have been overlooked.

Germination

Variation in germinative features, of course, follows different lines in the two subgenera. In subgen. *Proceres* virtually only the size of the promycelial cells and the sporidia vary, whereas in subgen. *Anthracoidea* the sporidia vary in number, size and shape and the pseudosterigmata in length and branching.

A. scirpi, the only undoubted *Anthracoidea* parasitizing a host outside Caricoideae, is highly noteworthy. Its sporidia are extraordinarily long (up to 30 μm, $M = 20$ μm) and only one is formed from each promycelial cell. This reduction in number is perhaps not an independent character, but simply a consequence of the voluminous sporidia, the mother cells already becoming exhausted after producing the first sporidium. The deviant sporidia may indicate that *A. scirpi* has undergone a long independent evolution, and that it is not the result of a recent "escapade" of some *Carex*-inhabiting species. As Kukkonen (1967 p. 39) remarked, it is perhaps not merely by chance that the host (*Trichophorum caespitosum*) belongs to a group within the genus *Scirpus* sensu latissimo which deviates from the rest, and from the Scirpoideae on the whole, by possessing an embryo of *"Carex* type" (Veken 1965), a type that otherwise is confined to Caricoideae–Cariceae.

A. eleocharidis represents an extreme in another direction. The 4–12 small sporidia (M = 6 μm long) are formed successively from each promycelial cell by sympodial prolification of the pseudosterigma, which eventually becomes zigzag-shaped, thus somewhat resembling the conidiophore of *Tritirachium* (Hughes 1953 p. 605).

In the other species the sporidia are relatively small (M = 7–13 μm long) and 2–4 are as a rule produced from each promycelial cell. The size and shape of sporidia and of pseudosterigmata afford good specific criteria, but seem to be of little value above species level, nor are they of any practical use for routine determinations.

The Anthracoidea species on Vignea

There are five Swedish (= Nordic) species of *Anthracoidea* on *Vignea*, and the European flora includes a further one.

Anthracoidea turfosa

One species, *A. turfosa*, belongs to *Proceres*. It only attacks members of *Dioicae* and their hybrids with *Heleonastes*. These sedges also fall within the host range of the small- and "smooth"-spored *A. karii*. A trace infection by *A. turfosa* on *C. heleonastes* has been found once amongst heavily infected *C. dioica* and with infected *C. dioica* × *heleonastes* in the vicinity.

As far as is known, *C. davalliana* does not take this smut, only *A. karii*. The North American *C. gynocrates* Wormskj. takes both. The North American *C. exilis* Dewey does take *A. turfosa*, which accords well with the view that this sedge belongs to *Dioicae* (instead of *Stellulatae*).

A. turfosa is easily recognized by its large spores (M = 21–24 μm long) with evenly thickened and rather smooth walls.

Anthracoidea fischeri

A second species, the echinosporous *A. fischeri*, has been revised by Nannfeldt & Lindeberg (1957 pp. 516–518) and by Kukkonen (1964 b pp. 170–172, 1969). In the Nordic countries it parasitizes *Heleonastes* (principal host: *C. canescens*), *Holarrhenae* (i.e. *C. disticha*), and *Paniculatae* (*C. diandra*). From a Nordic point of view it has a decidedly eastern–northeastern distribution. The host spectrum mentioned above already arouses attention, for *Holarrhenae* seems to take a rather isolated position, not hybridizing with any other section. Just east of Fennoscandia, in Latvia, a member of a fourth section, *C. vulpina* (*Stenorrhynchae*) takes a smut with the same morphology, and reports of smutted *C. vulpina* from eastern Germany, Poland, and Czechoslovakia may also refer to *A. fischeri*. In western Canada (British Columbia) such smuts, sometimes together with the *Crotalia* state, have been found on *Ovales* (*C. bebbii* Olney), *Paniculatae* (*C. cusickii* Mack. and *diandra*), and *Stellulatae* (*C. ?interior* Bailey).

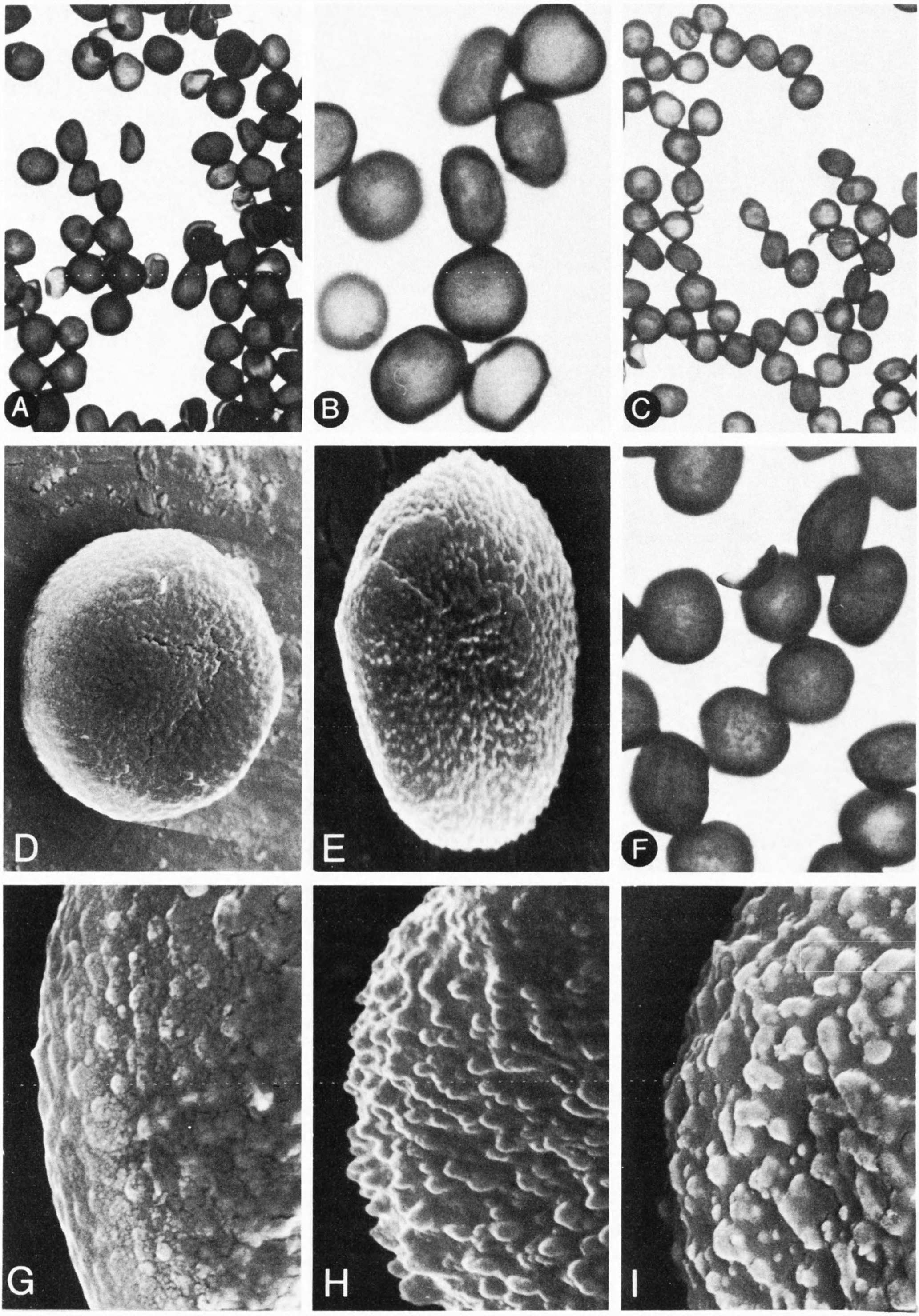
A. fischeri is easily recognized by its small subglobose spores (M = 14–16 μm) with long (1.0 μm), often apically flattened "spines". It is rather often accompanied by its conspicuous conidial state.

Anthracoidea aspera

A second echinosporous smut, *A. aspera*, with *C. chordorrhiza* (*Chordorrhizae*) as its principal host, has been treated in detail by Kukkonen (1964 b pp. 173–174, 1969).

A single sample found on *C. diandra* (*Paniculatae*) from Finland was studied by Lehtola (1940 pp. 79–81; cf. above), who found that the smut matched *A. aspera* so well, both as regards spore morphology and mode of germination, that he considered them to be conspecific, a view with which Kukkonen (1964 b) agreed although the voucher specimen cannot be found (Kukkonen in litt. 11.V. 1977). Unfortunately it is not known if smutted *C. chordorrhiza* also grew in the vicinity. Kukkonen (1964 b) also

Fig. 2. Spores of *Anthracoidea* species. – A, B, D, G: *A. karii* (A, B, D: Lundell & Nannf., F. exs. suec. 1573, on *C. echinata;* G: id. 1771, on *C. brunnescens*). – C, E, F, H, I: *A. arenaria* (C, F, I: Petr., Myc. gen. 1002, on *C. arenaria;* E, H: id. 1007, on *C. brizoides*). – A, C c. 400 ×; B, F c. 1100 ×; D, E c. 3000 ×; G, H, I c. 10,000 ×.


A
B
C
D
E
F
G
H
I

placed a smut from North America (Wyoming) on *C.* (?) *diandra* here.

Smuts on *Paniculatae* are on the whole very rare. A trace infection (a single sorus, UPS!) on *C. appropinquata* from the Swedish island of Gotland was also referred to *A. aspera* by Kukkonen (1964 b), and I agree. An old record of smut on *C. paniculata* (Tulasne 1847 p. 87 and repeated by numerous subsequent authors) cannot be substantiated, nor can the record by Lagerheim (1884 p. 104) of a smut on *C. diandra* from northern Sweden (Lule Lappmark) (Nannfeldt & Lindeberg 1957 p. 497).

Liro (1938 p. 22) based his *Ci. glareosa* on a single sample of smutted *C. glareosa* (*Heleonastes*) from the White Sea. The sample (H!) is not in a good condition, but the smut seems indistinguishable from *A. aspera*, as is a poor specimen (O!) on the same sedge from northernmost Norway.

A. aspera is characterized by slightly larger, oblong spores (M = 17–20 μm long), unevenly thickened walls with light-refractive spots and high, round-tipped papillae (up to 1.0 μm). The classification of the smuts on *C. glareosa* and on *Paniculatae* is only tentative.

Anthracoidea karii

Four taxa of small- and "smooth"-spored European *Vignea* smuts have been described, viz. *Ci. arenaria* (on *C. arenaria*), *Ci. caricis-dioicae* (on *C. dioica*), *Ci. karii* (on *C. brunnescens* and its allies), and *U. caricis β leioderma* (on *C. brizoides*). Liro (1938 pp. 25–27, 275–277) referred the smut very commonly found on *C. echinata* to *Ci. leioderma*. Lehtola (1940) and all subsequent authors followed.

The smallest spores (M = 14.3–16.1 μm long) are attributed to *Ci. caricis-dioicae* (Lehtola 1940 p. 82). On finding that her Swedish samples of a small-spored smut on *C. dioica* and *C. parallela* possessed decidedly larger spores (M = 15.9–18.3 μm long), B. L. hesitated to identify it as Lehtola's species, until we discovered (Nannfeldt & Lindeberg 1957 p. 564; cf. Kukkonen 1963 pp. 12–13) that on average Lehtola's measurements are 1.5 μm smaller than ours. Continued studies have convinced the present author that the *C. dioica* smut is morphologically indistinguishable from the *C. brunnescens* smut, and have shown that the numerous intersectional sedge hybrids are frequently infected by smuts of the same morphology.

During her studies B. L. also found that the *echinata* smut could not be kept apart from the *brunnescens* smut (i.e. *A. karii*) but did differ markedly from the *brizoides* smut (i.e. the original *Ci. leioderma*). My own extensive studies have confirmed her results, and the extremely rare hybrid *C. dioica* × *echinata*, in its single Swedish locality, was found to suffer from the same smut.

This implies a very wide host range, but all the hosts are directly or indirectly connected by (sterile) hybrids. The correct name of the composite species is *A. karii*. It is common and widespread on *C. dioica, parallela, echinata* and several members of *Heleonastes*, whereas it is rare or very rare on other, closely related members. Especially noteworthy is its rarity on *C. canescens*.

Anthracoidea arenaria

Judged from the type collection, *Ci. leioderma* looks at first sight very similar to *A. karii*, but closer examination reveals that the vast majority of the spores are immature and that spores approaching maturity are slightly longer, more oblong and irregularly angular, and their walls darker and unevenly thickened. This difference is confirmed by other collections from *C. brizoides*, for which the mean spore length is 16–20 μm. Some difference in verrucosity of the spores of the two smuts is just visible by light microscopy, but SEM reveals the difference to be real and very distinct (Fig. 2). The *brizoides* smut, instead, is morphologically indistinguishable from the smut found on *C. arenaria* (and *ligerica*). *A. arenaria* is the correct name for the consolidated species. For the sake of completeness it should be mentioned that Hirschhorn (1947 pp. 83–84) had already united these species, but this has not been generally accepted, because most of the other synonyms proposed in that paper are highly unjustifiable.

There are several records of smut on *C. leporina* (*Ovales*). Those that can be checked are mostly based on misnamed *C. brizoides*. A Bavarian record (Boidol & Poelt 1963 p. 18; M!) is correct, however. The smut agrees exactly with *A. arenaria*, and the host had been growing amongst smutted *C. brizoides*. This is evidently a case of accidental infection.

The records of smutted *C. leporina* from Finland (Åland and Helsingfors; Liro 1938 p. 544) are inextricable. Dr Kukkonen (in litt. 28.XII. 1976) informs me that no voucher specimens can be found (destroyed during World War II?) and that, having got a detailed description of the Åland locality, he visited it without refinding the smut. Since there is no reason for suspecting a misidentification of the host, we are probably faced with two more cases of accidental infection (but by which smut?).

Anthracoidea vankyi

The remaining European species is the hitherto undescribed Central European *A. vankyi* on *C. muricata* s.lat. (i.e. *C. divulsa, pairae,* and *spicata; Muhlenbergianae*). It is known from Spain in the west to Poland and Romania in the east, and perhaps to Germany and the Netherlands in the north (cf. under General distribution). Although the potential hosts are also present in Norden, it has never been found there.

The spores are angular, or even irregular, with hemispherical protuberances, their wall is very unevenly thickened, with light-refractive spots in the thickest areas, and distinctly verrucose.

Anthracoidea in N America

The North American *Vignea* flora is much richer and more diversified than the European, and the same evidently applies to the *Anthracoideae*.

The European *A. aspera, fischeri, karii,* and *turfosa* occur in North America too, partly on other hosts, but *A. arenaria* seems to be absent, and it is an open question whether the smut found on *Muhlenbergianae* (*C. occidentalis* Bailey; Clinton 1904 p. 402, 1906 p. 33) is in fact *A. vankyi*.

The following taxa have been described from North America: *A. eleocharidis* (on *C. eleocharis; Physodeae*) and *Ci. carpophila* var. *verrucosa* (on *C. ebenea* and others; *Ovales*). A nomen nudum is *U. caricis* [var.] *douglasii* (on *C. douglasii; Physodeae*). They will be treated as full species in the subsequent text.

A. eleocharidis (Kukkonen 1964 a), with small echinulate spores, is also known from Asia on *C. stenophylla* (closely related to *C. eleocharis*). *A. verrucosa,* with small, distinctly verrucose spores, occurs on several closely allied sedges in western North America and extends its distribution to Greenland (on *C. macloviana*). *A. douglasii* is a relatively large-spored species, which Kukkonen (1963 p. 37, 1964 a p. 275) supposes to belong to *Proceres*.

Planetella lironis, found on *C. maritima* (*Foetidae*) and *C. leiophylla* (*Eucarex–Atratae?;* cf. above) from northern Canada, could be regarded as an aberrant *Anthracoidea* (cf. Kukkonen 1964 a p. 276). The reports of smutted *C. maritima* from Greenland (Allescher & Hennings 1897 p. 40 as *Ci. caricis*) and from Asia (see below) are certainly not based on *Planetella*.

A number of North American hosts, either not or only superficially studied by me, are certainly infected by one or other of the known smut species, but other hosts, especially the taxonomically more isolated ones, are likely to house further species as yet undescribed, e.g. *C. aenea* Fern. (*Ovales*), *bromoides* Schkuhr (*Elongatae* vel *Deweyanae*), *deweyana* Schw. (*Elongatae* vel *Deweyanae*), *praegracilis* Boott (*Divisae;* germination studied by Kukkonen 1964 a p. 275), *praticola* Rydb. (=*pratensis* Drej.; *Ovales*), *siccata* Dewey (=*foenea* Willd. sensu Svens.; *Arenariae*), *straminiformis* Bailey (*Ovales*).

Anthracoidea in S America

Two *Vignea* smuts have been described from South America, viz. *U. cariciphila* Spegazzini (1925 p. 152) from Argentina on *C. bonariensis* Desf. (*Bracteosae*) and *Ci. pannucea* Liro (1935 p. 5) from Colombia on *C. bonplandii* Kunth (*Elongatae* vel *Deweyanae*). The former was transferred to *Cintractia* by Ciferri (1931 p. 58) but is certainly a *Farysia* ("pulviscula verde-olivaceo vivo", "sporae parvae olivaceae"). The material of *Ci. pannucea* can no longer be found in H (Kukkonen in litt. 28.XII.1976), but Kukkonen informs me (in litt. 11.V.1977) that he has seen two samples that he considers to belong to this very peculiar species, viz. one on *C. bonplandii* from Colombia (16.IX.1953 Jamillo & Mora) and one on "*C. longii* Mack." from Venezuela (5.II.1944 Steyermark). He thinks the species is an *Anthracoidea*.

I have seen smuts on two other South American sedges, viz. on *C. nebularum* Phill. (*Foeti-*

dae fide Kük. or *Divisae* fide Egorova) from Patagonia (Dusén. H!; Liro 1938 p. 252 as *Ci. caricis*) and on *C. ? gayana* Desv. (*Divisae*) from Chile (Valparaiso, Dusén, S!). The two smuts look very similar and are probably conspecific. They seem to be close to *A. verrucosa,* but have a thicker and darker spore wall with more conspicuous warts.

Anthracoidea in Asia

Also from Asia two *Vignea* smuts have been described, viz. *Ci. variabilis* S. Ito (1935 p. 92, 1936) from Japan on *C. arenicola* Fr. Schm. (*Divisae*), but also on *C. caespitosa* (*Acutae,* subgen. *Carex*), and *Cintractiomyxa caricis* Golovin (1952 p. 108) from Kazakstan on *C. pachystylis* J. Gay (*Physodes*). I have seen neither of these, and Ito's species is certainly heterogeneous. I have seen a sample on *C. arenicola* (Korea: Sgou-ouen 30.V.1901 Faurie; Liro 1938 p. 238; H!) but this can hardly be Ito's species, because the spores are not echinulate but rather smooth, resembling those of *A. karii.* Golovin's species is one of those whose spores are surrounded by a thick gelatinous coat (cf. above).

There are on the whole very few records of *Anthracoidea* from Asia. Besides the new species, some records by Liro (1938) and the records of *A. eleocharidis* (see under this species) only a single further *Vignea* smut find has been recorded, viz. that of *Ci. caricis* on *C. maritima* (*Foetidae*) from India (Punjab) by Pavgi & Mundkur (1949 p. 108) and Mundkur & Thirumalachar (1952 p. 43). According to the description this smut could well be *A. karii,* to which *C. dioica* ×*maritima* is known to be susceptible.

Key to the Nordic black ovariicolous smuts on Carex subgen. Vignea

Some sufficiently known species not occurring in the Nordic countries have been included.

1\. Spore wall with a broad (5–8 μm) dark equatorial band. Spores c. 10–16×9–14 μm. On *C. maritima* (and *C. leiophylla*) [Canada] .... *Planetella lironis*
– Spore wall without such a band (*Anthracoidea*) 2
2\. Spores large, 17–28×13–22 μm (M=20.5–24 μm long), rounded or only moderately angular 3
– Spores small–medium-sized, 12–23(–26)×8–19 μm (M=16–20 μm long or, when spore shape very irregular, up to 21.5 μm) 4
3\. Spore wall (almost) smooth. Internal swellings low, 1–2, rarely observed. On *Dioicae* and hybrids with *Heleonastes* .... 5. *A. turfosa*
– Wall with distinct warts (0.2–0.3 μm high). Internal swellings not observed. On *C. douglasii* [W. North America] .... *A. douglasii*
4\. Spore wall almost smooth–verruculose, warts up to 0.3 μm high 5
– Wall distinctly echinate with warts or spines at least as high as broad (0.5–1 μm high) 8
5\. Spore wall almost smooth 6
– Wall distinctly verruculose 7
6\. Spores regularly rounded, 13–21×9–19 μm (M=16–18.5 μm long). Wall evenly thickened. Internal swellings 2–3, often conspicuous. On *Dioicae, Heleonastes, Stellulatae,* and hybrids .... 4. *A. karii*
– Spores often angular, 13–23×11–19 μm (M=16–20 μm long). Wall often thicker at angles. Internal swellings present, but invisible in mature spores. On *Arenariae* .... 1. *A. arenaria*
7\. Spores rounded, in plan view subcircular–broadly elliptic, distinctly flattened, thin-walled (c. 1 μm). On *Ovales* [North America] .... *A. verrucosa*
– Spores angular–irregular. Wall unevenly thickened (1.5–4 μm), sometimes with light-refractive spots in the thickest areas. On *Muhlenbergianae* [Central Europe] .... *A. vankyi*
8\. Spore wall unevenly thickened (c. 1–4 μm) with light-refractive spots in the thickest areas. Spines up to 1.0 μm high. On *C. chordorrhiza, C. glareosa, Paniculatae* etc. .... 2. *A. aspera*
– Wall evenly thickened, relatively thin (c. 1.5 μm), no light-refractive spots 9
9\. Spines up to 0.5 μm high, blunt. Internal swellings not observed. On *C. stenophylla* s.lat. [Canada, Asia] .... *A. eleocharidis*
– Spines up to 1.0 μm high, often slightly flattened at tips. Internal swellings present. *Crotalia* state often conspicuous. On *Heleonastes* and hybrids, *C. disticha* etc. .... 3. *A. fischeri*

1. **Anthracoidea arenaria** (H. Syd.) Nannf. comb. nov. – Fig. 2 C, E, F, H, I

Cintractia arenaria H. Syd., Ann. Myc. 22 p. 289 (1924). – Typus (selected here): *Carex arenaria;* Germany, Pommern, Rügenwaldemünde VII.1893 P. Sydow (Syd., Ust. 5; hololectotypus: Hb. Syd. S!).

Ustilago Caricis β leioderma Lgh., Mitt. Badisch. Bot. Ver. 1888 p. 37 (1888). – *Cintractia Caricis* var. *leioderma* ("lejoderma") Bub., Verh. Zool.-Bot. Ges. Wien 48 p. 24 (1898). – *Cintractia leioderma* Cif., Ann. Myc. 29 p. 45 (1931). – *Anthracoidea leioderma* Kochm. & Maj., Grzyby (Mycota) 5 p. 111 (1973). – Typus: *Carex brizoides;* Germany, Baden, Bromberg nr. Freiburg i. Br. VI. 1888 G. Lagerheim (holotypus: S!; isotypi: Roumeg., F. gall. 4717).

Ustilago Vigneae Fuss a. *V. Schreberi* Fuss, Arch. Ver. Siebenbürg. Landeskunde, N.F. 14 p. 446 (1878; nom. nud.).

Spores in plan view (13–)15–21(–23) × (11–)13–18 (–19) µm (M = 16–20 µm long), subcircular–subelliptic and evenly rounded or mostly moderately angular or even rather irregular and pointed at one or both ends, only slightly flattened (10–15 µm thick). Wall c. 1.5–2 µm thick, markedly thicker at angles (up to 3 µm), rather dark. Internal swellings distinct in young still thin-walled spores, not (or hardly) visible in mature. Surface of young spores practically smooth, but later with low warts (0.2–0.3 µm high), clearly visible. Germination not studied.

Matr.: *(Arenariae) C. arenaria, brizoides* L., *ligerica, praecox.* – *(Arenariae* ×*Remotae) C. brizoides* ×*remota.* – *(Ovales) C. leporina.*

Exs.: (On *C. arenaria*) Kochm., Myc. pol. 170; Kochm., Ust. pol. 22; Lundell&Nannf., F. exs. suec. 849; Petr., Myc. gen 1002; Rbh., Herb. myc., ed.II:396 (p.p.; *"Ust. urceol."*); Samuelss., Fl. suec. exs. 348 Fung.; Smarods, F. latv. exs. 156 (*"Ci. Car."*); Syd., Ust. 5 (*"Ust. Car.";* typus), 14 (*"Ust. oliv."*), 442 (*"Ci. Car."*); Zillig, Ust. 2 (*"Ci. Car."*). – (On *C. brizoides*) Crypt. čechosl. exs. Fungi 11 (*"Ci. Car."*); Kochm., Myc. pol. 506; Krieg., F. saxon. 1851 (*"Ci. Car."*); Krypt. exs. Vindob. 3234 (*"Ci. lejod."*); Petr., Fl. Boh. Mor. exs. II:1 2107 (*"Ci. Car."*); Petr., Myc. gen. 1007 (*"Ci. lejod."*); Rbh., F. eur. 899 (*"Ust. urceol."* on *"C. bryoides"*); Roumeg., F. gall. 4717 (*"Ust. Car.* var. *leiod.";* typus); Schneid., Herb. Schles. P. 87 (*"Ust. urceol."*) fide Liro; Syd., Ust. 178 (*"Ci. Car.* var. *leiod."*); Weese, Eumyc. sel. exs. 311 (*"Ci. Car."*); Zillig, Ust. 71 (*"Ci. Car."*), 74 (*"Ci. Car."* on *"C. leporina"*). – (On *C. ligerica*) Baenitz, Herb. eur. 3465 Fung.; Syd., Myc. germ. 1875 (*"Ci. Car."*); Syd., Myc. march. 238 (*"Ust. oliv."*); Syd., Ust. 123 (*Ci. Car.*). – (On *C. praecox*) Const. & Negr., Herb. myc. rom. 2187 (*"A. car."*); Syd., Myc. march. 2624 (*"Ust. Car."*).

Swedish distribution

On *C. arenaria:* Coextensive with the host, common and mostly abundant. – Sk, Bl, Öl, Gtl, Vg, Srm, Upl.

On *C. ligerica:* Probably common and coextensive with the host, which is rare and has a very restricted area. – Bl, Öl, Gtl.

Zundel's (1953 p. 22) report of this species on *C. brizoides* is erroneous. *C. brizoides* is not a member of the Swedish flora. Savulescu (1957 p. 774) lists a Swedish specimen under the heading *brizoides,* but on the next page the host is correctly given as *C. echinata.*

Occurrence in the other Nordic countries

Denmark: Coextensive with *C. arenaria* and common (cf. Lind 1913 p. 263; O. Rostrup 1935 p. 26). Not observed on *C. ligerica.*

Finland: *C. arenaria* has a very restricted area in the extreme south. Four recent finds of the smut (Nyl; H, UPS!). Not known on the introduced *C. praecox.*

Norway: Some finds (Östf, Vestf, VAgd) on *C. arenaria.*

General distribution

Probably coextensive in Europe with its principal hosts. This is one of the few *Anthracoideae* that are common in the Central European lowlands. A single sample has been seen on *C. brizoides* ×*remota* (Germany, Rostock; Liro 1938 p. 275; UPS!) and one on *C. leporina* (Germany, Bavaria; Boidol & Poelt 1963 p. 18; M!) amongst infested *C. brizoides* (cf. above). – *C. arenaria* is introduced in North America but has not yet been found smutted there.

2. **Anthracoidea aspera** (Liro) Kukk.

Kukkonen, Ann. Bot. Soc. Vanamo 34:3 p. 73 (1963). – *Cintractia aspera* Liro, Mycoth. fenn. n. 41 (=Die Etiketten N:o 1–300 p. 15) (1934); Ann. Acad. Sci. Fenn. A:42 p. 18 (1938). – Typus: *Carex chordorrhiza;* Finland, Lapponia kemensis, Kittilä par., Sirkankylä 28.VII.1933 H. Roivainen & J. I. Liro (Liro, Mycoth. fenn. 41).

Cintractia scabra H. Syd., Ann. Myc. 33 p. 368 (1935). – Typus: *Carex chordorrhiza;* Sweden, Torne Lappmark, Kiruna, Ruopsok 8.VIII.1927 H. Smith (holotypus: Hb. Sydow S!; isotypi: Lundell & Nannf., F. exs. suec. ined.).

Cintractia glareosa Liro, Ann. Acad. Sci. Fenn. A:42 p. 22 (1938; diagn. german. tantum); Mycol. fenn., Die Etiketten N:o 301–600 p. 109 (1939). – Typus: *Carex glareosa;* Fennoscandia orientalis, Karelia keretina, Kantalaks, Pedosensk VII.1885 V. F. Brotherus (H!).

Spores subglobose–ellipsoid, usually slightly irregular or moderately angular, (15–)16–25

(–26) × 11–20(–22) µm (M = 17–20.5 µm long), slightly and irregularly flattened. Wall unevenly thickened, often with light-refractive spots in the thickest areas. Internal swellings 0–4, very variable in conspicuousness. Spines or warts of very different size, 0.1–1.0 µm high, tips rounded. Germination follows the pattern of subgen. *Anthracoidea* (fide Lehtola).

For detailed descriptions see Lehtola (1940 p. 74–81) and Kukkonen (1964 b p. 173, 1969 p. 271).

Matr.: (*Chordorrhizae*) *C. chordorrhiza*. – (*Paniculatae*) *C. appropinquata, diandra* fide Lehtola et Kukk. – (*Heleonastes*) *C. glareosa*.

C. glareosa does not take this smut in Greenland but *A. karii* instead, a fact which misled Savile (1952 p. 418) into regarding *Ci. glareosa* as a doubtful synonym of his *Ci. carpophila* var. *carpophila*. Liro's record (1938 p. 22) of *Ci. glareosa* from Greenland is based on E. Rostrup's (1888 p. 532) report of two finds of *U. caricis*. One (the Vahl specimen, C!) is *A. karii,* but the other is not to be found.

Exs.: (On *C. chordorrhiza*) Kari, F. exs. fenn. 103, 104; Liro, Myc. fenn. 41; Lundell & Nannf., F. exs. suec. 1554, 1555, ined.

Swedish distribution

On *C. appropinquata:* The only find (Kukkonen 1964 b p. 173; UPS!) consists of a single sorus (cf. above). – Gtl.

On *C. chordorrhiza:* In southern and central Sweden, perhaps restricted to the eastern parts. Increasing in frequency northwards. – Ög, Dlr, Hls, Jmt, LyL, LL, TL.

Occurrence in the other Nordic countries

Denmark: Unknown. *C. chordorrhiza,* the principal host, is very rare.

Finland: Known on *C. chordorrhiza* from all parts (Kukkonen 1964 b p. 174), evidently more common in the north. One find on *C. diandra* (Ob; Lehtola 1940 p. 79; doubtful, cf. above), one on *C. glareosa* from Fennoscandia orientalis (Kk; Liro 1938 p. 22).

Iceland: Unknown. Both *C. chordorrhiza* and *glareosa* are rather common.

Norway: Known on *C. chordorrhiza* from Akershus in the south to Troms in the north. One find on *C. glareosa* (Fnm; "prope Vadsöam" Deinboll; O!).

Spitzbergen: Not known. *C. glareosa* is a potential host.

General distribution

Liro (1938 p. 19) considered this smut (on *C. chordorrhiza*) to have a decidedly eastern distribution, being known from Russia and Siberia (cf. also Gutner 1941 p. 163) but not from Central Europe. The host, although almost circumpolar, is itself rather eastern in Europe (Hultén 1962 p. 94, map 85) and has become very rare in Central Europe. The smut is also known from North America (Alaska, British Columbia, Alberta, Ontario, Quebec) but there shows a greater morphological variability (Kukkonen 1964 b p. 174, cf. above). I have also seen a sample from Maine (K. K. Mackenzie 3194 Fung., S!).

Anthracoidea douglasii [Shear] Nannf. sp. nov. – Fig. 3 A, B

Ustilago Caricis [var.] *Douglasii* Shear var. nov. in Ell. & Ev., F. Columb. 1485 (1901; nom. nud.). – *Cintractia Caricis-Douglasii* Cif., Ann. Myc. 29 p. 43 (1931; nom. nud.). – Typus: *Carex douglasii;* U.S.A., Colorado, Gunnison 5.IX.1899 E. Bartholomew (Ell. & Ev., F. Columb. 1485; holotypus: S).

Sporae 16–27 × 14–20 µm (M = 21–22 µm longae), rotundatae vel raro paullum angulares. Paries 1.0–2.0 µm crassus, conspicue verrucosus, verrucis hemisphaericis, 0.2–0.3 µm altis, interdum binis confluentibus. Gibbera interna desunt.

Spores in plan view 16–27 × 14–20 µm (M = 21–22 µm long), subcircular–broadly elliptic, evenly rounded or subangular, moderately flattened (12–15 µm thick). Wall evenly thickened (1.0–2.0 µm thick), rather pale. Internal swellings not observed. Surface verrucose, warts 0.2–0.3 µm high, round or oblong, not infrequently confluent two and two, rather regularly spaced, forming no distinct pattern. Germination not studied.

Matr.: (*Divisae* fide Mack. vel *Douglasianae* fide Egorova) *C. douglasii* Boott.

Exs.: Ell. & Ev., F. Columb. 1485 (*"Ust. car. Dougl."*; typus); Ell. & Ev., N. Amer. F. 2259 (*"Ust. car."*); Griff., W. Amer. F. 209 (*"Ci. car."*), 209 a (*"Ci. car."*).

General distribution

May follow the host. Hitherto known from U.S.A. (Oregon, Nevada, Colorado) (Savile 1952 p. 427 as *Ci. limosa minor*).

Anthracoidea eleocharidis Kukk. – Fig. 3 F, H

Kukkonen, Trans. British Myc. Soc. 47 p. 274 (1964).

Spores in plan view 13–20(–21) × 11–15(–17) µm (M = 17–18 µm long), subcircular–elliptic, evenly rounded or slightly irregular, moderately flattened. Wall evenly thickened (1–1.5 µm). No internal swellings. Surface distinctly verrucose, warts up to 0.5 μm high, tips rounded. Germination follows the pattern of subgen. *Anthracoidea* (fide Kukkonen).

For full description and illustrations see Kukkonen 1964 a p. 274, 1964 b p. 172, 1969 p. 271.

Magnus (1895, 1896) found the mean spore length to be 15.7 μm in the collection studied (Bornmüller 1870), whereas I got M = 17.8 μm in the S copy of the same collection. My measurements were made in lactophenol and Magnus' certainly in water, which may explain the difference.

Matr.: (*Physodes*) *C. eleocharis* Bailey (type host), *stenophylla* Wg.

Exs.: 0.

General distribution

Known from Canada (Yukon) and U.S.A. (California) on *C. eleocharis* and from Central Asia (Iraq, Turkmenian S.S.R., Punjab, Kashmir) on *C. stenophylla* s.lat. Kukkonen (in litt. 11.V.1977) adds Turkey, Iran, and Afghanistan. The hosts belong to a widespread, almost circumpolar species complex, whose differentiation is still far from clarified (cf. e.g. Hultén 1962 p. 146, map 138, Raymond 1965 pp. 31–34, Egorova 1966 pp. 124–130). Although *C. stenophylla* s.str. is rather widely distributed in eastern and southeastern Europe, there are no European smut records.

3. **Anthracoidea fischeri** (Karst.) Kukk.

Kukkonen, Ann. Bot. Soc. Vanamo 34:3 p. 73 (1963).

For synonymy, detailed descriptions, illustrations, and exsiccata see Nannfeldt & Lindeberg (1957 pp. 516–519) and Kukkonen (1964 b pp. 170–171, 1969 p. 270).

Spores in plan view (13–)15–20(–22) × 10–18 μm (M = 16–18 μm long), circular–broadly elliptic and slightly flattened. Wall relatively thin with 1–5, mostly distinct internal swellings. Spines up to 1.0 μm high, rounded or slightly flattened apically. *Crotalia* state often present and conspicuous. Germination follows the pattern of subgen. *Anthracoidea* (fide Kukkonen).

Matr.: (*Heleonastes*) *C. ? arctaeformis* Mack. fide Kukk., *brunnescens* (& ×*canescens* ?), *canescens* (& ×*lachenalii* fide Liro & ×*lapponica* & ×*loliacea* & ×*mackenziei* & ×*tenuiflora*), *heleonastes*, *lapponica*, *mackenziei*, *tenuiflora*. – (*Stellulatae*) *C. ? interior* Bailey fide Kukk. – (*Paniculatae*) *C. cusickii* Mack. fide Kukk., *diandra*. – (*Vulpinae*) *C. vulpina*. – (*Holarrhenae*) *C. disticha*. – (*Ovales*) *C. bebbii* Olney fide Kukk.

Liro (1938 p. 528) listed *C. loliacea* as a host but Kukkonen (1964 b p. 171) found the sample to be *C. canescens* ×*loliacea*.

Swedish distribution

On *C. brunnescens:* The host grows almost all over Sweden except in the extreme south and becomes very common northwards. The single smut find is from the north. – Vb.

On *C. canescens:* Host common all over the country. The few smut finds only from the far north. Nevertheless a principal host? – Nb, LL, TL.

On *C. canescens* ×*lapponica:* One find on this little-known and certainly much overlooked hybrid. A neighbouring tuft had *A. karii*. – Nb (Överluleå par., Snödmossen 1929 O. R. Holmberg; UPS!).

On *C. canescens* ×*mackenziei:* The host is rather common in beach meadows wherever *C. mackenziei* grows. The smut is so far unknown from southern Sweden, where *C. mackenziei* is rare. – Gstr, Nb.

On *C. canescens* ×*tenuiflora:* One find only on this rather rare hybrid. – TL (Karesuando par., Karesvuopio 1929 E. Nordström; S!).

On *C. disticha:* The host is widespread in southern and central Sweden, but the smut is found only in the east. Certainly a principal host. – Ög, Upl, Gstr.

On *C. mackenziei:* Certainly much overlooked. The host is by far less conspicuous than its hybrid with *C. canescens*, and its culms wither early. Only two finds. – Gstr.

Occurrence in the other Nordic countries

Denmark: No finds. *C. canescens* and *C. disticha* are potential hosts.

Finland: Finds more numerous than in Sweden and on the whole concentrated to the north. *C. disticha* is found smutted only in the extreme south (Al, Ab) and *C. canescens* ×*mackenziei* has been found smutted from the north to Nylandia in the south. The known hosts are: *C. brunnescens* ×*canescens* (?), *canescens*, *c.* ×*lachenalii* (n.v.), *c.* ×*lapponica*, *c.* ×*loliacea*, *c.* ×*mackenziei*, *c.* ×*tenuiflora*, *diandra* (one find; Ob Tervola Loue 1961 Kukkonen 911; H, UPS!), *disticha*, *heleonastes*, *lapponica*, *mackenziei* (one find; Ab Painio 1969 Kukkonen; H, in litt. 11.V.1977), and *tenuiflora*. The then known finds were listed by Kukkonen (1964 b pp. 171–172).

The records by Liro (1938 pp. 20–22, 278–279, 528) are not all reliable, for he long considered that *C. canescens* and its hybrids were immune against *A. karii* (q.v.), *C. brunnescens* and its hybrids against *A. fischeri*, and in some cases he allowed the smuts to influence the determination of the host and vice versa.

Iceland: No finds. Potential hosts are *C. brunnescens*, *canescens*, and *mackenziei*.

Norway: Three finds only, on *C. canescens* (Hdm; O!) and on *C. canescens* ×*mackenziei* (Nrd, Trs; O!).

C. brunnescens, disticha, heleonastes, lapponica, and *tenuiflora* are further potential hosts.

General distribution

In striking contrast to the very wide host range of *A. fischeri* is its very limited geographical area. As pointed out previously (Nannfeldt & Lindeberg 1957 p. 517) the European distribution is decidedly northeastern. It is known on sect. *Heleonastes* only from Norway, Sweden and Finland (incl. Russian Fennoscandia) and on *C. disticha* only from Sweden and Finland. A morphologically indistinguishable smut on *C. vulpina* occurs in Latvia and a record of a small-spored smut (M = 13.5 × 10.3 μm) on the same host from eastern Germany (Brandenburg; Magnus 1895 p. 79, Jaap 1900 p. 262) also certainly belongs here, as also, probably, Eichler's report (sec. Kochman & Majewski 1973 p. 116) from Poland and Hruby's (1927 p. 156) from Czechoslovakia.

This species is also known from northwestern North America (Alaska, Distr. of Mackenzie, British Columbia) on *Heleonastes* (*C. canescens*) (Kukkonen 1964 b pp. 170–172). Morphologically indistinguishable smuts, on sects. *Ovales, Paniculatae,* and *Stellulatae* are also reported from northwestern North America (British Columbia) by Kukkonen (1964 b).

4. **Anthracoidea karii** (Liro) Nannf. comb. nov. – Fig. 2 A, B, D, G

Cintractia Karii Liro, Mycoth. fenn. n. 106 (=Die Etiketten N:o 1–300 p. 36) (1934); Ann. Acad. Sci. Fenn. A:42 p. 31 (1938). – Typus: *Carex brunnescens;* Finland, Lapponia enontekiensis, Enontekiö par., Vuontisjärvi, Peltovuoma 24.VII.1933 H. Roivainen & J. I. Liro (Liro, Myc. fenn. 106).

Cintractia Caricis-dioicae Lehtola, Acta Agral. Fenn. 42 p. 85 (1940). – Typus: *C. dioica;* Finland, no special collection designated.

Ustilago Vigneae Fuss b. *V. stellulatae* Fuss, Arch. Ver. Siebenbürg. Landeskunde N.F. 14 p. 446 (1878; nom. nud.).

Spores in plan view 13–21 × 9–19 μm (M = 16–18.5 μm long), subcircular–broadly elliptic, mostly very evenly rounded, only exceptionally slightly angular, strongly flattened (12–14 μm thick). Wall evenly thickened (up to 2 μm). Internal swellings 2–3, mostly distinct. Surface ranges from almost smooth to finely verruculose, warts up to 0.1 μm high, rounded, somewhat irregularly spaced but not forming a distinct pattern and not affecting the spore profile. Germination follows the pattern of subgen. *Anthracoidea* (fide Lehtola).

Matr.: (*Dioicae*) *C. davalliana, dioica, gynocrates* Wormskj., *parallela.* – (*Dioicae* × *Foetidae*) *C. dioica* × *maritima.* – (*Dioicae* × *Heleonastes*) *C. dioica* × *brunnescens* fide Liro & × *canescens* & × *heleonastes* & × *lachenalii* & × *tenuiflora, gynocrates* × ? *tenuiflora* fide Savile. – (*Dioicae* × *Stellulatae*) *C. dioica* × *echinata.* – (*Dispermae*) *C. disperma.* – (*Heleonastes*) *C. brunnescens* (& × *canescens* & × *lachenalii* & × *loliacea* & × *tenuiflora*), *canescens* (& × *heleonastes* & × *lachenalii* & × *lapponica* & × *loliacea* & × *tenuiflora*), *glareosa* (incl. *C. marina* Dewey), *heleonastes, lachenalii, lapponica, loliacea* fide Liro, *tenuiflora, trisperma* Dewey, *ursina* Dewey fide Fischer. – (*Stellulatae*) *C. angustior* Mack. fide Savile, *cephalantha* (Bailey) Bicknell fide Savile, *echinata, interior* Bailey fide Savile.

The four finds on *C. brunnescens* × *dioica* listed by Liro (1938 p. 32) may be either this species or *A. turfosa,* which has been seen on this hybrid from Norway, and the hosts may be hybrids with either *C. brunnescens* or *C. canescens* (cf. above under *A. fischeri*).

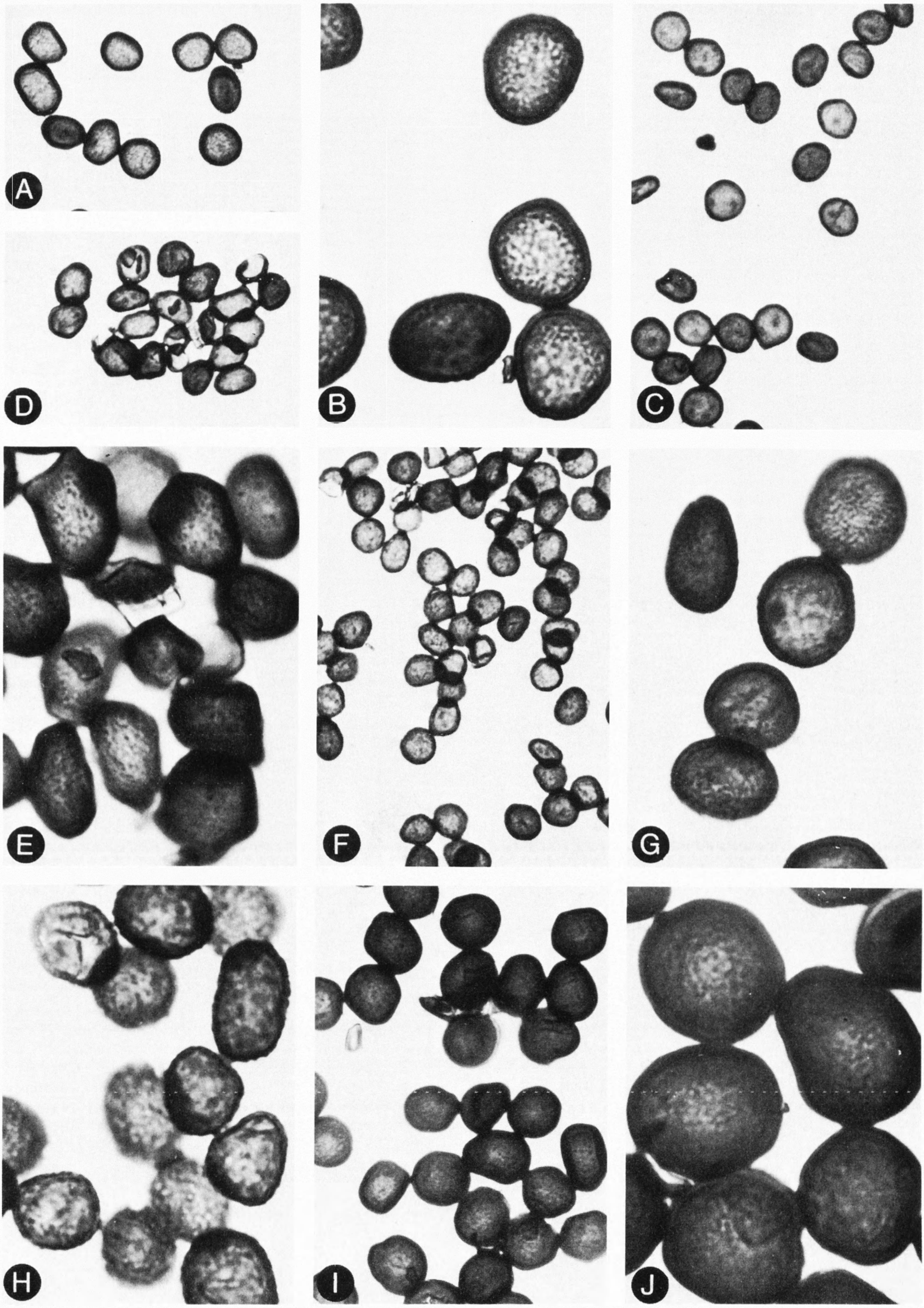
Exs.: (On *C. brunnescens*) Kari, F. exs. fenn. 277, 278; Liro, Myc. fenn. 106; Lundell & Nannf., F. exs. suec. 1571, 1572, 2761; Syd., Ust. 313 ("*Ust. Car.*" on "*C. can.*"); Vgr., M. rar. sel. 449 b ("*Ci. Car.*"). – (On *C. canescens*) Kari, F. exs. fenn. 221; Liro, Myc. fenn. 769 ("*Ci. Fisch.*"). – (On *C. canescens* × *loliacea*) Samuelss., Pl. Suec. exs. 364 Fung. – (On *C. canescens* × *tenuiflora*) Samuelss., Pl. Suec. exs. 367 Fung. – (On *C. cephalantha*) Seym. & Earle, Econ. F., Suppl. C5 (n.v.). – (On *C. dioica*) Lundell & Nannf., F. exs. suec. 645 b ("*Ci. turf.*", later changed into "*Ci. Car.-dioicae*"), 1568, 1569 (both as "*Ci. Car.-d.*"), 2762. – (On *C. echinata*) Kari, F. exs. fenn. 105, 106, 276 a, 276 b (all as "*Ci. leiod.*"); Linh., F. hung. 302 ("*Ust. Car.*"); Liro, Myc. fenn. 153 ("*Ci. leiod.*"); Lundell & Nannf., F. exs. suec. 1573, 1574 (both as "*Ci. leiod.*"); Schneid., Herb. Schles. P. 183 (n.v.); Ust. Jugosl. 60 ("*Ci. baccata*"); Zillig, Ust. eur. 124 ("*Ci. Car.*"). – (On *C. lachenalii*) Liro, Myc. fenn. 763 ("*Ci. Car.*"); Lundell & Nannf., F. exs. suec. 2763, 2764. – (On *C. lapponica*) Lundell & Nannf., F. exs. suec. ined.

Swedish distribution

On *C. brunnescens:* So far unknown in the south, common towards the north. Evidently a principal host. – Hrj, Jmt, Nb, LyL, PL, LL, TL.

On *C. brunnescens* × *canescens* (nov. matr.): Two finds from one locality on this very rare (or at least much overlooked) hybrid. – TL (Kiruna, Vittangi 1928, 1929 O. R. Holmberg; LD!, UPS!).

Fig. 3. Spores of *Anthracoidea* species. – A, B: *A. douglasii* (typus). – C, G: *A. verrucosa* (Savile 28 248). – D, E: *A. vankyi* (typus). – F, H: *A. eleocharidis* (Turkmenistan, Melnik; UPS). – I, J: *A. turfosa* (typus). – A, C, D, F, I c. 400 ×; B, E, G, H, J c. 1100 ×.


A
D
B
C
E
F
G
H
I
J

On *C. brunnescens* ×*lachenalii:* This hybrid and the very similar *C. canescens* ×*lachenalii* are common in the north. The present author has made no attempt to check the determinations. – Jmt, LL, TL. (Liro (1938 p. 278) lists an additional collection (from TL) by O. R. Holmberg, because he considered the attack by *A. karii* as a proof that Holmberg's determination of the host as *C. canescens* ×*lachenalii* was incorrect.)

On *C. brunnescens* ×*loliacea:* This hybrid is not so rare. – Hrj, LL, TL.

On *C. brunnescens* ×*tenuiflora:* Only one find on this very rare hybrid. – TL (Kiruna, Perkosvuoma 1935 C. G. Alm 418 Fung; LD!. Together with smutted *C. canescens* ×*tenuiflora.*).

On *C. canescens:* The host is very common all over Sweden. The smut is found only in the north and very rarely even there. – Vb, LL, TL.

On *C. canescens* ×*dioica:* This hybrid occurs throughout the country but is found smutted only towards the north. – Dlr, Hrj, Jmt, LL.

On *C. canescens* ×*heleonastes* (nov. matr.): Only one find on this very rare hybrid. – TL (Kiruna, Ö. Soppero Pereojavuoma 1928 O. R. Holmberg; UPS!).

On *C. canescens* ×*lachenalii:* Probably rather common on this hybrid, which is not infrequent (as on the very similar *C. brunnescens* ×*lachenalii,* q.v.). – Hrj, LyL, TL.

On *C. canescens* ×*lapponica* (nov. matr.): Two finds on this rare and little-known hybrid. – Nb (see *A. fischeri*), TL (Karesuando 1928 O. R. Holmberg; LD!, a single sorus).

On *C. canescens* ×*loliacea:* This hybrid is known from Central and North Sweden but has been found smutted only in the north. – PL, TL.

On *C. canescens* ×*tenuiflora:* This rare hybrid, restricted to North Sweden, seems to take this smut rather often. Cf. Liro (1938 p. 279). – LL, TL.

On *C. dioica:* The host grows all over the country, but this smut has not been found in the southern provinces and increases in frequency and abundance towards the north. *C. dioica* is evidently a principal host, but *A. karii* is less common than *A. turfosa* on it. – Srm, Upl, Vstm, Dlr, Hls, Hrj, Jmt, Vb, Nb, LyL, PL, LL, TL.

On *C. dioica* ×*echinata* (nov. matr.): This hybrid is extremely rare in Sweden, although the parent species are widely distributed. The smut has only been found in one locality, but there repeatedly. – Hrj (Tännäs par., Fjällnäs 1934, 1935, 1936 O. Östergren; 1946 B. Borgström; all UPS!).

On *C. dioica* ×*tenuiflora* (nov. matr.): Only a single tuft of this hybrid is so far known (Holmberg 1929 a p. 6; 1929 b p. 28; Hylander 1966 p. 68) and this (as well as adjacent tufts of *C. canescens* ×*tenuiflora*) bore this smut. – TL (Kiruna, Perkosvuoma 1928 C. G. Alm & O. R. Holmberg; LD!, S!, UPS).

On *C. echinata:* Evidently coextensive with its host and one of the few *Anthracoideae* which also occurs in the southern provinces but increasing in frequency northwards as far as the host grows. A principal host. – Sk, Hl, Sm, Ög, Vg, Bh, Srm, Upl, Vstm, Nrk, Dlr, Hls, Hrj, Jmt, Mpd, Vb, Nb, LyL.

On *C. lachenalii:* Probably coextensive with its host. – Hrj, LyL, LL, TL.

On *C. lapponica* (nov. matr.): This long-neglected host species occupies a very restricted area in the north (Hultén 1971 map 350). Only one Swedish find of this smut. – TL (Kiruna, Valkikurkkio 1959 E. Julin; UPS!).

On *C. parallela:* Probably coextensive with its host but rarer than *A. turfosa.* – TL.

On *C. tenuiflora* (nov. matr.): Only one poor sample. – Nb (Tärendö par. at the Tärendö River c. 3 km N of the parish church 1959 C. G. Alm; UPS!).

Liro (1938 p. 32) records a find on *C. brunnescens* × *dioica* (LL, leg. Wichura). This sample has not been seen, and may be the same as that cited (1938 p. 36) as *Ci. turfosa* on *C. canescens* ×*dioica,* which could not be found either.

Distribution in the other Nordic countries

Denmark: Known only on *C. echinata* (cf. Lind 1913 p. 263). Two other potential hosts are *C. canescens* and *dioica.*

The Færoes: Known on *C. echinata* (cf. Möller 1945 p. 71). Only one other potential host, viz. *C. dioica.*

Finland: Reported by Liro (1938 pp. 31–32, 278–279, 530) as *Ci. karii* on *C. brunnescens* (and its hybrids with *dioica, lachenalii,* and *loliacea*), *canescens,* and *loliacea;* as *Ci. leioderma* (1938 pp. 26, 275–276, 529) on *C. echinata* (numerous additions in Lehtola 1940), and as *Ci. caricis* (Liro 1938 pp. 8, 526) on *C. lachenalii.* The first certain finds on *C. dioica* were reported by Lehtola (1940), who was the first to make a distinction between the two smuts on *Dioicae.* To the above hosts can now be added: *C. heleonastes* (nov. matr.; Lk: Muonio 9.VII.1914 J. Montell; LD!), *parallela* (Le, a single find, compared with nearly 20 of *A. turfosa*), and the following hybrids: *C. canescens* × *dioica, c.* ×*lachenalii, c.* ×*lapponica* (Lk), *c.* ×*loliacea* (Lk, Le), *c.* ×*tenuiflora* (Li), *dioica* ×*heleonastes* (nov. matr.; Lk: Muonio Lompolovuoma 7.VII.1921 J. Montell; H!). As in Sweden the smut becomes less frequent towards the south.

Iceland: Seen only on *C. echinata* (cf. Larsen 1932 p. 516). Potential hosts are *C. brunnescens, canescens, dioica, glareosa,* and *lachenalii.*

Norway: Seen on *C. brunnescens* (AAgd–Fnm), *canescens* (Trs), *dioica* (Hdm–Fnm), *echinata* (common to Nrd in the north), *lachenalii* (Trs, Fnm), *lapponica* (Trs), and *parallela* (STrd, Trs) as well as on the following hybrids: *C. brunnescens* ×*lachenalii* (Hdm, Busk, STrd), *br.* ×*loliacea* (Trs), *canescens* × *dioica* (Hdm, STrd), *c.* ×*lachenalii* (Busk, Hrd, Opl, STrd, Nrd, Trs, Fnm), *dioica* ×*lachenalii* (nov. matr.; STrd: Oppdal, Sandådal in Storlidalen 1940 J. Haugen, O!, and Trs: Storfjord between Lulle and Fawresvarre 1937 P. Benum, O!), and *d.* ×*maritima* (STrd; Liro 1938 p. 242 as "*Ci. turfosa* kleinsporige Form"; UPS!). Also in Norway the smut decreases in frequency southwards. Potential hosts are *C. glareosa, heleonastes, loliacea, tenuiflora,* and several hybrids.

Spitzbergen: Not known. *C. glareosa, lachenalii,* and *parallela* are potential hosts.

General distribution

The host spectrum of this smut is wide, several of the hosts are widely distributed, as is the smut itself, but as far as Europe is concerned it seems to be rare in or absent from large parts of the lowlands. It is most frequently collected and reported on *C. echinata* (Scotland, France, Germany, Latvia, Poland, Switzerland, Austria, Czechoslovakia, Hungary, Romania etc.). I have seen it on *C. brunnescens* from Switzerland and Austria (Tirol). Liro (1938 p. 278) reports it from Italy, and Schellenberg's report (1911 p. 75) of a Swiss smut on *C. canescens* probably refers to *A. karii* on mis-identified *C. brunnescens*. There are several finds on *C. davalliana*. There are very few records of smutted *C. dioica* and since no material has been available, no decision can be made whether the smut is *A. karii* or *A. turfosa*.

In North America the conditions in the north seem to be much the same as in northern Europe. Thus *A. karii* is known from Greenland on *C. brunnescens, br.* ×*lachenalii, canescens* ×*lachenalii, glareosa, lachenalii, parallela,* and *ursina;* and from Alaska on *C. brunnescens, canescens, disperma, gynocrates, g.* ×*tenuiflora* (?), *lachenalii,* and *loliacea*. As in Europe the smut becomes less frequent southwards and its host range narrower. It just extends into the United States but only on a restricted number of hosts, e.g. on *C. angustior* (New Haven, Vermont), *brunnescens* (Vermont), *cephalantha* (Vermont), *interior* (Maine), and *trisperma* (Michigan; Povah 1935 p. 153).

5. **Anthracoidea turfosa** (H. Syd.) Kukk.
– Fig. 3 I, J

Kukkonen, Ann. Bot. Soc. Vanamo 34: 3 p. 24 (1963). – *Cintractia turfosa* H. Syd., Ann. Myc. 22 p. 289 (1924). – *Anthracoidea turfosa* Kochm. & Maj., Grzyby (Mycota) 5 p. 118 (1973). – Typus: *Carex dioica;* Norway, Finnmark, Alta Kåfjord VII.1895 G. Lagerheim (Syd., Ust. 75).

Spores in plan view (15–)17–26(–28) × (11–)13–22 (–25) µm (M = 22–24 µm long), rounded, broadly elliptic or rarely slightly irregular and angular, flattened (12–15 µm thick). Wall evenly thickened, dark, c. 2.5 µm thick. Internal swellings 1–2(–3), low, only rarely visible. Surface ranges from almost smooth to minutely verruculose; warts only 0.1 µm high or less, rounded or slightly elongate, occasionally confluent, somewhat irregularly spaced, but not forming a distinct pattern and hardly affecting the spore profile. Germination follows the *Proceres* scheme (fide Lehtola).

See Lehtola (1940 pp. 81–86).

Matr.: (*Dioicae*) *C. dioica* (& ×*parallela*), *exilis* Dewey, *gynocrates* Wormskj. fide Savile, *parallela*. – (*Dioicae* ×*Foetidae*) *C. dioica* ×*maritima*. – (*Dioicae* ×*Heleonastes*) *C. dioica* ×*brunnescens* & ×*canescens* & ×*heleonastes* & ×*lachenalii, parallela* ×*lachenalii*. – (*Heleonastes*) *C. heleonastes*.

The "kleinsporige Form" on *C. dioica* ×*maritima* mentioned by Liro (1938 pp. 17, 24) is *A. karii* (q.v.).

Boidol & Poelt (1963) cite *C. davalliana* and – with some doubts – also *C. baldensis* and *curvula* as hosts. Their *davalliana* sample (M!) shows typical *A. karii*. *C. baldensis* and *curvula* should be removed from *Vignea* (see above), and their smuts are specifically distinct. That found on *C. curvula* is close to *A. lindebergiae* (Kukk.) Kukkonen (1963 p. 63).

Exs.: (On *C. dioica*) Kari, F. exs. fenn. 101, 102; Krypt. exs. Vindob. 4504; Liro, Myc. fenn. 31, 779; Lundell & Nannf., F. exs. suec. 645 a; Syd., Ust. 75. [Non: Lundell & Nannf., F. exs. suec. 645 b (*"Ci. turf."*, corr. *"Ci. car.-d."*) q.e. *A. karii*.] – (On *C. parallela*) Krypt. exs. Vindob. 4402.

Swedish distribution

On *C. canescens* ×*dioica:* Restricted to the northern parts. – Hls, Ång, Vb, TL.

On *C. dioica:* Evidently coextensive with its host, commoner than *A. karii,* but likewise increasing in frequency and abundance towards the north. – Sm, Gtl, Vg, Bh, Srm, Upl, Vrm, Dlr, Hls, Hrj, Jmt, Ång, Nb, ÅsL, LyL, LL, TL.

On *C. dioica* ×*heleonastes:* Rare hybrid. – Hrj, TL (3 finds in all; cf. Liro 1938 p. 242).

On *C. dioica* ×*parallela* (nov. matr.): One find on this rare and little-known hybrid. – ÅsL (Vilhelmina par., Ransarluspen 1946 O. Rune 76 Fung.; S!, UPS!).

On *C. heleonastes:* A single sorus together with heavily infected *C. dioica* and with infected *C. d.* × *heleonastes* in the vicinty. – Hrj (Tännäs par., V. Malmagen 1933 J.A.N. 4664: UPS!; cf. Liro 1938 p. 242).

On *C. lachenalii* ×*parallela:* – TL (2 finds).

On *C. parallela:* coextensive with its host and much commoner than *A. karii*. – LyL, LL, TL.

Occurrence in the other Nordic countries

Denmark: No finds. *C. dioica* is a potential host.

The Færoes: Ditto.

Finland: As Liro (1938) did not distinguish between the two smuts on *Dioicae* all his records need to be re-examined. Lehtola (1940) found *A. turfosa* to be more common than *A. karii* and to be scattered all over the country. It is also common on *C. parallela*. I have seen it (in H) on the following hybrids, viz. *C. canescens* ×*dioica* (Lk), *dioica* ×*parallela* (Le, one find), and *lachenalii* ×*parallela* (Le).

The record (Liro 1938 p. 35) on *C. dioica* ×*heleonastes* is erroneous. The spores are immature but nevertheless the smut can be identified as *A. karii*.

Iceland: Some finds on *C. dioica*.

Norway: As in Sweden coextensive with *C. dioica* and *parallela*, commoner than *A. karii* and increasing in frequency and abundance towards the north. Seen also on the following hybrids: *C. brunnescens* × *dioica* (nov. matr.; Tel: Tinn, the Selstali fens 1933 J. Lid; O!), *canescens* × *dioica* (Oslo; Aurtjern at Ödegård (c. 1/2 km S of Nöklevatn) M. N. Blytt; O!), *dioica* × *lachenalii* (nov. matr.; Opl: Dovre, Midthö (at Vålåsjö) 980 m s. m. 1950 J. Lid; O!), and *dioica* × *maritima* (nov. matr.; Nrd: Narvik, Fagernes 1909 L. Trafvenfelt; UPS!).

Spitzbergen: No finds. *C. parallela* is a potential host.

General distribution

The host range of *A. turfosa* is rather narrow, as is its distribution. Apparently it does not follow its hosts everywhere, but is restricted to the northern regions. No finds are known from continental Europe, but it is uncertain whether some finds of smutted *C. davalliana* and *dioica* belong here and not to *A. karii* (q.v.).

In North America it is known on *C. gynocrates* (Quebec; Savile 1952 p. 426 as *Ci. limosa* var. *limosa*) and *exilis* (Quebec; Savile 1952 p. 427 as *Ci. pratensis;* Labrador, H!; and Nova Scotia fide Kukkonen in litt. 11.V.1977), but it is an open question whether other records on *C. exilis* belong here or perhaps to *A. karii*.

Anthracoidea vankyi Nannf. sp. nov. – Fig. 3 D, E

Typus: *Carex pairae;* Romania, Transilvania, in alpibus Csíki-havasok (M. Ciucului), mons Öcsém 1630 m s.m. 12.VII.1962 K. Vanky (holotypus: UPS, isotypus: Hb. Vanky).

Sporae 15–23(–26) × 12–20 μm (M = 18–21.5 μm longae), angulatae vel irregulares, elongatae, rarius ± isodiametricae. Paries valde inaequalis, 1.5–4 μm crassus, areolis crassissimis interdum ut loci lucem repercutientes apparentibus, verruculis c. 0.2 μm altis.

Spores 15–23(–26) × 12–20 μm (M = 18–21.5 μm long), angular–irregular, slightly and irregularly flattened, in plan view rarely ± isodiametric, mostly elongated, sometimes subtriangular or even subcordate, sometimes ± apiculate at one end. Wall of very uneven thickness (1.5–4 μm), often with light-refractive spots in the thickest areas. Internal swellings not observed. Surface distinctly verruculose, warts c. 0.2 μm high. *Crotalia* state not observed. Germination not studied.

Matr.: (*Muhlenbergianae*) *C. muricata* sensu lato, i.e. *divulsa, pairae,* and *spicata* (=*contigua* Hoppe). (No attempts have been made to revise the host determinations.)

Exs.: 0.

Additional specimens

France: Dép^t Alpes-Maritimes, Fontan in the Roja Valley 435 m (*C. divulsa*) 1963 F. Oberwinkler 4801 (M!). – Switzerland: K^t Wallis, Saas-Fee (*C. pairae* det. W. Koch) 1945 E. Mayor (ZT!); Zermatt 1876 Körnicke (H fide Kukkonen in litt. 11.V.1977); Zermatt-Zmutt (*C. pairae,* det. W. Koch) 1934 E. Gäumann (ZT!). – Italy: Trento, Rhaetian Alps, "Veltlin, unmittelbar nördlich Tirano, an der Strasse nach Pra Campo" 460–520 m s. m. (*C. divulsa*) 1965 W. Dietrich, E. Mayr, H. Hertel 5079 (M!). – Romania: Montibus Bîrsei, Poiana Brasov (*C. divulsa* ssp. *chabertii*) 1967 P. Olaru & M. Danciu (LD!, S!).

General distribution

So far, specimens have been seen from the Alps and Transilvania. The "*muricata*" smut recorded from France (Dép^t Hautes-Alpes; Massenot 1953 p. 404) and Poland (Walbrzych; Kochman & Majewski 1973 pp. 115–116), according to description and illustrations, exactly matches *A. vankyi.* Provided that the host determinations are correct other European records of "*muricata*" smut also certainly belong here, e.g. those from various parts of Switzerland by Körnicke (1877 p. 39), Boudier & Fischer (1894 p. CCXL), Schellenberg (1911 p. 75), Cruchet & Mayor (1918 p. 63), and Blumer (1946 p. 68), from Spain (Sierra Nevada) by Maire (sec. Massenot 1953 p. 404), from Germany (Leipzig) by Savulescu (1957 p. 788), from the Netherlands (Maastricht) by Oudemans (1893 p. 598). No finds from northern Europe. The identity of the smut on the North American *C. occidentalis* Bailey is unknown.

Anthracoidea verrucosa (Savile) Nannf. stat. nov. – Fig. 3 C, G

Cintractia carpophila (Schum.) Liro var. *verrucosa* Savile, Can. J. Bot. 30 p. 420 (1952). – Typus: *Carex ebenea;* U.S.A., Wyoming, Medicine Bow Mts, L. Marie 21.VIII.1941 W. G. Solheim 2009 (Myc. Saximont. exs. 439; n.v.).

Spores in plan view 14–23 × 13–17 μm (M = 18.5–20 μm), subcircular–broadly elliptic, regularly rounded, only exceptionally slightly angular, strongly flattened (9–12 μm thick). Wall thin (c. 1 μm), evenly thickened and rather pale, often with 1–3 internal swellings. Surface distinctly verrucose, warts rounded, rather evenly spaced, up to 0.3 μm high, distinctly visible in profile. Germination not studied.

Calculated from Ciferri's (1931 p. 48) measurements the mean spore length of Syd., Ust. 314, is only 16.6 μm, whereas I got M = 18.6 and 19.7 μm respectively, from two slides of the same collection. Ciferri probably measured the spores in water, and I – as always – in lactophenol, which may explain the difference.

Matr.: (*Ovales*) *C. ebenea* Rydb., ?*festivella* Mack., *macloviana* (incl. ssp. *pachystachya* (Cham.) Hult.), and according to Kukkonen (in litt. 11.V.1977) ? *illota* L. H. Bailey, *phaeocephala* Piper, *preslii* Steudel, *subfusca* W. Boott, and (*Bracteosae*) *C. hoodii* Boott.

Exs.: Myc. Saximont. exs. 439 (*C. ebenea;* typus; n.v.); Syd., Ust. 314 (*C. "festivella"; "Ci. car."*).

General distribution

To the known North American distribution (Alaska, British Columbia, Wyoming) southeastern Greenland can now be added (Akorninarmiut, "Dronning Marias Dal" 1931 B. Björlykke, O!, and 1932 J. Devold & P. F. Scholander, O!; Umanak Innfjorden 1932 J. Devold, O!) on *C. macloviana*. These finds have been published as *Ci. caricis* by Hagen (1947 p. 284; cf. Savile 1952 p. 420). Smutted *C. macloviana* is not reported from Europe.

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Garuleum subgen. Rutidocarpaea, a monotypic subgenus showing achene dimorphism

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Norlindh, T. 1977 12 30: Garuleum subgen. Rutidocarpaea, a monotypic subgenus showing achene dimorphism. *Bot. Notiser 130:* 377–380. Stockholm. ISSN 0006-8195.

Garuleum bipinnatum (Thunb.) Less., conspecific with *Dimorphotheca multifida* DC., is described and illustrated. Style characters show that the species belongs to *Garuleum;* it deviates, however, in having outer disc florets which are capable of producing well-developed achenes similar to those of *Dimorphotheca.* The latter condition may be the original one in *Garuleum.* The pollen morphology also deviates from that of the type species of *Garuleum.* The species is referred to a monotypic subgenus, *Garuleum* subgen. *Rutidocarpaea* (DC.) T. Norl. comb. nov. (basionym *Dimorphotheca* sect. *Rutidocarpaea* DC.).

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The genus *Garuleum* Cass. belongs to the Compositae–Calenduleae. It occurs in South and Southwest Africa and comprises only eight species. In his treatment of *Garuleum,* De Candolle (1836) also included *G. bipinnatum,* which was first collected by Thunberg in the Hantam ("Hantum") Mountains of Calvinia District, described by him as *Osteospermum bipinnatum* (Thunberg 1800, 1823) and transferred to *Garuleum* by Lessing (1832).

When publishing his new species *Dimorphotheca multifida* in 1838, De Candolle obviously failed to compare it with the very similar collections which he had determined about two years earlier as *Garuleum bipinnatum;* otherwise he would certainly have discovered that they were identical. By adding a question-mark, De Candolle indicated his doubts as to whether or not the species really belonged to *Dimorphotheca.* He established the section *Rutidocarpaea* to accommodate this species and noted that it resembled *Dimorphotheca* because the achenes of the disc florets were "plano-compressis", but that the disc florets were sterile.

A closer investigation showed that this taxon does not belong to *Dimorphotheca;* style characters determine its position in *Garuleum.* However, within *Garuleum* the species is unique in having disc florets which produce achenes with ripe seeds. Furthermore, it differs from the type of *Garuleum* (*G. pinnatifidum* (L'Hérit.) DC.) in that its pollen grains lack horizontal tectal areas and have a greater number of spines which are more closely set, etc. (Fig. 2; Praglowski unpubl.). In my opinion *G. bipinnatum* should be referred to a subgenus of its own and I have chosen to retain De Candolle's name, *Rutidocarpaea,* which thus has to be transferred to *Garuleum:*

Garuleum subgenus **Rutidocarpaea** (DC.) T. Norl. comb. nov.

Dimorphotheca sect. *Rutidocarpaea* De Candolle 1838 p. 72. – Typus: *Dimorphotheca multifida* DC. (= *Garuleum bipinnatum* (Thunb.) Less.)

Differt a subgenere *Garuleo:* floribus disci hermaphroditis fertilibus, achaeniis disci exterioribus semen includentibus illis *Dimorphothecae* similibus (floribus interioribus non fructificantibus).

The genus *Garuleum* merits further investigation, which should include pollen morphology;

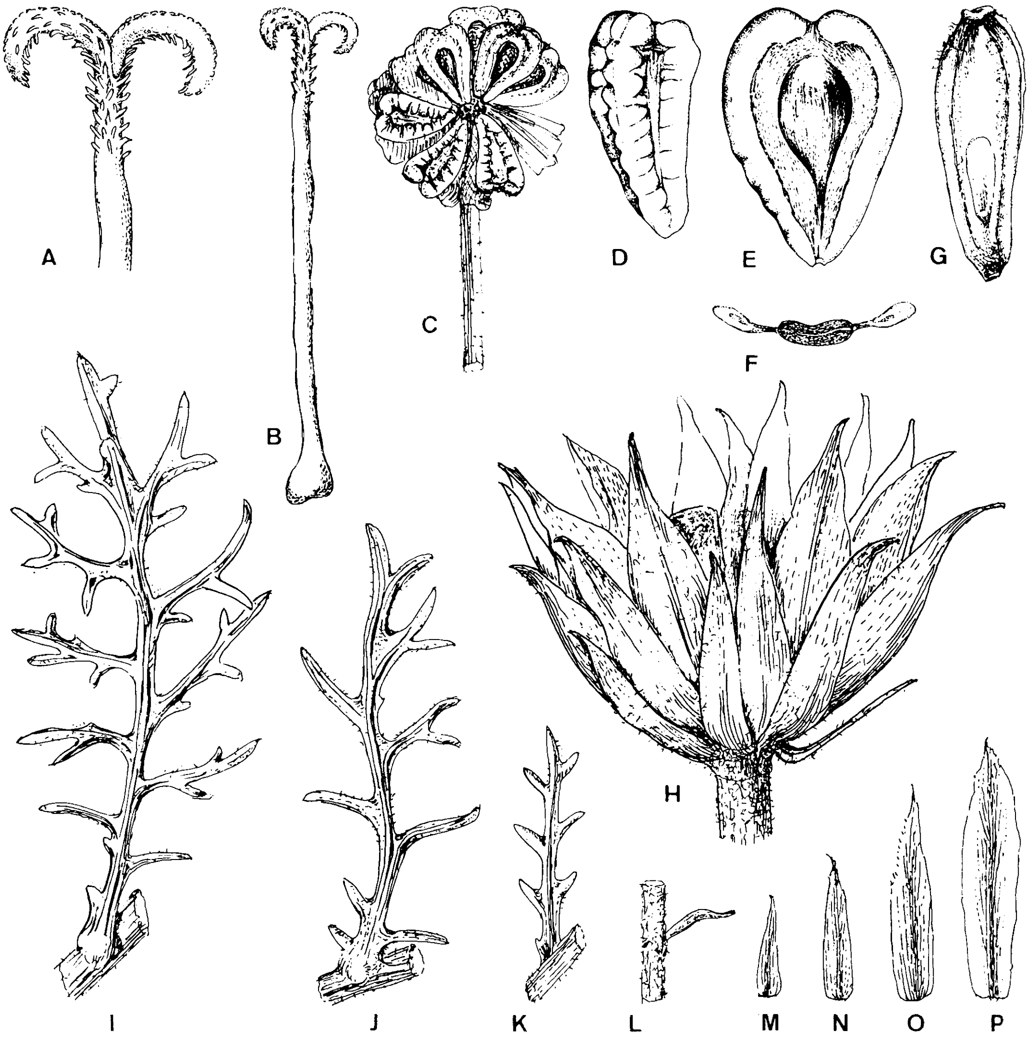

Fig. 1. *Garuleum bipinnatum*. – A: Upper part of style of disc floret, ×28. – B: Style of disc floret; note the bulbous base. ×14. – C: Capitulum with mature achenes of ray and disc florets, ×2. – D: Achene of ray floret, ×6.5. – E: Achene of outer disc floret with a well developed seed, ×6.5. – F: Cross section of achene of disc floret; the 14 years-old seed was somewhat shrivelled but still contained viscous oil, ×6.5. – G: Achene of inner disc floret with an abortive seed in the ovary, ×6.5. – H: Involucre; the achenes have fallen off. ×5.5. – I–K: Leaves from lower, middle and upper part of stem, ×3.5. – L: Part of peduncle with bract, ×3.5. – M–P: Series of involucral scales; M outermost, P innermost, ×5.5. – A, B: Wall s.n., Albany Distr., Committees Drift, 8.VIII.1938 (S). – C–G, M–P: Norlindh 5683, Albany Distr., Great Fish River Valley, 6.X.1963 (S). – H–L: Thunberg 20814, Calvinia Distr., Hantam Mountains, XI–XII.1774 (UPS).

this will probably result in the recognition of several sections.

Garuleum bipinnatum (Thunb.) Less. – Fig. 1,2

Lessing 1832 p. 194; De Candolle 1836 p. 309; Harvey 1865 p. 92; Marloth 1932 p. 243.

Osteospermum bipinnatum Thunberg 1800 p. 167 et ed. Schultes 1823 p. 717; Juel 1918 p. 717. – Holotype: Thunberg Herb. No. 20814, Calvinia "in Hantum" (UPS).

Dimorphotheca multifida De Candolle 1838 p. 73; Harvey 1865 p. 422. – Orig. coll.: Ecklon & Zeyher, Albany (G-DC No. 413 lectotype).

Perennial herb or subshrub, aromatic, viscid, with scattered short-stalked glands, up to 1.5 m tall. *Stems* arising from a woody rootstock up to 3 cm in diam., erect or ascendent, usually branched; stems and branches terete, striate or slightly furrowed, glabrous, in lower parts ± lignescent and covered by a brown-grey bark and remnants of leaf-sheaths, 1.5–3(–4) mm thick; internodes (except basal ones) 0.5–3 cm long. *Leaves* alternate, glabrous, 1–4 cm long, bipinnatipartite as well as pinnate, with lobes linear, subulate; primary lobes 3–6 on each side, up to 10 mm long; leaves decreasing in size and degree of lobation towards the inflorescence. *Capitula* solitary at the ends of stem and branches or more often arranged in loose corymbs; peduncles varying greatly in length, up to 12 cm, provided with few-dentate or entire bracts and upwards often densely covered with short-stalked glands. *Involucre* hemispheric, 5–8 mm high; scales imbricate, ± glandular (-puberulous) on the back, acuminate, 2–3-seriate, outer ones narrowly lanceolate, c. 3–4 mm long, innermost ones narrowly oblong-lanceolate, 5–6 mm long, with whitish-scarious margins and often violet tips. *Ray florets* (15–)20–25; ligule variously coloured, yellow, white (in two collections), blue, mauve, purple, violet etc., about twice as long as the involucre. *Disc florets* c. 60, yellow, about equalling the involucre; style branches provided with more or less distinct stigmatic papillae along margins. *Achenes* of ray florets glabrous, compressed triangular-obpyramidate, with angles partly entire, partly crenate, and sides irregularly cross-furrowed, truncate at apex, 4–5 mm long. Achenes of disc florets glabrous; outer ones surrounded by a wing with stiff, thickened margin, obovate and slightly emarginate at the tip or almost obcordate, c. 5 mm long and c. 3.5 mm broad; inner, sterile ones thin, pellucid, narrowly obovate, 5–6 mm long and c. 2 mm broad.

Garuleum bipinnatum is a xerophilic plant confined to the Cape Province, where it occurs mainly in the Karroo region. Some sixty herbarium specimens have been studied. Specimens having well-developed seeds, or nearly so, in the achenes of the outer disc florets are known from the following districts: Albany, Graaff Reinet, Laingsburg, Murraysburg and Oudtshoorn.

When visiting the Great Fish River Valley in 1963 I encountered specimens which agreed with De Candolle's *D. multifida,* except for the fact that the achenes of the outer disc florets contained well developed seeds. The specimens (Norlindh 5683) grew under favourable conditions and had bipinnatipartite leaves with numerous linear lobes.

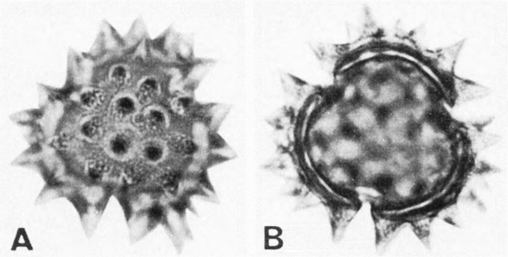

Fig. 2. Acetolysed pollen grains of *Garuleum bipinnatum*. – A: Polar view, high focus. – B: Optical cross section. – ×1000. Photomicrographs by Yvonne Arremo.

It seems that the achenes of the ray florets are nutritionally favoured, since in general they produce mature seed. The achenes of the outer disc florets probably develop only when nutrition is in excess. The achenes of the inner disc florets either do not receive sufficient food or they are sterile and the development of their ovaries is incomplete. There are numerous disc florets in each head but normally only a few of them produce ripe achenes, probably only under especially favourable conditions.

More detailed, recently obtained information about the variability of the flower colour in *Garuleum bipinnatum* has proved that it cannot be used as a distinguishing character, as earlier suggested by me.

Garuleum bipinnatum seems to be at an evolutionary stage, at which the female fertility of the disc florets is about to be lost. It is conceivable that the ancestral forms of *Garuleum* possessed fertile disc florets and that *G. bipinnatum* is primitive in this respect.

I intend to carry out supplementary investigations on the *Garuleum bipinnatum* complex. Above all, a better knowledge of the species would be gained by means of cultivation experiments.

Acknowledgements. I am very grateful to Dr J. Praglowski, Stockholm, for his palynological contribution to this paper, and to Miss Rita Baechler for the excellent illustrations. Thanks are also due to Dr Dorothy Guy-Ohlsson, who kindly checked the English. – The study is based mainly on material from the following herbaria: B, G, G-DC, PRE, S, UPS (abbreviations in accordance with Holmgren & Keuken 1974) and I wish to thank all those who have placed specimens at my disposal.

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Cryptocoryne dewitii N. Jacobsen sp. nov. (Araceae)

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Jacobsen, N. 1977 12 30: Cryptocoryne dewitii N. Jacobsen sp. nov. (Araceae). *Bot. Notiser 130:* 381–382. Stockholm. ISSN 0006-8195.

A new species of *Cryptocoryne* from Papua, New Guinea is described and illustrated.

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Cryptocoryne dewitii N. Jacobsen sp. nov.

Folia circiter 15 cm longa; laminae supra obscure virides, subtus pallidiores, 7–8 cm longae, anguste ovales, basi cordatae, margine leviter undulatae, in herbario complanatae irregulariter dentatas se praebentes. Spatha circiter 8 cm longa; tubus circiter 2 cm longus; limbus circiter 5 cm longus, anguste ovalis vel lanceolatus, lacteus vel flavidus, basi albidus, supra obscurior, extus cinnamomeus; collare faucale nullum; tubus inferior ut videtur alveolis nullis. Spadix circiter 1 cm longus; stigma ovale, breviter pedicellatum; corpora olfactoria irregularia; flores masculi circiter 30.

Holotypus die 16 Augusti anni 1971 in silva palustri paulum supra mare prope Kiunga Airstrip tractus Kiungensis regionis Papuanae Western District insulae New Guinea sub numero NGF 46818 a P. Katik lectus, siccus in Herbario Smithsoniano (US) depositus, isotypis in Herbario Leydensi (L) et Herbario Laensi (LAE).

The drawing is a reconstruction of the specimen at LAE. However, as the middle part of the spathe is missing, the spathe of the US specimen has been inserted instead. The upper part of the spathe is missing in the L specimen.

No stolons are present on the herbarium specimens, but they were doubtless broken off when the plants were dug up.

The species was found in lowland forest in the central western part of Papua, at an altitude of c. 70 m. The short tube of the spathe indicates an amphibious habit, and the plants were probably emersed at the time of flowering. The leaves are covered with a thin layer of mud and ochre. The colour of the limb was described as cream by the collector. The colours fade somewhat on drying and it is no longer possible to describe the colouration of the spathe more precisely. The outside of the limb seems to be more brownish than the rest. The herbarium specimens have denticulate leaf margins, an artefact obviously caused by pressing the slightly undulate leaf margins of the live plant.

The species is endemic to New Guinea, where *C. ciliata* (Roxb.) Schott and *C. versteegii* Engl. also occur. Rataj (1975) cited the collection of this new species under *C. versteegii* Engl., a species characterized by its green, fleshy leaves with an almost triangular leaf-blade (Engler 1920, de Wit 1971), a spathe with a yellow throat and collar and a very short, rugose, purple limb (Jacobsen 1977).

Cryptocoryne dewitii is characterized by ovate leaves with a slightly undulate margin, the rather wide, yellow to cream opening of the spathe, a rather flat, elongate limb, and the absence of a collar.

The species is named in honour of Prof. H. C. D. de Wit, nestor of the *Crypto's*.

Acknowledgement. I should like to thank Tyge Christensen for the Latin translation.

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Wit, H. C. D. de 1971: *Aquarienpflanzen.* Stuttgart.

Fig. 1. *Cryptocoryne dewitii.* – A: Habit.– B: Limb of the spathe. – C: Spadix. – A ×0.7, B × 1.6, C ×8.

Vessel types of the monocotyledons: a survey

Peter Wagner

Wagner, P. 1977 12 30: Vessel types of the monocotyledons: a survey. *Bot. Notiser 130:* 383–402. Stockholm. ISSN 0006-8195.

A literature survey of the occurrence of vessel types in roots, stems and leaves of the monocotyledons is presented. The information is arranged according to the classification suggested by Dahlgren, *Bot. Notiser 128:* 119–147 (1975). An agreement between type and distribution of vessels, systematic position, and habit is shown. Some minor modifications in the classification of the monocotyledons are suggested, e.g. *Hanguana* is better placed in Asparagales than in Poales, Bromeliales show greater affinity to Commelinaceae than to Lilianae in vessel characteristics and *Mayaca* and *Cartonema* deviate in their vessel anatomy from what is normal in Commelinales.

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The aim of the present compilation is to give an account of the distribution of vessels and vessel types in roots, stems and leaves of the monocotyledons. The system of classification used is mainly that suggested by Dahlgren (1975). Sometimes families suggested by Huber (1969) are preferred, in which case the appropriate taxon has been marked 'sensu Huber'. The perforation types found in the individual families and genera are tabulated at the end of this paper.

The information in this paper has been compiled from the various sources mentioned in the References. Whenever possible, information concerning the late metaxylem was used, because any differences in specialization are more pronounced in this part of the xylem. However, whether the information given concerns the metaxylem as a whole, or only the late metaxylem, is not always clearly stated in the papers. This may have distorted the picture to some degree. Systematic differences between authors also seem to be present. In the families dealt with in Cheadle's papers the frequency of scalariform perforation plates is invariably higher than e.g. in Metcalfe's 'Anatomy of the monocotyledons'.

The origin and specialization of vessels in the xylem of all parts of the plant in the monocotyledons were studied by Cheadle in a series of papers (1942–44). Using the principles outlined by Frost (1930) he concluded that vessel members originated from tracheids, that vessel members with long, scalariform perforation plates on very oblique end walls are the most primitive and that vessel members with simple perforation plates on transversely-placed end walls are the most specialized. During the phylogenetic development between these extremes, the vessel members have become shorter and, when thick, tend to have walls of constant width (Cheadle 1943 a). He established that the length of cells and the thickness of their walls, as well as their pitting details, should be used with great caution as indicators of specialization. The perforation plate is the most reliable tool for that purpose. He further concluded that vessels first originated in the roots, because in many plants vessels are found nowhere else and because the vessel members in the roots of species in which vessels are present throughout the plant are more specialized than similar elements in the shoot system; furthermore, the vessel members in the roots of species which lack vessels elsewhere are in general less specialized than those found in the roots of species in which vessels are widespread. Vessel members, however, may become more specialized in roots of species in which the shoot system lacks vessels (e.g. Alliaceae). Vessels originate, then, from the base of the stem upwards. This upward progression is paralleled by a change from vessels with long, scalariform perforation plates to vessels with short scalariform plates with few bars and simple perforations. In those species in which vessels occur in the stems and leaves, the perforation types of the vessels in the roots are always the most specialized and those in the leaves the most primitive (Cheadle 1943 b). In a few genera vessels are present in the roots and leaves and not in the stems (e.g. *Dracaena, Cordyline*), but no species is known in which the vessel perforation types are more specialized in the shoot system than in the roots.

The development and specialization of vessels in the late metaxylem preceded the similar development in the early metaxylem. The vessel members in the early metaxylem are never more specialized than those in the late metaxylem. Whatever the degree of specialization of the perforation plates in the late metaxylem, any type of perforation plate, excepting the more specialized, may occur in the early metaxylem. In some species vessels may be absent from the early metaxylem, but no cases have been reported in which vessels are present in the early but not in the late metaxylem (Cheadle 1944). Differences in specialization are more clearly seen when the late, rather than the early, metaxylem in all organs is compared (Cheadle 1944). Later studies by Cheadle and others have not affected these conclusions.

Huber (1969) proposed another view on the development of the vessel system. He suggested that vessels were originally present in both root, stem and leaves. In some evolutionary trends vessels were preserved in all parts and the vessel members eventually became more specialized (i.e. simple perforations were developed); in other trends the vessels in the shoot system, or eventually (in aquatics) in the entire plant, were lost. Huber argues, in opposition to Cheadle, that the root is a conservative organ and is therefore not prone to develop new cell types. It is more likely that it preserves cell types which have already been lost by the more progressive shoot system. Against this view, it may be argued that in spite of the unquestionably conservative anatomical characteristics of the root, this does invariably possess the most advanced vessel types in the whole plant, whether the stem and/or leaves possess vessels or not. This is unaffected by the fact that the progression of vessel specialization from the late to the early metaxylem is slower in the roots than elsewhere (Cheadle 1944).

Huber further argues that aquatic forms without vessels, mainly found in Alismatanae and Lemnaceae, are very specialized forms. Consequently, the absence of vessels must also be regarded as an advanced characteristic. This assumption is sustained by the occurrence of relatively advanced perforation types in the root vessels of the fairly 'primitive' marsh plants within Alismatanae (Alismataceae, Butomaceae).

Cheadle has established the unidirectional specialization of the vessels in the monocotyledons. The progression tracheid–scalariform perforation–simple perforation is irreversible. If vessels ever occurred in the ancestors of the above mentioned aquatics, their failure to develop is therefore a reduction in specialization, as there is no evidence that tracheids have ever been derived from vessels (Cheadle 1953). If the absence of vessels is a result of a reduction of the xylem, then this absence represents an advanced feature and does not contradict Huber's view concerning the advanced nature of the aquatics. This conceivable reduction in the xylem of the aquatics does go counter to the afore-mentioned general trend, that monocotyledons with vessels only in the roots have primitive vessels. To correlate and evaluate the degree of specialization of characteristics (and their phylogenetic significance) a large random sample is needed (Frost 1930), but the aquatic monocotyledons investigated are neither many, nor at random. According to my view they are more correctly treated as forming exceptions to the general evolutionary trend.

It should be emphasized that the irreversible specialization of the perforation plate makes this a most useful character for ruling out certain suggested phylogenetic relationships (Cheadle 1955, Cheadle & Tucker 1961). Vessel distribution and vessel characters, however, may only either suggest or confirm such relationships. Fig. 1, which depicts the distribution of the characteristics of vessels in the roots, stems and leaves of the monocotyledons, reveals certain features. In every order the roots invariably possess the most specialized vessels, if vessels are present at all. With a few exceptions in Asparagales

(Dracaenaceae, Dasypogonaceae, Nolinaceae and Xanthorrhoeaceae), in Velloziales and one genus (*Phytelephas*) in Arecanae, the degree of vessel specialization decreases in stems and leaves, even in the most advanced orders (e.g. Poales). The more primitive organization level in stems and leaves is, in some orders, expressed by a higher frequency of scalariform perforation plates (in the order as a whole, not necessarily in the individual genera) e.g. Poales, Cyperales, Juncales, Eriocaulales, Arecales, in others it is shown by an increase in the number of genera without vessels e.g. Bromeliaceae, Asparagales, Liliales, Stemonales, Velloziales, Haemodorales and Zingiberales. In certain cases vessels are not present at all in the shoot system, e.g. Arales, Philydrales, Taccales, Alismatales. A feature which is not evident from the figure or table is that the vessels in the stems and leaves are often of a more primitive type than those in the roots, since they have longer perforation plates with more numerous bars on the oblique end-walls. Sometimes the change in perforation type from root to stem is so pronounced that a shift from vessels to vessel tracheids takes place e.g. in Pontederiales and Philesiaceae.

It is also true that vessels are present in the shoot systems of orders in which plants with long internodes are prevalent e.g. Poales, Juncales, Eriocaulales, Cyperales, Typhales, Arecales and Dioscoreales. In orders in which bulb- or corm-forming plants are frequent, vessels are often not present in the shoot system, e.g. Asparagales, Liliales.

Alismatanae

Alismatales. Vessels are absent in stems and leaves but present in the roots of the investigated members of this order.

The perforation plates are scalariform (*Hydrocleys, Echinodorus*), scalariform and simple (*Limnocharis*) or predominantly simple (most species of Alismataceae; Stant 1964, 1967). This does not support the supposition, sometimes put forward, that Alismatales may be related to Ranunculales, because vessels are present in the stems and leaves, as well as in the roots, of the latter order.

Hydrocharitales. In the few members of this order studied vessels were only found in the roots of *Butomus*. Vessels are totally absent in Hydrocharitaceae and Aponogetonaceae, which probably represents a reduction, as hypothesized by Cheadle (1942) and Carlquist (1975). The vessels of *Butomus* have simple (Stant 1967) or mostly simple (Cheadle 1942) perforations.

Zosterales. Most aquatic genera of this order lack vessels. Vessels occur in roots of the marsh plants *Scheuchzeria* and *Triglochin,* but also in the investigated species of *Potamogeton;* the perforations are scalariform (Cheadle 1942).

Najadales. No members possess vessels (Cheadle 1942).

The general trend in Alismatanae seems to be that most land (marsh) plants have vessels in the roots but not in the stems and leaves. At least the more advanced aquatics entirely lack vessels. Scalariform perforation plates are found in Scheuchzeriaceae, Juncaginaceae and *Potamogeton.* Simple and scalariform perforations are found in *Butomus* and Alismataceae. Vessel characteristics seem to be highly correlated with growth habit and hence cannot be used indiscriminately for taxonomic purposes. Alismatales can be distinguished from Hydrocharitales by the possession of poly-aperturate pollen grains and a curved embryo, the presence of secretion vessels and the lack of anthocyanine pseudobases.

Lilianae

Dioscoreales. In the species studied vessels with scalariform perforation plates are present in roots, aerial stems and petioles, absent in leaf laminae and rhizomes (Braun 1957, Ayensu 1972). According to Cheadle's (1953) concept the presence of vessels in stems is a fairly advanced feature, a view supported (in this order) by the presence of highly-specialized xylem – and phloem – glomeruli in the nodes. Huber (1969) regards the presence of vessels in roots and stems as a rather primitive feature and derives several families within Lilianae from Dioscoreaceae, which he claims also forms a link with the dicotyledons. The presence of the above-mentioned xylem glomeruli makes the postulated primitiveness of the xylem disputable.

Stemonales. All the investigated species have root vessels with scalariform perforation plates; one, or perhaps two, species are known (both in Stemonaceae) which also have stem vessels with scalariform perforations (Tomlinson & Ayensu 1968). This supports the proposal by Huber (1969) and Ayensu (1968 a) that Stemonaceae, especially *Stemona* itself, are related to Dioscoreales. The presence of vessels (with scalariform perforations) only in the roots (Cheadle 1970) is a common feature among Lilianae and this characteristic is therefore not useful in assessing the affinities of Trilliaceae. The families are grouped together on a basis of absence of septal nectaries, presence of long connective appendages and on fruit anatomy.

Asparagales. In Smilacaceae scalariform perforations are found in the vessels. All the species investigated have vessels in the roots, 7 of 11 in the stems and 8 of 15 in the leaves (Cheadle 1970). Most taxa agree with Dioscoreaceae in the type and distribution of vessels to which family Smilacaceae is also for other reasons considered to be related (Huber 1969).

Some variation exists within Philesiaceae. In the roots, vessels with simple, or mostly simple, perforations are found in *Behnia* and *Eustrephus* (Fahn 1954 b, Cheadle & Kosakai 1975), vessels with simple and scalariform perforations (Cheadle & Kosakai 1975) or mostly simple (Fahn 1954 b) in *Geitonoplesium*, vessels with scalariform perforations (Cheadle & Kosakai 1975) or vessel-tracheids (Fahn 1954 b) in *Lapageria, Luzuriaga,* and *Philesia* and vessels with scalariform perforation plates in *Petermannia.* In the stems, Fahn (1954 b) found vessels with scalariform perforations in *Geitonoplesium* and vessel-tracheids in *Lapageria* and *Luzuriaga*; he reported finding only tracheids in the other genera which he investigated. Cheadle & Kosakai (1975) found vessels with scalariform perforations in *Eustrephus, Geitonoplesium, Lapageria, Luzuriaga, Philesia* and *Petermannia,* and tracheids only in *Behnia*. In the leaves, Fahn (1954 b) found vessel-tracheids in *Geitonoplesium*. Cheadle & Kosakai (1975) were uncertain about the presence of vessels (with scalariform perforations) in the leaves of *Eustrephus*. The discrepancies between the results of Fahn and of Cheadle and Kosakai, which may seem greater than they actually are, are due to the fact that the vessels are often very few and difficult to recognize, since they very much resemble tracheids. The heterogeneity of the family, most clearly seen in Fahn's results, may be taken to support Huber's conception that the family should be divided into smaller units (Philesiaceae, Luzuriagaceae and Petermanniaceae). The vessel distribution of *Petermannia* supports an affinity with Philesiaceae, rather than with Smilacaceae as is sometimes suggested (Tomlinson & Ayensu 1969).

In Convallariaceae the vessels in the roots have scalariform (*Aspidistra*), mostly scalariform, or mostly simple perforations (*Convallaria*). Some species in Polygonateae even have vessels (with scalariform perforations) in the stem (Cheadle & Kosakai 1971). Members of Herreriaceae have vessels with scalariform perforations in the stems, the roots not having been studied. Species of Asparagaceae have vessels with simple perforations in the roots and vessels with scalariform perforations in the stems (Cheadle & Kosakai 1971). In Ruscaceae a shift takes place from a primitive type, in which vessels, with scalariform perforation plates, are present only in the roots, to a presumably more advanced type with vessels with simple perforations in the roots and vessels with scalariform perforations in the stems; Cheadle (1970 p. 50) points out that he does not understand this mode of distribution. The occurrence of vessels in the stems of some of the genera in the families mentioned above may suggest a certain phylogenetic relationship with Smilacaceae, yet the perforations present in the root vessels are generally more advanced in type.

In Dracaenaceae and Nolinaceae sensu Huber (1969) the species studied have vessels in the roots and leaves, but not in the stems; vessel perforations in the leaves are scalariform, but are probably simple in the roots (Cheadle 1942). Cheadle (1943 b) suggests that the production of large numbers of tracheids in the bundles of the secondary tissues (both genera show secondary thickening) compensates for the failure to develope vessels. Carlquist (1975) notes that the establishment of a continuity between the vessels in the secondary tissues and the vessels in the upper primary stem would be a virtual impossibility morphogenetically; he also suggests stem succulence as providing an explanation. The species of Asteliaceae sensu Huber (1969) have vessels with scalariform perforation plates in the roots, but no vessels in the shoot system; those of Dianellaceae sensu Huber (1969) have vessels with mostly simple or with simple and scalariform perforation plates in the roots and likewise no vessels elsewhere (Cheadle & Kosakai 1971). Vessel characteristics seem to support Huber's assumption that the four last-mentioned families form quite separate groups.

Vessels with simple perforations were found in all the investigated species of Xanthorrhoeaceae, except in *Baxteria* and *Kingia*, which have scalariform perforations. Vessels occurred only in the roots, except in two genera (*Acanthocarpus* and *Xanthorrhoea*) in which vessels with long, scalariform perforation plates are found in the leaves. Arber (1925) found vessel cells in the stem of *Xanthorrhoea minor*, but Fahn (1954 a) found only tracheids. No vessels are present in the rhizomes. Secondary thickening occurs in *Lomandra*, *Xanthorrhoea* and possibly in *Kingia*. The type and distribution of the vessels do not contradict Huber's supposition that Xanthorrhoeaceae, Dracaenaceae and Asteliaceae are closely allied, but it does not support his theory that a closer relationship exists between *Xanthorrhoea* and Asteliaceae and between Dracaenaceae and the remaining genera in Xanthorrhoeaceae.

Hanguana (Hanguanaceae) has no vessels in either stems or leaves; the roots were not studied. The absence of vessels from the shoot system agree with the condition found in several families in Asparagales, but is in disagreement with a position in Flagellariaceae, in which family the genus is often placed. Smithson (1957) also reported other anatomical characters which separate *Hanguana* from *Flagellaria* and *Joinvillea*, but which suggest a certain relationship with Xanthorrhoeaceae.

In Asphodelaceae and Anthericaceae vessels are present in the roots and in seven of the genera studied also in the stems. The perforation plates in the root vessels are almost exclusively simple, except in Kniphofieae, in which scalariform as well as simple perforations are found, and in *Borya*, in which the perforations are scalariform. The perforations in the stem vessels are scalariform except in *Tricoryne* in which also simple perforations occur (Cheadle & Kosakai 1971). Secondary thickening occurs in *Aloe*. (Tomlinson & Zimmermann 1969). As far as vessel characteristics are concerned these two families, and Aphyllanthaceae sensu Huber, agree completely. They are kept separate mainly because of the occurrence of saponins in Asphodelaceae and because of differences in the embryo, microsporogenesis and karyotype.

In Agavaceae vessels are present in the roots. Perforations are simple in *Agave* and scalariform in *Hosta* (Cheadle & Kosakai 1971). Secondary thickening occurs in *Agave* and *Furcraea* (Tomlinson & Zimmermann 1969). *Hosta*, because of its herbaceous habit, is an atypical genus within Agavaceae. The vessel perforation type also resembles that found in *Hemerocallis* (Hemerocallidaceae), which Huber (1969), however, does not consider is related to *Hosta*.

In Hyacinthaceae and Alliaceae vessels are absent from the shoot system, but present in the roots. In Hyacinthaceae the perforations are scalariform and – in 5 of 22 investigated genera – scalariform and simple; in one genus (*Milula*) the perforations are mostly simple (Cheadle & Kosakai 1971). In Alliaceae the perforation plates are simple, simple and scalariform or (in *Agapanthus*) scalariform. It is noteworthy that the most primitive member of the family with regard to vascular characters, *Agapanthus*, is grouped together with the more advanced *Tulbaghia* in the tribe Agapantheae; Cheadle (1969) also notes that they are "bad tribe mates".

All the species of Amaryllidaceae studied have vessels only in the roots, the perforations being exclusively scalariform (Cheadle 1969). Huber (1969) considers this family to be the most advanced one in Asparagales; the vessel characteristics agree with those found in Hyacinthaceae, but are less advanced than those found in Alliaceae, Anthericaceae and Asphodelaceae.

In Hypoxidaceae vessels with scalariform perforation plates are found in the roots, though *Campynema* is possibly totally devoid of vessels (Cheadle 1968). Huber (1969) supposes that this family is more closely related to Asteliaceae than to Amaryllidaceae. Since in both families the vessels have scalariform perforations neither possibility can be excluded.

In the roots of Velloziaceae the vessel perforations are simple. Ayensu (1968 b) claims that all the species studied – except *Vellozia elegans* – have vessels with scalariform perforations in the leaves, but no vessels in the stem. He questions Cheadle's (1968) statement that vessels with scalariform perforations occur in the stems and

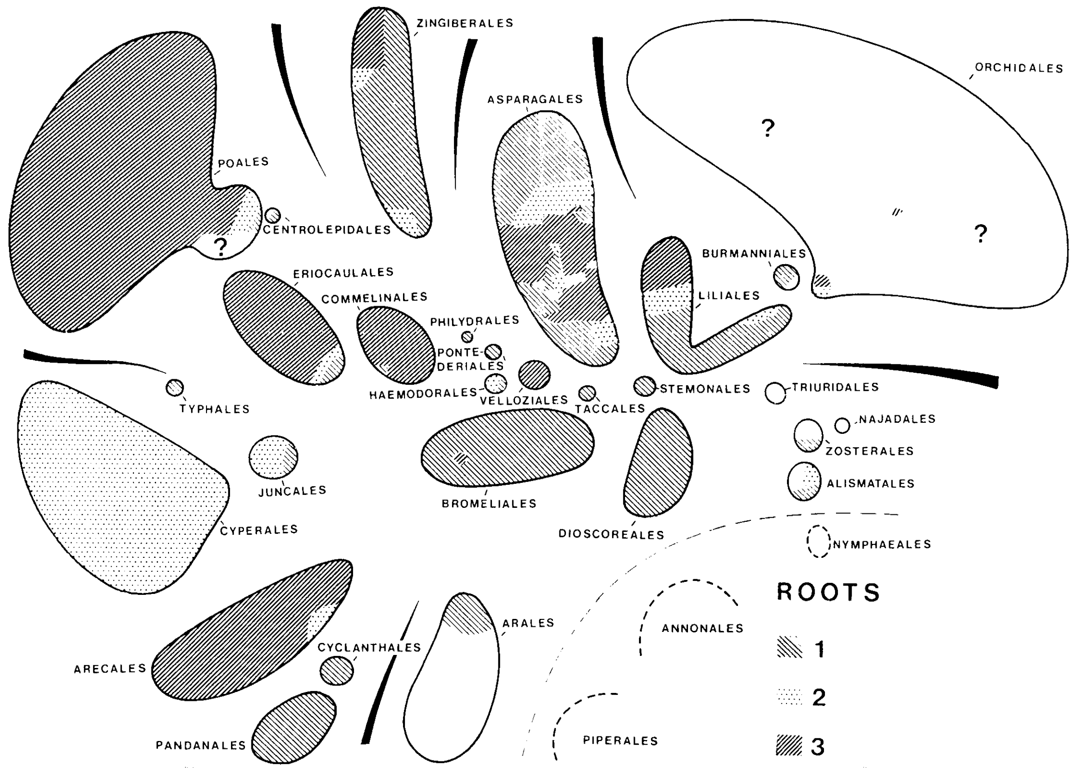


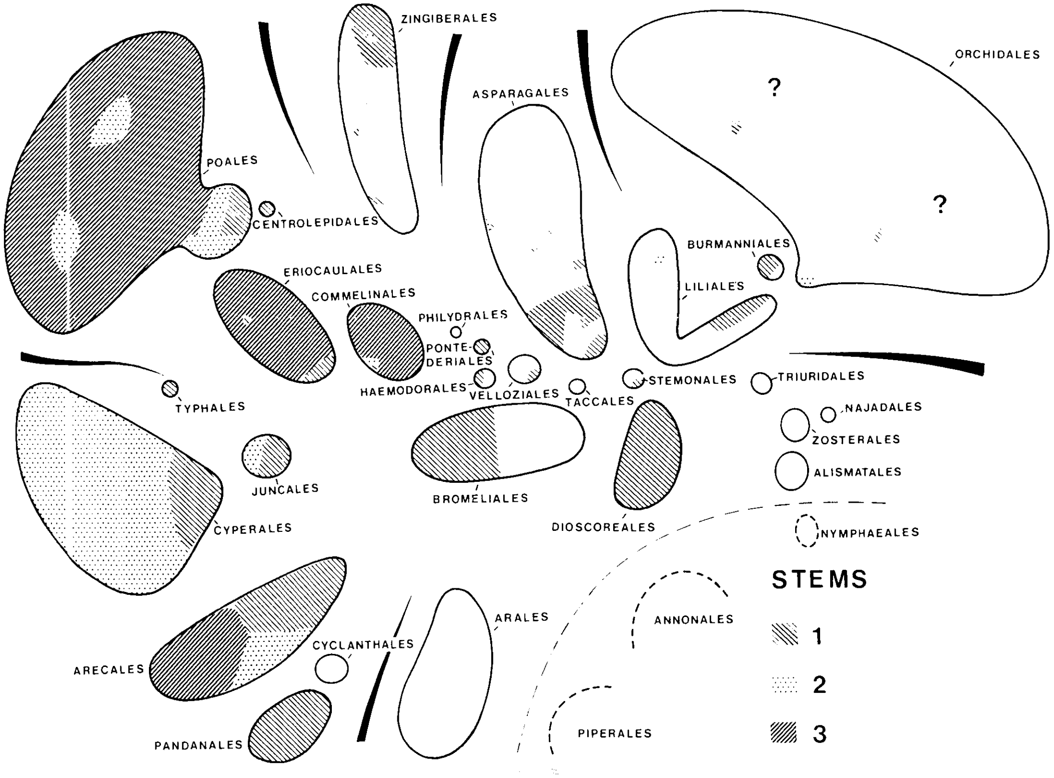
Fig. 1. Distribution of vessel types in roots, stems and leaves of the monocotyledons. The graphic representation of the orders is drawn up by Dahlgren and based on his system (Dahlgren 1975). Modifications have been made in accordance with a current revision of the system being carried out by Dahlgren and Huber, University of Hamburg. In the diagrams all the families have fixed places within the orders. – 1: Vessels with scalariform perforations only or vessel tracheids. – 2: Vessels with simple and scalariform perforations. – 3: Vessels with simple perforations only. – Orchidaceae is insufficiently investigated. No information was available about the presence of vessels in the stems and roots of some minor groups in Asparagales and in the roots of Flagellariaceae and Ecdeiocoleaceae. In Dioscoreales vessels are present in the petioles but not in the lamina; evidence is conflicting regarding their presence in the leaves of Restionaceae.

he assumes that macerated preparations may be contaminated with root material, because these cling tightly around the stem. Fahn (1954 b) found no vessels in the leaves of *Vellozia elegans*. Huber (1969) suggests that this family is best placed in an order of its own, Velloziales.

In Tecophilaeaceae vessels with scalariform perforations occur in the roots, but not elsewhere, an organization level equivalent to that found in the less specialized families within Asparagales (Cheadle 1969).

Liliales. The genera of Colchicaceae have vessels, with scalariform perforations, in the roots only (Cheadle & Kosakai 1971).

In Iridaceae most species have vessels with simple, or mostly simple, perforations in the roots, whereas the shoot system is devoid of vessels (Cheadle 1963). Two groups however deviate from this general condition, viz. (1) *Sisyrinchium*, in which vessels with mostly simple perforations occur in the stem and vessels with scalariform perforations occur in the leaves (in two species at least, in two other species only tracheids are present in the leaves), and (2) *Aristea, Klattia, Patersonia* and *Witsenia*, in which the vessels in the roots, as in Colchicaceae, have scalariform or mostly scalariform perforations (vessels are not present elsewhere in the plants). As regards vessel charac-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CENTROLEPIDALES
BURMANNIALES
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COMMELINALES
PHILYDRALES
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HAEMODORALES
VELLOZIALES
TACCALES
STEMONALES
TRIURIDALES
TYPHALES
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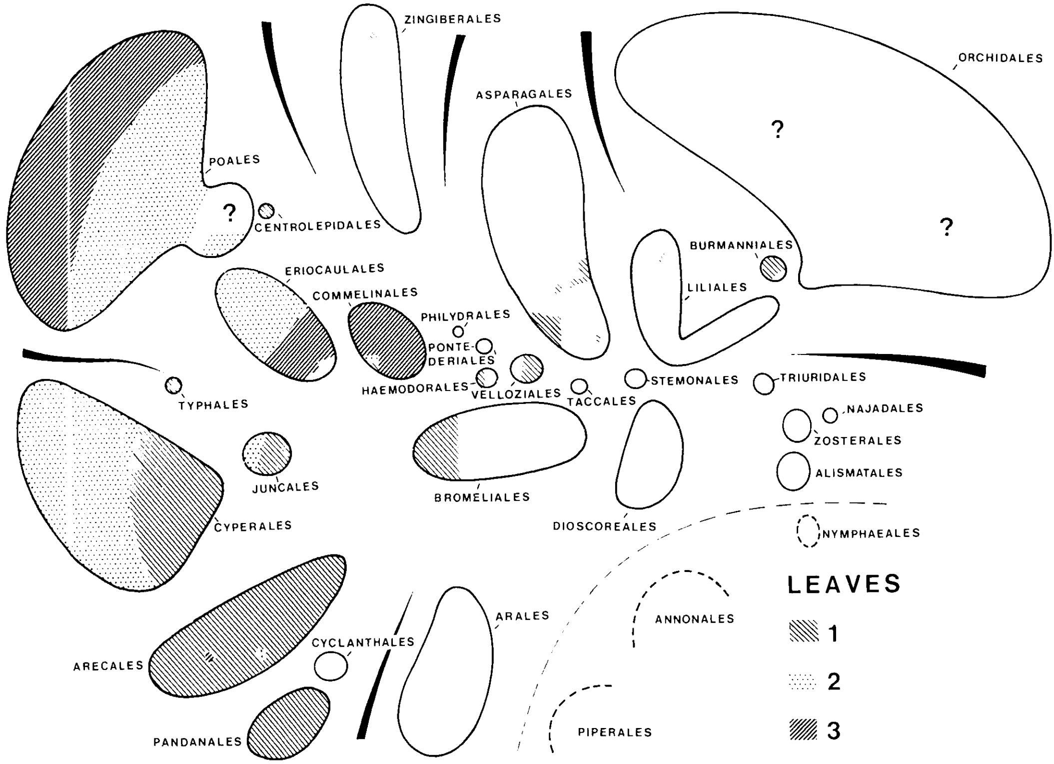
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teristics the latter group comes closest to Colchicaceae. The above-mentioned conditions support the tribal division suggested by Huber (1969). In *Klattia, Schizostylis* and *Witsenia* secondary thickening occurs (Tomlinson & Zimmermann 1969).

In Alstroemeriaceae vessels with scalariform perforations are found in the roots of *Bomarea, Schickendantzia* and *Alstroemeria*; in *Alstroemeria aurantiaca* the root vessels have mostly scalariform perforations. In the four genera investigated by Cheadle & Kosakai (1975), vessels with scalariform perforations were found in the stems. Huber (1969) regards the family as closely related to Colchicaceae and Liliaceae. The presence of vessels in the stems is a feature in common with *Sisyrinchium.*

Vessels are present in the roots of all the genera investigated in Liliaceae and Melanthiaceae, except in *Petrosavia,* in which genus no vessels occur. The perforation plates are scalariform (Cheadle & Kosakai 1971). In *Sandersonia* and *Tricyrtis* vessels with scalariform perforations are also present in the stem. The absence of vessels in *Petrosavia* (vessel tracheids may be present in the roots, the identification is difficult) may be connected with its saprophytic habit. Stant (1970) suggested placing *Petrosavia* in Triuridaceae, because of its anatomy, though with reservations. There is a fair possibility that parallel evolution has occurred, since Triuridaceae are likewise saprophytic. Colchicaceae, Liliaceae and Melanthiaceae agree in vessel characters. They are kept separate because of the presence of alkaloids, steroid saponins and raphides of calcium oxalate in Melanthiaceae.

Triuridales. Vessels are not present at all in the four Triuridales species investigated (only one of which is mentioned by name, viz. *Andruris sciaphila*). This feature is probably due to the mycoparasitic habit of the members of this family (Carlquist 1975).

Burmanniales. Burmannia disticha and *B. longifolia,* two autotrophic species, have vessels with scalariform perforation plates in roots, stems and leaves (Carlquist 1975). This is rather surprising considering their systematic position, although vessels do occur in the stems and leaves of Orchidales. None of the mycoparasitic species have been studied.

Orchidales. In Apostasiaceae the genus *Adactylus* has vessels, with mostly simple perforations, in the roots and vessels with simple and scalariform perforations in the stems; according to Cheadle (1968) it is devoid of vessels in the stems. In *Neuwiedia lindleyi* the presence of vessels in the roots is questionable (Cheadle 1968) and if present at all only scalariform perforations are found. According to Solereder & Meyer (1930) *Neuwiedia griffithii* has vessels with simple and scalariform perforations in the roots. In *Apostasia* vessels do occur in the stem, although the perforation type was not described. In Cypripediaceae *Phragmipedium* (5 spp.), *Cypripedium* (11 spp.) and *Selenipedium* (2 spp.) vessels with simple perforations are found in the roots. No vessels are found in *Paphiopedilum* (7 spp.) None of the genera investigated had vessels in the stems or leaves (Rosso 1966).

In Orchidaceae vessels are present in the roots of *Pogonopsis, Dendrobium, Vanda* and *Vanilla*; the perforation type is not described for any taxon, excepting *Vanilla aromatica,* in which the perforation plates are simple. Solereder & Meyer (1930) enumerate 8 genera with vessels in the stems, the perforation-type, however, being described only for two of them, and 6 genera with no vessels.

In *Epidendron* and *Scaphyglottis* vessels with scalariform perforations are present in the leaves. Cheadle (1942) mentions that one out of four species has vessels with simple and scalariform perforations in the roots and three have vessels with scalariform perforations, five out of 15 species have vessels with scalariform perforations in the stems (in 2 further species vessels are perhaps present in the stems). Generic names are only given exceptionally, however. According to the system of Dahlgren (1975) one of these genera would be placed in Cypripediaceae.

The insufficiency of the data on vessel characters in this order makes an assessment of the interrelationships almost impossible. A comparison with the conditions in other orders is also impeded by the presence of water-storing tissues (velamen) in the roots of Orchidales. The confusion is made worse by the suggestion of Withner et al. (1974) that the tracheids are vascular tracheids and that the absence of vessels should therefore be regarded as an advanced feature. However, it seems that the vessel types found in Cypripediaceae and Apostasiaceae are no less advanced then those found in Orchidaceae. According to Cheadle & Tucker (1961) and Carlquist (1975 fig. 8 p. 106) the vessels in Orchidaceae are generally more primitive than those in Apostasiaceae.

Haemodorales. The roots of most genera in both tribes of Haemodoraceae have vessels with mostly simple perforation plates. *Tribonanthes, Dilatris* and *Lanaria,* however, have scalariform perforations. In two genera in Haemodoreae, viz. *Lachnanthes* and *Xiphidium,* vessels are present in the shoot system. In *Lachnanthes* the presence of vessels in the leaves is uncertain (Cheadle 1942, 1968), while in *Xiphidium* the presence of vessels in the stems (Cheadle 1942) or in stems and leaves (Cheadle 1968) is doubtful. The remaining genera are devoid of vessels in either stems or leaves. Cheadle (1969) advocated a certain relationship between Haemodoraceae and Tecophilaeaceae. In the four species of Philydraceae investigated vessels with scalariform perforations are found in the roots and not elsewhere (Cheadle 1968, Fahn 1954 b). In this respect the family is considered to be more primitive than Haemodoraceae. The presence of scalariform perforation plates is a feature in common with Pontederiales, which also includes marsh (and aquatic) plants.

Taccales. The four species of Taccaceae studied have root vessels only, with long scalariform perforations; as the cell membrane may be present between some of the bars, the cells may be regarded as vessel tracheids (Cheadle 1968, Fahn 1954 b). Huber (1969) mentions the scalariform perforations as a feature in common with the dioscoreoid Liliiflorae.

Pontederiales. All the genera studied in Pontederiaceae have vessels with scalariform perforation plates in the roots; *Eichhornia crassipes, Heteranthera limosa* and perhaps *Pontederia cordata* also have vessels with scalariform perforations in the stems (Cheadle 1970). The type and distribution of vessels does not contradict the suggested relationship with Philydraceae and Haemodoraceae (Huber 1969), although the vessels in the latter family are of a more advanced type.

Bromeliales. In Bromeliaceae 14 of the 16 genera investigated have vessels with scalariform perforation plates in the roots, two have only simple perforations, 10 out of these 16 genera have vessels with scalariform perforations in the stems (*Aechmea* and *Dyckia* include species with or without vessels in the stems) and 7 have vessels with scalariform perforations in the leaves (Tomlinson 1969). The frequent occurrence of vessels in roots, stems and leaves indicates a relationship with families in Commelinales. However, since the perforation plates are simple in the latter order, this is considered more advanced. Within Lilianae, Bromeliaceae stand nearest to Dioscoreales with regard to vessel characteristics. Bromeliaceae is included in Lilianae because of the presence of steroid saponins, septal nectaries and helobial endosperm, but in several other features it agrees better with Commelinanae.

Commelinanae

Commelinales. In the 32 genera of Commelinaceae investigated vessels with simple perforations are found in roots, stems and leaves. In *Commelina, Rhoeo, Tradescantia* and *Zebrina,* however, scalariform perforation plates as well are found in stems and leaves (Tomlinson 1969, Cheadle 1942). In regard to vessel features the phylogenetic level of this family is the same as e.g. Xyridaceae and Poaceae. The genera of Xyridaceae studied have vessels with simple perforations in roots, stems and leaves (Tomlinson 1969).

Mayaca in the monogeneric Mayacaceae has vessels with long scalariform perforation plates in roots and stems and perhaps also in the leaves (Tomlinson 1969, Cheadle 1953). The vessels in the leaves may be vessel tracheids. The evolutionary line leading to Mayacaceae, like that leading to Cartonemataceae, apparently separated from the main line leading to Commelinaceae at a stage before vessels with simple perforations had been developed. *Cartonema spicatum* (Cartonemataceae) has mostly simple perforations in the root vessels, although a few scalariform are found too (Tomlinson 1969). Vessels are not present in stems and leaves at all, in which respect *Cartonema* differs conspicuously from other taxa in Commelinales.

In Rapateaceae the tribes Saxofridericieae and Schoenocephalieae have vessels with scalariform perforation plates in roots and stems. In the tribe Monotremeae simple perforations are present in the wider vessels of the roots, whereas scalariform perforations are present in the narrower ones; vessels with simple perforations are found in stems. In Rapateeae all genera have scalariform perforations in the roots and stems, except *Spathanthus* which has simple perforations (Carlquist 1969). Thus, within this family, the vessels exhibit a wide range of variation, from "rather primitive" (Saxofridericieae, Schoenocephalieae, Rapateeae p.p.) to "rather advanced" (Monotremeae, *Spathanthus*) conditions. In general, they are less advanced than the vessels found in Xyridaceae and Commelinaceae.

Eriocaulales. According to Tomlinson (1969) vessels with simple and, less frequently, scalariform perforations are found in roots, stems and leaves in all Eriocaulaceae genera studied, except *Tonina,* in which the stem has vessels with long, scalariform perforation plates. Cheadle (1942) states that *Eriocaulon articulatum* has scalariform perforations in all organs.

Juncales. Within Juncaceae the vessel characters in the genus *Juncus* vary. According to Cheadle & Kosakai (1973) four of the species studied have simple perforations in the roots and two have mostly scalariform, the remaining species varying between these extremes. In the stems five out of 12 species have mostly simple perforations, one scalariform and simple, and six mostly scalariform. In the leaves the perforations are simple and scalariform in two species, mostly scalariform in five, and only scalariform in three. In *Luzula* the root vessels have simple or mainly simple perforations, in the stems simple and scalariform perforations are found, in the leaves simple and scalariform or mainly scalariform. In the remaining genera the vessels in the shoot system have scalariform perforation plates and in the roots they have mostly or only scalariform (*Rostkovia*) except *Distichia,* in which the root vessels have mostly simple perforations. Cutler (1969) reported simple, scalariform and reticulate perforation plates in the vessels of these genera. It is evident that *Juncus* and *Luzula* are anatomically the most advanced genera in the family and *Rostkovia* the most primitive.

Thurnia (Thurniaceae) has vessels with scalariform perforations in roots, stems and leaves (Cutler 1969). Cheadle & Kosakai (1973) reported mostly scalariform perforations in the root vessels. As regards vessel characteristics this genus together with *Rostkovia* constitutes the most primitive part of Juncales.

Cyperales. In Cyperaceae Cheadle (1955) and Cheadle & Kosakai (1972) found vessels in roots, stems and leaves. Simple perforation plates prevail in the roots. In Cariceae mostly simple perforations are seen in the stems and mostly scalariform in the leaves. In Cryptangieae vessels with mostly scalariform perforations are present in the stems and leaves, except in *Cryptangium, Everardia* and *Lagenocarpus,* in which scalariform perforations only are found in both stems and leaves. The tribes Cypereae and Sclerieae have mostly simple to simple and scalariform perforation plates in the stems and simple and scalariform, or mainly scalariform, in the leaves. In Hypolytreae the stem vessels have mainly scalariform perforations and mostly or exclusively (*Chorizandra sphaerocephala*) scalariform perforations in the leaves. In Rhynchosporeae the vessels have mostly scalariform to scalariform and simple perforations in the stems and mostly scalariform in the leaves. Two species of *Cladium* and *Oreobolus* have scalariform plates only in both stems and leaves. *Carpha, Caustis* (one sp.), *Costularia, Cyathochaeta* and *Mesomelaena* (one sp.) have exclusively scalariform perforations in the leaves. The Scirpeae genera have vessels with simple and scalariform perforations in the stems and simple and scalariform or mainly scalariform in the leaves.

In tabular form Metcalfe (1971) reported on perforation types in 49 genera. The observations were made on longitudinal sections and the tables give only information about the observation of a perforation type in a given organ, not about the frequency of the different types. Metcalfe's results are therefore difficult to compare with those of Cheadle & Kosakai. The latter authors write that they "found no discrepancy in those species we had in common (with Metcalfe) except for our identification of scalariform perforation plates in addition to simple ones in a few organs". From the results of Cheadle & Kosakai and – to a certain extent – also from those of Metcalfe, it is evident, that vessels found in Cariceae and Cypereae have attained a more advanced level than those in Hypolytreae, Cryptangieae and Rhynchosporeae. Generally speaking, Cyperaceae exhibit more advanced vessel features than Juncales.

Centrolepidales. In the investigated genera in Centrolepidaceae vessels occur in roots, stems and leaves, except *Trithuria filamentosa,* which has no leaf vessels. Scalariform and reticulate perforations are found in the stems and mostly reticulate in the rhizomes (Cutler 1969).

Poales. Restionaceae. In the genera studied by Cutler (1969) vessels with simple perforation plates are present in the roots. The rhizomes of *Cannomois, Elegia, Hypolaena, Lyginia, Restio monocephalus* and *Staberoha* have vessels with simple perforations, whereas those of *Chondropetalum* have vessels with scalariform or fenestriform perforations. The erect stems of five genera studied had simple perforations, two genera had mostly simple, three genera had simple and scalariform and 10 genera scalariform perforations. 3 genera included species with either simple or scalariform to mostly simple perforations. Cheadle (1955) reported that in the roots of the ten species he studied, two had simple perforations, four mostly simple, three simple and scalariform and one mostly scalariform. In the stems of 12 species studied, one had simple perforations, four mostly simple, six simple and scalariform and one scalariform. In the leaves of 11 species he found vessels with mostly simple perforations in one, simple and scalariform in five, mostly scalariform in two, and in three species scalariform perforations only. Cutler (1969) found no vessels in the leaves.

Flagellariaceae. *Joinvillea* (sometimes placed in its own family, Joinvilleaceae) has vessels with mostly simple perforations in the stem and with scalariform perforations in the leaves; in the leaf-sheaths mostly simple perforations are seen. No information exists about vessels in the roots (Tomlinson 1969, Fahn 1954 b). *Flagellaria* has simple and scalariform perforations in the vessels of stems and leaf-sheaths, whereas the leaf laminae have vessels with scalariform perforations (Tomlinson 1969, Fahn 1954 b). (*Hanguana* is included under Asparagales.) In the stem of *Ecdeiocolea* (Ecdeiocoleaceae) vessels with simple and scalariform perforation plates occur; the perforation type in the root vessels has not been described (Cutler 1969).

Poaceae. According to Metcalfe (1960) all the grass genera investigated have vessels with simple perforations in roots, stems and leaves. Cheadle (1955) stated that the roots had simple perforations in 57 of 58 species studied and mostly simple in one. Simple perforations were found in the stems of 55 of 69 species investigated and mostly simple ones in 14. In the leaves, simple perforations were found in 33 of 63 species, mostly simple perforations in 26 and simple and scalariform plates in one species. The families of Poales agree with the other Commelinanae in having vessels in roots, stems and leaves. Restionaceae, Flagellariaceae and Ecdeiocoleaceae have more primitive vessel perforation types in stems and leaves than Poaceae. Poaceae, together with Commelinaceae, Xyridaceae and Eriocaulaceae, represent the highest organization level attained within Commelinanae.

Zingiberanae

Zingiberales. In Lowiaceae *Orchidantha* has vessels with scalariform perforations in the roots; the shoot system is devoid of vessels (Fahn 1954 b, Tomlinson 1959). Within Strelitziaceae, *Ravenala* has vessels with scalariform perforations in the roots, while in *Phenakospermum* and *Strelitzia* this type of vessel occurs in the stems as well, simple perforation plates being intermixed with scalariform in the root vessels of *Phenakospermum.* In *Heliconia* (Heliconiaceae) vessels with scalariform perforations occur in the roots only (Tomlinson 1969, Cheadle 1942).

In *Musa* and *Ensete* of Musaceae, vessels are present in the roots, their perforation plates being mostly simple, although scalariform and reticulate plates are also seen. Vessels with scalariform perforations have been found in the inflorescence axis of *Musa* (Tomlinson 1969, Cheadle 1942).

In *Alpinia,* Zingiberaceae, the root vessels have simple perforations, according to Solereder & Meyer (1930), scalariform according to Tomlinson (1969), while in *Catimbium, Elettaria* and *Elettariopsis* they have simple and scalariform or mostly scalariform perforations (Tomlinson 1956, 1969). In the remaining 15 genera investigated the perforation type is exclusively scalariform. Cheadle (1942) and Solereder & Meyer (1930) claimed that *Hedychium* is completely devoid of vessels, although Tomlinson (1956) reported finding vessels with scalariform perforation plates in the roots. Cheadle (1942) stated that in seven out of ten species (in his paper Zingiberaceae includes Costaceae) vessels are present in the stems; this was later corrected by Tomlinson (1956), who states that only one, *Renealmia,* has stem vessels. Within Costaceae, *Costus, Dimerocostus* and *Tapeinochilus* have vessels with scalariform perforations in the roots only, but in *Dimerocostus* also in the stem (Tomlinson 1956). In *Canna* (Cannaceae) the root vessels have mostly simple perforations (Tomlinson 1961).

In the genera of Marantaceae studied by Tomlinson (1969) vessels occurred in both roots and stems. In *Donax, Halopegia, Hypselodelphis, Ischnosiphon, Marantochloa, Megaphrynium* and *Thaumatococcus* the root vessels have simple perforations, while in the remaining 10 genera they have scalariform perforations only. The perforation plates in the stem vessels are scalariform, except in *Hypselodelphis,* where there are simple ones as well.

The vessel characters of Zingiberales are less advanced than those of Commelinanae, and on a level with those of Asparagales and Liliales. Rather primitive perforation types are found in the roots of Strelitziaceae, Lowiaceae, Heliconiaceae, Musaceae and Costaceae, while vessels with primitive perforation plates also occur in the stems of one or two genera in Strelitziaceae and Costaceae. Zingiberaceae possess more advanced vessel types in the roots than do the other families, but vessels are found in the stems of one genus only. In *Canna* the roots have vessels with perforation plates of advanced type and simple perforations are rather frequent in the roots of Marantaceae. In the latter family, vessels in the stems are not uncommon in genera with well developed stems and therefore the vessel type of this family may be considered the most advanced within Zingiberales.

Typhanae

Typhales. Sparganium (Sparganiaceae) and *Typha* (Typhaceae) have vessels with scalariform perforation plates in roots, stems and leaves (Cheadle 1942). Neither the type nor the distribution of vessels contradict the often-assumed connection with Pandanales and agree with the condition found in various Commelinanae genera as well. In Arecales, with which group a certain affinity is also suggested, the vessels have more advanced perforation types in the roots and sometimes also in the stems, a fact which does not however exclude some kind of relationship. Typhales, if related to Arecales at all, must have separated from the ancestors of this order before the simple perforation type had developed. Similar considerations apply to the relationships with groups within Commelinanae. In Araceae (Arales) vessels with scalariform perforations are found only in the roots and as regards vessel anatomy this family is distant from Typhales.

Arecanae

Arecales. In 20 out of 26 palm genera investigated the root vessels had simple perforations, two (*Verschaffeltia* and *Chamaerops*) had mostly simple, and two (*Nypa* and *Chamaedorea*) scalariform perforations only (Tomlinson 1961 b). In 10 of the genera investigated the stem vessels had simple perforation plates, three had mostly simple, two simple and scalariform and 10 genera had exclusively scalariform perforation. In *Phytelephas* no vessels were found in the stem, although they were present in the leaves. Vessels with simple perforations are found in the leaves of *Plectocomia,* while vessels with simple and scalariform plates are present in *Calamus* leaves. In the leaves of the remaining species scalariform perforations prevail, while eight genera have reticulate as well. Cheadle (1942) found simple and scalariform perforation plates in the roots of 21 species (the simple perforation plates prevailed in the late metaxylem): in the stems he found vessels with simple and scalariform plates in eight species and vessels with scalariform alone in 15, and in the leaves of 22 species he found scalariform perforation plates.

In the palms the occurrence of vessels in roots, stems and leaves supports the assumed connection with Pandanales. In the latter order, however, the perforation plates are scalariform and it ought therefore be regarded as the more primitive. The vessel characters do not rule out affinities to groups within Poales and Cyperales.

Relationships with Cyclanthales seem to be more distant, because of the primitive vessel tracheids found in that order. Vessel features indicate no relationship of Arecales with Arales.

Pandanales. Freycinetia and *Pandanus* have vessels with scalariform perforations in roots, stems and leaves (Cheadle 1942). This does not contradict the assumed relationships with Arecales, Typhales and Cyclanthales.

Cyclanthales. In the roots and leaves of the genera of Cyclanthaceae studied vessel tracheids with very long scalariform 'perforation plates' are present, while in the stems only tracheids have been found (Fahn 1954 b). A connection with Pandanales, or perhaps with Arecales (in Arecales no stem vessels are present in *Phytelephas*) cannot be excluded. It must be emphasized, however, that the vessel tracheids represent a much more primitive type of conductive system than that found in Pandanales and Arecales.

Aranae

Arales. In Araceae *Acorus* and *Arisaema* have vessels with scalariform perforations in the roots. *Lemna* and *Spirodela* (Lemnaceae) are completely devoid of vessels (Cheadle 1942). If the occurrence of vessels only in the roots is regarded as a primitive feature (as suggested by Cheadle) it is hardly possible to derive Arales from the ancestors of Arecanae. On the other hand, a common origin with groups close to Asparagales does not seem unlikely. If the absence of vessels is regarded as a reduction, then it represents an advanced feature, in which case it would be more justifiable to derive Aranae from ancestors of Pandanales. A comparison of the vessel characters of Piperales and Arales (a connection between these two families is sometimes suggested) would lead to an absurd conclusion, however, since there is no proof that the conductive system in fact arose in the same way in these two families.

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Data base

The following table lists the types of perforation plates occurring in roots, stems and leaves of the monocotyledonous genera, for which information was found in the literature. The only results that can be accepted without reservation are those from papers in which information is given on the actual genera and species studied. Information given about the perforation types of families or tribes only, has been entered under the name of the family or tribe stated by the author. Cheadle often gives information about vessel types for a whole family, not for the individual genera. Therefore only those genera for which a detailed anatomical description is found are included in the table. Where information on specific genera is given, this has been inserted in the table under the generic name.

The descriptions have been standardized and classified into five groups (which coincide with those used by Cheadle). Results from papers in which the proportion of different perforation types are not given, have been classified by the present author if possible. If no information was given about the vessel characteristics of specific organs or genera, a blank entry has been made in the table.

Code to the table: si exclusively simple perforations – si>sc mostly simple perforations – sc=si scalariform and simple perforations in about equal numbers – sc>si mostly scalariform perforations – sc exclusively scalariform perforations – – absence of vessels demonstrated – + vessels present but perforation type unknown – sc* vessel tracheids. – Punctuation marks: , is used if a family or a genus comprises species deviating from each other as regards perforation types, / is used when conflicting evidence on the perforation type is found in the literature and ; is used if two perforation types are described from an organ without any information about their frequency. – is used if the perforation types vary between the classes noted.

Taxon	Root	Stem	Leaves
Alismatales			
Limnocharitaceae			
Hydrocleys	sc	–	–
Limnocharis	si=sc	–	–
Alismataceae			
Alisma	si>sc	–	–
Baldellia		–	–
Damasonium		–	–
Echinodorus	sc	–	–
Limnophyton	si>sc	–	–
Luronium	si>sc	–	–
Ranalisma		–	–
Sagittaria 2 spp.	si>sc	–	–
Wisneria	si>sc	–	–
Hydrocharitales			
Butomaceae			
Butomus	si>sc	–	–
Hydrocharitaceae			
Vallisneria	–	–	–
Elodea	–	–	–
Aponogetonaceae			
Aponogeton	–	–	–

Taxon	Root	Stem	Leaves
Zosterales			
Scheuchzeriaceae			
Scheuchzeria	sc	–	–
Juncaginaceae			
Triglochin	sc	–	–
Potamogetonaceae			
Potamogeton 5 spp.	sc	–	–
Ruppia	–	–	–
Zosteraceae			
Zostera	–	–	–
Zannichelliaceae			
Zannichellia	–	–	–
Najadales			
Najadaceae			
Najas	–	–	–
Dioscoreales			
Dioscoreaceae[1]	sc	sc	
Stemonales			
Stemonaceae			
Croomia	sc	–	–
Stemona	sc	sc	–
Stichoneuron	sc	sc?	–
Trilliaceae			
Medeola	sc	–	–
Paris 4 spp.	sc	–	–
Scoliopus	sc	–	–
Trillium 2 spp.	sc	–	–
Asparagales			
Smilacaceae	sc	sc,–	sc,–
Heterosmilax 4 spp.			sc,–
Rhipogonum 4 spp.			–
Smilax 7 spp.			
Philesiaceae			
Behnia	si>sc	–	
Eustrephus 2spp.	si	sc/–	sc?/–
Geitonoplesium	si=sc/si>sc	sc	sc*/–
Lapageria	sc*/sc	sc*/sc	–
Luzuriaga 5 spp.	sc*/sc	sc*/sc	–
Philesia	sc*/sc	–/sc	–
Petermannia	sc	–/sc	–
Convallariaceae			
Convallarieae			
Convallaria	si>sc		–
Aspidistreae			
Aspidistra	sc	–	–
Polygonateae[2]	si=sc,sc>si	sc,–	–
Ophiopogoneae[3]	si=sc,sc	–	
Herreriaceae			
Herreria 4 spp.		sc	
Asparagaceae			
Asparagus 4 spp.	si	sc	
Ruscaceae			
Ruscus 2 spp.	sc	–	
Danae	sc	sc	
Semele	si	sc	
Nolinaceae			
Nolina	si?	–	sc
Dracaenaceae			
Dracaena	si?	–	sc
Asteliaceae[4]	sc	–	–
Dianellaceae[5]	si=sc,si>sc	–	–
Phormiaceae			
Xanthorrhoeaceae			
Acanthocarpus	si	–	sc
Baxteria	sc?	–	–
Calectasia 2 spp.	si	–	–
Chamaexeros 2 spp.	si	–	–
Dasypogon 2 spp.	si	–	–
Kingia	sc	–	–
Lomandra 34 spp.	si	–	–
Xanthorrhoea 14 spp.	si	–/sc	sc
Hanguanaceae			
Hanguana		–	–
Asphodelaceae			
Asphodeleae p.p.	si	–,sc	
Agrostocrinum		sc	
Asphodelus		sc	
Bulbine 4 spp.		–	
Bulbinopsis		–	
Herpolirion		–	
Nanolirion		–	
Aloineae[6]	si	–	
Kniphofieae[7]	si=sc	–	
Anthericaceae			
Asphodeleae p.p.[8]	si	–,sc	
Anthericum		sc	
Arthropodium 2 spp.		sc	
Caesia 2 spp.		–,sc	
Johnsonieae[9]	si,sc	–,sc>si	–
Borya	sc		
Johnsonia		sc	
Tricoryne		sc>si	
Aphyllanthaceae	si>sc	–	–
Aphyllanthes			
Agavaceae			
Hosta 2 spp.	sc	–	–
Agave	si	–	–
Hemerocallidaceae			
Hemerocallis	sc	–	–
Hyacinthaceae			
Scilleae[10]	sc>si	–	–
Albuca 2 spp.	si=sc		
Camassia	si=sc		
Dipcadi	si=sc		
Drimia	sc		
Drimiopsis	sc		
Eucomis	sc		
Galtonia	si=sc		
Hyacinthus	sc		
Lachenalia 2 spp.	sc		
Litanthus	sc		
Muscari	sc		
Ornithogalum 3 spp.	si=sc		
Polyxena 2 spp.	sc		
Rhadamanthus	sc		

Taxon	Root	Stem	Leaves
Bowieeae[11]	sc	–	–
Miluleae			
Milula	si>sc		
Massonieae			
Massonia	sc		
Alliaceae			
Agapantheae	sc>si	–	–
Agapanthus 3 spp.	sc		
Tulbaghia 4 spp.	si		
Allieae[12]	si>sc	–	
Gilliesieae[13]	si=sc	–	–
Amaryllidaceae			
Galantheae[14]	sc	–	–
Amaryllideae[15]	sc	–	–
Crineae[16]	sc	–	–
Zephyrantheae[17]	sc	–	–
Haemantheae[18]	sc	–	–
Ixiolirieae	sc	–	–
Ixiolirion			
Eucharideae[19]	sc	–	–
Eustephieae			
Phaedranassa	sc	–	–
Hippeastreae[20]	sc	–	–
Narcisseae			
Narcissus 2 spp.	sc	–	–
Hypoxidaceae			
Campynema	–/sc?	–	–
Curculigo 2 spp.	sc	–	–
Hypoxis 7 spp.	sc	–	–
Pauridia	sc	–	–
Velloziaceae			
Barbacenia 3 spp.	si	–	–/sc
Barbaceniopsis	si	–	sc
Vellozia 2 spp.	si	–/sc	–/sc
Tecophilaeaceae[21]	sc	–	–
Liliales			
Colchicaceae			
Iphigenieae[22]	sc	–	–
Colchiceae			
Colchicum	sc	–	–
Anguillarieae[23]	sc	–	–
Uvularieae[24]	sc	–	–
Iridaceae			
Sisyrinchieae[25]	si	–,si>sc	–,sc
Sisyrinchium 4 spp.		si>sc	–,sc
Aristeae	sc,si>sc	–	–
Aristea 3 spp.	sc		
Klattia 2 spp.	sc		
Patersonia 3 spp.	sc		
Schizostylis	si>sc		
Witsenia	sc		
Tigrideae[26]	si	–	–
Irideae[27]	si	–	–
Ixieae[28]	si>sc	–	–
Croceae[29]	si	–	–
Gladioleae[30]	si	–	–
Antholyzeae[31]	si>sc	–	–
Alstroemeriaceae			
Alstroemeria 3 spp.	sc>si,sc	sc	–
Bomarea 3 spp.	sc	sc	–
Leontochir		sc	–
Schickendantzia	sc	sc	–
Liliaceae[32]	sc	–	–
Melanthiaceae			
Narthecieae	sc	–	–
Aletris			
Veratreae[33]	sc	–	–
Tricyrtideae[34]	sc	sc	–
Heloniadeae[35]	sc	–	–
Petrosavia	–/sc	–	–
Triuridales			
Triuridaceae			
Andruris 4 spp.	–	–	–
Burmanniales			
Burmanniaceae			
Burmannia 2 spp.	sc	sc	sc
Thismiaceae			
Corsiaceae			
Orchidales			
Apostasiaceae			
Adactylus	si>sc	si=sc/–	
Apostasia		+	
Neuwiedia	si=sc/–?		
Cypripediaceae			
Cypripedium 11 spp.	si	–	
Paphiopedilum 7 spp.	–	–	–
Phragmipedium 5 spp.	si	–	–
Selenipedium 2 spp.	si	–	–
Orchidaceae			
Appendicula		+	
Dendrobium	+	–	
Dichaea		sc	
Epidendrum		–	sc
Habenaria		–	
Isochilus		+	
Neottia		+	
Oncidium		–	
Phalaenopsis		–	
Physosiphon		+	
Pleurothallis		+	
Pogonopsis	+		
Renanthera		–	
Scaphyglottis			sc
Thunia		+	
Vanilla 2 spp.	si	sc	
Vanda	+	–/+	
Haemodorales			
Haemodoraceae			
Haemodoreae[36]	si>sc	–	–
Dilatris	sc		
Lachnanthes		sc	sc?
Lanaria	sc		
Xiphidium		sc?	sc

Taxon	Root	Stem	Leaves
Conostyleae[37]	si>sc	–	–
Tribonanthes 3 spp.	sc		
Philydraceae[38]	sc	–	–
Orthothylax	sc	–	–
Taccales			
Taccaceae			
Schizocapsa	sc*	–	–
Tacca 3 spp.	sc*	–	–
Pontederiales			
Pontederiaceae			
Eichhornia 2 spp.	sc	–,sc	–
Heteranthera 3 spp.	sc	–,sc	–
Monochoria 6 spp.	sc	–	–
Pontederia 2 spp.	sc	–,sc?	–
Reussia	sc	–	–
Bromeliales			
Bromeliaceae			
Acanthostachys	sc	sc	sc
Aechmea	sc	sc,–	–
Ananas	sc	–	–
Billbergia	sc	–	–
Cryptanthus	sc	sc	sc
Dyckia	sc	sc,–	–
Guzmania	sc	sc	–
Hechtia	sc	sc	sc
Hohenbergia	sc	sc	sc
Neoglaziovia	sc	–	–
Nidularium	sc	–	–
Ochagavia	sc	–	–
Orthophytum	sc	sc	sc
Pitcairnia	si	sc	sc
Quesnelia	sc	–	–
Vriesia	si	sc	sc
Commelinales			
Commelinaceae			
Aneilema 8 spp.	si	si	si
Anthericopsis	si	si	si
Aploleia	si	si	si
Ballya	si	si	si
Belosynapsis 2 spp.	si	si	si
Callisia 6 spp.	si	si	si
Campelia	si	si	si
Cochliostema 2 spp.	si	si	si
Coleotrype	si	si	si
Commelina 10 spp.	si	si>sc	si>sc
Cuthbertia 2 spp.	si	si	si
Cyanotis 16 spp.	si	si	si
Dichorisandra 2 spp.	si	si	si
Floscopa 2 spp.	si	si	si
Forrestia	si	si	si
Geogenanthus	si	si	si
Gibasis 2 spp.	si	si	si
Hadrodemas			si
Murdannia 5 spp.	si	si	si
Palisota 4 spp.	si	si	si
Phaeosphaerion		si	si
Pollia 5 spp.	si	si	si
Polyspatha 2 spp.	si	si	si
Rhoeo	si	si>sc	si>sc
Setcreasea	si	si	si
Siderasis			si
Stanfieldiella	si	si	si
Tinantia	si	si	si
Tradescantia 12 spp.	si	si>sc/si=sc	si>sc/si=sc
Triceratella	si	si	si
Tripogandra 3 spp.	si	si	si
Zebrina	si	si/si=sc	si/si=sc
Mayacaceae			
Mayaca 3 spp.	sc	sc	sc*/sc?
Cartonemataceae			
Cartonema	si>sc	–	–
Xyridaceae			
Abolboda 3 spp.	si	si	si
Achlyphila	si	si	si
Xyris 30 spp.	si	si	si
Rapateaceae			
Rapateeae			
Cephalostemon	sc	sc	–
Duckea 3 spp.	sc	sc	–
Rapatea 7 spp.	sc	sc	–
Spathanthus 2 spp.	si	si	si
Monotremeae[39]	si=sc	si	–
Schoenocephalieae[40]	sc	sc	–
Saxofridericieae[41]	sc	sc	–
Eriocaulales			
Eriocaulaceae[42]	si>sc	si>sc	si>sc
Eriocaulon 8 spp.	si/sc?	si/sc?	sc
Tonina		sc	
Juncales			
Juncaceae	si–sc>si	si>sc–sc>si	si>sc–sc
Distichia 2 spp.	si>sc		sc/–
Juncus 28 spp.	si–sc>si	si>sc–sc>si	si=sc–sc
Luzula 12 spp.	si,si>sc	si=sc	si=sc,sc>si
Marsippospermum	sc>si	sc	sc
Oxychloe 3 spp.	sc>si	sc	sc
Prionium	sc>si	sc	sc
Rostkovia	sc	sc	sc
Thurniaceae			
Thurnia 2 spp.	sc>si/sc	sc	sc
Cyperales			
Cyperaceae			
Cariceae[43]	si>sc	sc>si–si=sc	sc>si
Carex* 45 spp.	si	si;sc	si,sc
Schoenoxiphium* 3 spp.	si;sc?	si;sc	si;sc
Uncinia* 4 spp.		si;sc	
Cryptangieae[44]	si>sc	sc>si,sc	sc>si,sc

Taxon	Root	Stem	Leaves
Afrotrilepis 2 spp.	si	si;sc	si;sc?
Calyptrocarya* 2 spp.	sc		
Cephalocarpus		si;sc	si
Coleochloa		si	si
Cryptangium°		sc	sc
Didymiandrum	si	sc	
Everardia°		sc	sc
Lagenocarpus* 2 spp.		sc	sc
Cypereae[45]	si>sc	si=sc–si>sc	sc>si–si=sc
Cyperus* 13 spp.		si;sc?	
Kyllingia 2 spp.		si;sc?	si;sc
Mariscus* 6 spp.		si	si;sc?
Pycreus 2 spp.		si	
Hypolytreae	si=sc–si>sc	sc>si	sc,sc>si
Chorizandra°			sc
Chrysithrix*	si;sc?	si;sc	si;sc
Hypolytrum 13 spp.	sc	sc	sc
Lepironia		si	
Mapania		sc	
Scirpodendron	si;sc	sc	
Rhynchosporeae[46]	si>sc	sc>si–si=sc	sc>si
Asterochaete		si	si
Carpha°			sc
Caustis* 3 spp.	si;sc?	si,sc	sc,sc>si
Cladium* 4 spp.	sc,sc>si	sc,sc>si	sc,sc>si
Costularia°			sc
Cyathochaeta*		si	si,sc?
Dichromena		si	
Elynanthus	si	si;sc	si
Epischoenus* 2 spp.	si	si	
Evandra		sc	
Gahnia* 5 spp.		si;sc	si
Gymnoschoenus*			si;sc?
Lepidosperma* 3 spp.	si,sc?		si
Machaerina* 3 spp.		si,sc?	sc/si;sc?
Macrochaetium		sc	
Mesomelaena* 3 spp.	si	si	si;sc?
Neesenbeckia		si	si;sc?
Oreobolus°		sc	sc
Ptilanthelium		si	
Reedia*	si	si;sc	si;sc?
Rhynchospora* 3 spp.		si	si
Schoenus* 6 spp.		si	sc
Tetraria* 4 spp.		si	si;sc
Tetrariopsis*		si;sc	si
Trianoptiles*		sc	si
Sclerieae[47]	si>sc	si=sc–si>sc	sc>si–si=sc
Scleria* 10 spp.		si;sc	si
Scirpeae[48]	si>sc	si=sc	sc>si–si=sc
Eleocharis* 4 spp.		si	
Eriophorum* 3 spp.		si	si
Ficinia* 4 spp.		sc	si;sc?
Fuirena		si	si
Lipocarpha* 2 spp.		si;sc	si;sc?
Scirpus* 14 spp.	si	si;sc	
Centrolepidales			
Centrolepidaceae			
Aphelia 4 spp.		sc	sc
Centrolepis 8 spp.		sc	sc
Gaimardia 3 spp.		sc	sc
Pseudalepyrum 2 spp.	sc	sc	sc
Trithuria 2 spp.	sc	sc	sc,–
Poales			
Restionaceae	si	si–sc	si>sc–sc
Anthochortus		sc	–
Calorophus 3 spp.	+	si	–
Cannomois 6 spp.	+	sc=si	–
Chaetanthus		si	
Chondropetalum	si	sc	–
Coleocarya		sc	
Dielsia 2 spp.		sc	
Elegia 21 spp.		sc	–
Harperia		sc	
Hopkinsia		si	–
Hypodiscus 9 spp.	+	sc=si	–
Hypolaena 7 spp.	+,si	sc,si	–
Lepidobolus 3 spp.	+	si	–
Leptocarpus 19 spp.	+	si,si>sc	–
Lepyrodia 17 spp.	+	sc=si	–
Loxocarya 6 spp.		+	–
Lyginia 2 spp.	+	sc	
Mastersiella 5 spp.	+	si>sc	–
Meeboldina		sc	
Onychosepalum		+	
Phyllocomos		sc	–
Restio 85 spp.	+,si	sc	–/sc*
Sporadanthus	+	si>sc	–
Staberoha 5 spp.	si	+	–
Thamnochortus 20 spp.	+	si	–
Willdenowia 8 spp.		sc,sc=si	–
Flagellariaceae			
Flagellaria		si>sc	sc>si
Joinvillea 2 spp.		si>sc	sc,si>sc
Ecdeiocoleaceae			
Ecdeiocolea	+	sc=si	–
Poaceae[49, 50]	si–si>sc	si–si>sc	si–si=sc
Zingiberales			
Lowiaceae			
Orchidantha 3 spp.	sc	–	–

Taxon	Root	Stem	Leaves
Strelitziaceae			
Phenakospermum	sc>si	sc	–
Ravenala 3 spp.	sc	–	
Strelitzia 5 spp.	sc	sc	–
Heliconiaceae			
Heliconia 7 spp.	sc	–	–
Musaceae			
Ensete 3 spp.	si=sc	–	–
Musa 7 spp.	si>sc	–	–
Zingiberaceae			
Aframomum	sc	–	–
Alpinia 4 spp.	si/sc	–	–
Brachychilum	sc	–	–
Boesenbergia	sc	–	–
Burbidgea	sc	–	–
Camptandra 2 spp.	sc	–	–
Catimbium 2 spp.	sc>si	–	–
Cautleya	sc	–	–
Curcuma 2 spp.		–	–
Elettaria	si=sc	–	–
Elettariopsis	sc>si	–	–
Geostachys	sc	–	–
Globba 4 spp.	sc	–	–
Hedychium 4 spp.	sc/–	–	–
Hornstedtia 2 spp.	sc	–	–
Kaempferia 6 spp.	sc	–	–
Renealmia 2 spp.	sc	sc	–
Roscoea 3 spp.	sc	–	–
Scaphochlamys 3 spp.	sc	–	–
Zingiber 2 spp.	sc	–	–
Costaceae			
Costus 9 spp.	sc	–	–
Dimerocostus	sc	sc	
Tapeinochilus	sc	–	–
Cannaceae			
Canna 5 spp.	si>sc	–	–
Marantaceae			
Ataenidia	sc		
Calathea 12 spp.	sc		
Ctenanthe	sc		
Donax	si		
Halopegia	si		
Hypselodelphis	si	si>sc	
Ischnosiphon	si		
Maranta 2 spp.	sc		
Marantochloa 6 spp.	si	sc	
Megaphrynium	si		
Monotagma 2 spp.	sc		
Phrynium	sc		
Sarcophrynium	sc	sc	
Stromanthe 3 spp.	sc		
Thalia 2 spp.	sc	sc	
Thaumatococcus	si	sc	
Trachophrynium	sc		
Typhales			
Sparganiaceae			
Sparganium 5 spp.	sc	sc	sc?
Typhaceae			
Typha 2 spp.	sc	sc	sc
Arecales			
Arecaceae			
Areca	si	sc	sc
Bactris 2 spp.	si	si	sc
Borassus	si	si	sc
Calamus 11 spp.	si	si	si=sc
Caryota 6 spp.	+	+	+
Chamaedorea	sc	sc	sc
Chamaerops	si>sc	si>sc	sc
Chrysalidocarpus	si	sc	sc
Coccothrinax			sc
Copernicia			sc
Corypha	si		
Cryosophila			sc
Daemonorops	si	si	sc
Elaeis	si	si	sc
Howeia	si	sc	sc
Hyphaene 2 spp.	si	si	sc
Latania	si		sc
Licuala	si	sc	sc
Livistona	si	sc	sc
Lodoicea			sc
Myrialepis		si	sc
Nannorhops			sc
Nypa	sc		
Paurotis			sc
Phoenix	si	sc	sc
Pholidocarpus			sc
Phytelephas	si	–	sc
Pinanga		sc	sc
Plectocomia	si	si	si
Pritchardia			sc
Ptychosperma	si	sc	sc
Raphia	si	si	sc
Raphidophyllum		si>sc	sc
Rhapis		sc	sc
Sabal			sc
Salacca	si	si	sc
Sclerosperma		si=sc	
Serenoa	si	si=sc	sc
Thrinax			sc
Trachycarpus		si>sc	sc
Trithrinax			sc
Veitchia			sc
Verschaffeltia	si>sc		
Wallichia	si		
Washingtonia			sc
Zombia			sc
Pandanales			
Pandanaceae			
Freycinetia	sc	sc	sc
Pandanus 2 spp.	sc	sc	sc

Taxon	Root	Stem	Leaves
Cyclanthales			
Cyclanthaceae			
Carludovica	sc*	–	sc*
Cyclanthus	sc*	–	sc
Ludovia	sc	–	sc
Arales			
Araceae[51]	sc		
Lemnaceae[52]	–	–	–

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[1] *Dioscorea* (97 spp.), *Rajania* (4 spp.), *Tamus* (2 spp.), *Stenomeris* (2 spp.), *Avetra, Trichopus* – [2] *Clintonia, Drymophila* (2 spp.), *Maianthemum, Polygonatum, Smilacina* (2 spp.) – [3] *Liriope, Mondo* – [4] *Astelia, Milligania* (3 spp.) – [5] *Dianella* (4 spp.), *Stypandra* (2 spp.), *Walleria* – [6] *Aloe* (10 spp.), *Apicra* (3 spp.), *Chortolirion, Gasteria* (2 spp.) – [7] *Blandfordia* (2 spp.), *Kniphofia, Notosceptrum* – [8] Also *Chamaescilla, Chlorophytum* (2 spp.), *Chlorogalum, Dichopogon, Paradisea, Thysanotus* (2 spp.), *Xeronema* – [9] Also *Bartlingia* (3 spp.), *Sowerbaea* – [10] Also *Scilla* (2 spp.), *Urginea, Veltheimia* (2 spp.) – [11] *Bowiea, Eriospermum, Schizobasis* – [12] *Allium* (6 spp.), *Bloomeria, Brodiaea, Muilla, Nothoscordum* (2 spp.) – [13] *Miersia, Trichlora* – [14] *Galanthus, Leucojum* (2 spp.) – [15] *Amaryllis, Brunsvigia* (2 spp.), *Nerine* (4 spp.) – [16] *Ammocharis, Crinum* (6 spp.), *Cybistetes, Cyrtanthus, Vallota* – [17] *Cooperia* (2 spp.), *Gethyllis, Zephyranthes* (2 spp.) – [18] *Buphane, Clivia* (2 spp.), *Haemanthus* (2 spp.), *Strumaria* (2 spp.) – [19] *Calostemma, Eucharis, Eurycles, Hymenocallis, Stenomesson* (2 spp.) – [20] *Hippeastrum* (2 spp.), *Sprekelia* – [21] *Conanthera* (2 spp.), *Cyanella* (2 spp.), *Odontostomum, Tecophilaea* – [22] *Androcymbium* (2 spp.), *Ornithoglossum, Reya* – [23] *Anguillaria, Baeometra, Dipidax, Neodregea* – [24] *Gloriosa, Kreysigia, Schellhammeria, Uvularia* (2 spp.), *Walleria* – [25] *Bobartia, Diplarrhena, Libertia, Orthrosanthus* – [26] *Ferraria, Hexaglottis, Homeria* – [27] *Dietes, Hermodactylus, Iris* (7 spp.), *Moraea* (2 spp.) – [28] *Dierama* (2 spp.), *Freesia, Geissorhiza, Hesperantha, Ixia, Lapeyrousia, Micranthus, Pillansia, Watsonia* – [29] *Galaxia, Romulea* (2 spp.), *Syringodea* (2 spp.) – [30] *Babiana* (2 spp.), *Crocosmia, Gladiolus, Melasphaerula, Sparaxis* (2 spp.), *Synnotia, Tritonia* (3 spp.), *Tritoniopsis* – [31] *Anaclanthe, Anapalina* (3 spp.), *Antholyza, Curtonus, Petamenes* – [32] *Calochortus, Erythronium, Fritillaria, Lilium* (4 spp.), *Tulipa* – [33] *Veratrum, Zygadenus* – [34] *Sandersonia, Tricyrtis* – [35] Also *Chaemaelirion, Chionographis, Helonias, Ypsilandra* – [36] Also *Haemodorum* (4 spp.), *Phlebocarya, Wachendorfia* – [37] Also *Anigozanthos* (4 spp.), *Blancoa, Conostylis* (4 spp.), *Macropidia* – [38] Also *Helmholtzia, Philydrum, Pritzelia* – [39] *Maschalocephalus, Monotrema* (4 spp.) *Potarophytum, Windsorina* – [40] *Guacamaya, Epidryos, Schoenocephalium* (3 spp.) – [41] *Phelpsiella, Saxofridericia* (2 spp.), *Stegolepis* (2 spp.) – [42] Also *Lachnocaulon* (3 spp.), *Leiothrix, Paepalanthus* (4 spp.), *Syngonanthus* (2 spp.) – [43] Genera of Cyperaceae investigated by Cheadle & Kosakai and Metcalfe are marked *, whereas genera studied only by Cheadle & Kosakai are marked° and those mentioned only by Metcalfe are unmarked – [44] Also *Becquerelia** – [45] Also *Dulichium*°, *Remirea* – [46] Also *Tricostularia*° – [47] Also *Diplacrum*°, *Kobresia*° (2 spp.) – [48] Also *Bulbostylis*°, *Fimbristylis*° (2 spp.) – [49] Genera of Poaceae investigated (genera mentioned by Metcalfe (1950) and Cheadle (1955) are marked *, whereas genera studied only by Cheadle are marked ° and those mentioned only by Metcalfe are unmarked): *Acroceras, Aegilops* (3 spp.), *Aeluropus, Agropyron** (4 spp.), *Agrostis** (2 spp.), *Aira, Alloteropsis* (2 spp.), *Alopecurus* (3 spp.), *Ammophila**, *Ampelodesmos, Andropogon** (2 spp.), *Anomochloa, Anthochloa, Anthoxanthum**, *Apluda, Aristida* (5 spp.), *Arrhenatherum, Arthraxon, Arundinaria*°, *Arundinella* (2 spp.), *Arundo**, *Avena** (2 spp.), *Beckeropsis* (3 spp.), *Bothriochloa* (2 spp.), *Bouteloua**, *Brachiaria* (4 spp.), *Brachypodium* (2 spp.), *Bromuniola, Bromus** (8 spp.), *Brylkinia, Buchloe, Calamagrostis**, *Calamovilfa, Capillipedium, Catapodium, Cenchrus** (3 spp.), *Centotheca, Chloris** (6 spp.), *Chrysopogon, Cleistachne, Coelachne* (3 spp.), *Coelachyrum, Coix, Coleanthus, Cortaderia* (2 spp.), *Corynephorus, Cymbopogon* (5 spp.), *Cynodon* (3 spp.), *Cynosurus, Cyrtococcum* (2 spp.), *Dactylis**, *Dactyloctenium* (2 spp.), *Danthonia** (16 spp.), *Deschampsia**, *Desmostachya, Deyeuxia, Diarrhena, Dichanthium* (3 spp.), *Dichelachne, Digitaria** (5 spp.), *Dimeria, Distichlis, Echinochloa** (2 spp.), *Ectosperma, Ehrharta* (2 spp.), *Eleusine* (2 spp.), *Elymus* (6 spp.), *Elyonurus* (2 spp.), *Enneapogon, Eragrostiella, Eragrostis* (6 spp.), *Eriachne, Erianthus, Euchlaena, Euchlaezea, Euclasta, Eulalia* (2 spp.), *Festuca* (5 spp.), *Fingerhuthia, Garnotia, Glyceria** (2 spp.), *Gymnopogon* (4 spp.), *Gynerium*°, *Hakonechloa, Helictotrichon* (3 spp.), *Hemarthria, Heteranthelium, Heteranthoecia, Heteropogon, Hierochloe* (2 spp.), *Hilaria*°, *Holcus** (2 spp.), *Hordelymus, Hordeum** (4 spp.), *Hyparrhenia, Imperata, Indopoa, Isachne* (3 spp.), *Ischaemum* (2 spp.), *Koeleria* (2 spp.), *Lagurus, Lamarckia, Leersia** (2 spp.), *Leptaspis, Leptocarydion, Leptochloa* (2 spp.), *Lolium**, *Lophatherum, Loudetia* (2 spp.), *Lycochloa, Lygeum, Megastachya, Melica** (3 spp.), *Melinis, Micraira, Microlaena, Microstegium, Miscanthidium, Miscanthus* (2 spp.), *Molinia* (2 spp.), *Muhlenbergia**, *Munroa, Nardus, Neurolepis* (2 spp.), *Neyraudia*°, *Olyra, Oplismenus* (2 spp.), *Orcuttia, Oropetium, Oryza, Oryzopsis** (3 spp.), *Panicum** (7 spp.), *Parapholis, Pariana* (3 spp.), *Paspalidium, Paspalum** (4 spp.), *Pennisetum* (2 spp.), *Pentapogon, Perotis* (2 spp.), *Phaenosperma, Phalaris** (3 spp.), *Pharus, Phleum**, *Phragmites**, *Phyllorachis**, *Plectrachne* (3 spp.), *Pleioblastus*°, *Pleuropogon*°, *Poa** (3 spp.), *Pogonarthria, Pogonatherum, Polypogon* (2 spp.), *Pommereulla, Psammochloa, Pseudanthistiria, Puccinellia* (2 spp.), *Rhynchelytrum, Rhytachne, Richardsiella, Rottboellia, Saccharum* (3 spp.), *Sacciolepis* (4 spp.), *Schizachyrium, Secale**, *Setaria** (5 spp.), *Sieglingia, Snowdenia, Sorghum**, *Spartina** (2 spp.), *Sphaerocaryum, Spinifex, Sporobolus** (9 spp.), *Stenotaphrum* (2 spp.), *Stipa* (6 spp.), *Streptochaeta, Streptogyna, Tetrarrhena, Themeda* (4 spp.), *Thysanolaena**, *Tragus* (2 spp.), *Tridens?, Trikeraia, Triplopogon, Tripsacum**, *Triraphis, Trichachne, Tristachya* (2 spp.), *Triticum** (3 spp.), *Uniola, Urochloa, Vetiveria, Zea**, *Zizania** – [50] Genera of Bambuseae investigated: *Arthrostylidium* (2 spp.), *Arundinaria* (12 spp.), *Atractocarpa, Bambusa* (2 spp.), *Cephalostachyum, Chloothamnus, Chusquea** (2 spp.), *Dendrocalamus** (2 spp.), *Dinochloa, Gigantochloa, Greslania, Guadua, Guaduella, Melocalamus, Melocanna, Merostachys, Nastus* (2 spp.), *Ochlandra, Oreobambos, Oxytenanthera, Phyllostachys** (6 spp.), *Pseudostachyum, Puellia, Schizostachyum, Shibataea* (2 spp.), *Thyrsostachys* – [51] *Acorus, Arisaema* – [52] *Lemna, Spirodela*.

Morphology and intraspecific variation in Geastrum triplex Jungh.

Stellan Sunhede

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Swedish material of *Geastrum triplex* Jungh. has been studied in the field and in the laboratory. The morphology and intraspecific variation of mature or nearly mature fruitbodies are described and illustrated with photographs and drawings. More than 3150 fruitbodies have been investigated. SEM-pictures show spores, capillitial threads and the surface of the endoperidium. The use of the name *Geastrum triplex* Jungh., instead of *G. indicum* (Klotzsch) Rauschert, is explained.

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The author has studied the biology and collected fruitbodies of *Geastrum* species in southern Sweden during more than 450 days in the field the last seven years (mainly September–December). Especially the islands of Öland, Gotland and Gotska Sandön have been investigated. This is the second paper discussing the morphology and intraspecific variation in mature or nearly mature fruitbodies of Swedish species of *Geastrum*. An earlier paper (Sunhede 1974 b) dealt with *G. umbilicatum* Fr.; in that paper the great variation in different characteristics of mature fruitbodies of *Geastrum*, as well as the importance of field experience, was pointed out.

The material of *Geastrum triplex* Jungh. examined in this study comprises c. 2700 specimens from the author's herbarium and c. 450 specimens from GB, LD, S, UPS and UPSV. For methods, see Sunhede (1974 b). Unless otherwise stated, all measurements of fruitbodies have been made on dry specimens. Routine investigations with the microscope have been performed in 2% KOH, in lactic blue and Melzer's reagent. All measurements reported were made in KOH. Spores were also measured in lactic blue. There was no significant difference in spore measurements between KOH and lactic blue preparations. I prefer the KOH preparations because the spore outline is more distinct. The basidial development in *G. triplex* will be discussed in a forthcoming paper.

Exoperidium

Young fruitbodies, just prior to opening, are often partly or wholly visible on the ground (Fig. 2 A, B). They are rounded with a small tip at the top, more or less onion-shaped, rarely irregular, light brownish and 1.5–6 cm broad or more (Figs. 2 A, B, E, F; 4 C; 5 A: j). At the base of loosened, unexpanded specimens there may be a mycelial tuft consisting of whitish hyphae intermixed with debris (Fig. 4 C: b, e, f, j, k). The exoperidium splits from the apex in a stellate manner, more or less deeply, into 3–10 (mostly 5–7) regular or irregular rays of varying shape (Figs. 2 A, B, C; 4 B: c; 5 B; 7 B). The rays often recurve under the unsplit part of the exoperidium (Figs. 1 B, D, F, 3 A: d–j; 4 A: a, c, B: b, d, f) but may also take up other positions (Figs. 3 A: a, B; 4 B: c; 5 A: d). The margins of the rays may be recurved (Figs. 3 A: a, 4 A: a, c, B: c). The rays are non-hygroscopic.

The exoperidium of expanded fruitbodies may be saccate (Figs. 1 A, D; 4 B: a, b; 5 A: f, h), somewhat saccate (Fig. 5 A: d, e, i), plane (Fig. 5 A: c, g) or arched (Figs. 1 F, 4 A: a, c; 5 A: a, b). The frequency of the different shapes is illustrated in Fig. 7 B. The maximal diameter of expanded fruitbodies (cf. Fig. 3 A) varies between 2.3. and 15.1 cm. A specimen with the exoperidium forced out into stellate configuration (cf. Fig. 5 B) had a maximum diameter of 18 cm. When collected in the field (as rather fresh) the corresponding diameter was 22.4 cm.

The fleshy pseudoparenchymatic layer in a fresh, just opened fruitbody is whitish to sordid white and up to 5 mm thick or more. The colour changes with age to pale buff to brown of different shades. Older specimens (Fig. 1 E, F) are dark brown. In expanding fruitbodies the central region of the fleshy layer often breaks loose from that of the rays (Fig. 2 C) forming a collar or a cup around the endoperidium (Figs. 1 A–D, F; 4 A: a, c, d). The pseudoparenchymatic layer of the rays may crack in different ways or peel off. With wet conditions in nature the fleshy tissue seems to gelatinize gradually but it may persist for a long time. When drying the fleshy layer shrinks, becomes hard and brittle, and its colour changes to some degree.

The middle, fibrous layer of the exoperidium is rarely – even in old specimens – totally free from pseudoparenchymatic and mycelial remnants. When free (Fig. 4 B: e) it is pale brownish to dirty grey and papery coriaceous.

The third and the outermost layer, the mycelial stratum, is brownish, rather thick and persistent. It often cracks radially in a characteristic pattern (Fig. 3 C), or sometimes more irregularly. The mycelial layer may begin to crack in unexpanded fruitbodies (Fig. 2 B, arrows). Generally, it is free or nearly free from dirt and debris (Fig. 2 A, B). The basal mycelium (cf. Fig. 4 C: b) leaves a scar at the point of attachment when the expanding fruitbody is loosened from the ground (Figs. 3 C; 4 B: d).

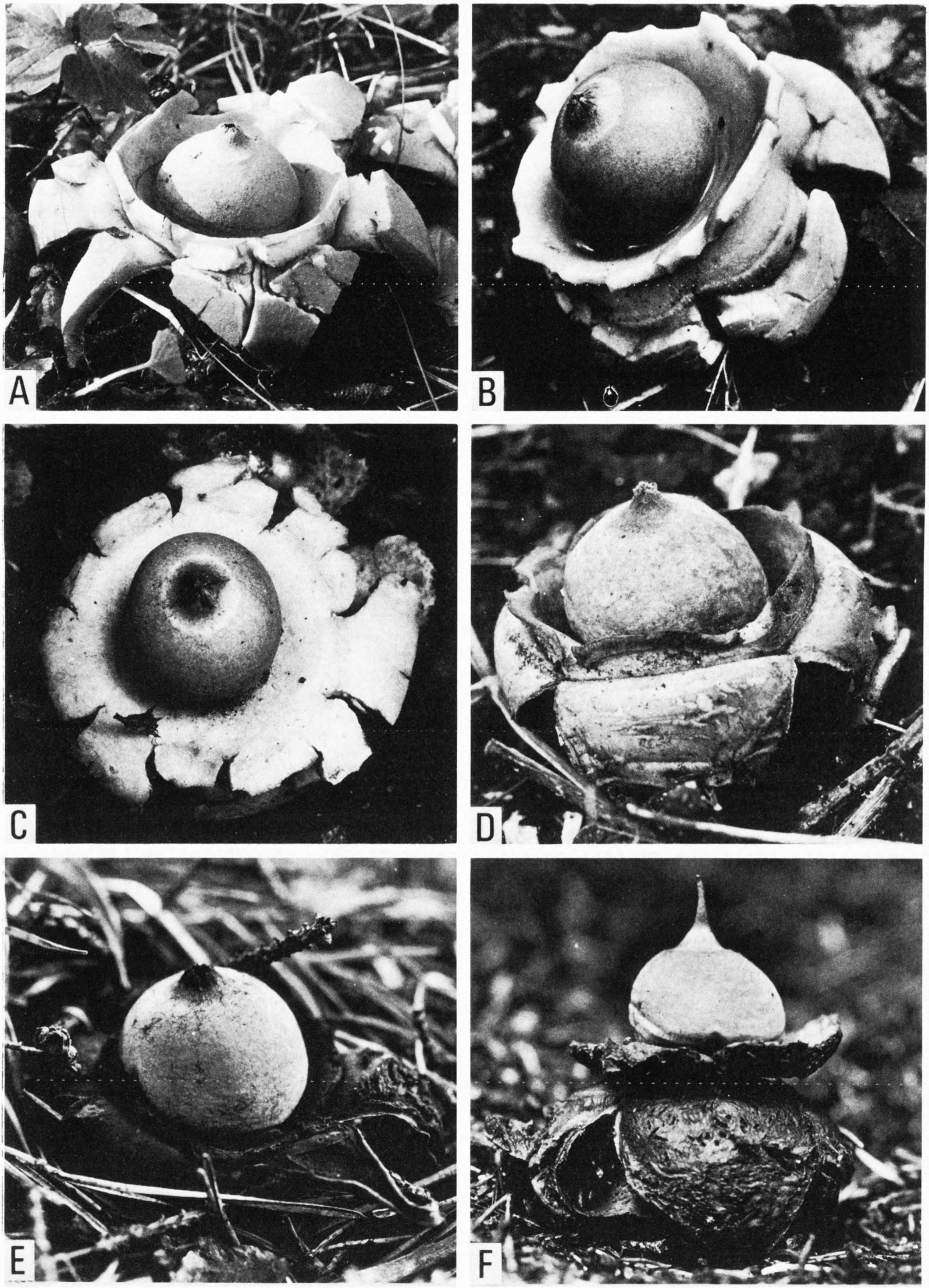
Endoperidium

The endoperidium is often sessile. A short pedicel (stalk) may be seen when the fleshy layer of the exoperidium has disappeared (Figs. 4 B: e; 5 A: i; 6 A: b, c, B: k). The pedicel is rounded to oblong in cross section. The endoperidium is generally more or less globose, but may be depressed globose, depressed, laterally compressed, pyriform, obpyriform, oblong (seen from above) or irregular. The size, shape and position of the peristome also influence the general shape of the endoperidium. Examples of the variation in size and shape are given especially in Figs. 3 A; 5; 6 A but also in Figs. 1; 2 A, C; 3 D, E; 4 A, B. An apophysis occurs rarely (Fig. 6 B: k). The maximum diameter of the endoperidium is 10.8–54 mm and the height (normal peristome included) is 10–41 mm. The outer side of the endoperidial wall is smooth. The colour is generally of rather pale greyish or pale brownish shades or sometimes seemingly darker brown due to spore deposits. Argillaceous endoperidia are rarely observed. Endoperidia with dark areas or spots of unknown origin have been observed in a few specimens (Fig. 3 E).

There is normally one stoma, usually at the top of the endoperidium, but specimens with two and six stomata have been observed (Figs. 3 D; 6 A: p, q). A stoma is rarely lacking (Fig. 6 A: g). Besides the true stoma there may be one or more regular holes in the endoperidial wall, made by insects, e.g. the beetle *Lycoperdina succincta* L. Such holes function in spore liberation (Sunhede 1974 a).

The peristome is mostly fibrillose. It is often well delimited (definite) from the rest of the endoperidium, due to different colour (darker or lighter) and/or through topographical demarcation (Figs. 1 B, C; 2 A, C, D; 3 A: a; 6 B: a, b, d–j). It is sometimes indefinite (Figs. 1 D, E; 6 B: c). The normal peristome is often more or less mammiform (Figs. 1 A–E; 4 A: a, c, d; 6 A: a–c) and up to 6 mm high. It is sometimes prolonged into a beak (Figs. 1 F; 2 D; 6 A: k, B: i). The peristome field is more or less circular (up to 15 mm or more in diameter) but may be oblong (Fig. 6 B: g, j). Occasionally there is only a

Fig. 1. *Geastrum triplex*. Fully expanded fruitbodies, in natural habitat, most of them with the rays recurved under the exoperidial discs. – A–C: Fresh specimens with an intact, whitish fleshy layer. – D: Rather fresh fruitbody where the fleshy layer has nearly dried up. – E, F: Older specimens with a dark-brown fleshy layer. – A, D, E: Exoperidia saccate. – B, C, F: Exoperidia arched. – A–F: The central part of the fleshy layer has formed a collar around the endoperidium. The collar may be deeply cup-shaped (A, B, D), shallowly cup-shaped (F) or plane (C). The collar in (C) is cracked at its margin. – A–C, F: Specimens with a well defined peristome field. – D, E: Endoperidium with an indefinite peristome-field. – A–E: Endoperidia with mamilla-like peristome. – F: Endoperidium with the peristome prolonged into a beak. – A, D: Bohuslän, Marstrand 14.X.1974. – B, C: Västergötland, Göteborg 10.X.1974. – E, F: Gotland, Bunge parish 4.XII.1972. Photo: Stellan Sunhede.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simple hole surrounded by the non-fibrillose endoperidial wall (Fig. 6 A: h, i). Examples of the shape, height and position of the peristome are given especially in Figs. 1; 2 D; 5 B and 6.

From the inner side of the endoperidial wall capillital threads radiate towards a central capillitial mass emerging from a pseudocolumella (Fig. 7 A: a, b, d). Capillitial threads from the top of the pseudocolumella may occasionally be so long that a bundle of them protrudes through the stoma. In vertical section through the center of the pseudocolumella, it appears to be more or less club-shaped or sometimes rounded (Figs. 2 E: e, F: e; 7 A: a, b, d, e, h). In cross section it is normally round to oblong (Fig. 7 A: c, f, g, i).

Microscopic characteristics

The *spores* are normally globose and, including the processes, the diameter is (4–)4.5–5.5(–6) µm. Smaller but not fully developed spores have been observed. The processes vary in shape and size. They are often high warts with a more or less flat top, but may be plate- or ridge-shaped (straight or curved) and have a height reaching 3/4 µm. Younger spores are cyanophilous but most of the fully developed, well pigmented spores do not stain blue. Their reaction in Melzer's reagent appears to be negative. The colour of the spore wall in KOH is yellow-brown. The processes have a darker tint.

The SEM pictures (Fig. 8 A–C) show the processes to be cylindrical or somewhat conical with rounded or flat, often expanded, tops. Sometimes the processes coalesce. The sides may be furrowed and there may be root-like ridges at the base of the processes.

The brown *capillitial threads* are more (Fig. 7 A: l) or less thick-walled, have gradually narrowing tips (Fig. 7 A: m) and a diameter of (1.5–) 2–9(–11) µm. They may be smooth or nearly so or have a cyanophilous cover of warts or matter of different shapes (Figs. 7 A: l, m; 8 D–F). They do not stain in Melzer's reagent. Their colour in KOH is yellow-brown.

In a vertical section through the centre of the endoperidium the whitish *pseudocolumella* clearly stands out against the brown mass of capillitial hyphae and spores (Fig. 2 E). The hyphae of the pseudocolumella gradually pass into capillitial threads so that there is no distinct border to the pseudocolumella in a mature fruitbody (Figs. 2 E; 7 A: a, b, d). The interwoven hyphae from the centre of the tough pseudocolumella are thick-walled, cyanophilous and (1.5–)2–7.5 µm broad.

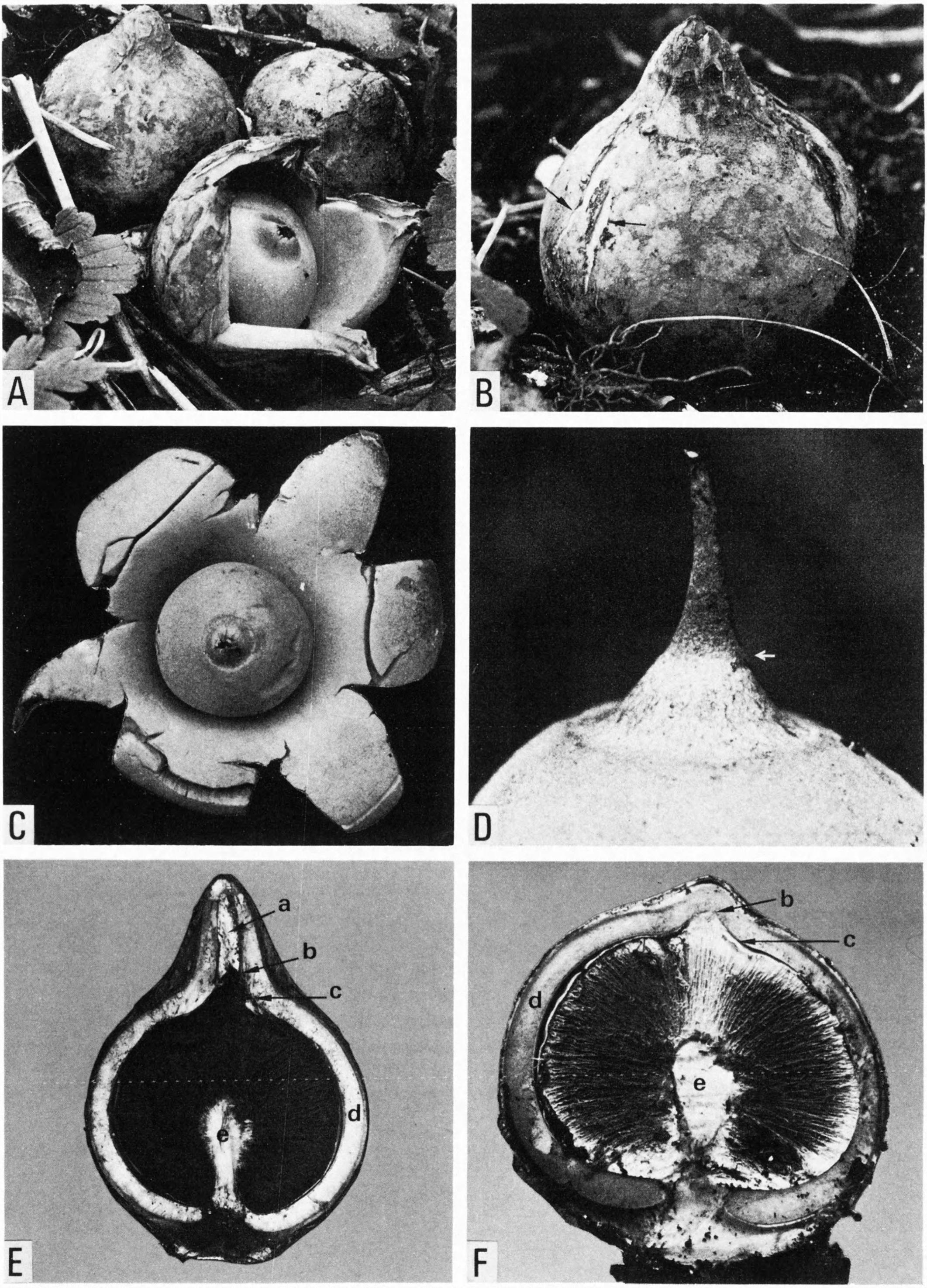
The hyphae of the *endoperidial wall* (Figs. 7 A: n, o; 8 A) are thick-walled and (1.5–)2–5(–7) µm broad.

The *pseudoparenchymatic layer* of the exoperidium consists of bladder-like cells (Fig. 7 A: p) of varying sizes. The hyphae of the *fibrous layer* are thick-walled (like those in Fig. 7 A: n, o), cyanophilous and 2–6(–8) µm broad. The *mycelial layer* is built up of thin-walled (or slightly thick-walled) hyphae with clamp connections (Fig. 7 A: j, k) and (1.5–)2–5(–6) µm broad. Similar hyphae are sparsely distributed on other sites of the fruitbody (cf. Fig. 8 A, arrow).

Discussion

Junghuhn (1840 p. 287) described *Geastrum triplex* (ut *Geaster*) on specimens from Java. I have examined the type collection (Herb. F. Junghuhn in H. L. B. No. 97) kept in Leiden. It consists of one divided, unexpanded, onion-shaped specimen and eight expanded ones. The specimens are severely damaged, possibly due to insects. In five of them there is no endoperidium (except some remnants in two fruitbodies). On the four remaining specimens the peristome and other parts of the endoperidial wall are

Fig. 2. *Geastrum triplex*. Fruitbodies. – A, B: Young epigeal fruitbodies in natural habitat. – A: Two onion-shaped specimens and one where the exoperidium has recently split to expose an endoperidium with a well defined mouth area. – B: Young onion-shaped fruitbody just splitting at the top. Note the cracks in the mycelial layer (arrows). – C: Fresh expanded specimen where the central part of the fleshy layer begins to break loose from that of the rays. – D: Endoperidium with a beak-like peristome. The arrow marks the height of a normal peristome, compare (b) in (E) and (F). Note the well defined peristome field. – E, F: Vertical sections through the centre of two young fruitbodies where the exoperidium still enclose the endoperidium and the gleba. (d) fleshy layer of the exoperidium and (e) pseudocolumella. – E: Prominently onion-shaped fruitbody where the peristome is prolonged into a beak (a), like that seen in (D). (b) and (c) correspond to the same letters in (F). – F: Subglobose fruitbody with an almost mature gleba. The arrows (b) and (c) mark the height of the peristome. – A, B: Bohuslän, Marstrand 14.X.1974. – D: Sunhede 5600. Photo: Stellan Sunhede.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destroyed. In all the expanded specimens there are remnants of a pseudoparenchymatic collar. Fig. 3 on Junghuhn's plate also shows a deep pseudoparenchymatic cup around the endoperidium. The peristome of the endoperidium on his Figs. 2 and 3 is very similar to that of Fig. 6 B: a in this paper.

Palmer (1968 p. 116) notes: "Junghuhn's plate shows a deeply cupulate specimen with a blue endoperidium which I have never seen in European specimens". In Swedish specimens, I have not observed endoperidia with that pale bluish-grey colour that is shown on Junghuhn's Figs. 2 and 3, but pale grey or whitish grey endoperidia occur. The colour of the endoperidial wall of the fruitbodies in the type specimen is brownish but there are areas with a whitish or greyish tint. In the light microscope there seems to be a slight difference in the spore ornamentation compared with most spores in Swedish specimens. I do not think that this difference is taxonomically significant.

Palmer, who examined part of the type collection, noted: "... found it so severely insect-damaged that, although it looked like what I would call *G. triplex,* I was reluctant to form any definite conclusions". We have to be careful when dealing with incomplete fruitbodies of *Geastrum*. However the similarities between the Swedish specimens and the type (together with Junghuhn's description and Figs.) are so great compared with the differences mentioned that I consider them to be the same taxon. The best preserved specimen in the type collection is designated as lectotype.

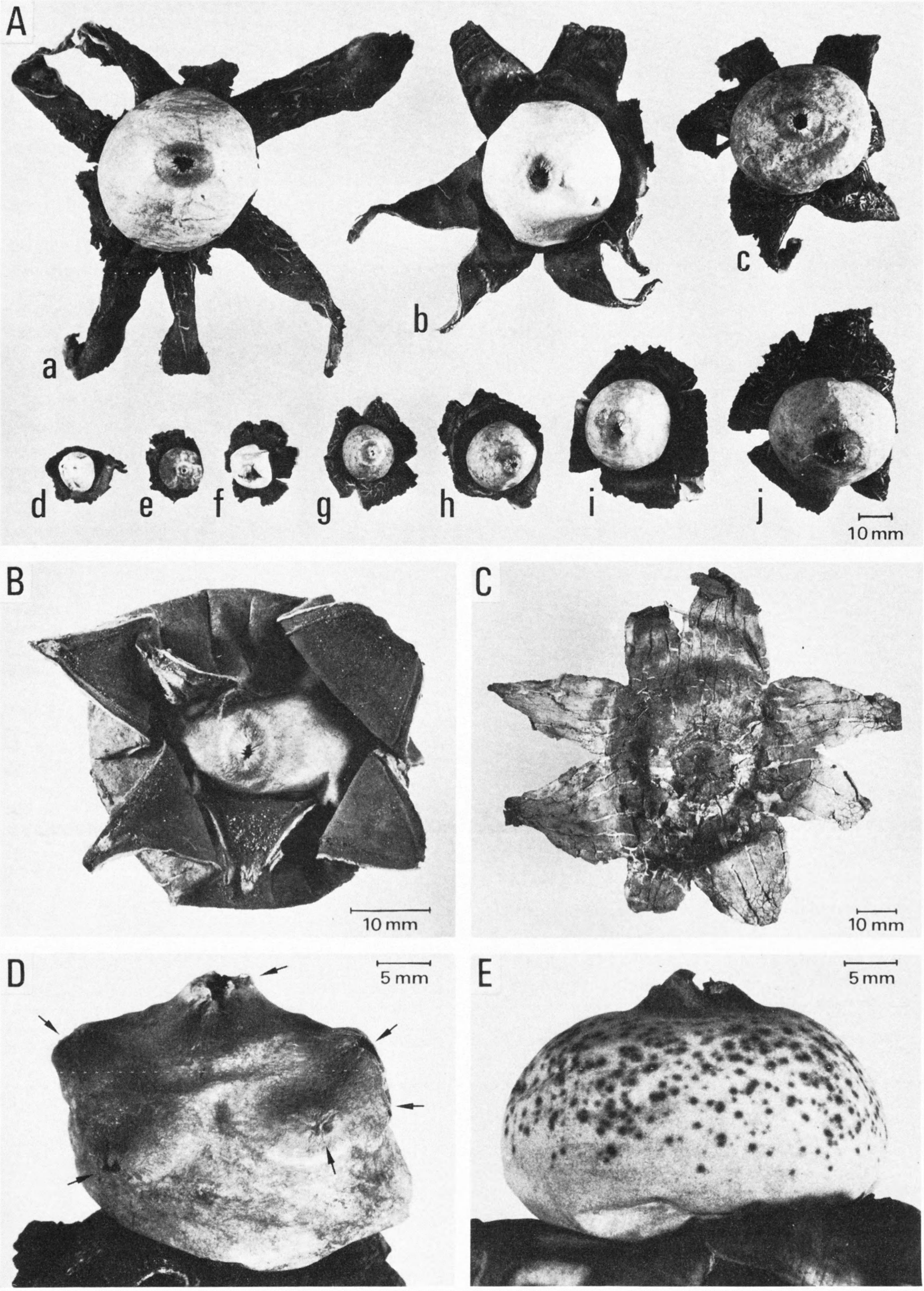
Klotzsch (1832) described *Cycloderma indicum* om material from "India occidentali". Hollós (1904 p. 53) who examined the material in Berlin stated that it was an immature fruitbody of *Geastrum triplex* Jungh. Lloyd (1904) was not sure of the identity of *C. indicum* but was of the opinion that it could not be an unopened *G. triplex*. Rauschert (1959) made the combination *Geastrum indicum* (Klotzsch) Rauschert on the basis of Hollós's (1904) report. The type of *Cycloderma indicum* was probably destroyed during the second world war (Palmer 1968). The description and the figures by Klotzsch are not detailed enough to show whether the fungus is *G. triplex* or another fungus. The epithet *indicum* can be considered to be a nomen dubium.

Unexpanded fruitbodies of *G. triplex* may have a root-like basal plug of mycelium and debris. I have seen this only on a Hungarian specimen growing on sandy soil near Pécs. Rounded young unexpanded fruitbodies (Fig. 4 C: e, i) show in section a normal mammiform mouth (Fig. 2 F). Young prominently onion-shaped fruitbodies (Fig. 4 C: a, b) show in section a mouth prolonged into a beak (Fig. 2 E: a). This beak normally breaks when the exoperidium bursts and remnants of it may sometimes be seen at the end of the rays. Such specimens were called *G. cryptorhynchus* by Hazslinszky (1874, 1876). Sometimes, however, the beak remains intact even in expanded specimens (Fig. 1 F; 2 D; 6 A: k, B: i). The beak is not hollow. Remnants of it may remain as a plug in the stoma (Fig. 6 B: f, h). Specimens where the exoperidial rays are prolonged into slender tips (Fig. 5 B: b, c) originate from prominently onion-shaped young fruitbodies.

Most of the fully expanded specimens of *G. triplex* have a pseudoparenchymatic collar or cup. Such "triplex-collars" or "cups" may, even though rather rare, be present in other non-hygroscopic species of *Geastrum*. I have observed this phenomenon in *Geastrum coronatum* Pers., *G. fimbriatum* Fr., *G. minimum* Schw., *G. quadrifidum* Pers., *G. rufescens* Pers., *G. umbilicatum* Fr. (Sunhede 1974 b) and *Trichaster melanocephalus* Czern.

As a deviation from the normal the endoperidium of *Geastrum* spp. may have two or more peristomes. Staněk (1952 a, b) reports this deviation in nine species from Czechoslovakia. The phenomenon seems to be rare in *G. triplex* where only five specimens with two and one

Fig. 3. Fruitbodies of *Geastrum triplex*. All, except (E), are dry. – A: Variation in size of fruitbodies, specimens rather old and dark. All, except (a), have some or all of their rays recurved under the exoperidial discs. (a) with an elliptical well-defined peristome field. – B: Fruitbody which has dried during the splitting of the exoperidium and where the rays have bent (back) over the endoperidium. – C: Specimen seen from below, where the exoperidial rays under wet condition have been forced into one plane. Note the radiating cracks in the mycelial layer and the dark central scar where the fruitbody was earlier attached to the mycelium in the ground. – D: Polystomatous fruitbody with six stomata (arrows). – E: Endoperidium (wetted) with dark areas and dots of unknown origin. – D: Sunhede 2102. – E: Sunhede 5588. Photo: Stellan Sunhede.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with six stomata (Figs. 3 D, 6 A: p, q) were found among 3150 specimens examined.

For further information concerning *G. triplex* the reader is referred to Hollós (1904), Lohwag (1929), Palmer (1955, 1968), Staněk (1958), Demoulin (1968), Reid (1976), Boiffard (1976) and literature cited in these works.

The investigation has shown that the morphological variation within *G. triplex* is unexpectedly large and that no character alone is quite reliable för determinations. When normally developed the fungus is characteristic and easily determined, but for less experienced observers deviating specimens may be difficult to recognize, especially when they grow singly. I have not found any significant variation between fruitbodies from different mycelia except that in size a.s.o. directly depending on humidity and fertility of the soil, nor any geographical variation in the Swedish material of *G. triplex*. There is no reason to believe that Swedish specimens named *G. triplex* represent more than one taxon.

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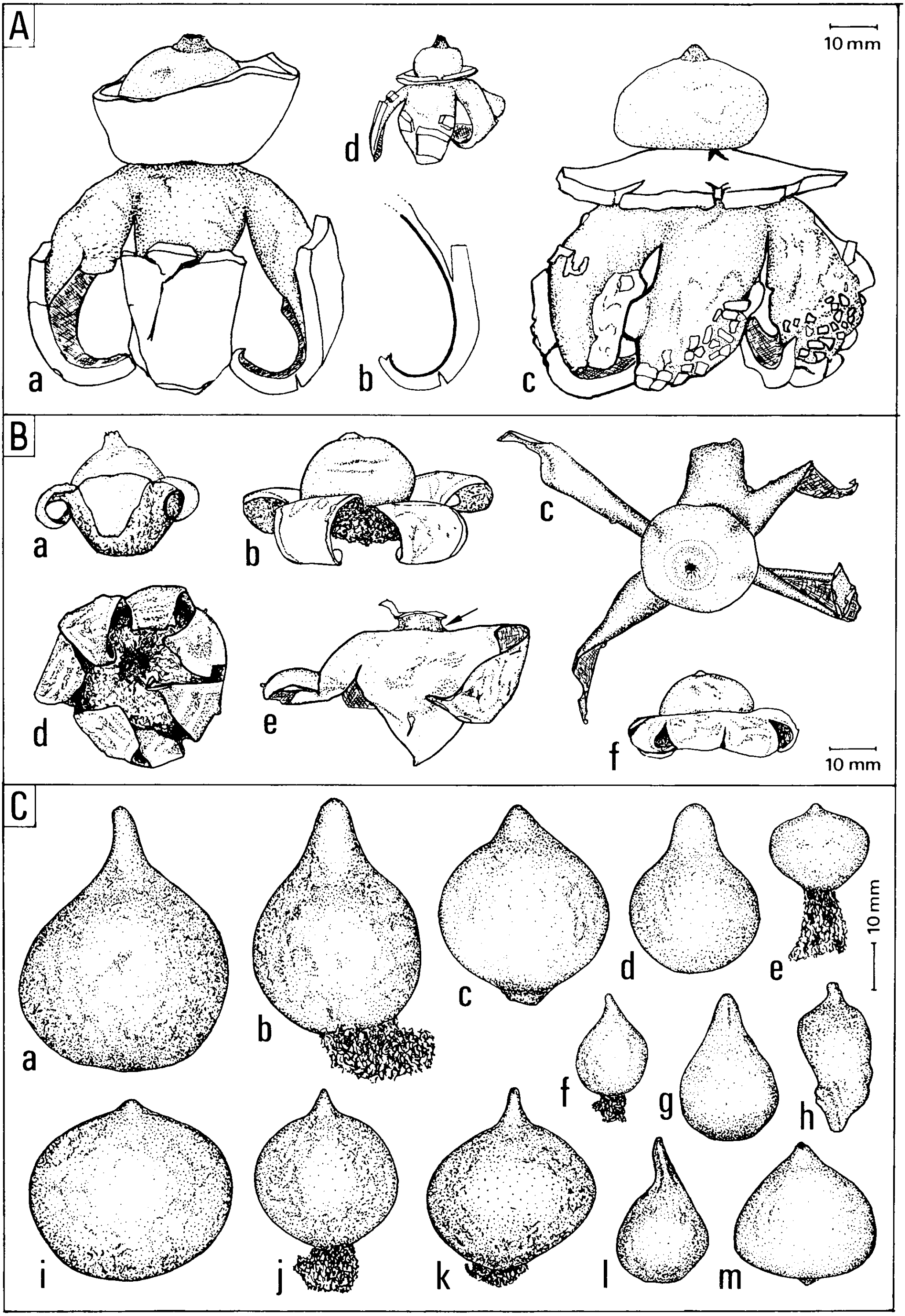
Fig. 4. Fruitbodies of *Geastrum triplex*. – A: Fresh specimens. (a) with a deep pseudoparenchymatic cup around the endoperidium, (d) with a shallow cup and (c) with a disc-shaped collar. (b) is a longitudinal section through the right ray in (a). The thick black line in the section represents the mycelial and fibrous layer of the exoperidium and the clear area the pseudoparenchymatous tissue. (a, c, d) the margins of at least the basal halves of the rays are recurved. – B: Dry fruitbodies. (a, b, f) rather small, saccate to somewhat saccate specimens where no pseudoparenchymatic collar has developed. (c) old fruitbody, where the margins of the rays are enrolled from both edges. (d) specimen seen from below with the rays recurved under the exoperidial disc. Note the central mycelial scar. (e) fruitbody with only the fibrous layer of the exoperidium and a short endoperidial stalk (arrow) remaining. – C: Shape and size of young fruitbodies. (a–f, i–k) fresh and (g, h, l, m) dry specimens. (g, l) one fruitbody seen from different angles. (b, e, f, j, k) specimens with basal mycelial tufts.

Fig. 5. *Geastrum triplex*. Dry fruitbodies, simplified drawings. – A: (a–i) vertical sections through the axis of fruitbodies showing the curvature of the exoperidium and the position and to some extent the shape of the endoperidium (dotted area). (c, d) with a prominent pseudoparenchymatic collar. (i) slightly stalked endoperidium. (a, b) exoperidium arched, (c, g) exoperidial disc plane or nearly so, (d, e, i) somewhat saccate and (f, h) prominently saccate. (j) young fruitbody (Hungarian specimen) with a root-like plug of whitish hyphae intermixed with debris. – B: Fruitbodies (from above) where the exoperidia under wet conditions have been forced into a horizontal plane. Note the more or less regular splitting of the exoperidium, the depth to which it has been cleft, the shape of the rays and the form of the endoperidia. (b, c) exoperidial rays with slender tips. – A: j Sunhede 3575.

Fig. 6. *Geastrum triplex*. – A: Variation in shape and size of endoperidium and peristome shown in side views (a–p) and top views (q–s). All endoperidia are dry except that in (c) which is wetted and has swollen. (b) dry state of specimen in (c). (l, m) and (p, q) two fruitbodies in different wiews. (a–p) position of exoperidium only indicated. (b, c) short-stalked endoperidium. (g) specimen with no stoma, (p, q) with two stomata. (h) endoperidium with an irregular hole in the wall. (k) endoperidium with a prolonged peristome. (o) endoperidium with a hat-shaped rest of the exoperidium covering the mouth. – B: (a–j) details of different types of peristomes. All specimens dry except that in (b). (a) is the same specimen as (b). Note the fringed peristome edge in (a). (a, b, d–j) endoperidia with a more or less definite peristome-field. (c) with an indefinite peristome-field. (f, h) stoma plugged with hyphae from the region marked with (a) in 2 E. (g, j) one specimen with an elongated peristome-field seen in different views. (i) peristome prolonged into a beak, partly covered with a hat of exoperidial remnants. (k) dry specimen with an apophysis and with a short endoperidial stalk.

Fig. 7. *Geastrum triplex*. – A: Shape of the pseudocolumella and microscopical characteristics. (a, b, d) vertical sections through the centre of the endoperidium and through the exoperidium showing the shape of the pseudocolumella. Capillitial threads from the inner side of the endoperidial wall radiate towards a central capillitial mass emerging from the pseudocolumella. (c, f, g, i) are horizontal sections through the broadest part of pseudocolumellas. (e, h) side views of a flat pseudocolumella from different angles. (j) young thin-walled and (k) somewhat thick-walled older clamp-bearing hyphae from the mycelial layer. (l) part of a thick-walled capillitial thread with a narrow lumen and with cyanophilous matter on the surface. (m) end of a capillitial thread with well-defined cyanophilous matter on the surface. (n, o) thick-walled hyphae from the endoperidial wall. (p) section through the fleshy layer of a fresh specimen showing bladder-like hyphal cells. – B: Diagrams showing variation of different characteristics of the fruitbody. The analyzed characteristics are: number of exoperidial rays, shape of exoperidium (see below) and largest diameter of endoperidium. s = saccate, [s] = somewhat saccate, p = plane and a = arched.

Fig. 8. *Geastrum triplex*. SEM photos of endoperidial surface, spores and capillitial threads. – A: Endoperidial surface with spores. Most of the hyphae are thick-walled, the arrow points at a thin-walled collapsed hypha. – B, C: Spores from Swedish specimens except that in C: c which is from the type specimen. – D, E, F: Segments of capillitial threads covered with irregular as well as well-defined cyanophilous matter. – A: 2100 ×. – B: 14000 ×. – C: a, b 7300 ×; c 8000 ×; d 7600 ×. – D, E: 6300 ×. – F: 4700 ×. – Photo: Stellan Sunhede.



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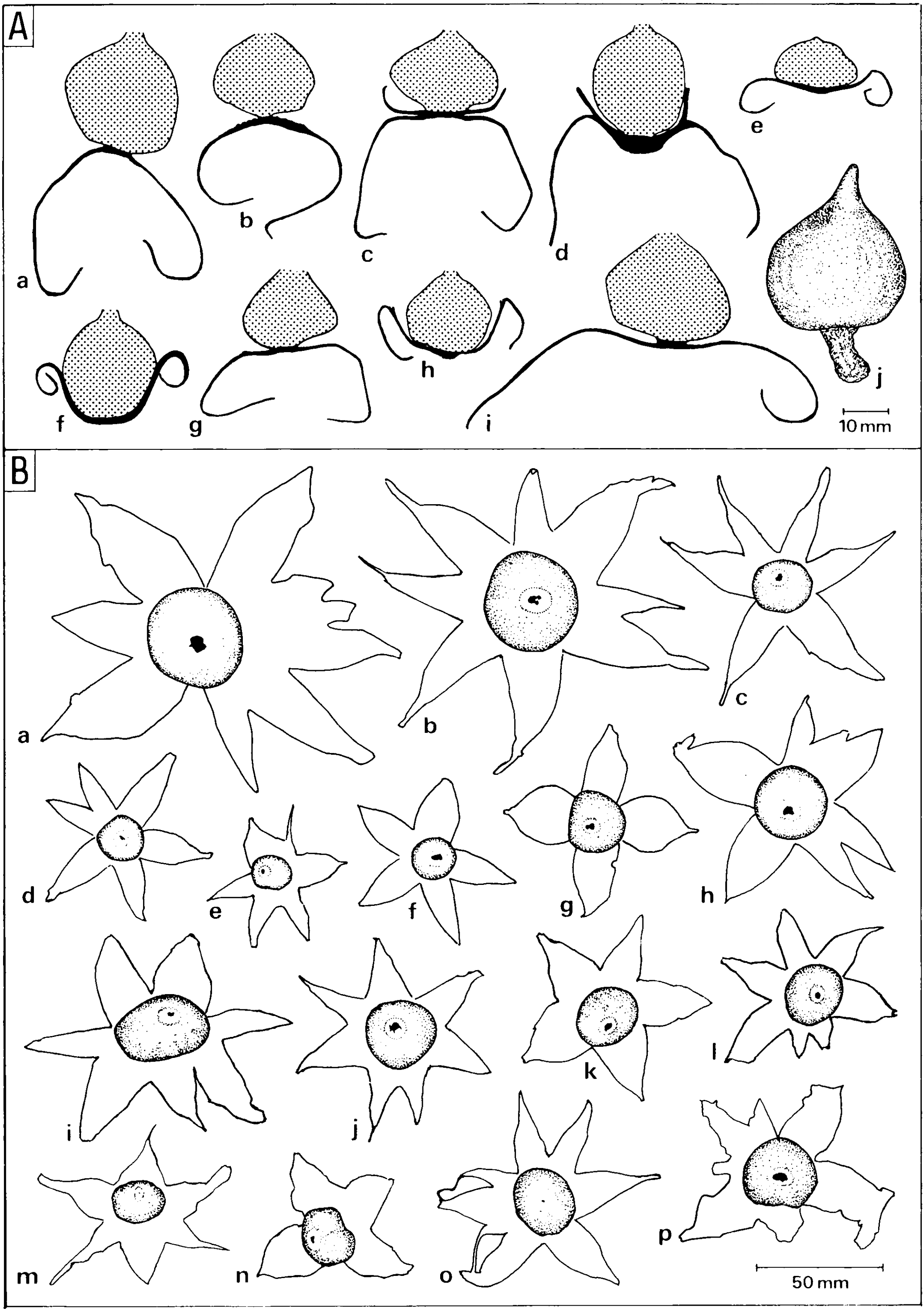

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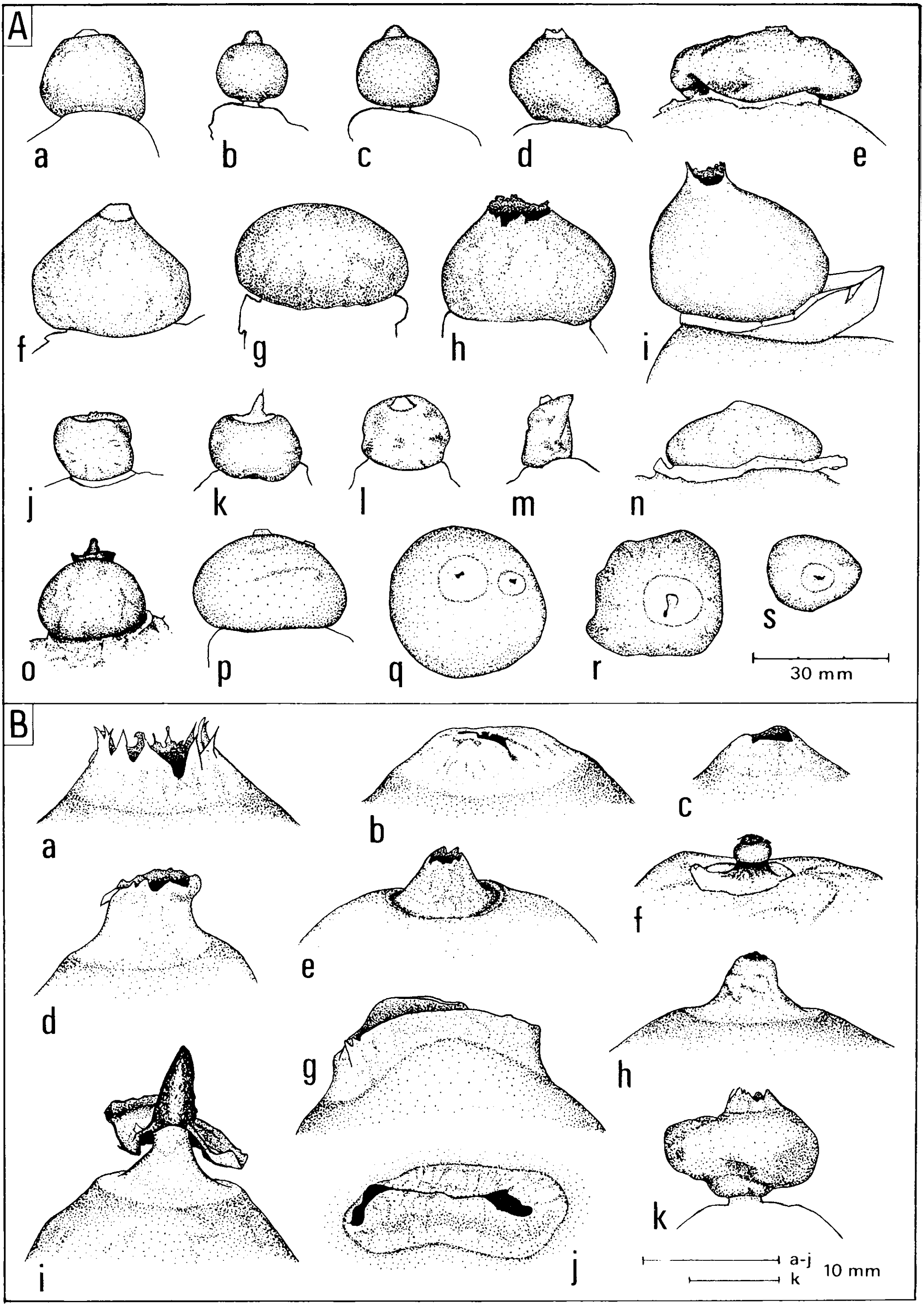

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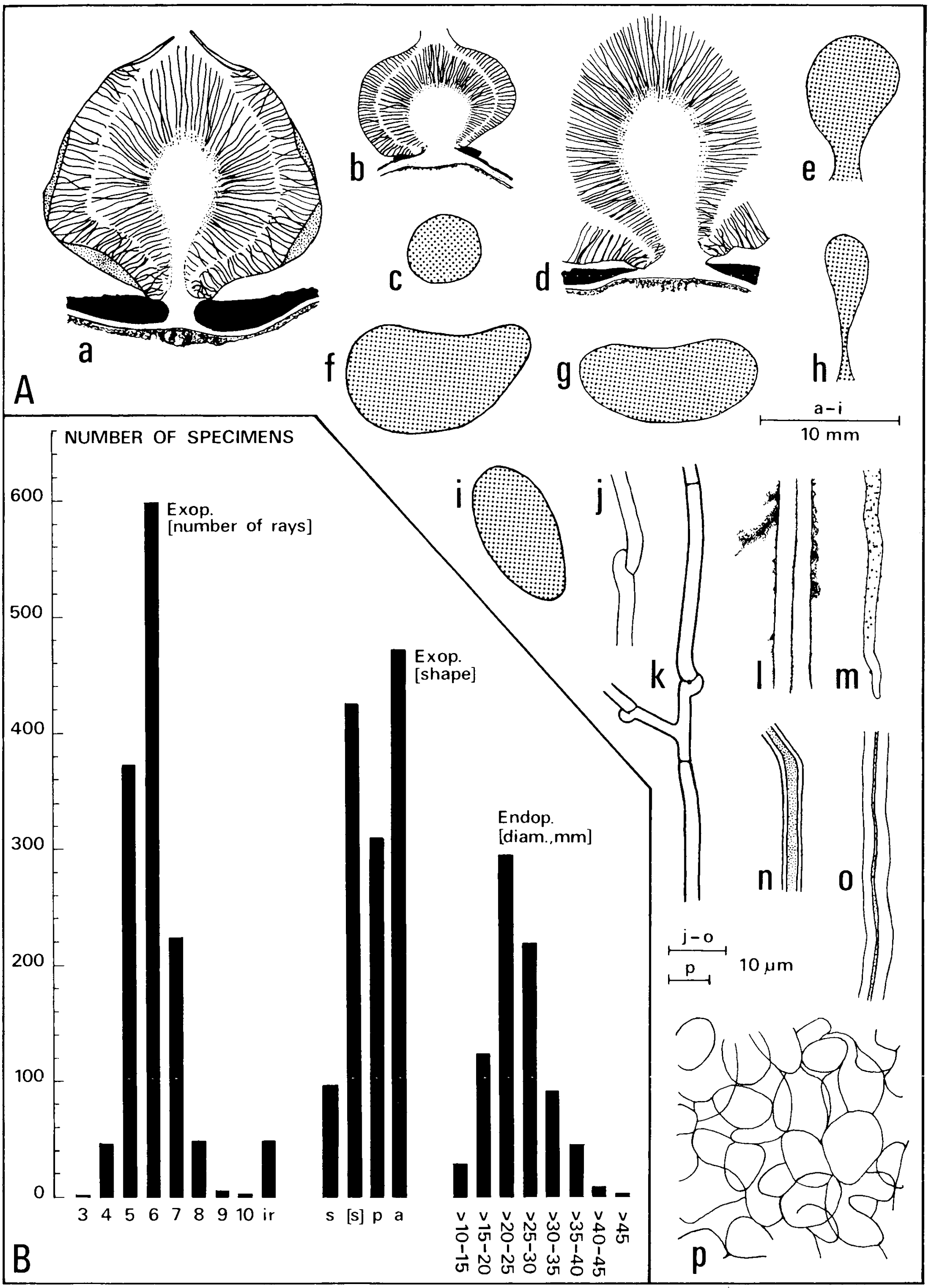
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Fig. 7

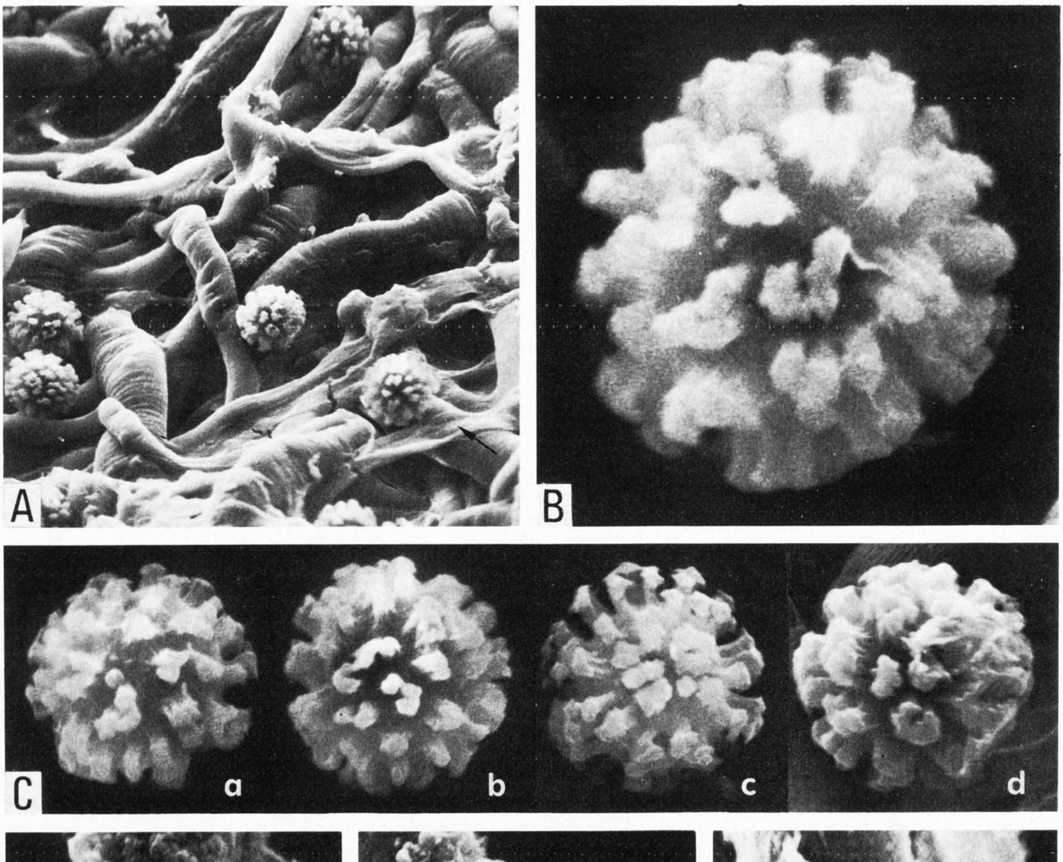

Fig. 8.

Species of Epidendroideae (Orchidaceae) new to Ecuador

Bernt Løjtnant

Løjtnant, B. 1977 12 30: Species of Epidendroideae (Orchidaceae) new to Ecuador. [AAU Ecuador project, contribution no. 9.] *Bot. Notiser 130:* 417–425. Stockholm. ISSN 0006-8195.

Lepanthes villosa Løjtnant is described as new and the new combinations, *Malaxis hoppii* (Schltr.) Løjtnant and *M. nasuta* (Schltr.) Løjtnant are made. Four species, *Dichaea lankesteri, Maxillaria campanulata, M. foliosa* and *M. friedrichsthalii* are reported for the first time from S America and 42 other taxa are reported as new to Ecuador.

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The species enumerated here are new to Ecuador (except for *Cryptocentrum jamesonii* and *C. latifolium*), and *Dichaea lankesteri, Maxillaria campanulata, M. foliosa* and *M. friedrichsthalii* are also new to S America. The collections were made during the 1st and 2nd Danish Botanical Expeditions to Ecuador (Holm-Nielsen & Jeppesen 1968, Holm-Nielsen et al. 1975). Most of the determinations were made during my stay at the Orchid Herbarium of Oakes Ames, Harvard University in 1976.

The first set of the collections are deposited at AAU. Duplicate sets have been sent to AMES, SEL, S, MO, HB, K, MBM, COL, QCA and Q. The drawings of flowers and floral parts have been made from material preserved in FAA.

Bifrenaria picta (Schltr.) C. Schweinf.

C. Schweinf. in Bot. Mus. Leafl. 11: 246, 1944.

Collected in the area around the Bomboiza Mission in prov. Morona-Santiago in SE Ecuador according to Padre Angel Andreetta who donated this plant to us. Holm-Nielsen et al. 4327 (in cultivation and preserved in FAA). – Also Colombia (type) and ?Panama (Schweinfurth 1944 b).

Brachionidium tetrapetalum (Lehm. & Kränzl.) Schltr.

Schltr. in Feddes Rep. Beih. 7: 241, 1920.

The type collection from Colombia is the only one hitherto known of this species (cf. Garay 1956). It is perhaps conspecific with *B. serratum* Schltr. from Peru (Leslie A. Garay, pers. comm.), but the type of that taxon was destroyed during World War II.

Ecuador, prov. Carchi, Páramo El Angel, in the pass on the road El Angel–Tulcán, very humid *Espeletia* paramo, 3750–3850 m (78°54'W, 0°41'N), 15.5.1973, Holm-Nielsen et al. 5454.

Brassia rhizomatosa Garay & Dunsterv.

Garay & Dunsterv., Venz. Orch. Ill. 3: 46, 1965.

Ecuador, prov. Cotopaxi, Quevedo–Latacunga road, tropical rain forest and old *Citrus* plantation, c. 700 m (79°11'W, 0°55'S), 5.4.1973, Holm-Nielsen et al. 2967. – Also Venezuela.

Brassia spathacea Lind. & Rchb. f.

Lind. & Rchb. f. in Bonpl. 2: 279, 1854.

Ecuador, prov. Napo, 1 km E of the oil pump station on the road Papallacta–Baeza, gallery vegetation along Rio Papallacta, 2050 m (78°W, 0°21'S), 6.6. 1973, Holm-Nielsen et al. 6982. – Also Colombia.

Campylocentrum colombianum Schltr.

Schltr. in Feddes Rep. Beih. 7: 205, 1920.

Ecuador, prov. Los Rios, surroundings of Montalvo (foothills of the Andes, c. 40 km E of Babahoyo), rain forest with coffee and cocoa plantations, 100–200 m (79°17'W, 1°47'S), 30.3–2.4.1973, Holm-Nielsen et al. 2595, 2639. – Also Colombia.

Campylocentrum fasciola (Lindl.) Cogn.

Cogn. in Mart. Fl. Bras. 3,6: 520, 1906.

Ecuador, prov. Los Rios, surroundings of Montalvo (foothills of the Andes, c. 40 km E of Babahoyo), rain forest with coffee and cocoa plantations, 100–200 m (79°17'W, 1°47'S), 30.3–2.4.1973, Holm-Nielsen et al. 2719. – Also Guatemala, Br. Honduras, Honduras, Costa Rica, Panama, West Indies, Venezuela, Br. Guiana (type), Surinam, Brazil, Peru and Colombia.

Cryptocentrum hoppii Schltr.

Schltr. in Feddes Rep. Beih. 27: 103, 1924.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34'W, 3°29'S), 23.4.1973, Holm-Nielsen et al. 4241. – Also Colombia.

Cryptocentrum jamesonii Benth.

Benth. in Benth. & Hook., Gen. Pl. 3: 557, 1883.

A comparison of the types of *C. jamesonii* (Ecuador) and *C. calcarata* (Schltr.) Schltr. (Costa Rica) has shown that they are probably conspecific. The lip of *C. calcarata* is, like that of *C. jamesonii,* evenly tapered from the concave base and the constrictions described and illustrated by Schlechter (1906, 1913, 1931) represent folds rather than constrictions. There seems, however, to be a slight difference in leaf width: 3–5 mm in the type of *C. jamesonii,* occasionally up to 7 mm in *C. calcarata.*

C. lehmannii (Rchb. f.) Garay is easily distinguishable from *C. jamesonii* (Garay 1958). *C. lehmannii* is a rarely collected species described from Ecuador and it has not been recorded from outside that country. However, I found a Colombian specimen of it (Lehmann 8582, Colombia, West Andes of Popayan, 1500–2300 m, AMES) among the undetermined material of *Cryptocentrum* at AMES.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 33, dry rocky slopes with grass and scattered shrubs, 1800–1850 m (79°04'W, 3°59'S), 21.4.1973, Holm-Nielsen et al. 4124.

Cryptocentrum latifolium Schltr.

Schltr. in Feddes Rep. Beih. 19: 247, 1923.

The collection cited below belongs to the typical variety of this species, which seems to have been reported from Costa Rica (type) and Panama only. However, its var. *brachypetalum* Garay is known from a few collections from Colombia and Ecuador (Garay 1953). The Ecuadorean specimen of *Cryptocentrum* illustrated by Withner (1959) as *C. jamesonii* represents the typical form of *C. latifolium.*

Besides the species of *Cryptocentrum* reported here, we have found three further but yet unidentified species in Ecuador.

Ecuador, prov. Cotopaxi, Quevedo–Latacunga road, tropical rain forest and old *Citrus* plantation, 700 m (79°11'W, 0°55'S), 5.4.1973, Holm-Nielsen et al. 2962. – Quevedo–Latacunga road, rocky slopes with rain forest, 800–950 m (79°10'W, 0°55'S), 5.4.1973, Holm-Nielsen et al. 3008.

Dichaea anguina Schltr.

Schltr. in Feddes Rep. 27: 82, 1929.

Ecuador, prov. Morona-Santiago, Pachicutza, at "Escuela Fiscomisional Cardinal Döpfner", km 140 on the road Loja–Gualaquiza, tropical rain forest with cleared areas along Río Zamora and along the road, 900–1000 m (78°34'W, 3°37'S), 26–27.4.1973, Holm-Nielsen et al. 4487. – Also Bolivia (type) and ? Venezuela (Schweinfurth 1967).

Dichaea brachypoda Rchb. f.

Rchb. f., Beitr. Orch. Centr.-Amer. 78, 1866.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 33, dry rocky slopes with grass and scattered shrubs, 1800–1850 m (79°04'W, 3°59'S), 21.4.1973, Holm-Nielsen et al. 4131. – Also Costa Rica (type), Venezuela, Surinam, Colombia and Brazil.

Dichaea lankesteri Ames

Ames in Sched. Orch. 4: 56, 1923.

Ecuador, prov. Pichincha, "Finca Carlita", at km 13 on the road Santo Domingo de los Colorados–Chone, secondary rain forest and slopes with secondary herb vegetation, 550 m (79°14'W, 0°15'S), 10.6.1973, Holm-Nielsen et al. 7034. – Prov. Cotopaxi, Quevedo–Latacunga road, km 46 from Quevedo, NE-exposed slopes with rain forest, c. 600 m (79°11'W, 0°55'S), 4.4.1973, Holm-Nielsen et al. 2901. – Also Costa Rica (type) and Honduras.

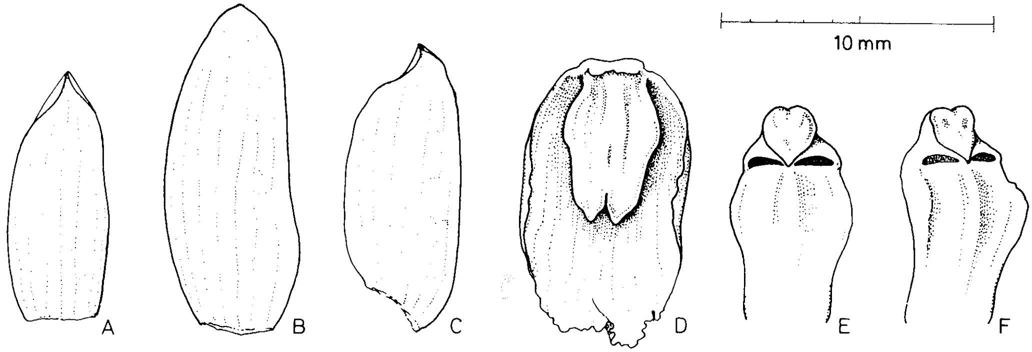

Fig. 1. *Kefersteinia laminata.* – A: Dorsal sepal. – B: Lateral sepal. – C: Petal. – D: Lip. – E–F: Column. – Holm-Nielsen et al. 6058.

Dichaea maculata Poepp. & Endl.

Poepp. & Endl., Nov. Gen. ac Sp. Pl. 2: 3, 1838.

Ecuador, prov. Morona-Santiago, Shuinia Nait, small mountain ridge c. 8 km SE of Misión Bomboiza, tropical rain forest, 900–1000 m (78°33'W, 3°30'S), 24.4.1973, Holm-Nielsen et al. 4420. – Also Peru (type) and Costa Rica.

Dichaea tenuis C. Schweinf.

C. Schweinf. in Amer. Orch. Soc. Bull. 21: 510, 1952.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34'W, 3°29'S), 23.4.1973, Holm-Nielsen et al. 4199. – Also Peru.

Diothonea gratissima Rchb. f.

Rchb. f. in Bot. Zeit. 10: 772, 1852.

Ecuador, prov. Cotopaxi, Quevedo–Latacunga road, above Pilaló, in cloud forest, mostly steep slopes, c. 3200–3300 m (78°56'W, 0°58'S), 8.4.1973, Holm-Nielsen et al. 3275. – Also Colombia (cf. Schweinfurth 1944 a).

Fernandezia ionanthera (Rchb. f. & Warsz.) Schltr.

Schltr. in Feddes Rep. 16: 349, 1920.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 14, mountain ridges with elfin forest and open bogs, 2750–2770 m (79°09'W, 4°S), 19–20.4.1973, Holm-Nielsen et al. 3985. – Also Peru.

Kefersteinia laminata (Rchb. f.) Schltr.

Schltr. in Feddes Rep. Beih. 7: 267, 1920.

This species has apparently been known from the type collection only, which is of uncertain origin (Colombia?). It belongs to the genus *Kefersteinia* because it has a substigmatic longitudinal keel on the column (Fig. 1).

It is generally assumed that Reichenbach gave his species the alternative name *Kefersteinia laminata;* however, he only referred the species to the section *Kefersteinia* within the genus *Zygopetalum.* The legitimate combination under *Kefersteinia* was made incidentally by Schlechter. B. J. Jackson listed in 1895 the name *Kefersteinia laminata* in Index Kewensis, but this combination is not valid since it was listed merely as a synonym to *Zygopetalum laminatum.*

Ecuador, prov. Carchi, Valle de Maldonado, km 71 on the road Tulcán–Maldonado, steep forested slopes, 2100–2200 m (78°06'W, 0°54'N), 20.5.1973, Holm-Nielsen et al. 6058.

Lepanthes dasyphylla Rchb. f.

Rchb. f. in Flora 69: 557, 1886.

Ecuador, prov. Carchi, Valle de Maldonado, km 71 on the road Tulcán–Maldonado, steep forested slopes, 2100–2200 m (78°06'W, 0°54'N), 20.5.1973, Holm-Nielsen et al. 6072, 6073. – Also Colombia.

Lepanthes villosa Løjtnant sp. nov. – Fig. 2

Orig. coll.: Ecuador, prov. Carchi, Valle de Maldonado, km 67 on the road Tulcán–Maldonado, montane forest, 2400 m (78°04'W, 0°53'N), 20.5.1973, Holm-Nielsen, Jeppesen, Løjtnant & Øllgaard 6151. Epiphyte, pendent. Labellum red-brown. Flowers purple-brown with smaller pale greenish areas. Leaves with red-brownish veins (AAU holotype).

Plantae epiphyticae, pendentes; *caulibus primariis*

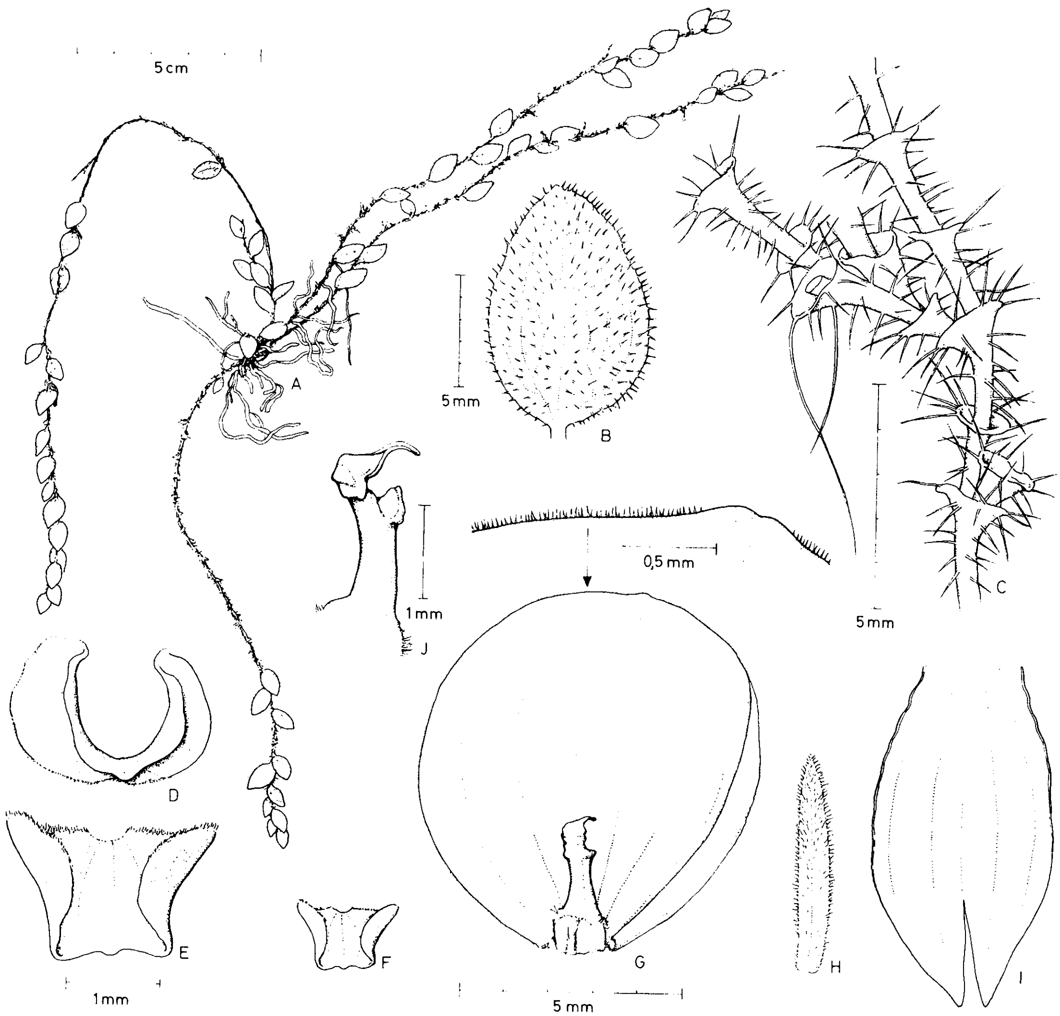

Fig. 2. *Lepanthes villosa*. – A: Habit. The plant is pendent under natural conditions. – B: Leaf. – C: Stems. – D–F: Lip. – G: Dorsal sepal and column. – H: Petal. – I: Lateral sepals. – J: Column. – Holotype.

gracilibus, simplicibus vel parum ramosis, vaginis infundibuliformibus, setis acutis obtectis; *caulibus secundariis* perpaucis, unifoliatis; *foliis* ellipticis, carnosis, dense setosis, in vivo usque ad 13 mm longis, 8.5 mm latis, 3-nerviis; *inflorescentiis* solitariis, unifloris; *pedunculo* folio breviore; *sepalo postico* orbiculari, hemisphaerico, valde concavo, margine ciliato, 7-nervio, 8.5 mm longo, 8 mm lato; *sepalis lateralibus* inter se usque ad tertiam partem apicalem connatis, ovato-lanceolatis, acutis, 4-nerviis, usque ad 8.5 mm longis, 4 mm latis; *petalis* lineari-lanceolatis, uninerviis, villosis, usque ad 5 mm longis, 0.7 mm latis; *labello* reniformi, minute apiculato, 3-nervio, usque ad 1.5 mm longo, 2.5 mm lato; *columna* gracili; *rostello* porrecto.

This new species differs from all hitherto described species of the section *Brachyclada* Rchb. f. by the long, linear and villose petals.

The specific name is descriptive of the villose petals, villosa meaning hairy.

Liparis laticuneata C. Schweinf.

C. Schweinf. in Bot. Mus. Leafl. 15: 104, 1951.

The leaves of our collection are somewhat smaller (up to 2.5 × 1.6 cm) and the lips are slightly broader and shorter than those of the

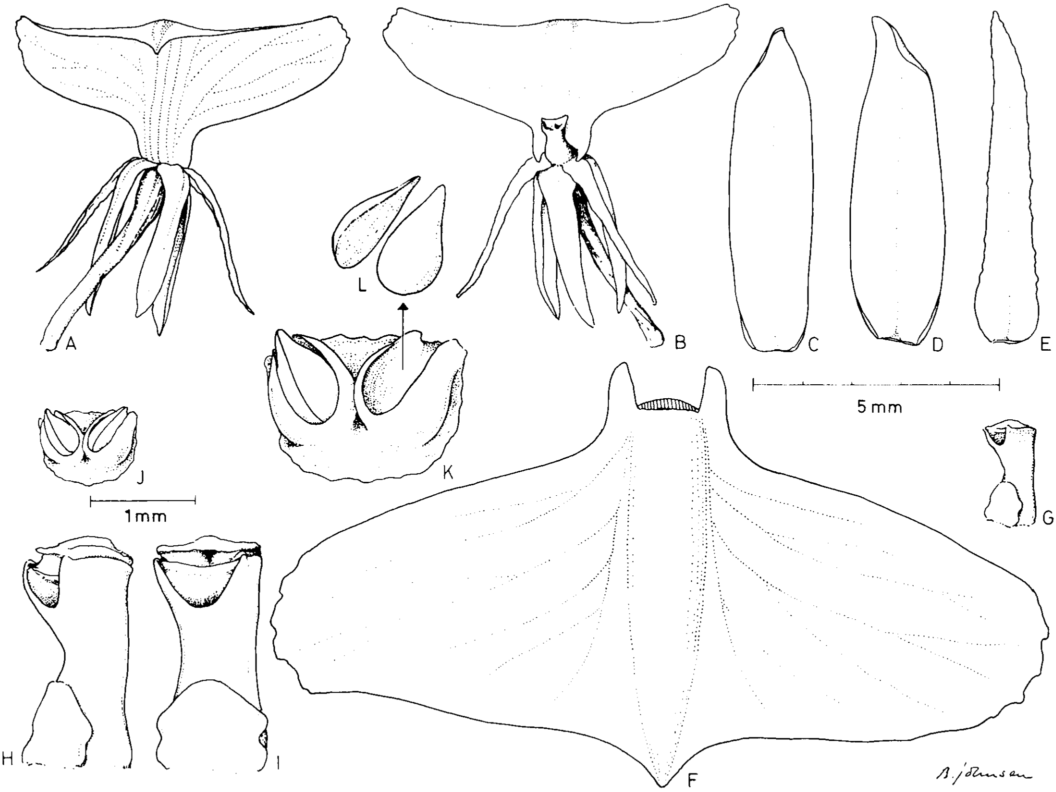

Fig. 3. *Liparis laticuneata*. – A–B: Flower from the lower part of the inflorescence. – C: Dorsal sepal. – D: Lateral sepal. – E: Petal. – F: Lip, spread out. –G–I: Column. – J–K: Anther. – L: Pollinia. – Holm-Nielsen et al. 4646.

type. However, the flowers vary even within a single inflorescence: the flowers situated lower down are thus bigger and have shorter and broader lips than the upper flowers (Fig. 3).

Ecuador, prov. Loja, km 51 on Pan American Highway of Loja, shrub, 2–4 m high, dominated by xerophytic vegetation, 2900 m (79°15'W, 3°45'S), 1.5.1973, Holm-Nielsen et al. 4646. – Also Peru.

Malaxis hoppii (Schltr.) Løjtnant comb. nov.

Basionym: *Microstylis Hopii* Schltr. in Feddes Rep., Beih. 27: 21, 1924.

Since the genus *Microstylis* Nutt. ex Lindl. is easily accommodated within *Malaxis* Soland. ex Sw. the above new combination has been made. The epithet should be spelled *hoppii* since the species is named to honour the collector, W. Hopp.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 24–25, steep rocky slopes, covered with scrub, 1950–2100 m (79°05'W, 3°59'S), 15.4.1973, Holm-Nielsen et al. 3451. – Also Colombia.

Malaxis lobulata L. O. Wms.

L. O. Wms. in Lilloa 5: 6, 1939.

Ecuador, prov. Azuay, km 91 on Pan American Highway N of Loja, dry scrub, 1–3 m high, 2900 m (79°10'W, 3°25'S), 5.5.1973, Holm-Nielsen et al. 5109. – Also Colombia.

Malaxis nasuta (Schltr.) Løjtnant comb. nov.

Basionym: *Microstylis nasuta* Schltr. in Feddes Rep. 27: 35, 1929.

Ecuador, prov. Cotopaxi, Quevedo–Latacunga road, above Macuchi, low herb and grass vegetation on stony-clayey soil, c. 1600 m (79°03'W, 0°56'S), 6–

9.4.1973, Holm-Nielsen et al. 3039, 3043, 3428. – Also Bolivia.

Maxillaria affinis (Poepp. & Endl.) Garay

Garay in Caldasia 8: 527, 1962.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, common in rain forest, c. 800 m (78°34'W, 3°29'S), 23.4.1973, Holm-Nielsen et al. 4249. – Also Colombia and Peru (type).

Maxillaria brachybulbon Schltr.

Schltr. in Feddes Rep. Beih. 19: 55, 1923.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34'W, 3°29'S), 23.4.1973, Holm-Nielsen et al. 4198. – Also Honduras, Costa Rica (type), Panama, Venezuela and Colombia.

Maxillaria campanulata C. Schweinf.

C. Schweinf. in Bot. Mus. Leafl. 5: 94, 1938.

The original description of *M. campanulata* states that the species has several inconspicuous warts in the middle of the lip near the base. Our collection fits the type except in having a small cluster of unicellular hairs instead of warts in the middle and near the base of the lip. These hairs break off easily, leaving scars which resemble small warts. It is my opinion that the warts described by Schweinfurth represents scars of the above-mentioned unicellular hairs. The hairs may represent food-hairs, since this type of pollinator attractant as well as pseudopollen is common within *Maxillaria* (Porsch 1908, Pijl & Dodson 1969).

Ecuador, prov. Carchi, Valle de Maldonado, km 71 on the road Tulcán–Maldonado, steep forested slopes, 2100–2200 m (78°06'W, 0°54'N), 20.5.1973, Holm-Nielsen et al. 6047. – Also Costa Rica.

Maxillaria christobalensis Rchb. f.

Rchb. f. in Bot. Zeit. 10: 857, 1852.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34'W, 3°29'S), 23.4.1973, Holm-Nielsen et al. 4242, 4245. – Pachicutza, at "Escuela Fiscomisional Cardinal Döpfner" km 140 on the road Loja–Gualaquiza, tropical rain forest with cleared areas along Río Zamora and along the road, 900–1000 m (78°34'W, 3°37'S), 26–27.4.1973, Holm-Nielsen et al. 4537. – Also Peru.

Maxillaria equitans (Schltr.) Garay

Garay in Bot. Mus. Leafl. 18: 208, 1958.

Ecuador, prov. Morona-Santiago, Pachicutza, at "Escuela Fiscomisional Cardinal Döpfner" km 140 on the road Loja–Gualaquiza, tropical rain forest with cleared areas along Río Zamora and along the road, 900–1000 m (78°34'W, 3°37'S), 26–27.4.1973, Holm-Nielsen et al. 4515. – Also Peru, Colombia (type), Brazil, Guyana and Venezuela.

Maxillaria foliosa Ames & C. Schweinf.

Ames & C. Schweinf. in Sched. Orch. 8: 60, 1925.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34'W, 3°29'S), 23.4.1973, Holm-Nielsen et al. 4195. – Also Costa Rica.

Maxillaria friedrichsthalii Rchb. f.

Rchb. f. in Bot. Zeit. 10: 858, 1852.

Ecuador, prov. Morona-Santiago, Pachicutza, at "Escuela Fiscomisional Cardinal Döpfner" km 140 on the road Loja–Gualaquiza, tropical rain forest with cleared areas along Río Zamora and along the road, 900–1000 m (78°34'W, 3°37'S), 26–27.4.1973, Holm-Nielsen et al. 4536. – Also from Mexico to Br. Honduras, Guatemala (type) and Panama.

Maxillaria mapiriensis (Kränzl.) L. O. Wms.

L. O. Wms. in Caldasia 5: 16, 1942.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 39, rocky area with steep scrub-covered slopes, 1600–1650 m (79°04'W, 3°59'S), 21.4.1973, Holm-Nielsen et al. 4034. – Also Bolivia (type), Colombia and Venezuela.

Maxillaria nasuta Rchb. f.

Rchb. f., Beitr. Orch. Centr.-Amer. 104, 1866.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34'W, 3°29'S), 23.4.1973, Holm-Nielsen et al. 4247. – Also from Mexico to Guatemala, Costa Rica (type), Venezuela, Colombia, Peru and Bolivia.

Maxillaria parviflora (Poepp. & Endl.) Garay

Garay in Bot. Mus. Leafl. 21: 258, 1967.

Ecuador, prov. Morona-Santiago, Pachicutza, at "Escuela Fiscomisional Cardinal Döpfner" km 140 on the road Loja–Gualaquiza, tropical rain forest with cleared areas along Río Zamora and along the road, 900–1000 m (78°34'W, 3°37'S), 26–27.4.1973, Holm-Nielsen et al. 4519, 4520. – Also Peru.

Maxillaria platyloba Schltr.

Schltr. in Feddes Rep. Beih. 9: 104, 1921.

Ecuador, prov. Loja, road Loja–Zamora, 1 km W of the pass (km 13), dry grass slopes, shrubby mountain slopes, and elfin forest, 2725–2750 m (79°09'W, 4°S), 17.4.1973, Holm-Nielsen et al. 3662; also at km 14, 2750–2770 m, 19–20.4.1973, Holm-Nielsen et al. 3946. – Also Peru.

Octomeria grandiflora Lindl.

Lindl. in Bot. Reg. 28: misc. 64, 1842.

Besides the cited collection of *O. grandiflora,* a different but fruiting species of *Octomeria* was collected in prov. Morona-Santiago and it is certain that several species of *Octomeria* will yet be discovered in the Amazonian part of Ecuador. The genus is new to Ecuador.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 24–25, steep rocky slopes, covered with scrub, 1950–2100 m (79°05'W, 3°59'S), 15.4.1973, Holm-Nielsen et al. 3445. – Also Trinidad, Venezuela, ? Bolivia and Brazil (type).

Odontoglossum auriculatum Rolfe

Rolfe in Kew Bull. 1892: 140.

Ecuador, prov. Carchi, Valle de Maldonado, km 60 on the road Tulcán–Maldonado, cleared slopes along the road and denser cloud forest, 2700 m (78°04'W, 0°51'N), 18.5.1973, Holm-Nielsen et al. 5702; also at km 67, 2600 m (78°04'W, 0°53'N), 21.5.1973, Holm-Nielsen et al. 6215. – Also Venezuela and Colombia (type ?).

Odontoglossum longipes Rchb. f. & Warsz.

Rchb. f. & Warsz. in Bonpl. 2: 100, 1854.

Schweinfurth (1970) was inclined to believe that *O. longipes* is conspecific with *O. longifolium* Lindl. from Ecuador. However, after examining records of the types of both species, I hesitate to concur with Schweinfurth's view that the differences between *O. longipes* and *O. longifolium* are merely a result of ecological differences.

Ecuador, prov. Loja, road Loja–Zamora, 1 km W of the pass (km 13), dry grass slopes, shrubby mountain slopes, and elfin forest, 2725–2750 m (79°09'W, 4°S), 17.4.1973, Holm-Nielsen et al. 3686. – Also Peru.

Odontoglossum rhynchanthum Rchb. f.

Rchb. f. in Gard. Chron. 1,3: 380, 1887.

Reichenbach described the species as "*Odontoglossum rhynchanthum* X" as he thought it might be a hybrid between *O. purum* Rchb. f. and *O. lindleyanum* Rchb. f. & Warsz., both from "New Granada". It is uncertain whether *O. rhynchanthum, O. purum,* and *O. lindleyanum* are described upon material from what is now known as N Ecuador or from Colombia. We found *O. rhynchanthum* close to the Colombian border, together with *O. armatum* Rchb. f. and *O. auriculatum* Rolfe, two species which are closely related to *O. purum* and *O. lindleyanum.*

Ecuador, prov. Carchi, Valle de Maldonado, km 71 on the road Tulcán–Maldonado, steep forested slopes, 2100–2200 m (78°06'W, 0°54'N), 20.5.1973, Holm-Nielsen et al. 6066.

Odontoglossum scabiosum (Kränzl.) Schltr.

Schltr. in Feddes Rep. Beih. 7: 284, 1920.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 14, mountain ridges with elfin forest and open bogs, 2750–2770 m (79°09'W, 4°S), 19–20.4.1973, Holm-Nielsen et al. 3956, 3984. – Also Colombia.

Odontoglossum spathaceum Lindl.

Lindl., Fol. Orch., Odontoglossum 18, no. 50, 1852.

Ecuador, prov. Carchi, Valle de Maldonado, km 53 on the road Tulcán–Maldonado, steep slopes in cloud forest, 3150–3250 m (78°03'W, 0°50'N), 17–18.5.1973, Holm-Nielsen et al. 5614. – Prov. Imbabura, timber line vegetation on the Hacienda Yura Cruz, 10 km N of Ibarra, 3700–3800 m (78°05'W, 0°22'N), 25.5.1973, Holm-Nielsen et al. 6487. – Prov. Cotopaxi, Quevedo–Latacunga road, above Pilaló, at the timber line, 3450–3500 m (78°56'W, 0°58'S), 8.4.1973, Holm-Nielsen et al. 3298. – Also Colombia.

Oliveriana brevilabia (C. Schweinf.) Dressl. & N. Will.

Dressl. & N. Will. in Amer. Orch. Soc. Bull. 39: 324, 1970, in adnot.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 33, dry rocky slopes with grass and scattered shrubs, 1800–1850 m (79°04'W, 3°59'S), 21.4.1973, Holm-Nielsen et al. 4123. – Also Peru (type) and Colombia.

Oncidium cocciferum Rchb. f. & Warsz.

Rchb. f. & Warsz. in Bonpl. 2: 101, 1854.

Ecuador, prov. Carchi, Valle de Maldonado, km 67 on the road Tulcán–Maldonado, montane forest, 2400 m

(78°04'W, 0°53'N), 20.5.1973, Holm-Nielsen et al. 6149. – Also Colombia (type) and Peru.

Pachyphyllum pectinatum Rchb. f.

Rchb. f., Xen. Orch. 3: 22, 1878.

Ecuador, prov. Carchi, Valle de Maldonado, km 67 on the road Tulcán–Maldonado, montane forest, 2600 m (78°04'W, 0°53'N), 21.5.1973, Holm-Nielsen et al. 6223. – Also Bolivia (type) and Peru.

Pachyphyllum squarrosum Lindl.

Lindl. in Ann. & Mag. Nat. Hist. 15: 107, 1845.

Ecuador, prov. Carchi, Valle de Maldonado, km 53 on the road Tulcán–Maldonado, steep slopes in cloud forest, 3250–3300 m (78°03'W, 0°50'N), 22.5.1973, Holm-Nielsen et al. 6252. – Also Colombia.

Pityphyllum laricinum (Kränzl.) Schltr.

Schltr. in Feddes Rep. Beih. 7: 163, 1920.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 24–25, steep rocky slopes, covered with scrub, 1950–2100 m (79°05'W, 3°59'S), 15.4.1973, Holm-Nielsen et al. 3437. – Also Peru.

Pleurothallis gelida Lindl.

Lindl. in Bot. Reg. 27, misc.: 91, 1841.

Ecuador, prov. Carchi, Valle de Maldonado, km 71 on the road Tulcán–Maldonado, steep forested slopes, 2100–2200 m (78°06' W, 0°54'N), 20.5.1973, Holm-Nielsen et al. 6077. – Prov. Cotopaxi, Quevedo–Latacunga road, steep rocky slopes along Río Pilaló with scattered trees, subtropical rain forest on fat clay, 1200–1300 m (79°09'W, 0°52'S), 7.4.1973, Holm-Nielsen et al. 3110, 3111. – Also from Florida, C America and the West Indies (type) to Colombia and Peru.

Pleurothallis rhopalocarpa Schltr.

Schltr. in Feddes Rep. Beih. 10: 43, 1922.

Ecuador, prov. Carchi, Valle de Maldonado, km 67 on the road Tulcán–Maldonado, montane forest, 2600 m (78°04'W, 0°53'N), 21.5.1973, Holm-Nielsen et al. 6227, 6228. – Also Bolivia.

Rodriguezia carnea Lindl.

Lindl. in Bot. Reg. 29, misc.: 72, 1843.

R. carnea will certainly prove to have a wider distribution in the equatorial Andes than indicated by the scarce collections as *R. carnea* is easily confused with *R. lanceolata* Ruiz & Pavón (*R. secunda* H.B.K.) which is often reported to be widely distributed in the American tropics. *R. carnea* differs from *R. lanceolata* by the lip which is distinctly constricted and bilamellate in the middle and not cuneate at the base.

Ecuador, prov. Napo, Archidona (77°48'W, 0°54'S), 27.6.1968, Holm-Nielsen & Jeppesen 1018. – Also Colombia.

Scaphyglottis bicornis (Lindl.) Garay

Garay in Bot. Mus. Leafl. 21: 255, 1967.

Ecuador, prov. Carchi, Valle de Maldonado, km 67 on the road Tulcán–Maldonado, montane forest, 2400 m (78°04'W, 0°53'N), 20.5.1973, Holm-Nielsen et al. 6150, 6156; also at 2600 m, 21.5.1973, Holm-Nielsen et al. 6221. – Also Colombia (type) and Venezuela.

Trichocentrum recurvum Lindl.

Lindl. in Bot. Reg. 29, misc.: 9, 1843.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34'W, 3°29'S), 23.4.1973, Holm-Nielsen et al. 4197. – Also Guyana.

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Seed coat structure of Old World Lupinus species

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The seed surface of 8 Old World *Lupinus* species was studied by SEM. At least 4 different seed coat patterns were discerned, according to which the species are arranged in four groups: (1) *L. albus* L. and *L. graecus* Boiss. & Sprun.; (2) *L. luteus* L.; (3) *L. angustifolius* L. and *L. micranthus* Guss.; (4) *L. pilosus* Murr., *L. palaestinus* Boiss. and *L. cosentinii* Guss. For comparison 6 New World species were also examined: *L. albicaulis* Torr., *L. arboreus* Sims, *L. aschenbornii* S. Schau., *L. montanus* H. B., *L. mutabilis* Sweet and *L. succulentus* Dougl. These were all found to have a comparatively uniform seed coat pattern.

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The data presented here are part of a wider biosystematic research project on native *Lupinus* populations in Israel, the aims of which have been explained elsewhere (Pazy et al. 1977). To assess interspecific relationships, characters not previously studied in *Lupinus* are being investigated.

To study the inter- and intraspecific variation of the seed coat of Old World lupins, several accessions of each of the 6 species (7 taxa) growing in Israel were examined; for comparison two other Mediterranean and 6 New World species were also investigated.

Material and methods

The sources of the seeds studied are listed in Table 1. Seeds were either collected by us in the field or obtained from various seed collections, more rarely taken from herbarium material. Vouchers are deposited in our seed collection or at HUJ.

In a preliminary study hand-cut sections of dried seeds were studied under a light microscope. The main investigations were SEM studies of seeds coated with gold-palladium, using a Cambridge S4/10 microscope. The micrographs were taken in the central part of the seed coat.

Observations

The general seed coat structure of *Lupinus*, as seen in the hand sections, agrees with that reported for other Leguminosae (Corner 1951, 1976). The different seed coat patterns are the result of differences in the organization of the uppermost layer, the palisade cells, and of various substances deposited on their surface. The following species groups were discerned.

(1) *L. albus* and *L. graecus* (Fig. 1).

The testa surface is strongly granulated. It is also covered with ridges either arranged in a regular pattern which makes the surface appear foveolate (*L. albus*, Fig. 1 A, B) or irregularly scattered (*L. albus*, Fig. 1 C, D; *L. graecus*, Fig. 1 E, F). According to the distance between the ridges, these may represent elevated cell walls or some parts of cell walls. It is possible that the foveolate appearance of some *L. albus* seed coats is due to the collapse of the tangential cell walls (cf. Brisson & Peterson 1976).

(2) *L. luteus* (Fig. 2).

The testa surface is covered with shallow, "volcano-like", protuberances which differ from those of the preceding group in shape and pattern. Each protuberance probably corresponds to a single cell. Their upper margin is surrounded by a thick amorphous layer which we assume to be cutinous. Otherwise, the seed surface is smooth, not covered by granules as in *L. albus* and *L. graecus*.

We compared seeds from wild populations from Israel (Fig. 2 A, B) and the Iberian peninsula (Fig. 2 C, D) with seeds from a cultivated line (Fig. 2 E). The shape and spacing of the protuberances on the seed coats of *L. luteus* from Israel seem to differ slightly from those of the plants from other sources. Fig. 2 F shows an extreme case, which must be regarded, however, with some suspicion, because these seeds were obtained from a herbarium specimen and might not have reached full maturity.

(3) *L. micranthus* and *L. angustifolius* (Fig. 3).

The testa looks as if it had been strewn over with some amorphous substance. This covering is mainly formed of short 'threads', which lie between and on top of the rounded protuberances. In *L. albus* and *L. graecus* the surface granulation has a different appearance.

Some variation occurs within the group. The diameter of the protuberances is smaller in *L. micranthus* (Fig. 3 A, B) and *L. angustifolius* var. *angustifolius* (Fig. 3 C, D) than in *L. angustifolius* var. *basalticus* (Fig. 3 E). The large seeds of a sample of *L. angustifolius*, probably an introduced species in Israel, have a less granulated surface and the shape of the protuberances is somewhat different (Fig. 3 F).

(4) *L. palaestinus, L. pilosus* and *L. cosentinii* (Fig. 4).

The seed coat structure of all these species, known as the rough-seeded lupins, is generally similar. We consider the protuberances to be fascicled palisade cells. They are much larger than those of the other species and are discernible without optical aids. In *L. pilosus* (Fig. 4 A), which has the largest protuberances, they may exceed 300 μm in height, about twice the height of those of *L. palaestinus* (Fig. 4 B). In the single sample of *L. cosentinii*, they seem even shallower and wider.

The surface of each protuberance (Fig. 4 D) most resembles the continuous surface of the seeds of some of the species from the New World (Fig. 5 A–C).

In these three species a thin membrane covers the whole seed below the tops of the protuberances. However, it is easily torn apart, even after careful handling, like in nature, and only fragments remain (Fig. 4 B).

(5) Species from the New World (Fig. 5).

Six out of a total of at least 100 New World species were chosen at random. Their seed surfaces are fairly similar, being irregularly ridged, smooth or granular, perhaps most resembling that of *L. albus* and *L. graecus*. They vary, however, in the extent of granulation and in the shape and arrangement of the ridges.

Discussion

Species for which a close relationship has been previously proven or assumed, have a similar seed coat structure. *L. albus* and *L. graecus* (group 1) are closely related, and the latter is often assumed to be the wild progenitor of the former (for a summary see Gladstones 1974, who regards them as varieties of the same species). *L. palaestinus, L. pilosus* and *L. cosentinii* (group 4) are generally considered to have many morphological characters in common. The first two have the same chromosome number (Pazy et al. 1977); *L. cosentinii,* though differing in chromosome number, has even been united with *L. pilosus* to form a single species (*L. varius* L.; Amaral Franco & Pinto da Silva 1968, Chamberlain 1970, Zohary 1972).

Similarity of seed coat structure, however, may also occur in species which are not closely related: *L. angustifolius* and *L. micranthus* (group 3) differ greatly in morphological characters as well as in chromosome numbers. Their seed coat structures, however, are very similar.

Intraspecific variation has been found in some cases: e.g. native and introduced *L. angustifolius* (Fig. 3 C–E and 3 F); wild and cultivated *L. luteus* (Fig. 2 A–D and 2 E), in the latter case confirmed by cytogenetic studies (Kazimierski & Kazimierska 1975).

No comprehensive SEM studies of the seeds of leguminous genera seem to have been published yet (Brisson & Peterson 1976 p. 492). In any case, the variation displayed by the Old World species of *Lupinus* seems impressive and the contrast with the relative uniformity of the seed coats of the six New World species is striking. Further studies of a wider array of New

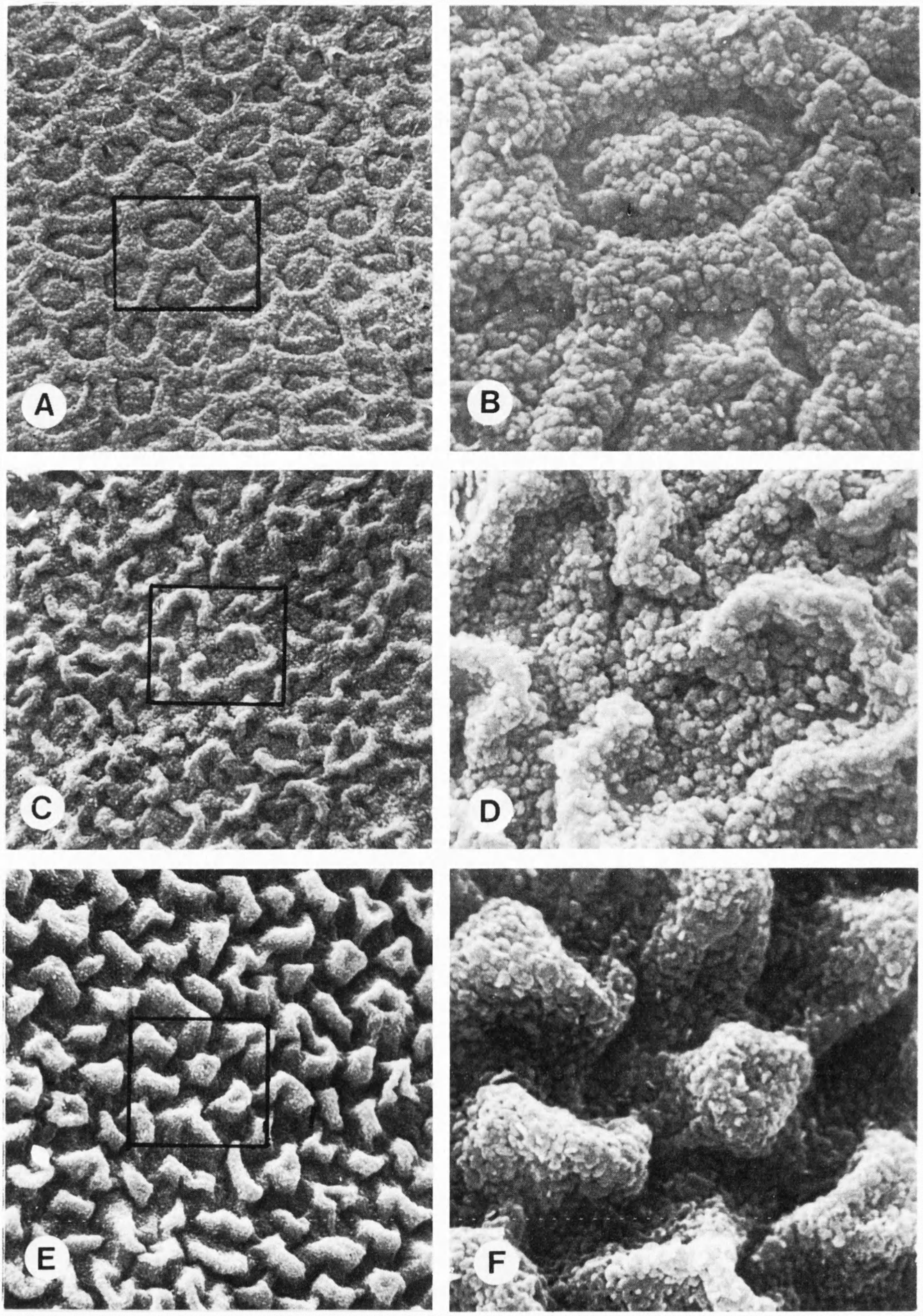

Fig. 1. Seed coats. A–D: *L. albus*. – A, B: Regularly ridged. – C, D: Irregularly ridged. – E, F: *L. graecus*. – A, C, E × 650, B, D, F × 2600.

Table 1. Collections of *Lupinus* species studied. – Old World species: *L. albus* to *L. pilosus*. New World species: *L. albicaulis* to *L. succulentus*.

Species	Reference	Origin	Fig.
L. albus L.	C/14	Cult. (Bot. Garden, HUJ)	
	C/11	Cult. (Pl. Introd. Service, Bet Dagan)	
	Herb. HUJ	Cult.? Golan Heights, Birket Ram	1 A, B
	C/22	Cult. (A. Horovitz, Tel-Aviv)	1 C, D
	C/55	Cult. (E. A. Bell, King's College, London No. 7)	
L. angustifolius L. var. *angustifolius*	ANG-P/75-3	Israel, Sharon Plain, Nordia	
	ANG-P/75-4	Israel, Sharon Plain, Raanana junction	3 C, D
L. angustifolius var. *basalticus*	C/3	Israel, W. Galilee (A. Horovitz Lb-21)	3 E
	C/4	Israel, W. Galilee (A. Horovitz Lb-20)	
	C/5	Israel, W. Galilee (A. Horovitz Lb-24)	
	ANG-P/76-12	Israel, Upper Galilee, Yiron (introduced)	3 F
L. cosentinii Guss. (*L. varius* ssp. *varius*)	C/18	Morocco (Zentr. Inst. Genet. Kulturpfl. Gatersleben)	4 E, F
L. graecus Boiss. & Sprun.	C/20	Greece (Zentr. Inst. Genet. Kulturpfl. Gatersleben)	1 E, F
L. luteus L.	C/58	Israel, Sharon Plain, Herzliya (Pl. Introd. Serv., Bet-Dagan, as *L. aureus*)	2 A, B
	LUT-P/75-4	Israel, Sharon Plain, Raanana junction	
	Herb. HUJ	Israel, Sharon Plain, Gan Shmuel	2 F
	C/19	Cult. (Zentr. Inst. Genet. Kulturpfl. Gatersleben)	
	Herb. HUJ	Spain, Algeciras	
	C/17	Portugal, Cult. (Zentr. Inst. Genet. Kulturpfl. Gatersleben)	2 C, D
	C/21	Cult. (Wageningen)	2 E
L. micranthus Guss.	MIC-P/75-5	Israel, W. Galilee, Kefar Liman	3 A, B
	MIC-P/75-6	Israel, Upper Galilee, Mt. Meron	
	C/37	Crete, Paleochora-Kandanos (J. Katznelson No. 30)	
L. palaestinus Boiss.	PAL-P/75-2	Israel, Sharon Plain, Ilanoth	4 B–D
	C/10	Israel, Sharon Plain, Tel Barukh	
	PAL-P/75-1	Israel, Sharon Plain, Tel-Tsur	
L. pilosus Murr. (*L. varius* ssp. *orientalis*)	C/2	Israel, Shomron, Wadi Milek (A. Horovitz Lv-31)	4 A
	C/7	Israel, Jezreel Valley, Dovrath–Tel Adashim	
	C/8	Israel, Upper Galilee, Rosh Pinna	
	PLO-P/76-11	Israel, Upper Galilee, Amiad	
	C/9	Israel, Lower Galilee, Mitspe	
	PLO-P/76-10	Israel, Upper Jordan Valley, N of Ein Gev	
	C/23	Crete (Zentr. Inst. Genet. Kulturpfl. Gatersleben)	
	C/56	Crete, Kandanos (J. Katznelson No. 32 A)	
L. albicaulis Torr.	C/40	? (E. A. Bell, King's College, London)	5 F
L. arboreus Sims	Herb. HUJ	California, Rose 33228	5 B
L. aschenbornii S. Schau.	Herb. HUJ	Mexico, Rudd 1028	5 C
L. montanus H. B.	Herb. HUJ	Mexico, Rudd 1029	5 E
L. mutabilis Sweet	C/24	Cult. (Zentr. Inst. Genet. Kulturpfl. Gatersleben)	5 A
	C/41	Cult. (E. A. Bell, King's College, London)	
L. succulentus Dougl.	Herb. HUJ	California, Rudd 3436	5 D

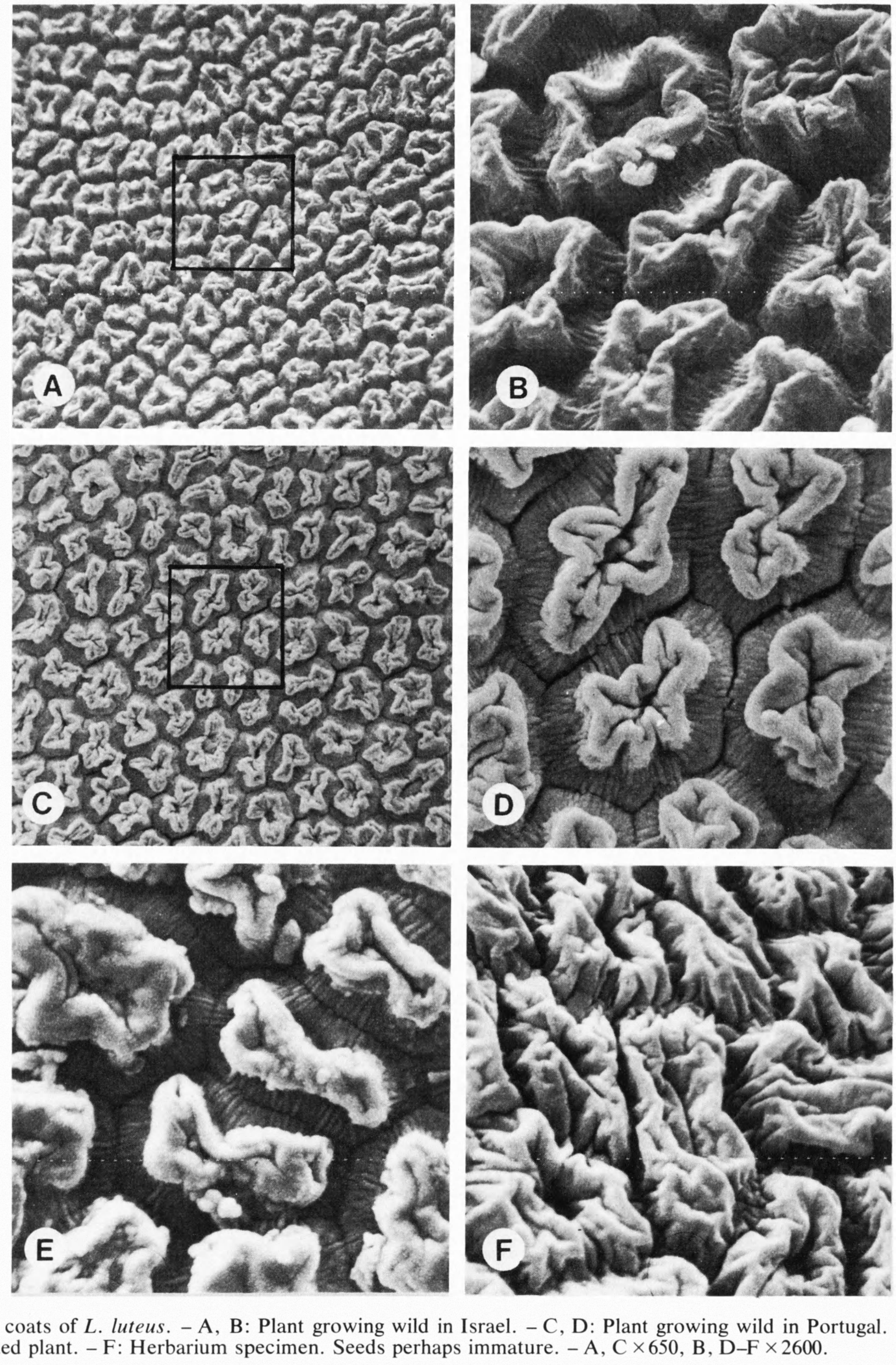

Fig. 2. Seed coats of *L. luteus*. – A, B: Plant growing wild in Israel. – C, D: Plant growing wild in Portugal. – E: Cultivated plant. – F: Herbarium specimen. Seeds perhaps immature. – A, C ×650, B, D–F ×2600.

World species are desirable to discover whether or not this uniformity is representative. The observations made so far, seem at all events to agree with the patterns of chromosome numbers found for the Old World lupins (cf. Pazy et al. 1977). According to the variation in both seed surface and chromosome number, the relatively few Old World *Lupinus* species may be regarded as being representatives of isolated species groups.

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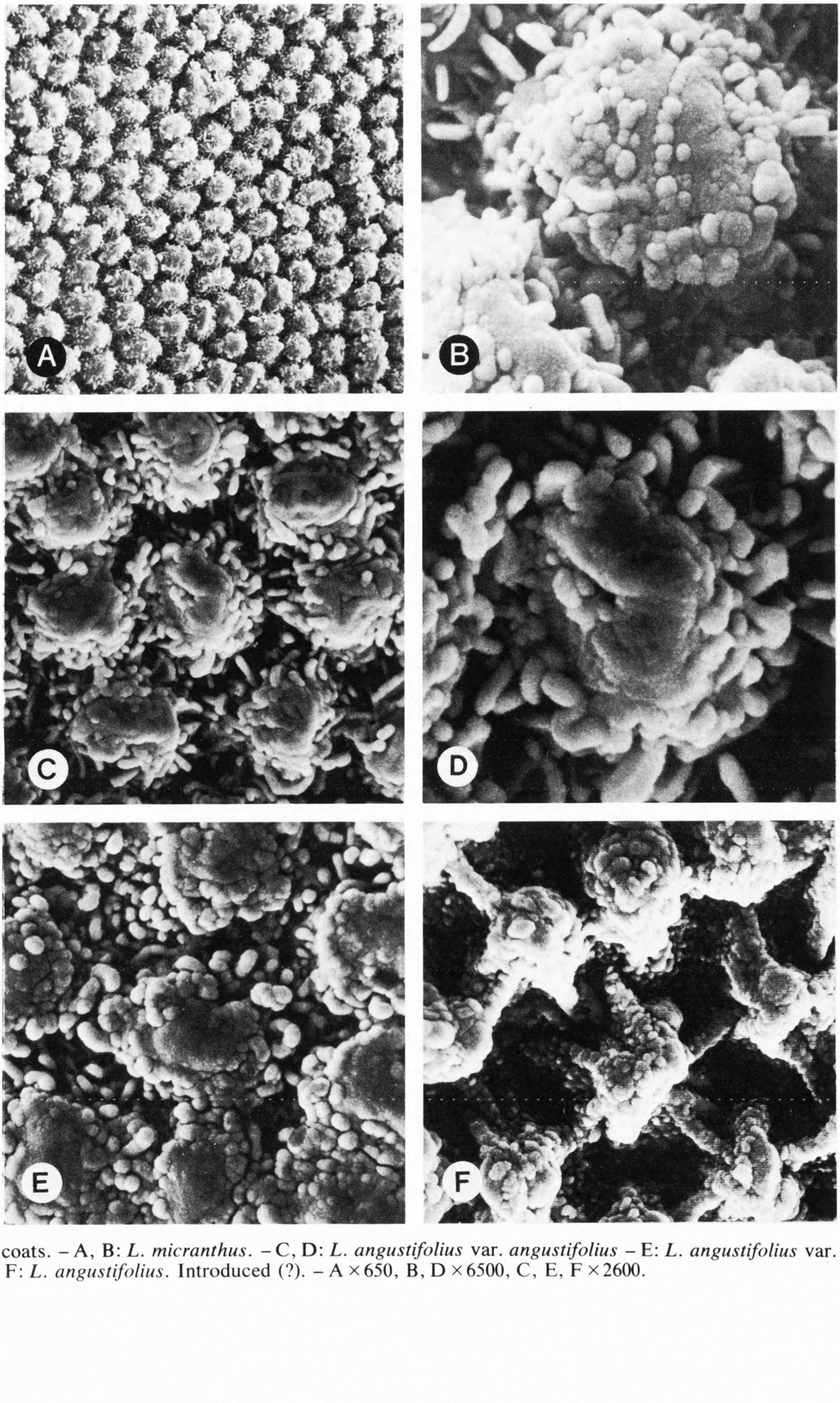

Fig. 3. Seed coats. – A, B: *L. micranthus*. – C, D: *L. angustifolius* var. *angustifolius* – E: *L. angustifolius* var. *basalticus*. – F: *L. angustifolius*. Introduced (?). – A ×650, B, D ×6500, C, E, F ×2600.

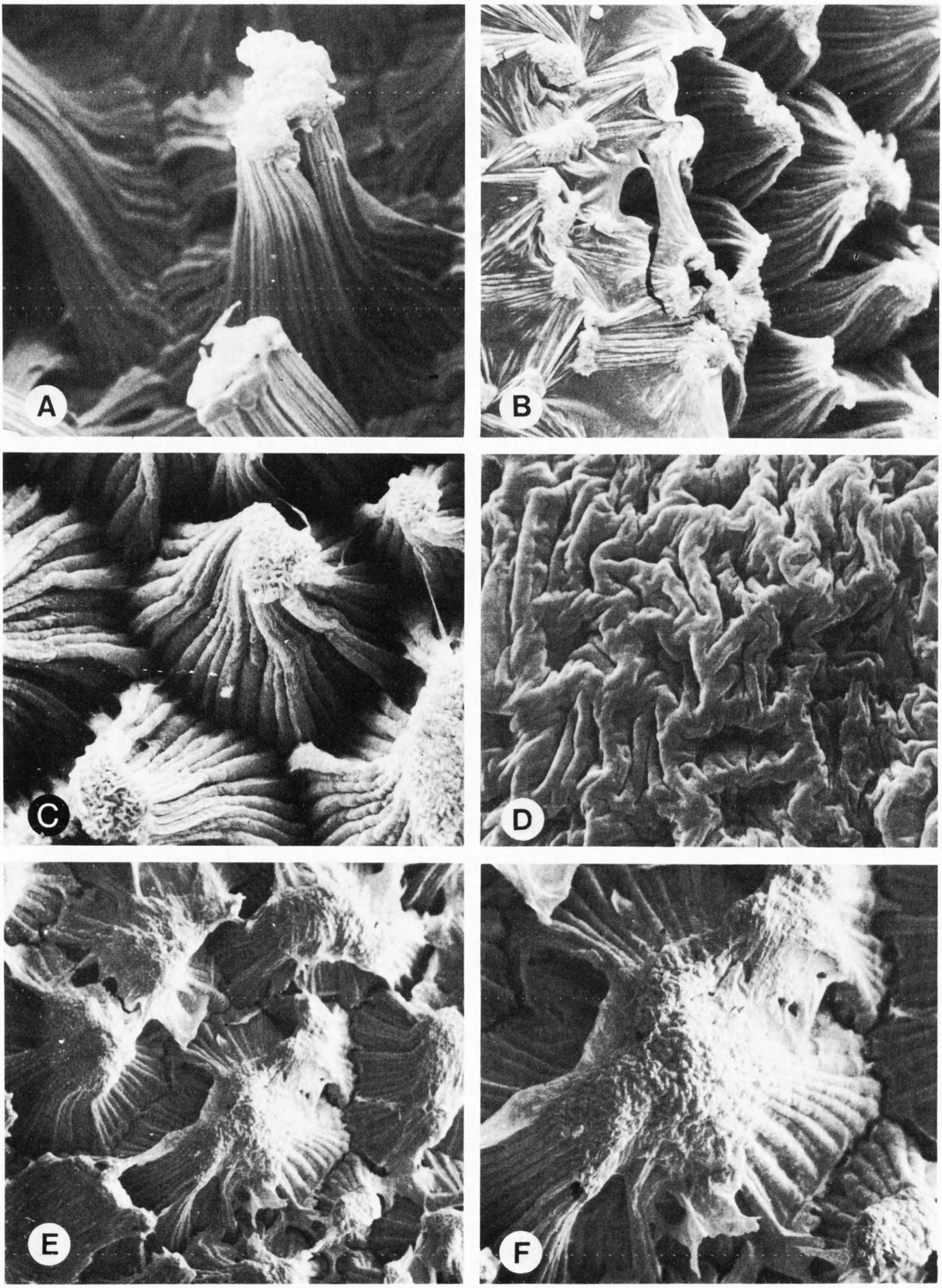

Fig. 4. Seed coats. – A: *L. pilosus*. – B–D: *L. palaestinus*. – B: Part of the seed with intact membrane. – C: Seed coat without membrane. – D: Surface of fascicled palisade cells. – E, F: *L. cosentinii*. – A, B, E × 130, C, F × 260, D × 2600.

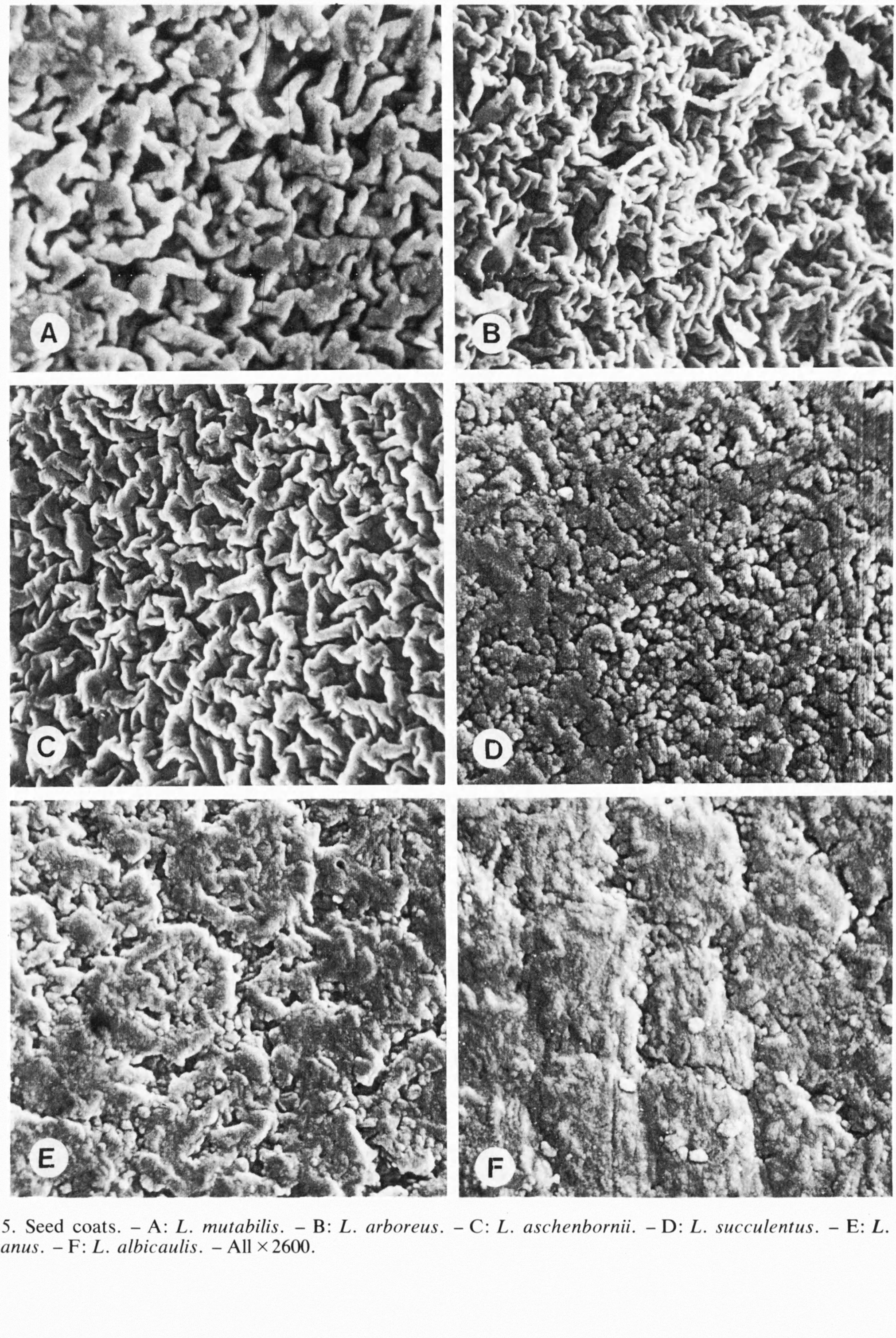

Fig. 5. Seed coats. – A: *L. mutabilis*. – B: *L. arboreus*. – C: *L. aschenbornii*. – D: *L. succulentus*. – E: *L. montanus*. – F: *L. albicaulis*. – All ×2600.

Chromosome numbers for some Leguminosae from Iraq

Abdul-Ridha A. Al-Mayah and Ihsan A. Al-Shehbaz

Al-Mayah, A.-R. A. & Al-Shehbaz, I. A. 1977 12 30: Chromosome numbers for some Leguminosae from Iraq. *Bot. Notiser 130:* 437–440. Stockholm. ISSN 0006-8195.

Chromosome numbers are reported for 79 collections representing 49 species in 19 genera of Leguminosae. Of these, 12 are first reports. Observations deviating from those of previous reports are discussed. Meiotic irregularities were observed in several species. The karyotypes of a few species are described for the first time.

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In the present paper, chromosome counts are reported for wild and cultivated species of Leguminosae from Iraq. Unless otherwise indicated, the counts given here are in accordance with those of previous reports as listed in the indices edited by Fedorov (1969) and Moore (1973, 1974), and are presented without further comment. For those species where meiosis was not quite regular, the types of irregularities are briefly discussed. The nomenclature follows Townsend (1974).

Flower buds or root tips were fixed in Carnoy's fluid. Meiotic material was squashed in aceto-carmine or aceto-orcein after treating the buds with boiling HCl for a few seconds and then washing them in water for 15–30 minutes. Most root tips were pretreated with 0.002 M 8-hydroxyquinoline for 3–4 hours at room temperature. Roots of *Vigna* species and of *Lathyrus vinealis* were pretreated with 0.5% colchicine for 2–3 hours at room temperature. Most root tips were squashed in aceto-carmine following the conventional method. Those of the genera *Medicago* and *Melilotus* were squashed in aceto-orcein after boiling them in the stain for 5 minutes and twice repeating the boiling process. Lacto-propionic-orcein was used for the roots of *Glycyrrhiza* and *Onobrychis* following the procedure of Dyer (1963).

Under each species, the chromosome number(s) given is followed by the name(s) of the physiographic districts and localities for the material on which the chromosome count(s) were made. We have followed Guest (1966) in assigning each physiographic district to a given locality. The abbreviations IAS and AAM stand for I. A. Al-Shehbaz and A. A. Al-Mayah respectively. An asterisk following the diploid number indicates that the count was made from the somatic cells of the pistil. All other diploid counts were obtained from root tips. All voucher specimens are deposited in the Baghdad University Herbarium (BUH), where they are available for inspection.

This paper is part of a M. Sc. thesis submitted by the senior author to the University of Baghdad.

Albizia lebbeck (L.) Benth. – n = 13. LCA: Wazeeriya, Baghdad, AAM 75205 (cult.). This is probably the second count for this species, after that made by Patil (1958).

Amorpha fruticosa L. – n = 20. LCA: Wazeeriya, Baghdad, AAM 76146 (cult.).

Astragalus dactylocarpus Boiss. – n = 8. LCA: Sudur, AAM 7631. This is the first report for this species.

Astragalus laguriformis Freyn – 2n = 14. MAM: Sharanish, AAM 75280. This is the first report for this species. All chromosomes are medium-sized. Two pairs are metacentric and the remaining five pairs are submetacentric.

Astragalus mossulensis Bunge – n = 8. LEA: Wadi Al-Ahmar, N of Muqdadiya, AAM 75149. Ledingham & Rever (1963) previously reported 2n = 32 for this species.

Astragalus russelii Banks & Sol. – n = 8. DSD:

Jabal Sanam, AAM 76415. This is the first report for this species. Townsend (1974) indicated that the species is restricted to northern and north-central Iraq. However, we have examined a large number of specimens that were not available to him, and the species does seem to extend all the way to the southern part of the country.

Astragalus zubairensis Eig – n = 8. DWD: Ukhaidhir, AAM 76136. This is the first report for this species.

Glycyrrhiza glabra L. var. *glandulifera* (Waldst. & Kit.) Reg. & Herd. – n = 8. LBA: Mikhrag, N of Fao, AAM 75192. This is the first report for this variety. It agrees with the other reported counts for the species, as well as with counts reported for other species of the genus.

Hymenocarpus circinnatus (L.) Savi – n = 8. MRO: Bekhal, IAS & AAM 76194.

Lathyrus annuus L. – n = 7. LCA: Saddat Al-Hindiya, AAM 7641.

Lathyrus aphaca L. – n = 7, 2n = 14*. LBA: Mikhrag, N of Fao, AAM 7620. LCA: Saddat Al-Hindiya, AAM 7642.

Lathyrus chloranthus Boiss. & Bal. – n = 7, 2n = 14*. MRO: Nawanda, southern slope of Algird Dagh, IAS & AAM 76295. This is the first report for this species.

Lathyrus cicera L. – n = 7, 2n = 14*. MAM: Sulaf, IAS & AAM 76229.

Lathyrus gorgoni Parl. – n = 7, 2n = 14*. LEA: Harooniya, AAM 7657.

Lathyrus inconspicuus L. – n = 7, 2n = 14*. MAM: Bamerni, near Sarsang, IAS & AAM 76260.

Lathyrus pratensis L. – n = 7. MRO: Sidikan, IAS & AAM 76287. Chromosomal fragments were occasionally observed. The association of two bivalents with the nucleolus at diakinesis indicates that secondary constrictions are present on two out of the seven pairs of chromosomes.

Lathyrus tuberosus L. – n = 7. MRO: Between Darband and Chouman, IAS & AAM 76296.

Lathyrus vinealis Boiss. & Noë – 2n = 14. MRO: Hirdi, IAS & AAM 76289; Haj Omran, IAS & AAM 76302. This is the first report for this species. The karyotype is made up of a pair of long metacentric chromosomes, a pair of long submetacentric chromosomes, four pairs of medium-sized submetacentric chromosomes and one pair of small metacentric chromosomes.

Lens orientalis (Boiss.) Hand.-Mazz. – n = 7, 2n = 14*. MRO: Chouman, IAS & AAM 76173. This is the first report for this species. Counts of n = 7 were reported for other species of the genus.

Lotus corniculatus L. var. *corniculatus* – n = 6, 2n = 12*. LBA: Ma'qil, AAM 7607. Diploids and tetraploids based on x = 6 have been reported for this genus.

Medicago sativa L. – 2n = 32. DSD: Najaf, AAM 75132 (cult.). LBA: Mikhrag, N of Fao, AAM 75193 (cult.).

Melilotus alba Med. – n = 8, 2n = 16. LBA: Basra, AAM 75183.

Melilotus indica (L.) All. – n = 8, 2n = 16. LCA: Baghdad, AAM 7531.

Onobrychis crista-galli (L.) Lam. – n = 8, 2n = 16*. DGA: Adhaim, AAM 7510.

Onobrychis galegifolia Boiss. – 2n = 16. MAM: Amadiya, AAM 75218. This is the first report for this species.

Onobrychis haussknechtii Boiss. – 2n = 16. FPF: Badra, IAS & AAM 76154. This is the first report for this species.

Pisum formosum (Stev.) Alef. – 2n = 14. MAM: Swara Tuka, AAM 75332. This is the first report for this species. All the chromosomes are nearly equal in size. Six pairs are submetacentric, one of which has a secondary constriction. The seventh pair is metacentric.

Pisum sativum L. – n = 7. MAM: Sulaf, IAS & AAM 76227. MRO: Bekhal, IAS & AAM 76191. In a few cells six bivalents and two univalents were observed at diakinesis and first metaphase. Lagging chromosomes were occasionally observed at first anaphase.

Scorpiurus muricatus L. var. *subvillosus* (L.) Lam. – n = 7, n = 8. LEA: Wadi Al-Ahmar, AAM 7547. In some plants eight bivalents were observed in most cells at first metaphase. However, few cells showed seven bivalents and two univalents. In other plants seven bivalents, or five bivalents and four univalents were observed. This taxon certainly needs a more detailed study in Iraq. Heyn & Raviv (1966) showed that polyploidy based on x = 7 is involved in all the morphological extremes they studied in this species.

Securigera securidaca (L.) Deg. & Doerfl. – n = 6. LBA: Basra, AAM 7518.

Sesbania cannabina (Retz.) Poir. – n = 6. LCA: Baghdad, AAM 75241 (cult.). This is the first report for the species.

Sesbania sesban (L.) Merrill – n = 6. LCA: Baghdad, AAM 76340 (cult.). In a few cells five bivalents and two univalents were observed at first metaphase, while in others lagging chromosomes were seen at second anaphase.

Sophora gibbosa (DC.) Yakovl. – n = 9. DLJ: Thirthar, AAM 76522. This is the first report for the species. Counts of n = 9 have been reported previously for many species of the genus.

Trifolium echinatum M.B. – n = 8. LEA: Harooniya, AAM 7555.

Vicia assyriaca Boiss. – n = 6. MAM: Between Amadiya and Sulaf, IAS & AAM 76221. MRO: Bekhal, IAS & AAM 76186. Our count for the species differs from that (2n = 14) reported by Plitmann (1970).

Vicia ervilia (L.) Willd. – n = 7. MAM: Between Dohuk and Zawita, IAS & AAM 76249. MRO: Chouman, IAS & AAM 76174. – 2n = 14. MJS: Karsi, IAS & AAM 75123. The karyotype of this species is made up of one pair of small acrocentric chromosomes with satellites, a pair of medium-sized metacentric chromosomes, a pair of long metacentric chromosomes, two pairs of long submetacentric chromosomes and two pairs of long acrocentric chromosomes.

Vicia faba L. (all cult.) – n = 6. LBA: Mikhrag, N of Fao, AAM 7611. DSD: Safwan, AAM 7651. n = 7, 2n = 14. LCA: Baghdad, AAM 75450.

Vicia hybrida L. – n = 6, 2n = 12*. MAM: Between Dohuk and Zawita, IAS & AAM 76217. MRO: Salah ad-Din, IAS & AAM 76206; Bekhal, IAS & AAM 76189. FPF: Koma Sang, near Mandali, IAS & AAM 76151. Five bivalents and two univalents were occasionally observed at first metaphase, while one or two lagging chromosomes were seen in a few cells at first anaphase.

Vicia koeieana Rech. f. – n = 7. MRO: Bewas, IAS & AAM 76281: Hirdin, IAS & AAM 76283; Bassan, IAS & AAM 76293. Our count agrees with the earlier one reported by Plitmann (1970). In the three collections cited above, a number of meiotic irregularities were observed. A few cells showed five bivalents and a quadrivalent or six bivalents and two univalents at first metaphase. One or two lagging chromosomes or one or two chromosomal bridges were observed in many cells at first anaphase.

Vicia michauxii Spreng. – n = 7, 2n = 14*. MAM: Between Dohuk and Zawita, IAS & AAM 76254; Sulaf, IAS & AAM 76237. MRO: Salah ad-Din, IAS & AAM 76203; Chouman, IAS & AAM 76170. The only previous count available for this species is 2n = 12. This was made by Coutinho some 32 years ago (Fedorov 1969).

Vicia narbonensis L. – n = 7. MAM: Sulaf, IAS & AAM 76223; Kani Sang, IAS & AAM 76224; Zawita, IAS & AAM 76246. MRO: Chouman, IAS & AAM 76168; Bekhal, IAS & AAM 76187. Chromosomal fragments or one or two lagging chromosomes were observed in a few cells at first or second anaphase.

Vicia palaestina Boiss. – n = 7, 2n = 14*. MRO: Bekhal, IAS & AAM 76190. MJS: Karsi, IAS & AAM 75124. Four bivalents and six univalents were occasionally observed at first metaphase.

Vicia peregrina L. – n = 7, 2n = 14*. MAM: Sulaf, IAS & AAM 76230. MRO: Salah ad-Din, IAS & AAM 76202. Six bivalents and two univalents were observed in a few cells at first metaphase. Our counts agree with those reported by Kuzmanov & Markova (1973) and Zohary (1972) but not with those of Plitmann (1970).

Vicia sativa L. var. *sativa* – n = 6, 2n = 12*. MRO: Bekhal, IAS & AAM 76188; Salah ad-Din, IAS & AAM 76208. FPF: Mandali, IAS & AAM 76152. LCA: Baghdad, AAM 7646.

Vicia sativa var. *amphicarpa* Boiss. – n = 5, 2n = 10*. LCA: Saddat Al-Hindiya, AAM 7640. In many cells four bivalents and two univalents or three bivalents and four univalents were observed at first metaphase. Plitmann (1973) and Kuzmanov & Markova (1973) have reported n = 7 for this species.

Vicia sericocarpa Fenzl – n = 6, 2n = 12*. MRO: Chouman, IAS & AAM 76178. Lagging chromosomes or chromosomal fragments or bridges were occasionally observed at first anaphase.

Vicia tenuifolia Roth – n = 7. MAM: Sarsang, IAS & AAM 76241; Zawita, IAS & AAM 76245. Six bivalents and two univalents or five bivalents and four univalents were observed in a few cells at first metaphase. Chromosomal fragments were occasionally seen at first anaphase. All the previous counts for this species reported 2n = 24, although counts of 2n = 14 and 2n = 28 have been reported for *V. cracca* L. Townsend (1974) stated that the Iraqi material which he treated as *V. tenuifolia* was intermediate between the typical plant and *V. cracca* subsp. *stenophylla* Vel. Davis (1970), on the other hand, considered *V. tenuifolia* to be a subspecies of *V. cracca*. Our cytological findings are thus compatible with the view held by Davis.

Vicia villosa Roth – n = 7. MRO: Hirdin, IAS & AAM 76284; Haj Omran, IAS & AAM 76297; Bassan, IAS & AAM 76292.

Vigna radiata (L.) Wilczek – 2n = 22. MAM: Sharanish, AAM 75303 (cult.).

Vigna unguiculata (L.) Walp. – 2n = 22. LCA: Adhamiya, Baghdad, AAM 76306 (cult.).

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Embryology of Trichodesma (Boraginaceae)

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The embryology of *Trichodesma indicum* R. Br. and *T. zeylanicum* R. Br. has been studied. The development of the anther conforms to the dicotyledonous type. The tapetal cells become multinucleate and the nuclei tend to fuse and form polyploid nuclei. A few cells, underlying the archesporial initials on the connective side of the anther, enlarge and become vacuolated and multinucleate, resembling the tapetum. The pollen grains are shed at the two-celled stage. The stylar canal is filled with a transmitting tissue which extends over the micropyle of the anatropous ovules and abuts onto the placenta, behaving like an obturator. The megaspore tetrads are linear in *T. indicum* and consistently T-shaped in *T. zeylanicum.* A tendency towards nucellar apospory was observed in both species. The aposporic embryo sacs degenerate at the two-nucleate (sometimes at the four-nucleate) stage. The endosperm is nuclear. Embryo development follows the Asterad type, conforming to the Polygonum variation in *T. indicum* and the Lamium variation in *T. zeylanicum.* The pericarp is differentiated into a one-layered epicarp, a 6–8-layered, resiniferous mesocarp and a one-layered endocarp with radially elongated cells. The cells bordering the interlocular septum become strongly thickened and behave like the endothecial cells in the anther. The seed coat is 8–10-layered with a tanniniferous innermost layer.

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The genus *Trichodesma* belongs to the tribe Cynoglosseae (Boraginaceae) and includes about 21 species distributed within tropical and subtropical Africa, Asia and Australia. In South India, this genus is represented by two species, viz. *Trichodesma indicum* and *T. zeylanicum* (Gamble 1928).

Extensive morphological, anatomical and cytological studies have been made on the subfamily Boraginoideae. Recent work is that of Khanna (1964 a, b) on *Trichodesma amplexicaule, Mertensia platyphylla* and *M. paniculata,* Fathima (1967) on *Trichodesma zeylanicum,* Nagaraj & Fathima (1968) on *Adelocaryum coelestinum* and Khaleel (1974) on *Cynoglossum denticulatum.*

The present investigation deals with anther development, micro- and megasporogenesis, development and organization of the megagametophyte, fertilization, endosperm and embryo development, and the structure and development of the pericarp and seed coat in *Trichodesma indicum* R. Br. and *T. zeylanicum* R. Br.

Material and methods

The material was collected from various localities near to Bangalore, Bannerghatta and Mysore in Mysore State, India. Young flower buds, open flowers, fruits and nutlets were fixed in FAA and embedded in paraffin wax. Sections, 5–15 μm thick, were cut and stained in Heidenhain's iron alum haematoxylin with eosin as a counterstain. Sections of fruits and seeds were stained with safranin and fast green. Fresh ovules were dissected to study the endosperm. They were also treated with lactic acid or KOH at 50–60°C and stained with cotton blue to study the course of the vascular strands.

Flower

The flowers of *Trichodesma* are actinomorphic, bisexual and hypogynous. The calyx consists of five densely hispid lobes that are hastate at the base in *T. indicum* and rounded in *T. zeylanicum*. The corolla consists of five pale-blue petals united to form a tube, which in *T. zeylanicum* is equal in length to that of the rounded lobes. Two glandular spots are present on each lobe at the throat of the corolla tube in *T. indicum*. The stamens are connivent, densely hirsute, and their tips are spirally twisted, ending in hair-like points. The ovary is superior, bicarpellary, syncarpous and bilocular in the early stages, but later becomes quadrilocular due to the development of a false septum, each locule then containing a single anatropous ovule on an axillary placenta. The style is terminal and the stigma is simple. The fruit is pyramidal, containing a central quadrangular carpophore with four bays each bearing an ovoid, oblong nutlet adnate to the torus. The nutlets are smooth. The floral parts develop in an acropetal succession.

The stylar canal consists of a transmitting tissue composed of compactly arranged, elongated, glandular cells. The transmitting tissue extends over the micropyle and abuts onto the placenta, behaving like an obturator (Fig. 3 A, B). It continues spreading along the upper part of the funiculus and finally covers the upper part of each locule. It persists until the later stages of embryo development.

Microsporogenesis and anther development

Trichodesma indicum and *T. zeylanicum* are protandrous. A young anther in transection is rounded in outline and consists of a mass of homogeneous cells. It soon becomes four-lobed and a plate of four to five hypodermal cells, each possessing conspicuous nuclei and dense cytoplasm, develops in each of the four lobes (Fig. 1 A). Periclinal divisions in these cells result in the formation of a primary parietal layer and a primary sporogenous layer (Fig. 1 B). The primary parietal layer divides periclinally to form two secondary parietal layers (Fig. 1 C). The outer secondary parietal layer divides again, while the inner one functions as the tapetum (Fig. 1 D, E). Thus the anther wall consists of four layers, viz., epidermis, endothecium, middle layer and tapetum (Fig. 1 E). The tapetal cells are uninucleate initially but become multinucleate in later stages with the appearance of vacuoles in the cytoplasm (Fig. 1 E). The nuclei in some of these cells have a tendency to aggregate and fuse, forming polyploid nuclei with many nucleoli. After its cells have elongated radially and tangentially, at about the time the microspores are formed, the endothecium develops fibrillar bands of thickenings. The middle layer degenerates and the outer tangential walls of the epidermal cells become heavily cutinized (Fig. 1 N). The development of the anther wall thus corresponds to the dicotyledonous type (Davis 1966).

A few cells which underly the archesporial initials on the connective side of the anther, enlarge and become vacuolated. They become binucleate when the archesporial cells divide and later multinucleate, resembling the tapetal cells (Fig. 1 B–D). They persist until microsporogenesis is completed and then degenerate along with the tapetal cells. They appear to take part in the nutrition of the developing microsporocytes before the tapetal cells are formed.

The cells of the primary sporogenous layer undergo a number of periclinal and anticlinal divisions to form a massive sporogenous tissue (Fig. 1 C–E). The microsporocytes enlarge and become rounded before dividing meiotically (Fig. 1 F–H). The cell divisions are simultaneous and result in tetrahedral and decussate microspore tetrads (Fig. 1 I, K). In *T. zeylanicum* isobilateral tetrads are also formed. The microspores separate and develop a thick wall (Fig. 1 L, M). The centrally placed nucleus migrates to one side of the microspore and divides mitotically to form a lenticular generative cell and a large vegetative cell. The generative cell detaches itself and becomes engulfed in the cytoplasm of the vegetative cell and lies near the nucleus of the same (Fig. 1 M). The pollen grains are triporate and possess a smooth exine. They are shed at the two-celled stage.

Anther dehiscence takes place at the junction of the pollen sacs, where the endothecial cells lack fibrillar thickenings and the epidermal cells are slightly smaller. Each locule opens out independently (Fig. 1 O, P).

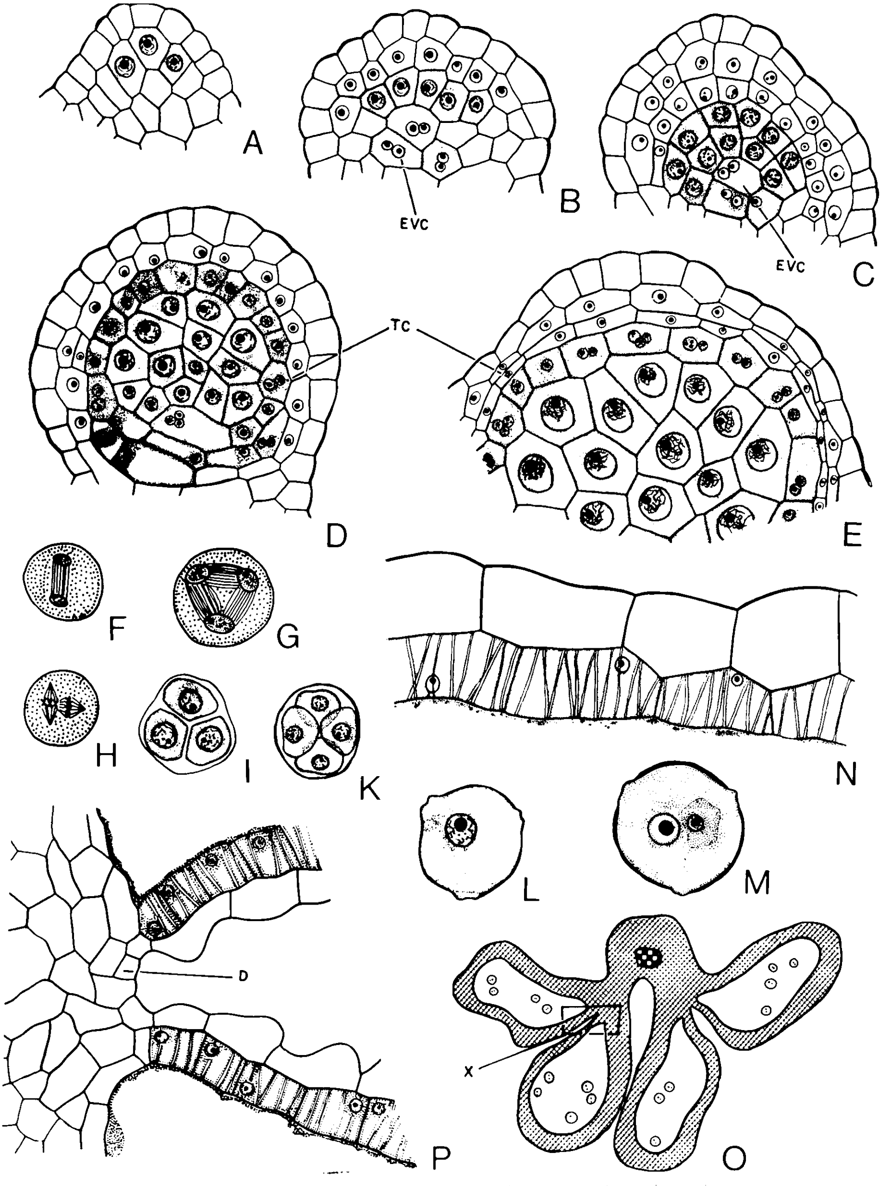

Fig. 1. Microsporogenesis and anther development in *Trichodesma indicum*. – A: TS of anther lobe showing archesporial initials. – B: TS of anther lobe showing primary parietal cells, primary sporogenous cells and enlarged vacuolated cells. – C: TS of anther lobe showing secondary parietal layers, sporogenous cells and enlarged vacuolated cells. – D: TS of anther lobe showing wall layers, tapetum and sporogenous tissue. – E: TS of portion of anther lobe showing wall layers, tapetum and microsporocytes. – F–H: Meiosis. – I, K: Tetrahedral and decussate microspore tetrads. – L, M: Pollen grains. – N: TS of portion of anther wall showing epidermis, fibrillar endothecium and degenerating tapetum. – O: TS of anther showing the region of dehiscence. – P: Portion marked X in Fig. 1 O enlarged. – A–H, N, P × 265, I–M × 530, O × 30. – D region of dehiscence, EVC enlarged vacuolated cells, TC tapetal cells.

Megasporogenesis and megagametophyte development

The ovules are anatropous, unitegmic and tenuinucellar. They arise on the axillary placenta as small papillate outgrowths and are supplied with a single vascular strand which branches inside the massive integument, the branches running close to the epidermis.

A single hypodermal archesporial initial differentiates in the nucellar dome and is recognizable by its dense cytoplasm and conspicuous nucleus. Occasionally two to three archesporial cells differentiate. However, only one of them functions further and the others degenerate (Fig. 2 A, B). The functional archesporial cell enlarges and becomes the megasporocyte (Fig. 2 C). Meiotic divisions in the megasporocyte result in linear tetrads in *Trichodesma indicum* (Fig. 2 D–F) and T-shaped tetrads in *T. zeylanicum.* The chalazal megaspore enlarges and functions further, while the three micropylar spores degenerate (Fig. 2 G–I).

The development of the gametophyte corresponds to the Polygonum type (Maheshwari 1950), see Fig. 2 H–L. The antipodals degenerate after fertilization. The two polar nuclei fuse either during or after fertilization.

The cells of the nucellar epidermis become disorganized at about the time that a four-nucleate gametophyte is formed. The surrounding nucellar cells also become crushed during this process, which brings the gametophyte into direct contact with the innermost layer of the integument (Fig. 2 K, L). However, no endothelium is organized.

A tendency towards nucellar apospory was observed. The aposporic embryo sacs initiate as enlarged cells below the archesporial cells and range from four to twelve in number (Fig. 2 B, C). They develop the characteristic vacuolation of aposporic embryo sacs and attain a regular polarity, thus simulating two-nucleate embryo sacs (Fig. 2 D–F). They seldom develop further and degenerate as the normal gametophyte enlarges. Rarely, however, they may reach a four-nucleate stage. The remnants of crushed, degenerating aposporic embryo sacs are visible during the various stages of gametogenesis as dark-staining masses.

Endosperm

The endosperm is nuclear, conforming to the Borago type (Svensson 1925). Division of the primary endosperm nucleus always precedes that of the zygote (Fig. 3 C) and about 16–32 free nuclei are formed (Figs. 3 D–G, 4 A, B). After a few more divisions, centripetal wall formation takes place, as a result of which the endosperm becomes cellular (Fig. 4 C–F). At this stage, small granules of reserve food material are found in the endosperm cells. When the embryo has reached the heart-shaped stage, most of the endosperm is consumed, leaving only one or two layers of cells. The endosperm is completely consumed as the embryo reaches maturity, so that none remains in the seed.

Embryo

The development of the embryo conforms to the Asterad type. In *Trichodesma indicum,* it develops according to the Polygonum variation and in *T. zeylanicum* according to the Lamium variation (Johansen 1950).

The zygote enlarges considerably before it divides transversely, resulting in the formation of a short terminal cell *ca* and a long basal cell *cb* (Figs. 5 A, B, 6 A, B). The next division in the terminal cell *ca* is by a vertical wall, whereas the basal cell *cb* divides by a transverse one, resulting in a T-shaped proembryonal tetrad (Figs. 5 C, D, 6 C). The upper two tiers of cells in the proembryonal tetrad are designated as *ci* and *m*. The two juxtaposed cells formed by the division of the cell *ca* divide vertically in a plane perpendicular to the previous one and organize the quadrant *q* (Figs. 5 F–I, 6 D–F). Meanwhile, the middle cell *m* divides vertically and the basal cell *ci* divides transversely resulting in an eight-celled embryo, the cells of which are placed in four tiers and are designated as *n'*, *n, m* and *q* respectively (Figs. 5 E, 6 F). In *T. indicum* this is followed by a transverse division in the cells *q* forming two tiers of an octant *l* and *l'* (Fig. 5 K, L). The cell *m* undergoes two vertical divisions (Fig. 5 K). The four cells of the tier *m* thus formed, and of the tier *l'* undergo periclinal divisions to form dermatogen *de* (Fig. 5 L, M). Further divisions in the embryonal mass after the second periclinal division are irregular (Fig. 5 M–S). The region *l* forms the stem tip, tier *l'*

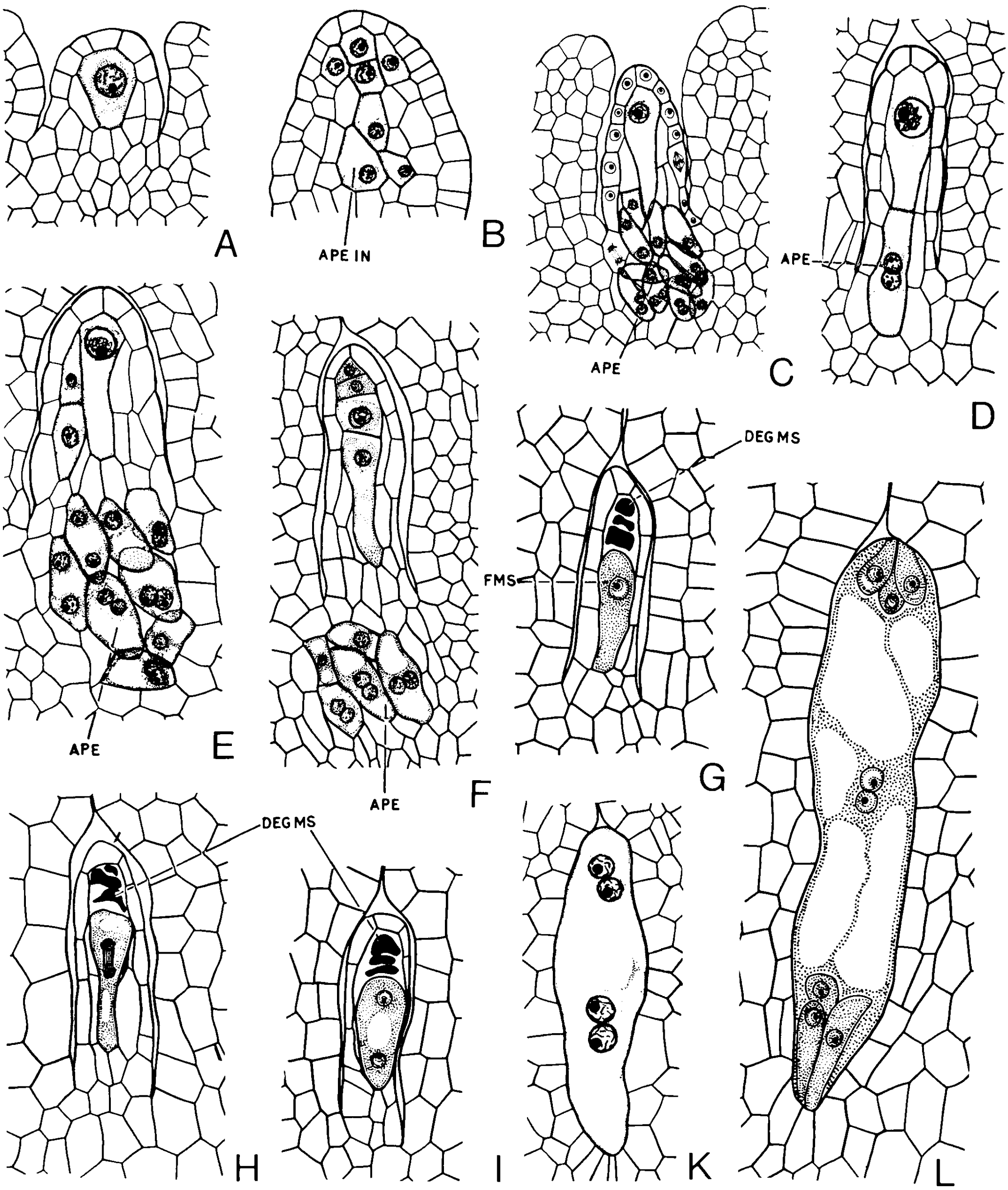

Fig. 2. Megasporogenesis and megagametophyte development in *Trichodesma indicum*. – A: LS of nucellus showing an archesporial cell. – B: LS of nucellus showing multiple archesporium and aposporic embryo sac initials. – C–E: LS of nucellus showing megasporocyte and aposporic embryo sacs. – F: LS of nucellus showing linear tetrad of megaspores and aposporic embryo sacs. – G–L: LS of nucellus showing successive stages in the development of the megagametophyte. – APE aposporic embryo sacs, APE IN aposporic embryo sac initials, DEG MS degenerating megaspores, FMS functional megaspore. – All × 310.

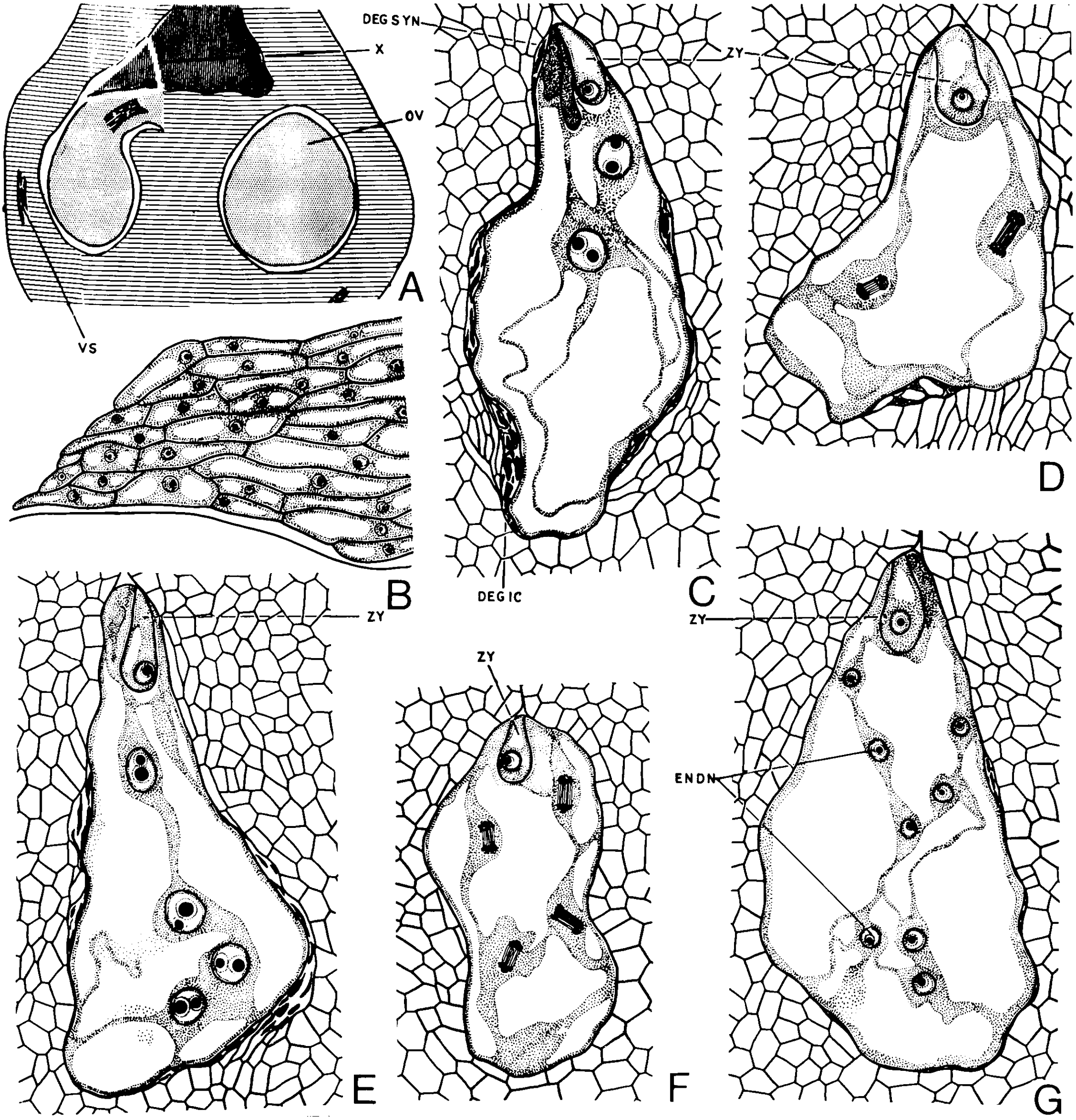

Fig. 3. *Trichodesma zeylanicum*. – A: LS of ovary showing obturator. – B: Portion marked X in Fig. 3 A enlarged. – C–G: LS of ovule showing zygote and successive stages in the development of the endosperm. – DEG SYN degenerating synergids, DEG IC degenerating cells of the integument, ENDN endosperm nuclei, OV ovule, VS vascular strand, ZY zygote. – A ×35, B ×325, C–G ×230.

gives rise to a part of the hypocotyl, while the remaining portion of the hypocotyl is derived from *m*. By this time the cell *n* has divided vertically and *n'* undergoes a transverse division to form *o* and *p* (Fig. 5 L–N). A suspensor of three to four cells is formed by two successive transverse divisions of *p* (Fig. 5 S). The terminal cell of the suspensor may undergo an oblique or a vertical division (Fig. 5 O, S). Cell *o* also divides forming two superposed cells, of which the upper after a transverse and the lower after a vertical division together form the initials for the

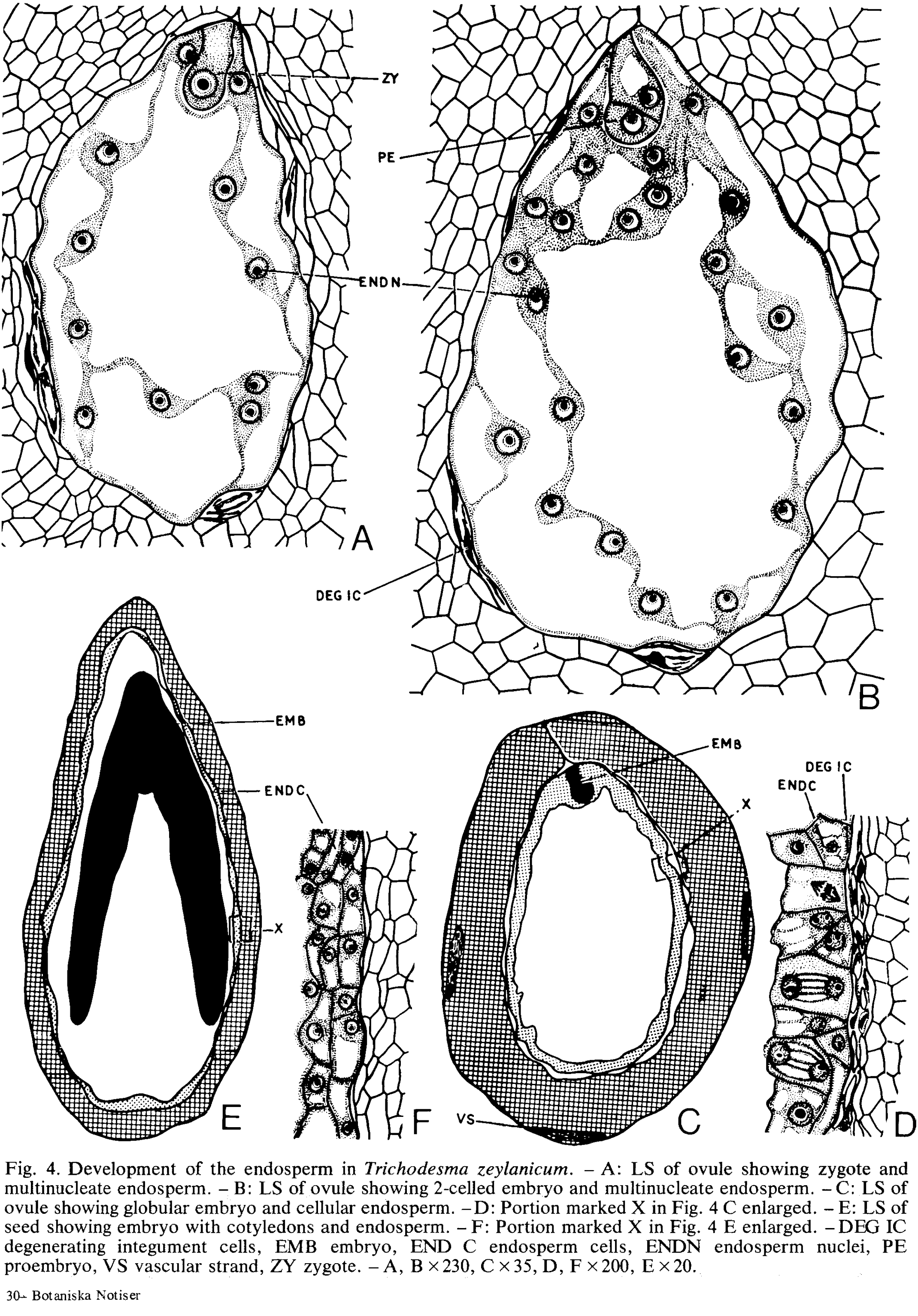

Fig. 4. Development of the endosperm in *Trichodesma zeylanicum*. – A: LS of ovule showing zygote and multinucleate endosperm. – B: LS of ovule showing 2-celled embryo and multinucleate endosperm. – C: LS of ovule showing globular embryo and cellular endosperm. – D: Portion marked X in Fig. 4 C enlarged. – E: LS of seed showing embryo with cotyledons and endosperm. – F: Portion marked X in Fig. 4 E enlarged. – DEG IC degenerating integument cells, EMB embryo, END C endosperm cells, ENDN endosperm nuclei, PE proembryo, VS vascular strand, ZY zygote. – A, B ×230, C ×35, D, F ×200, E ×20.

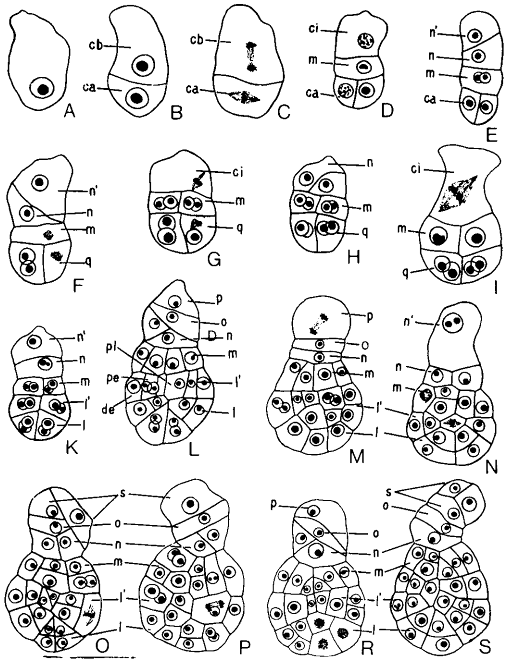

Fig. 5. Development of embryo in *Trichodesma indicum*. – Abbreviations as given under Fig. 6. – All × 150.

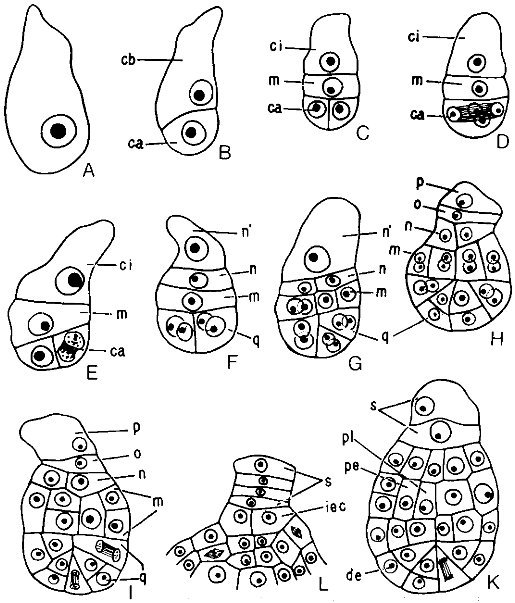

Fig. 6. Development of embryo in *Trichodesma zeylanicum*. – *ca* apical cell, *cb* basal cell, *ci* lower daughter cell of *cb*, *de* dermatogen, *iec* initials for root cortex, *l* upper tier of octant, *l'* lower tier of octant, *m* middle cell of tetrad, *n* upper daughter cell of *ci*, *n'* lower daughter cell of *ci*, *o* upper daughter cell of *n'*, *p* lower daughter cell of *n'*, *pe* periblem, *pl* plerome, *q* quadrant, *s* suspensor. – All × 150.

root, while the two cells formed by *n* give rise to the root cortex. Therefore, the cell *ca* contributes to the development of the embryo proper and a portion of the hypocotyl, while the cell *cb* gives rise to the hypophysis, hypocotyl and suspensor. Embryo development thus corresponds to the Polygonum variation of the Asterad type (Johansen 1950).

In *T. zeylanicum* a sixteen-celled embryo arises by a bipartition of each cell of the eight-celled embryo. Cell *n'* divides by a transverse wall to form *o* and *p*, the cell *n* meridionally into two juxtaposed cells and the two cells of the tier *m* divide by vertical walls to form four circumaxially placed cells (Fig. 6 G, H). The four elements of *q* undergo divisions by oblique walls, each wall having its outer insertion almost in the centre of the peripheral wall and its inner insertion at a point about a half to three-quarters of the way along the horizontal wall which separates *q* from *m* (Fig. 6 G, H). Of the cells thus formed, the upper cell nearest to the axis gives rise to the epidermal initials and subepidermal initials. The outer cells, away from the axis, undergo vertical divisions and become continuous with the epidermal initials (Fig. 6 I–L). The inner cells divide tangentially to form the periblem *pe* and the plerome *pl* respectively (Fig. 6 K). Thus the entire apical cell is destined for the formation of the cotyledonary portion and the stem apex.

The portion *m* consists of four circumaxially placed cells at the 16-celled stage of the embryo. They divide by vertical walls and separate the epidermal initials. Later on, transverse divisions in the derivatives of these cells result in the hypocotyledonary portion of the embryo (Fig. 6 G–I). The lower portion of the hypocotyl is formed by *n*. The cell *o* may undergo a transverse division or give rise directly to the initials for the root cap, *iec* (Fig. 6 L). The cell *p* divides once or twice by transverse walls and forms a 2–4-celled suspensor (Fig. 6 L). The sequence of development thus conforms to the Lamium variation of the Asterad type (Johansen 1950).

Pericarp

During the early stages of development, the pericarp consists of undifferentiated parenchymatous cells, with a well-developed epidermis made up of tangentially elongated cells (Fig. 7 A, B). In the mature fruit the pericarp is divisible into an endocarp, a mesocarp and an epicarp.

Before fertilization a young ovary shows eight to ten layers of cells, with the vascular strand traversing the centre (Fig. 7 A, B). After fertilization the inner epidermis of the ovary wall is gradually transformed into the endocarp, after its cells have developed thickenings along the inner tangential walls (Fig. 7 C–F). The mesocarp consists of six to eight layers of resiniferous cells. The cells of the outer epidermis elongate vertically and develop thickenings all over their outer tangential and radial walls. They become heavily cutinized during the later stages and constitute the epicarp (Fig. 7 C–F).

The cells bordering the interlocular septum are elongate and resemble those of the pericarp during the early stages, but as the epicarp differentiates the inner tangential and the radial walls of these cells become strongly thickened and possess a narrow, triangular lumen (Fig. 7 E, G). These cells behave similarly to those of the endothecium in the anther. They appear to help in the dispersal of the nutlets. The three to four layers of cells which underly these thickened cells are thin-walled and parenchymatous; they are followed by the innermost cells which are reticulately thickened (Fig. 7 G).

Seed coat

The seeds are oblong and the seed coat is undifferentiated during the early stages of development. Mature seeds possess a thin, papery seed coat. At the mature megagametophyte stage the integument is composed of 20–22 layers of cells (Fig. 8 A, B). Immediately after fertilization, the cells of the inner layers of the integument start to break down continuously until the mature embryo is formed (Fig. 8 C–H). At this stage the seed coat consists of about ten layers of cells, subdivided into an epidermal layer of tanniniferous cells, a middle zone of parenchymatous cells and an inner zone of thickened cells. The vascular strand runs close to the epidermis (Fig. 8 G). The seeds are never released from the fruit; the dispersal unit is the nutlet.

Discussion

A regular placental obturator is absent in Boraginoideae. However, in *Trichodesma indicum* and *T. zeylanicum,* as well as in *T. amplexicaule* (Khanna 1964 b), the stylar canal is filled with a transmitting tissue which extends over the micropylar region and behaves as an obturator. A similar feature has been observed in *Mertensia platyphylla* (Khanna 1964 a).

In the species of *Trichodesma* under study, a few cells underlying the archesporium become tapetal in function by developing vacuoles and undergoing precocious nuclear divisions. Such a feature has not been reported in any other member of Boraginaceae, excepting *Cynoglossum amabile* (Millsaps 1940), in which the first row of meristematic cells adjacent to the sporogenous tissue develop into a tapetum.

Occurrence of nucellar apospory in Boraginaceae was first reported for *Cynoglossum denticulatum* (Khaleel 1974). Four to five aposporic embryo sac initials differentiated just below the archesporial cells and developed up to the 2- or 4-, rarely 8-nucleate stage. However, they all degenerated as the normal gametophyte enlarged. Subsequently this phenomenon has also been reported for *Cordia alba* and *C. obliqua* (Khaleel 1975). In *C. alba* the aposporic embryo sacs occur in the form of six to eight enlarged binucleate cells. However, they thereafter degenerate, providing an additional source of nutrition for the gametophyte. In *C. obliqua,* not only is the number of aposporic embryo sac initials six to twelve, but the phenomenon itself is much more advanced. The aposporic embryo sacs develop up to the eight-nucleate stage, following the same sequence of cell divisions as the normal gametophyte, compete with the same and eventually suppress it by their vigorous enlargement. *T. indicum* and *T. zeylanicum* show similarities with *C. denticulatum* and *C. alba* in this aspect. The frequent enlargement of the nucellar cells, with a definite polarity and embryo sac like appearance suggests a tendency towards nucellar apospory. The aposporic embryo sac initials are four to twelve in number and differentiate below the archesporial cell. They rarely develop up to the four-nucleate stage

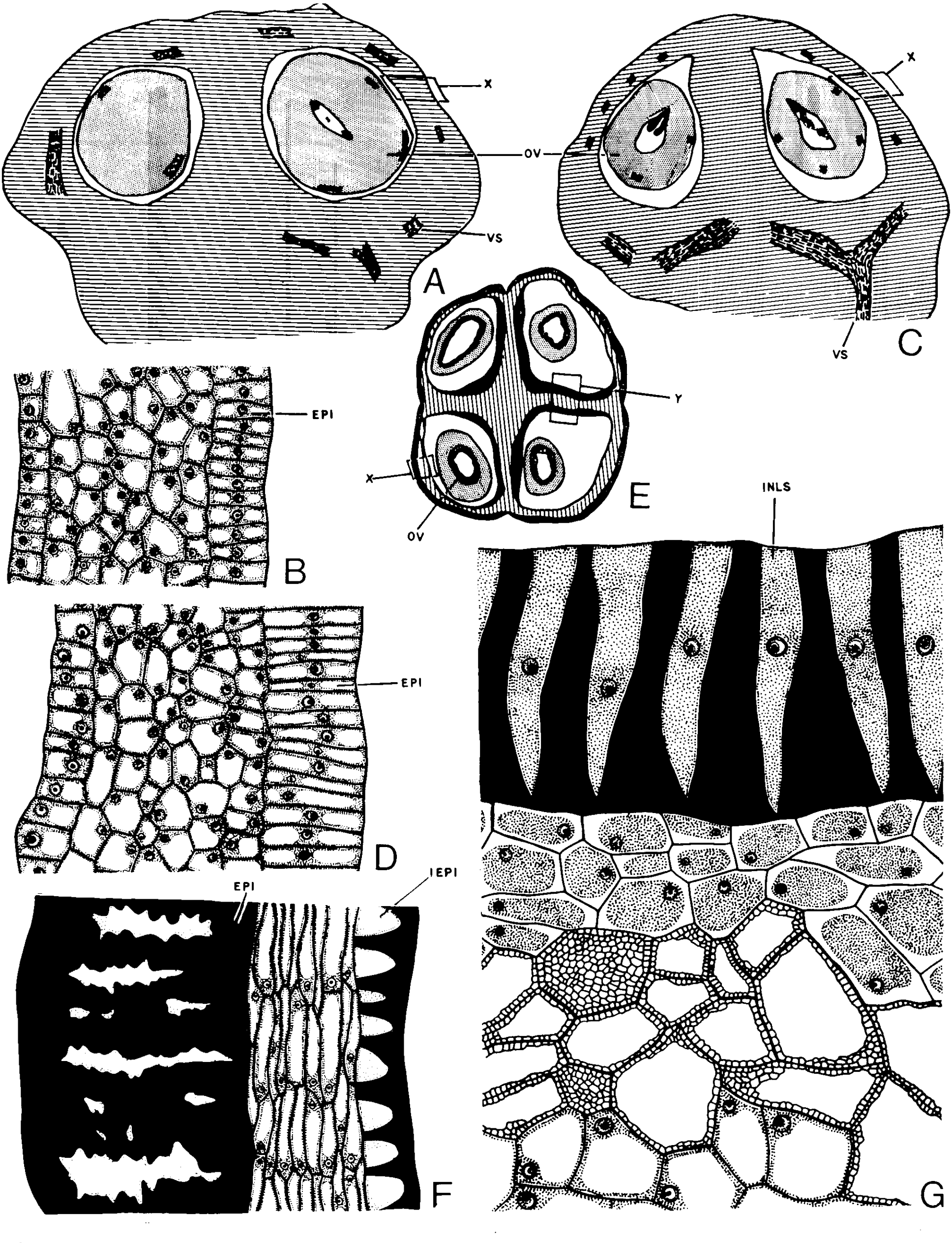

Fig. 7. Development of pericarp in *Trichodesma zeylanicum*. – A: LS of ovary with mature megagametophyte. – B: Portion marked X in Fig. 7 A enlarged. – C: LS of ovary with nuclear endosperm. – D: Portion marked X in Fig. 7 C enlarged. – E: TS of mature fruit. – F: Portion marked X in Fig. 7 E enlarged. – G: Portion marked Y in Fig. 7 E enlarged. – EPI epidermis, IEPI inner epidermis, INLS interlocular septum, OV ovule, VS vascular strand. – A ×30, B, D, F ×290, C ×20, E ×5, G ×150.

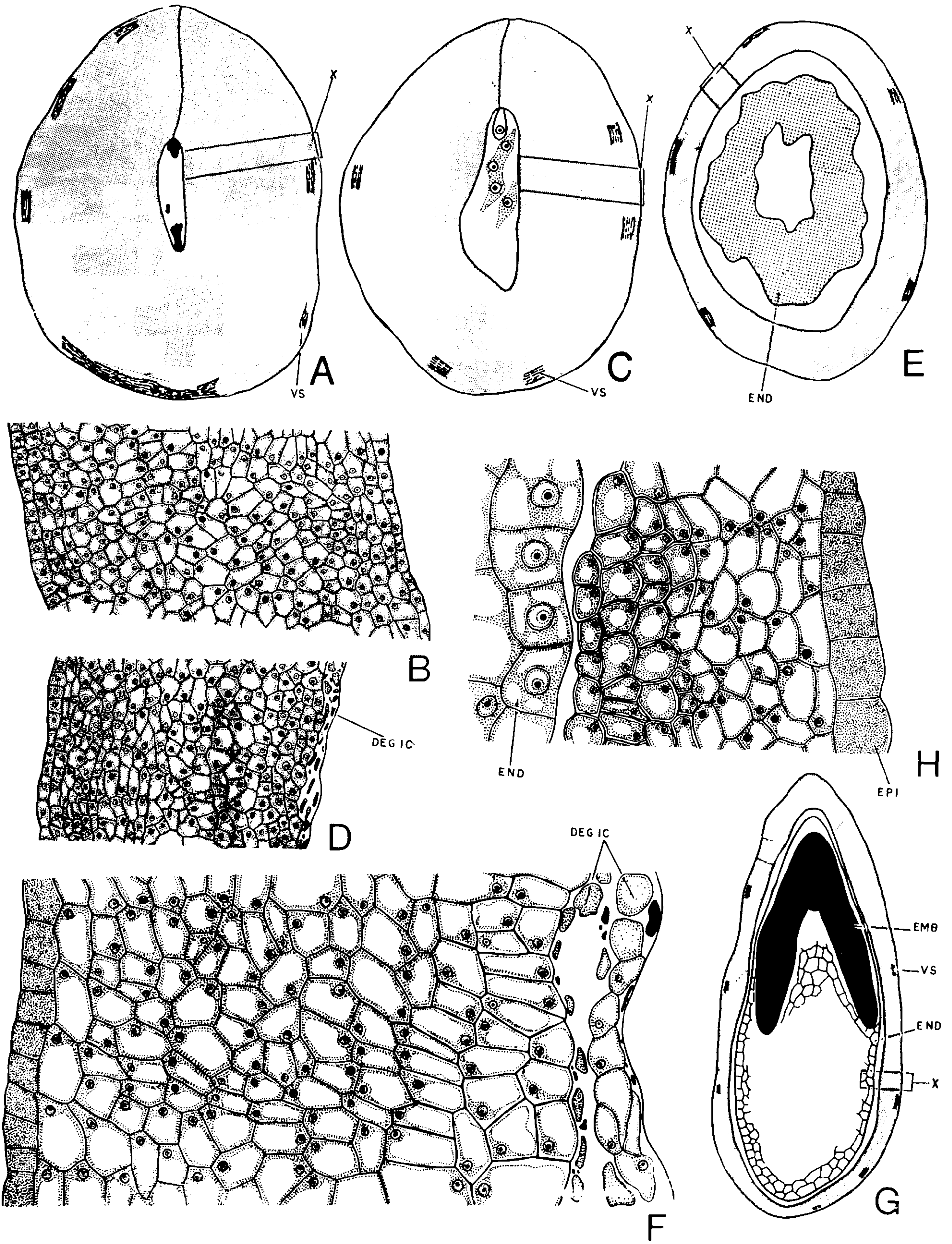

Fig. 8. Development of seed coat in *Trichodesma zeylanicum*. – A: LS of ovule with a mature megagametophyte. – B: Portion marked X in Fig. 8 A enlarged. – C: LS of ovule with 4-nucleate endosperm. – D: Portion marked X in Fig. 8 C enlarged. – E: TS of ovary with multinucleate endosperm. – F: Portion marked X in Fig. 8 E enlarged. – G: LS of mature seed. – H: Portion marked X in Fig. 8 G enlarged. – DEG IC degenerating integument cells, EMB embryo, END endosperm, EPI epidermis, VS vascular strand. – A, C × 90, B, D, E × 150, F, H × 300, G × 15.

and degenerate as the normal gametophyte enlarges.

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A key to the species of Cyathus (Nidulariaceae)

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A dichotomous key to the forty-two species of the fungus genus *Cyathus* (Nidulariaceae) is presented. Salient characters employed in the key are described, annotated and illustrated.

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Because only forty-two species in the fungus genus *Cyathus* are recognized as valid in my recently published monograph of the Nidulariaceae (Brodie 1975), it might appear that a key for identification could be constructed with ease. I was reluctant to produce such a key, for a number of reasons which were discussed in some detail in my monograph. The most cogent reason is my conviction that too many *Cyathus* species are still known only from scanty collections. Moreover, any key which can really guide a mycologist who lacks experience with this group of fungi must separate groups of species on the basis of divaricating phrases which are as unequivocal as possible, and the "all or none" nature of such descriptions tends to encourage too great a reliance on the key itself as a substitute for careful phrase-by-phrase comparison with the full official descriptions.

However, several mycologists have urged that a key should be published and the present paper is offered in an effort to meet the apparent need.

Terms used in the key

The terms have been listed approximately in the order in which they appear in the key.

In my monograph (Brodie 1975) I discussed at length the difficulties involved in applying the various criteria by means of which the species of *Cyathus* have been separated. This discussion was intended to alert mycologists to an awareness of the range of variation that exists in almost all species in colour, shape, size, etc. The reader should therefore consult the monograph (pp. 126–132) before using the accompanying key. For the convenience of those who may not have the monograph at hand, an illustrated glossary is given herewith to define or explain as clearly as possible the terms used in the present key. Page numbers cited in the key give the principal reference *in my monograph* to the species concerned.

The *first time* each term or descriptive phrase is used in the key, reference is made by brackets (T 1 to T 36 inclusive) which indicate corresponding items in the list of notes and illustrations.

T1 *Peridium* (Fig. 1 A). The fruit body as a whole, exclusive of the basal emplacement if this structure is present.

T2 *Plicate* (Fig. 1 A, G, M, X). Ridged, grooved or folded parallel to the length of the peridium. In some species, the external plicae may be hidden because of the shaggy outer surface (Fig. 1 X). As a precaution, hairs should be rubbed off one specimen if there is doubt as to whether it is externally plicate or not.

T3 *Not plicate or non-plicate* (Fig. 1 B, F, H, L, N, O, Y). An occasional specimen of a non-plicate species will show some lengthwise folds as the result of drying, but such folds are not regular in width or spacing. Moreover, in some plicate species, the folds are very faint; in such cases they are regularly distributed, however (Fig. 1 D). Many species are plicate internally (Fig. 1 G, X) in addition to externally.

T4 *Tunica present* (Fig. 1 R). The tunica when present is an outermost layer of the peridiole. It can frequently be identified with certainty by using a needle to pick at a moist peridiole under the binocular microscope. More certain identification usually necessitates examination of a free-hand section of a peridiole, when a tunica is then seen as a firm (sometimes flimsy) layer of hyphae on the outside of the firmer darker cortex (a one-layered cortex is shown in Fig. 1 I, a two-layered in Fig. 1 K but no tunica is present in either).

T5 *Tunica absent* (Fig. 1 G, I, K). When there is no tunica at all, the peridiole usually appears dark and shiny on the outside (Fig. 1 G). In free-hand sections, a delicate tunica may easily be lost; for this reason, it is wise to examine sections of more than one peridiole.

T6 *Peridium dark-coloured* (Fig. 1 B, X). Colour intensity provides a useful key divarication but should be considered cautiously because of the variation in colour within certain species. Most descriptions refer to the colour of dry specimens. The colour is usually some shade of brown, from buff to deep chocolate or almost black.

T7 *Peridium light-coloured* (Fig. 1 D). As noted above, a few specimens of such a species as shown in Fig. 1 D may be considerably darker than others. The colour range is from ivory or grey to light buff.

T8 *Outer surface of peridium hirsute, shaggy, woolly* (Fig. 1 B, hirsute; Fig. 1 N, shaggy; Fig. 1 H, woolly). There are many degrees of "woolliness"; in general what is meant is seen in the contrast between the uneven lengths of hyphae making up the covering (Fig. 1 H) and the even length of the hyphae composing the outer wall of a species such as the one shown in Fig. 1 F.

T9 *Outer surface of peridium covered with fine matted hairs* (Fig. 1 C, F). Hyphae of outer layer of wall essentially all of the same length giving the appearance of a *fine* pile (Fig. 1 F) as compared with a coarse or shaggy pile (Fig. 1 H). Such a fine pile is commonly called the *tomentum*.

T10 *Peridia provided with long conspicuous hairs* (Fig. 1 O; Fig. 1 T, lower half; Fig. 1 D, lower half). The hairs are *in addition* to a fine under pile and stand out as easily-discerned bristles of various sorts as in Fig. 1 O, T. There are also long hairs in the woolly types (e.g. Fig. 1 H) but the hairs are irregular, usually matted and not specifically oriented *downwards* as they are clearly in Fig. 1 T.

T11 *External hairs aggregated into conical tufts* (Fig. 1 O). Shown clearly at the bottom of Fig. 1 O. Note that such tufts are *conical:* compare Fig. 1 T, where aggregation of hyphae produces long hairs, but not cones of hairs.

T12 *External hairs aggregated into mounds* (Fig. 1 N). This condition is frequently referred to in descriptions as *tufted tomentum*.

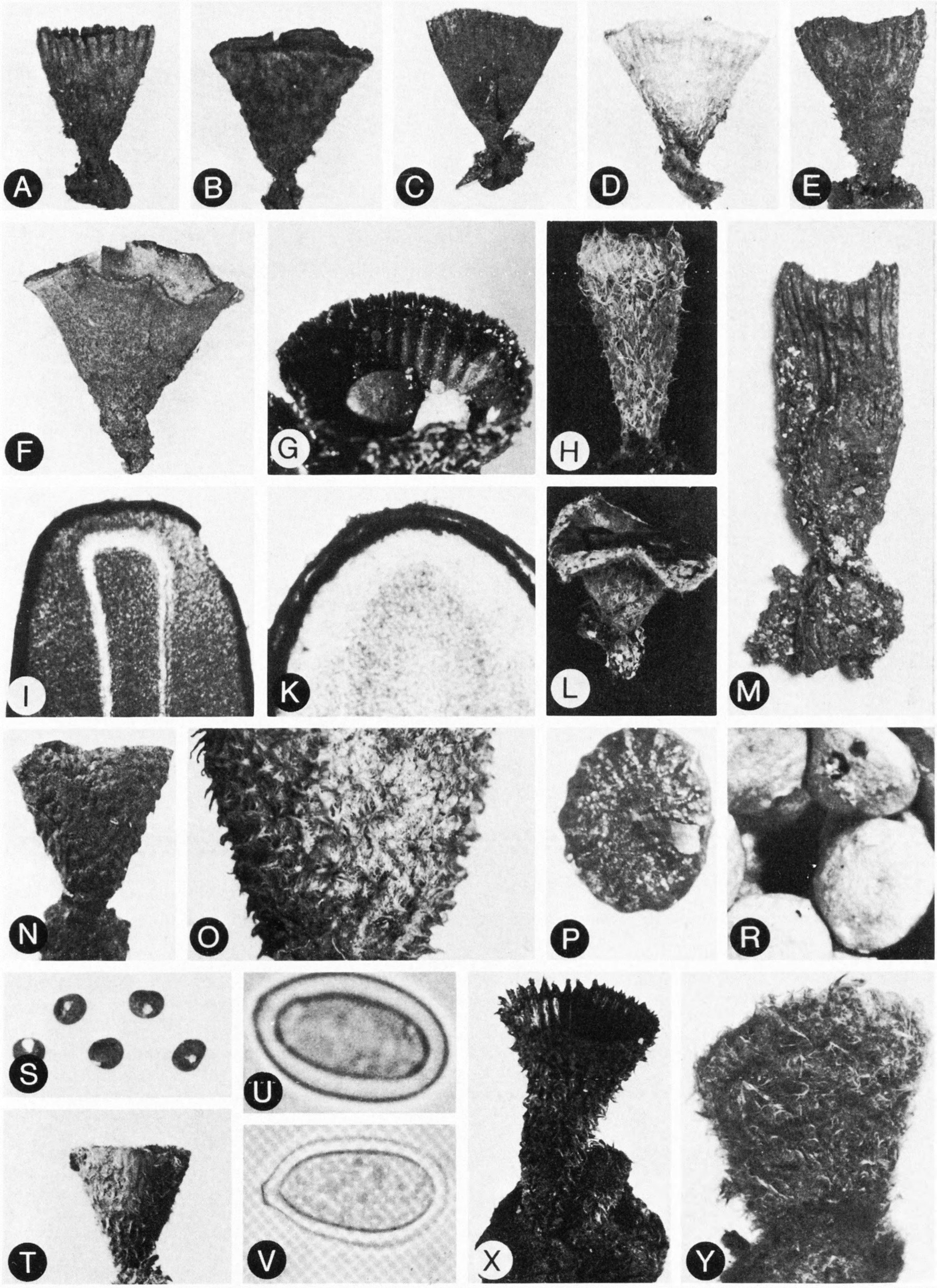
T13 *External hairs distinctly curled* (= curly tomentum, etc. of descriptions) (Fig. 1 Y). This is a woolly tomentum but hyphae or groups of hyphae form tight curls, easily seen under a binocular microscope.

T14 *Peridia slender* (= not broad relative to height) (Fig. 1 H, M). Such types often have a slender base but not invariably.

T15 *Peridia broad* (= broad relative to height). Fig. 1 F especially, and Fig. 1 A–D, N, T.

T16 *Peridia flaring out widely at the mouth* (Fig. 1 L, B). There is an abrupt change in the angle of the peridium wall in the upper third.

Fig. 1. Taxonomic features, *Cyathus* (for details see text under Terms used in the key). Photographs are similar to many I have published in various journals but in no case identical. – A: *C. poeppigii,* ×3. – B: *C. triplex,* ×3. – C: *C. berkeleyanus,* ×3. – D: *C. bulleri,* ×3. – E: *C. limbatus,* ×3. – F: *C. earlei,* ×3. – G: *C. poeppigii,* ×7. – H: *C. stercoreus,* ×6. – I: *C. limbatus,* ×70. – K: *C. gracilis,* ×90. – L: *C. olla,* ×3. – M: *C. gayanus,* ×4. – N: *C. intermedius,* ×4. – O: *C. gracilis,* ×10. – P: *C. crispus,* ×20. – R: *C.* sp. indet., ×20. – S: *C. olla,* ×2. – T: *C. pallidus,* ×4. – U: *C. gracilis,* ×1500. – V: *C. africanus,* ×2000. – X: *C. striatus,* ×5. – Y: *C. crispus,* ×6.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T17 *Peridia not flaring out* (Fig. 1 A, C, N). No abrupt change in angle of wall. Note: as might be expected, there are many intermediate conditions, e.g. Fig. 1 E, F, X.

T18 *Spores ellipsoid* (Fig. 1 U, V). The spore outline approximates an ellipse with one dimension markedly exceeding the other.

T19 *Spores ovoid, globose, etc.* (not illustrated). These terms are used in the ordinary sense. Note: there is often considerable variation in shape among spores of a single specimen. If most are ellipsoid, that is the term used.

T20 *Spores apiculate* (Fig. 1 V). A distinct projection of some kind is visible at one end of the spore, at least under the oil immersion lens. According to present views this should be called a hilum; the term 'apiculate' is retained because it is used so frequently in older publications.

T21 *Spores not apiculate* (Fig. 1 U). No distinct projection at either end.

T22 *Peridia small or large* (no reference to illustrations is made because peridia are shown at various magnifications). These terms are helpful only in a very general way since within one species (e.g. *Cyathus stercoreus*) peridia may vary from 3 mm in height to as much as 10 mm).

T23 *Emplacement conspicuous, compact* (Fig. 1 M, N, X). The hyphae incorporate some substrate, and the basal structure is a *firm mass* which usually remains attached to the peridium proper.

T24 *Emplacement conspicuous, byssoid* (Fig. 1 Y). Basal hyphae only loosely aggregated, never a firm ball.

T25 *Emplacement inconspicuous* (Fig. 1 T, D).

T26 *Peridioles regular in outline* (circular or ellipsoid) (Fig. 1 G).

T27 *Peridioles irregular in outline* (reniform or subtriangular) (Fig. 1 S).

T28 *Peridioles smooth* (Fig. 1 G, R).

T29 *Peridioles wrinkled.* May be radiately wrinkled (Fig. 1 P) or irregularly wrinkled (not illustrated).

T30 *Cortex one-layered* (Fig. 1 I).

T31 *Cortex two-layered* (Fig. 1 K). Again, caution is urged! A one-layered cortex overlaid by a tunica may easily be classified as a two-layered cortex. In a true two-layered cortex, each layer is dense and of approximately the same width in section.

T32 *Mouth (or lip) of peridium setose* (Fig. 1 X).

T33 *Mouth of peridium not setose* (Fig. 1 F).

T34 *Mouth of peridium fimbriate* (Fig. 1 G). Note: at very high magnification, some hyphae of the lip or mouth can always be seen even in a specimen such as shown in Fig. 1 F which would be designated "not fimbriate".

T35 *Peridia with slender stalk* (Fig. 1 B, C).

T36 *Peridia without (clearly defined) stalk* (Fig. 1 E, H).

Key to the groups of Cyathus

1\. Peridia (T1) distinctly plicate (T2) or ridged lengthwise, externally or internally or both 2
– Peridia distinctly not plicate (T3) or ridged lengthwise 3
2\. Tunica present (T4); peridia dark (T6) or light-coloured (T7), hirsute to shaggy (T8) ... Group VII (p. 173)
– Tunica absent or extremely delicate and fragile; peridia mostly very dark; peridioles dark . Group VI (p. 171)
3\. Peridia covered externally by fine, matted hairs (T9) but very few or no long, conspicuous hairs (T10) .... Group I (p. 154)
– Peridia woolly externally and provided with conspicuous, long hairs 4
4\. Tunica absent; peridioles shiny black .... Group V (p. 168)
– Tunica present; peridioles not shiny black 5
5\. External hairs of dark-coloured peridium distinctly aggregated into conical tufts (T11) or into mounds (T12); peridia mostly slender (T14), not broad at mouth relative to height .... Group IV (p. 164)
– External hairs of peridium not clearly aggregated into tufts (T9), peridia mostly broad relative to height (T15) 6
6\. Peridia mostly light-coloured and (outside) having conspicuous, long, downward-pointing hairs (T10); spores mostly ovoid (T19), thin-walled .... Group II (p. 161)
– Peridia mostly dark-coloured; long hairs rare or inconspicuous; spores mostly ellipsoid (T18), thick-walled .... Group III (p. 163)

Group I

The *olla* group; peridia commonly *flaring out widely* (T16) in the upper third, clearly not longitudinally ridged, though sometimes weakly transversely ridged on the inside; comparatively smooth-textured, the tomentum consisting of fine, appressed hairs; in some, aggregated into tufts or low mounds but usually *devoid of long, conspicuous hairs;* spores mostly ovoid, thin-walled.

Like many other species, *C. olla* appears in many "forms" which differ from one another in size, colour and form. The only one of these to which I applied a name is forma *anglicus* (Lloyd) Brodie, a description of which is given in my monograph (Brodie 1975 p. 155).

1. Peridia small (T22), not over 5 mm in height or breadth, usually less 2
– Peridia larger, mostly 7 mm wide at mouth or more, up to 15 mm 3
2. Spores small, ovoid, 8–9× 12–14 μm .... *C. pygmaeus* Lloyd (p. 157)
– Spores longer, ellipsoid, 10–12 × 18–20 μm .... *C. minimus* Pat. (p. 157)
3. Spores with obvious apiculus (T20) .... *C. africanus* Brodie (p. 159)
– Spores without obvious apiculus (T21) 4
4. Peridia thick-walled; mouth abruptly flared outwards, recurved; emplacement conspicuous (T23, T24); peridioles large, irregular (T27) in outline .... *C. olla* (Batsch) ex Pers. (p. 154)
– Peridia not conspicuously thick-walled; mouth not abruptly flaring outwards 5
5. Cortex two-layered (T31); peridia internally shiny white or silvery 6
– Cortex one-layered (T30); peridia internally not shiny white or silvery 7
6. Spores globose, 8 μm .... *C. canna* Lloyd (p. 158)
– Spores ovoid, 10–12× 12–22 μm .... *C. earlei* Lloyd (p. 156)
7. Peridia 5–6 mm in height and width 8
– Peridia 10–17 mm high, 7–10 mm wide 9
8. Spores small, 4× 5–6 μm; cups with straight sides .... *C. microsporus* Tul. (p. 158)
– Spores large, variable, 8–12 × 10–12 μm .... *C. colensoi* Berk. (p. 156)
9. Spores ellipsoid, 5–8× 8–11 μm 10
– Spores ovoid, 11× 13 μm, thick-walled .... *C. badius* Kobay. (p. 160)
10. Interior of cups dark brown, faintly plicate .... *C. hookeri* Berk. (p. 159)
– Interior of cups light brown, not plicate .... *C. confusus* Tai & Hung (p. 160)

Group II

The *pallidus* group; peridia *not* distinctly *flaring out abruptly* at the mouth (T17), mostly light-coloured and not plicate; basal texture of peridium wall fine, but bearing *conspicuous, long, downward-pointing hairs.* Inner peridium wall smooth. Spores mostly ovoid, thin-walled. Tunica thin.

1. Peridia small, mostly 5–6 mm in height or width; sides of peridia curved; colour pale straw, light buff, occasionally darker; spores mostly ellipsoid, 4–8× 8–15 μm .... *C. pallidus* Berk. & Curt. (p. 161)
– Peridia large, mostly 7–8 mm in height or width; sides of peridia straight; colour pale buff with a yellow tinge; spores mostly subglobose, 5–7 ×5–9 μm .... *C. julietae* Brodie (p. 161)

Group III

The *triplex* group; peridia mostly *dark*-coloured, sometimes having faint plication, visible *only* internally; outer surface with a few spreading (sometimes tufted) hairs; inner surface smooth, silvery white; cortex one-layered, subhomogeneous *or* distinctly two-layered, spores mostly ellipsoid, thick-walled; tunica thin or absent.

1. Mouth of peridium beset with conspicuous stiff setae (T32); tunica absent; peridioles large and conspicuously plump .... *C. setosus* Brodie (p. 164)
– Mouth of peridium lacking conspicuous setae (T33); tunica present; peridioles not conspicuously plump 2
2. Spores 8–10 μm long; cortex one-layered; peridioles 1–1.5 mm; external hairs in occasional tufts .... *C. sinensis* Imaz. (p. 164)
– Spores 12–14 μm long or more; cortex two-layered; peridioles 2 mm or more; external hairs not in tufts .... *C. triplex* Lloyd (p. 163)

Group IV

The *gracilis* group; peridia not plicate *or* extremely faintly plicate; tomentum hyphae *clearly* aggregated into nodular (T12) or pyramidal tufts (T11). Spores ellipsoidal, moderately thick-walled; tunica thin.

1. Peridia slender, with slender stalk (one third length of whole peridium); external hairs aggregated into sharp, conical tufts; cortex two-layered .... *C. gracilis* Brodie (p. 164)
– Peridia not slender or long-stalked; external hairs aggregated into low irregular mounds; cortex one-layered 2
2. Peridium wall thin (0.1–0.2 mm); no stiff conspicuous hairs around mouth (T33); spore walls thin (1.5–2 μm) 3
– Peridium wall thick (0.3 mm); conspicuous stiff hairs around peridium mouth (T34); spore wall thick (2.5–4 μm) .... *C. crassimurus* Brodie (p. 167)
3. Peridium very faintly (and broadly) plicate inside; tomentum of broad nodules; peridioles 1.3–1.5 mm; spores 10–12 × 18–22 μm .... *C. elmeri* Bres. (p. 167)
– Peridium not plicate externally or internally; tomentum in small, sharply defined nodules (T12); peridioles 2 mm; spores 10 × 16 μm .... *C. intermedius* (Mont.) Tul. (p. 166)

Group V

The *stercoreus* group; peridia *not plicate;* outer peridium wall bearing abundant hairs of irregular length, giving a *shaggy* or woolly appearance; peridioles *black* or dark, devoid of tunica; spores *large, subglobose*.

1. Spores large, 30–40 μm or more, globose 2
– Spores small, 8–16 μm, ellipsoid .... *C. fimicola* Lloyd in Stev. & Cash, nom. illeg. (p. 169)
2. Few long, shaggy hairs; hairs of tomentum often aggregated into low mounds; reddish band just below outer lip of peridium .... *C. pictus* Brodie (p. 169)
– Many long, shaggy hairs; hairs of tomentum sometimes irregularly adherent but not into mounds; no band on peridium mouth; peridioles conspicuously shiny black ...... *C. stercoreus* (Schwein.) de Toni (p. 168)

Group VI

The *poeppigii* group; peridia *distinctly plicate* externally and internally; outer peridium wall hirsute to shaggy, in age wearing to smooth, strong brown; *peridioles dark* to black; spores large, globose or ellipsoid; tunica absent.

1. Peridioles small, 1 mm, rarely 1.5 mm 2
– Peridioles larger, minimum 1.75 mm, maximum 3 mm 3
2. Peridia gold-coloured to pinkish brown; external hairs in tight curls (T13); peridioles radiately wrinkled (T29) .... *C. crispus* Brodie (p. 181)
– Peridia not gold or pinkish; external hairs not in curls; peridioles black, not wrinkled (T28); on manure .... *C. costatus* Lloyd in Stev. & Cash nom. illeg. (p. 172)
3. Peridia dark brown 4
– Peridia light brown, russett or olive, irregularly shaggy externally 6
4. Peridia narrow and tall (to 15 mm); peridioles 3 mm, spores subglobose, large, 20–32 μm .... *C. gayanus* Tul. (p. 172)
– Peridia broadly conic, 10 mm high or less; peridioles 2 mm 5
5. Plicae marked and close, the grooves about 0.5 mm apart; spores large, 30–50 μm *C. poeppigii* Tul. (p. 171)
– Plication less marked but distinct and coarse, the grooves about 0.75–1 mm apart; spores 10–12 × 16–22 μm .... *C. limbatus* Tul. (p. 172)
6. Peridia shiny brown; spores 11–15 × 16–22 μm, thin-walled .... *C. olivaceo-brunneus* Tai & Hung (p. 173)
– Peridia inside not shiny brown; spores smaller, 8.5–10 × 16–19 μm, thick-walled .... *C. cheliensis* Tai & Hung (p. 173)

Group VII

The *striatus* group; peridia distinctly *plicate* internally, sometimes obscurely so externally; outer peridium wall hirsute to shaggy; spores mostly ellipsoidal; *tunica present;* emplacement firm and conspicuous in many species (T23).

1. Peridia strikingly elongate, 12–20 mm high, not over 7 mm wide, externally dark brown, shaggy 2
– Peridia not usually elongate, mostly in range, 7–10 mm high, 6–8 mm wide 3
2. Peridioles 2.5–3 mm; spores ellipsoid, 11–13 × 5–6 μm, thick-walled ... *C. novae-zeelandiae* Tul. (p. 176)
– Peridioles 1 mm; spores ovoid, 8 × 5 μm .... *C. chevalieri* Hariot & Pat. (p. 177)
3. Peridioles distinctly ellipsoid (T26) and rugulose (T29); spores ellipsoid, 10 × 16 μm .... *C. ellipsoideus* Brodie (p. 181)
– Peridioles circular in outline or irregular (T27), not ellipsoid or rugulose 4
4. Peridioles small, 1 mm or less; peridia only faintly plicate externally; cups ferrugineous .... *C. rudis* Pat. (p. 177)
– Peridioles larger, mostly 2 mm (range 1.5–3 mm) 5
5. Peridium wall thick; external hairs distinctly aggregated into tufts; emplacement large, solid; peridia grey-coloured, rarely light fawn .... *C. helenae* Brodie (p. 175)
– Peridium wall not thick; external hairs not in tufts; emplacement variable (T24, T25) 6
6. Peridia very pale, linen-coloured, outside having a few long, down-pointing hairs; epiphragm snow white with tawny hyphal tufts .... *C. bulleri* Brodie (p. 179)
– Peridia usually darker brown 7
7. Peridia externally very dark brown, almost black, internally conspicuously white or silvery; peridia wide and short; spores ellipsoid, 12 × 16–22 μm 8
– Peridia in various shades of brown, internally not contrasting white or silvery 9
8. Peridioles small, not over 1.5 mm .... *C. nigro-albus* Lloyd (p. 176)
– Peridioles larger, 2 mm or more .... *C. montagnei* Tul. (p. 176)
9. Peridioles mostly irregular in outline, angular or triangular; spores not less than 8–5 × 10–20 μm 10
– Peridioles not angular in outline 11
10. Outer lip of peridium with band of tufted reddish-brown hyphae .... *C. annulatus* Brodie (p. 179)
– Lip devoid of distinct, coloured band .... *C. striatus* (Huds.) ex Pers. (p. 173)
11. Spores very small, subglobose, 4–7 × 6–9 μm; peridioles variable in size, commonly elliptical in outline .... *C. berkeleyanus* (Tul.) Lloyd (p. 178)
– Spores larger, ovoid to globose, 6.5 × 9–11 μm; peridioles circular in outline *C. pullus* Tai & Hung (p. 179)

Comments

The keys presented herewith have been used with a fair degree of success by graduate students in botany who had little or no previous acquaintance with Birds' Nest Fungi. Undoubtedly, however, difficulties will be encountered by some persons using the keys; I should, therefore, be grateful to have such difficulties reported to me so that adjustments can be made if possible. As is true for any key that embraces all the recognized species in the world, the matter of geographical distribution as given in descriptions or monographs should not be overlooked. If, for example, erroneous judgement in the use of a dichotomy in the key should lead to the identification of a specimen collected in central Canada as *Cyathus colensoi,* which is known only from New Zealand and Australia, one should consider the identification as highly improbable. It is possible, however, for exotic species to appear adventitiously, especially in greenhouses and on imported nursery stock (Brodie 1975).

Addendum

In a recently-published review (*Kew Bull. 32:* 260–261), D. M. Dring has stated that I am incorrect in my use of the term 'double-layered cortex'. Recording to Dring, "the outer part of the 'double-layered cortex' is so obviously in reality just a part of the tunica, being constructed of filamentous not isodiametric cells as is the true cortex". Only further research will resolve the problem of the proper nomenclature to be applied. Meanwhile, the descriptive terms as I have used them herein do serve to separate the taxonomic entities covered by the keys.

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Brodie, H. J. 1975: *The Birds' Nest Fungi.* Toronto.

A study of the genus Litschauerella (Corticiaceae)

John Eriksson and Leif Ryvarden

Eriksson, J. & Ryvarden, L. 1977 12 30: A study of the genus Litschauerella (Corticiaceae). *Bot. Notiser 130:* 461–465. Stockholm. ISSN 0006-8195.

An examination of authentic Bourdot-Galzin material of *Litschauerella* showed that there is only one species in the genus as we know it today. Spore size and spore ornamentation, previously used as specific characters, are shown to be very variable and no discontinuity could be demonstrated which would support a separation into several species. The typification of *Peniophora clematitis* Bourd. & Galz. and *P. abietis* Bourd. & Galz. is discussed.

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In connection with our treatment of the genus *Litschauerella* Oberw. (Eriksson & Ryvarden 1976 p. 838) we found that the previous arrangement of species in the genus was difficult to maintain. The reason was that SEM pictures revealed the spore ornamentation to be far more variable than previously assumed. In our provisional treatment, we recognized two species, one growing on *Clematis* (*Peniophora clematitis* Bourd. & Galz.) with spores about 5 µm in diameter, and one (*Peniophora abietis* Bourd. & Galz.), growing on conifer wood with spores somewhat larger, viz. 7–9 µm in diameter. Oberwinkler (1965) also accepted two species although he put them in different genera. However, Weresub (1961), Boidin (1958) and Liberta (1960) treated the species as synonyms. Weresub (1961 pp. 1480–1581) gave very detailed descriptions of the two species based on syntype material from L, S, TRTC and UPS. She noticed particularly the difference in spore size between specimens from the two types of substrate. Both she and Boidin (1958) noticed that in some specimens collected on *Clematis*, there occurred some very large spores, up to 15 µm in diameter. Boidin considered these spores to be a result of polyploidy.

Our SEM pictures published in 1976 show that spores from collections made on *Clematis* have more or less cubical warts with a square base, while those from the coniferous hosts seem to have more or less rounded warts with a rounded base. However, a collection from Sweden (Eriksson 4157) has more or less smooth spores. Furthermore a collection made by Corbière has spores with somewhat elongated ridges, partly fused together to form a more irregular ornamentation. All other characters, such as cystidia (which are very distinctive in *Litschauerella*) and hyphae were the same, and it was clear that if a separation into several species was desirable, it would have to be based exclusively on the spores.

However, we were suspicious when it appeared that, possibly, 4 species were contained within this restricted number of collections. Further, many spores that appeared smooth under the light microscope, appeared distinctly ornamented when viewed under the scanning electron microscope. Thus, it would be impossible, if the species concepts were to be based on the spore ornamentation alone, to determine the species without the aid of a scanning electron microscope.

Table 1. Authentic and examined collections of *Litschauerella clematitis,* all collected by Galzin, except for number 10 (collected by L. Corbière).

Number	Galzin number	Bourdot number	Herb.	Locality (all in France)	Date	Substrate (according to labels)	Spore size (μm)
1	–	7920	S	Pl. de l'Aveyron, Trou d'Enfer, près Millau	8.V.1911	*Clematis alba*	5.5–15
2	6935	–	PC	Aveyron, Arnac	10.XI.1910	Sapin pectiné *(Abies pectinata)*	7–9
3	7573	–	S	Aveyron, Loubotis	Nov. 1910	*Clematis alba*	4.5–6
4	8949	7933	S	Aveyron, Pisse Vielle, près St. Sernin	26.IV.1911	*Clematis*	5
5	9640	7949	PC	Aveyron, Bouisson	4.VII.1911	*Clematis*	5
6	9486	7987	S	Aveyron, Arnac	29.V.1911	Sapin	5
7	10389	8946	S	Aveyron, Labastide	11.XI.1911	Genévrier (*Juniperus*)	9–12
8	15869	–	PC	Aveyron, Pisse Vieille	25.VII.1911	*Clematis*	4–5
9	17605	14866	PC, U	Aveyron, St-Estève	5.V.1915	*Juniperus*	7–9.5
10	–	32950	PC	Manche, Cherbourg	17.VI.1921	*Pinus*	7–7.5

In an effort to solve some of the problems mentioned above, we borrowed all available material collected or determined by Bourdot and Galzin (Table 1). The spores in all collections were measured and then photographed under a scanning electron microscope.

Spore size

It is apparent from Table 1 that most collections made on coniferous substrates have spores 7–12 μm in diameter. However, collection no. 6, made on *Abies,* has spores which are only about 5 μm in diameter (10 spores measured). This size is within the normal range for collections made on *Clematis* (see Table 1). The substrates have evidently not been mixed as the specimen lived on a piece of bark about 2 × 2 cm and about 4 mm thick and *Clematis* has thin, herbaceous stems.

Although most of the collections made on *Clematis* have rather small spores, 4–6 μm in diameter, there are some spores in collection no. 1 which reach 15 μm in diameter (see Fig. 2 B).

Thus, on both types of substrates there are specimens which deviate from the normal range of spore sizes. The inevitable conclusion is that spore size cannot be used as a character to separate the species in *Litschauerella* based on the facts now available.

Spore ornamentation

Fig. 1 A and B show the spores of two collections, both made on *Picea.* It is evident that the warts vary in shape from cubical to rounded. Fig. 1 C illustrates a form (from *Picea*) with weakly developed ornamentation, while Fig. 1 D shows more or less smooth spores (a collection made on *Picea*), probably slightly shrunken during drying. Fig. 2 A illustrates the spores from the Corbière collection (10 in Table 1) which was made on *Pinus* in France. Here the ornamentation is deviating from that of the other collections on coniferous substrates.

Fig. 2 B is a picture of the large spores from Bourdot 7920 collected on *Clematis* at the type locality and on the same date as the type. It is evident that the ornamentation is of the same

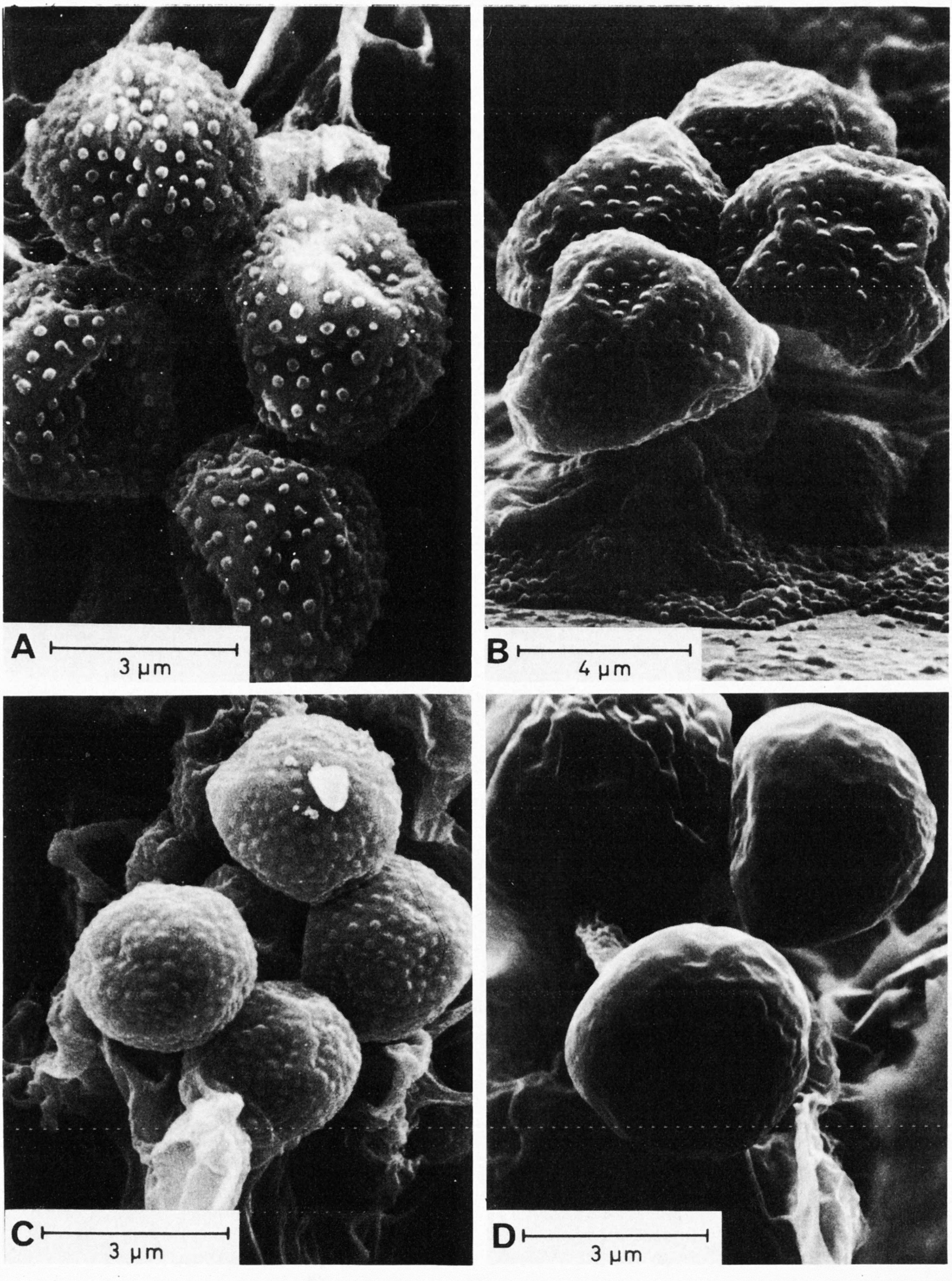

Fig. 1. Scanning electron micrographs of spores of *Litschauerella clematitis*. – A: Form from coniferous substrate with well developed warts. Hjortstam 3787 c. – B: Form from coniferous substrate with low, rounded warts. Larsson 2029. – C: Form from coniferous substrate with weakly developed warts. Eriksson 8570. – D: Form from coniferous substrate with almost smooth spores. Eriksson 4157. – Photo: Leif Ryvarden.

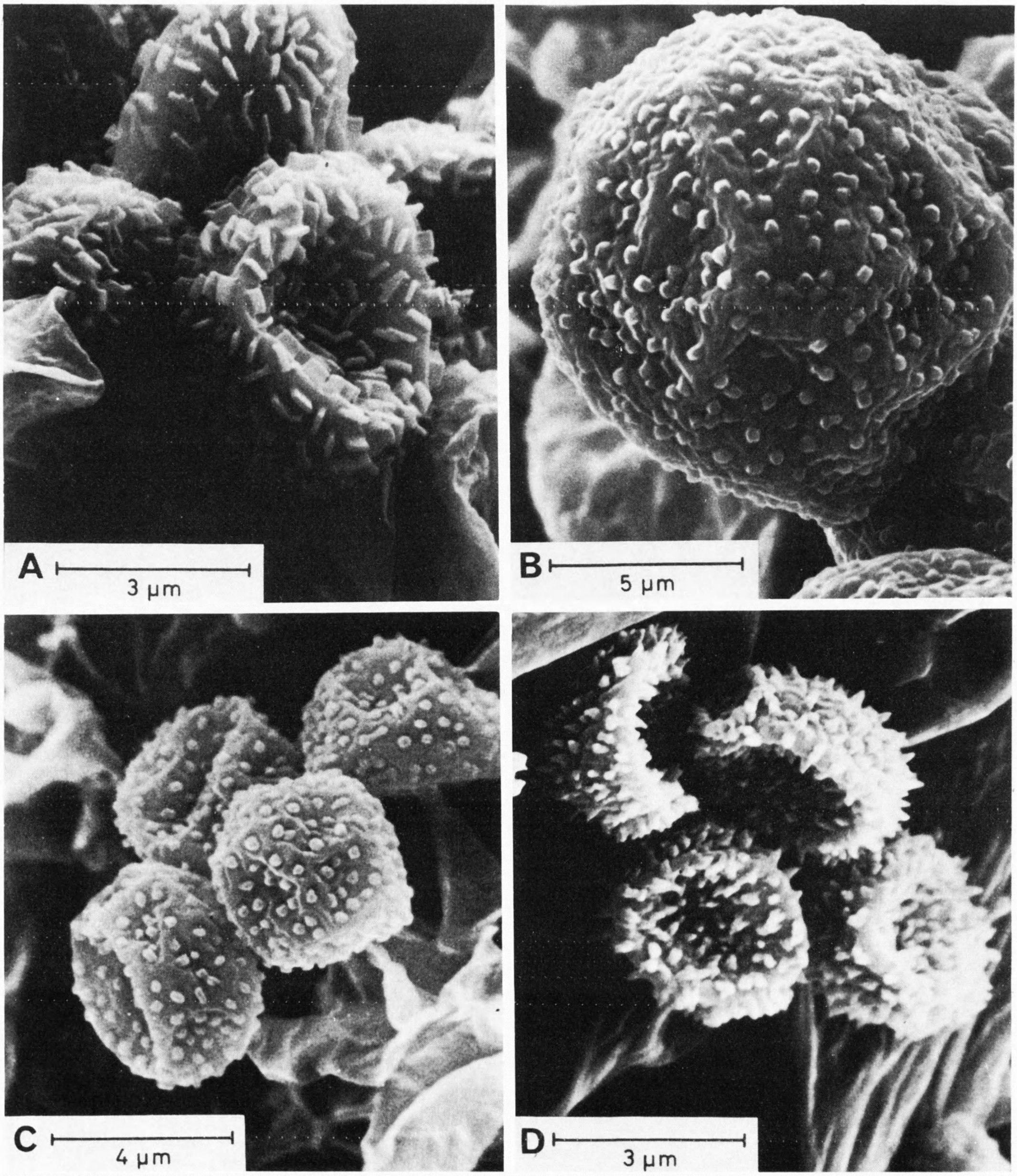

Fig. 2. Scanning electron micrographs of spores of *Litschauerella clematitis*. – A: Form with short plates on the spores, on *Pinus*. Corbière 5. – B: Form from *Clematis* with large spores. Bourdot 7920. – C: Form from *Clematis* with spores of normal size, cf. Fig. 2 B. Galzin 15869. – D: Form from *Clematis* with conical warts. Galzin 7573. – Photo: Leif Ryvarden.

type as that on the spores from collections made on conifer wood. Fig. 2 C shows spores from a collection made on *Clematis*, but which are of normal size. Fig. 2 D shows spores of a collection also made on *Clematis* (coll. no. 3) but with another type of ornamentation. With regard to other characters it is in complete accordance with the other ones made on *Clematis*.

Conclusion

Spore ornamentation is very variable and there are transitions from smooth spores to ornamented ones at least from coniferous substrates. Further, on both types of substrates, there are deviating forms which clearly indicate that spore ornamentation is not a stable character.

We have come to the point of view that there is only one species in *Litschauerella*, *L. clematitis* (Bourd. & Galz.) Erikss. & Ryv., and that there is no sound basis for separating the taxa involved into several species. A separation must eventually be based on spore ornamentation, and would necessitate the use of a scanning electron microscope and would be without value for mycologists in general.

Typification

P. clematitis. Weresub (1961) selected as lectotype coll. Bourdot 7943–Galzin 9001, but Oberwinkler (1965) challenged this view. He proposed Galzin 9640 as lectotype as it "stimmt exact mit der Originalbeschreibung überein", which was not the case, according to Oberwinkler, with the lectotype selected by Weresub. We have not taken SEM pictures of Bourdot 7943, but of Bourdot 7920 which was collected at the same locality on the same day and also on *Clematis* (Fig. 2 B). We measured the spores and found that some of them reached 15 μm in diameter, although the majority measured about 5 μm in diameter. This is in accordance with the original diagnosis, and we see no reason to reject Weresub's choice.

P. abietis. Weresub (1961) selected as lectotype the collection Galzin 9468–Bourdot 7988. This collection has spores deviating from the normal size for collections made on coniferous substrate (see Table 1, coll. no. 6). In his original description Bourdot states that the spores are 6–8 μm in diameter. Thus, the selected lectotype is somewhat abnormal, and we propose Galzin 6935 as new lectotype for *P. abietis*.

Acknowledgements. The curators of the herbaria in Paris, Uppsala and Stockholm are thanked most sincerely for their cooperation in lending us authentic Bourdot–Galzin material. We also wish to thank Dr L. Weresub, Ottawa, for valuable suggestions and Dr J. Ginns, Ottawa, for revising the English text.

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Laeticorticium pulverulentum (Corticiaceae) validated

John Eriksson and Leif Ryvarden

Eriksson, J. & Ryvarden, L. 1977 12 30: Laeticorticium pulverulentum validated. *Bot. Notiser 130:* 466. Stockholm. ISSN 0006-8195.

Laeticorticium pulverulentum Erikss. & Ryv. is validly published, rectifying a previous invalid publication.

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Laeticorticium pulverulentum Eriksson & Ryvarden sp. nov.

A Laeticorticio roseo differt sporis minoribus, autumno maturis, et statu imperfecto pulverulento.

Typus: Sweden, Uppland, Vänge par., Fiby urskog, on *Populus tremula,* 1937-10-26, Lundell 2030 (Herb. Eriksson).

In the Corticiaceae of North Europe vol. 4 (Eriksson & Ryvarden 1976) we made a mistake in proposing two different ranks simultaneously for the same taxon. In doing so, we violated article 34 of the International Code of Botanical Nomenclature, and none of the names is validly published. We want to rectify this error and therefore propose it as a species here.

Acknowledgements. We want to thank professor J. A. Nannfeldt and Dr L. Weresub for drawing our attention to the invalidity of our previous publication of *L. pulverulentum.*

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Eriksson, J. & Ryvarden, L. 1976: *The Corticiaceae of North Europe. Vol. 4. Hyphodermella–Mycoacia.* Oslo.

New taxa of Zygophyllum from Egypt

Amal I. Hosny

Hosny, A. I. 1977 12 30: New taxa of Zygophyllum from Egypt. *Bot. Notiser 130:* 467–468. Stockholm. ISSN 0006-8195.

Zygophyllum decumbens Del. var. *megacarpum* A. Hosny var. nov. and *Z. aegyptium* A. Hosny sp. nov. are described and illustrated.

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Zygophyllum sect. *Bipartia* v. Huyssteen comprises 2 species in Egypt. *Z. simplex* Del. is widespread in Africa and the W parts of Asia. It shows considerable variation in leaf shape, colour of petals and stamens and in fruit size. In Egypt, however, it is fairly constant and the variation exhibited seems to be related to differing environmental conditions. *Z. decumbens* Del. is restricted to the Red Sea region. In Egypt a robust variety is present which differs from the type in having larger flowers and fruits. It is here described as *Z. decumbens* var. *megacarpum*.

The species of *Zygophyllum* sect. *Mediterranea* Engler are all closely allied and are often confused. The author is preparing a thesis, entitled "Revision of the *Zygophyllum* species of sections *Bipartia* v. Huyssteen and *Mediterranea* Engler in Egypt", under the supervision of Professor M. N. El Hadidi. During revision of the material of *Z. album* L. fil. in BM, CAI, CAIM and K, it turned out that at least two species and several varieties have been included under this name. One new species from this complex, *Z. aegyptium,* is described here.

Zygophyllum decumbens var. **megacarpum** A. Hosny var. nov.

Holotypus: Egypt, Eastern Desert (Da. sept.), Cairo–Suez road, 115 km from Cairo, 4.1976, N. El Hadidi and A. Hosny s.n. (CAI).

Frutex quam varietas typica robustior, usque ad 35 cm altus. Inflorescentia cymosa ter vel quater ramificans. Flores magni, sepala 3×2 mm, petala 4×1.5 mm, stamina 8–10, filamenta 3.5 mm longa. Capsula magna, turbinata, 4–6×4–8 mm, pedicello 6.5 mm.

More robust than the type, up to 35 cm. Inflorescence cymose, branched 3–4 times. Flowers large, sepals 3×2 mm, petals 4× 1.5 mm, stamens 8–10, filaments 3.5 mm. Capsule turbinate, 4–6×4–8 mm, pedicel 6.5 mm.

Distribution: Along the Red Sea coasts of Sudan and Somalia, and along the coasts of the Gulf of Aden. In Egypt (Fig. 2) along the Cairo–Suez road and in wadis along the Red Sea coast.

Zygophyllum aegyptium A. Hosny sp. nov. – Fig. 1

Holotypus: Egypt, Mediterranean region (Mma), Ras El Bar near Damietta, 7.1976, A. El Gazzar s.n. (CAI).

Differt a *Z. albo* ramis floriferis ad nodos bifloris vel trifloris (in *Z. albo* unifloris) et capsulis majoribus.

Green, glabrous shrub 30–60 cm high; internodes cylindrical, slightly hairy, 2.5–4 cm. Leaves 2-foliolate, leaflets unequal, obovate to oblanceolate, 7–11 mm long, apex rounded; petiole cylindrical, 9–16 mm; stipules minute. Inflorescence cymose with 2–3 flowers at each node. Flowers stalked, pedicel 2 mm; sepals 5, ovate, 4×2 mm; petals 5, spathulate, 5×3 mm, white; stamens 10, filaments 3 mm, staminal scales 2 mm long, entire; ovary spherical, hairy, style 1 mm, terminal. Capsule glabrous or slightly hairy,

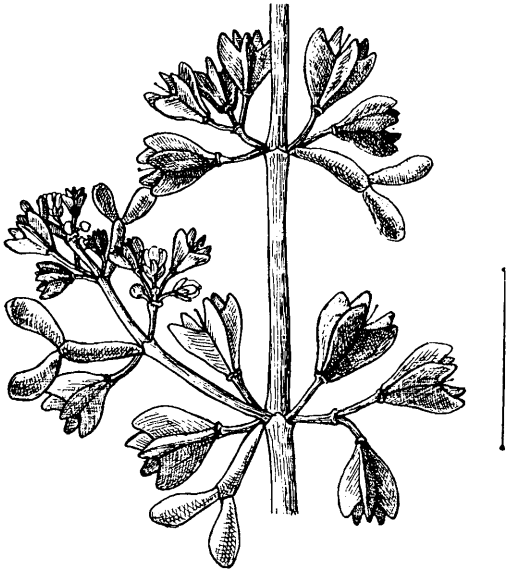

Fig. 1. *Zygophyllum aegyptium*. Scale 2 cm.

obconical, 5-partite, 5–9 mm long, 5–8 mm broad, apex retuse; pedicel short, 4–5 mm.

Z. aegyptium is easily distinguished from *Z. album* since the flowering branches bear 2–3 flowers at each node (only one in *Z. album*). This makes *Z. aegyptium* look more luxuriant during the flowering stage. The difference is even more marked during the fruiting stage. The branches of *Z. album* are lax, bearing only one capsule at each node and the capsule itself hardly exceeds 5 × 5 mm. In *Z. aegyptium*, the branches bear several capsules at each node and the capsules are larger, thereby giving the branches a characteristic, dense appearance.

Distribution: Mediterranean region and the Isthmic Desert in Egypt (Fig. 2). Specimens from Tunisia, Libya and Cyprus were also seen by the author.

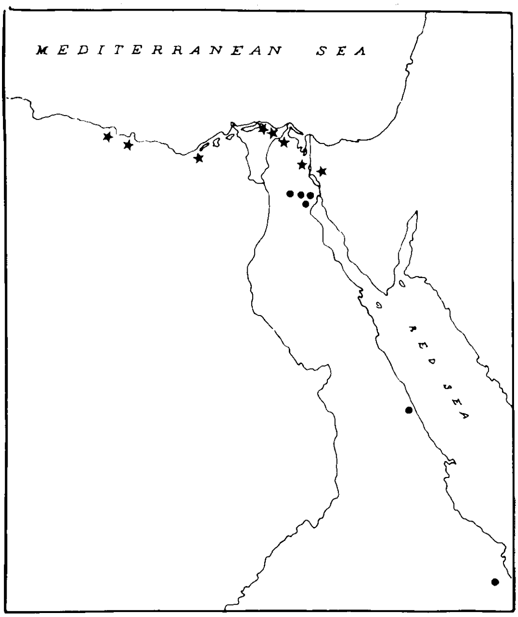

Fig. 2. Distribution of ★ *Zygophyllum aegyptium*, ● *Z. decumbens* var. *megacarpum*.

Collections: Egypt. Western Mediterranean region: Mersa Matrouh, 7.1959, Ghabour (CAI) – Ras El Hekma, growing on sandy dunes, 5.1963, Täckholm et al. (CAI) – Alexandria, El Maks, 5.1908, Bornmüller 10504 (BM). – *Eastern Mediterranean region:* Burg El Borollos, 9.1952, Kassas (CAI) – Emad, 3 km W of Burg El Borollos, 8.1961, Täckholm et al. (CAI) – Baltim, 8.1968, El Hadidi (CAI) – Along the road from Damietta to Ras El Bar, 8.1961, Täckholm & Kassas (CAI) – Ras El Bar, 7.1976, El Gazzar (CAI). – *Isthmic desert:* Desert road between Qantara and Ismailia, 7.1952, Amin (CAI) – E bank of Suez Canal at Ismailia, Lupton (BM).

Acknowledgements. I am most grateful to Miss D. Hillcoat and Dr W. Stearn (BM) and to Mr L. Forman (K) for herbarium facilities. The drawings were made by Mr M. El-Gohari. Financial support from the Salén Foundation, Stockholm, is gratefully acknowledged.

A new species in the Cerastium alpinum group from Mt Olympus, Greece

Hermann Merxmüller and Arne Strid

Merxmüller, H. & Strid, A. 1977 12 30: A new species in the Cerastium alpinum group from Mt Olympus, Greece. *Bot. Notiser 130:* 469–472. Stockholm. ISSN 0006-8195.

Cerastium theophrasti Merxm. & Strid is described from calcareous scree in the summit area of Mt Olympus. It differs from related taxa by its glandular pubescence and larger seeds with long, acute tubercles. The chromosome number, $2n=36$, is the lowest yet recorded in the *C. alpinum* complex.

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Cerastium theophrasti Merxm. & Strid sp. nov. – Fig. 1

Cerastium uniflorum "Murith" (recte: Clairv.) var. *mitkaënse* Wagner, Feddes Repert. 38: 282 (1935).

Cerastium alpinum L. var. *glanduliferum* Koch sensu Stojanov & Jordanov, God. Sof. Univ. 34: 173 (1938).

Cerastium uniflorum Clairv. sensu Quézel & Contandriopoulos, Candollea 20: 55 (1965).

Orig. coll. Greece. Mt Olympus, summit area, E-facing slope below the peak of Mitikas, along path to Refuge C, 2700 m, calcareous scree, Strid 13029, 10.7.1977 (ATH holotype, C, G, LD, M, W, isotypes).

Herba caespitosa, perennis, ubique dense glanduloso-pilosa. Inflorescentia (1–)2(–3)-flora, pedunculis post anthesin deflexis. Bracteolae omnino herbaceae vel apice anguste scariosae. Sepala lanceolata, margine scariosa. Petala alba, bifida, sepalis circiter 1.4 longiora. Capsula paene recta ostio haud obliquo. Semina 1.45–1.75 mm longa, tuberculis longis acutis dense obsita. Numerus chromosomatum $2n=36$.

Caespitose perennial with a thin, more or less vertical, branched root and numerous, prostrate to ascending, 2–6 cm long non-flowering shoots. *Flowering shoots* ascending to erect, 4–9 cm long. *Stems* and peduncles terete, 0.6–0.8 mm in diameter. *Leaves* on non-flowering and flowering shoots similar, opposite, narrowly elliptical to oblanceolate, obtuse, 7–11(–14) × 2.5–4 mm, crowded towards the apex of non-flowering shoots; internodes on flowering shoots 5–14 mm. Older parts of stems rather densely covered with dead, inward-curving leaves which are obovate to broadly oblanceolate and somewhat smaller than the green leaves. *Inflorescence* 1–2- or occasionally 3-flowered; the flowers emerging in the axils of a pair of bracts which are entirely herbaceous and similar to the uppermost leaves, though somewhat smaller. *Peduncles* 10–25 mm, straight and erect at anthesis, conspicuously deflexed (but remaining straight) after anthesis. First flower usually lacking *bracteoles;* second flower with a pair of herbaceous (or sometimes scarious-tipped), elliptical, acute, 3–5 × 1–2 mm large bracteoles attached 1/4–1/3 from the base of the peduncle. *Sepals* lanceolate, subacute, 5–7 × 2–2.5 mm, with a scarious margin which is usually c. 0.5 mm wide near the apex and extends almost to the base in 2 of the sepals, narrower and confined to the upper 1/3 in the others. Whole plant, including stems, leaves, bracts, bracteoles, peduncles and calyces, densely covered with straight, spreading, colourless *glandular hairs* (white in dried material) which are 0.15–0.20 mm long on the leaves, somewhat longer and more variable (up to 0.45 mm) on the peduncles; whole plant thereby sticky; *eglandular hairs lacking*. *Flowers* broadly campanu-

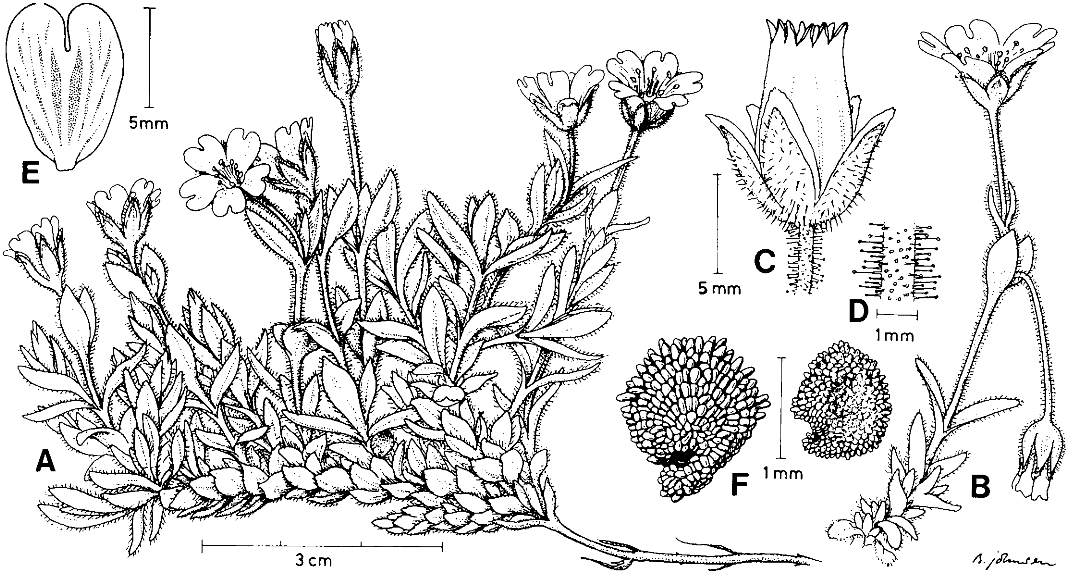

Fig. 1. *Cerastium theophrasti,* drawn from a cultivated specimen (Strid 9874). – A: Habit. – B: Inflorescence. Note the deflexed pedicel after flowering. – C: Ripe capsule. – D: Portion of pedicel to show glandular pubescence. – E: Petal. – F: Seed of *C. theophrasti* (left) compared with seed of *C. alpinum* from Britain (right).

late, with a sweet scent. *Petals* obovate, 7–9.5 × 4.5–5.5 mm, white except for the pale greenish base, with coarse, raised veins above, bifid to 1/4–1/3. *Filaments* subulate, 4–5 mm long, outward-curving, white, with small (c. 0.6 × 0.4 mm), dorsifixed, versatile, yellow anthers which dehisce c. 2 days before the stigmas become receptive. *Ovary* spherical at anthesis, pale green, smooth, c. 2 mm in diameter. Styles c. 3 mm long, white, outward-curving and slightly expanded in the upper part, papillose and receptive on the upper one mm of the adaxial side. *Mature capsule* 8–10 mm long, nearly straight, c. 4 mm wide at the base, gradually tapering and c. 3 mm wide at the apex (below the teeth); teeth c. 0.8 mm long, triangular, subacute, patent, with recurved sides; mouth of capsule not oblique. *Seeds* medium brown, 1.45–1.75 mm, acutely long-tuberculate, the tubercles rugose at base. *Chromosome number* 2n = 36.

Since the type collection was gathered on an excursion with the Botanical Society 'Theophrastos' of Copenhagen we find it appropriate to let the specific epithet commemorate the father of botany as well as the society named after him.

Other collections: Olympos, 2600 m, J. Wagner, Iter Graecum 1934, 1.8.1934 (M, type of *C. uniflorum* var. *mitkaënse*) – Auf Felsen und Felsschotter auf den Gipfeln Skala und Skolion, auf cca. 2700–2900 m Meereshöhe; in Ritzen der Felsmauer, auf den Gipfeln Stefani und Mitika, cca. 2800–2900 m, Stojanov & Jordanov, 21.–25.7.1937 (apparently in SOM, not seen) – Skolio, 2900 m, Stamatiadou 3972, 2.8.1968 (ATH) – Ditto, 2700–2750 m, Stamatiadou 6867, 10.7.1969 (ATH) – Am Mytikas-Gipfel, 2917 m, Roessler 6413, 4.7.1968 (M) – Grosschutthang an der Stefani-Nordwand, 2600 m, Sauer, 28.7.1969 (Herb. Univ. Saarbrücken) – Hagos Antonios, in saxosis calc., 2600–2700 m, Rechinger 38773, 27.7.1970 (M, W) – Summit area of Ag. Antonios, 2700–2800 m, Strid 1313, 24.7.1970 (C) – N and W slopes of Ag. Antonios, 2650 m, calcareous scree, Strid 1410, 27.7.1970 (C) – Ridge between Skala and Mitikas, 2800–2900 m, calcareous scree and rock crevices, Strid 1483, 28.7.1970 (C, W) – Skolio-Gipfel, 2900 m, Greuter 9720, 26.7.1971 (ATH, G) – S of Skala peak, 2740 m, glacial cirque with humid limestone scree, Kornaś 97, 26.–30.8.1973 (KRA) – Osthänge der Skala, 2600–2800 m, Podlech 25797, 10.8.1973 (M) – Above Refuge A, along path to Ag. Antonios, 2600 m, calcareous scree, Strid 9874 & 10092, 19.8. & 22.8. 1975 (seed coll., cult. in Bot. Garden Copenhagen, vouchers in C).

Cerastium theophrasti is fairly widespread in the summit area of Mt Olympus, where it grows on calcareous scree and occasionally in rock crevices. It is strictly alpine and has not been recorded below c. 2600 m. It grows together with several other Olympus endemics such as: *Alyssum handelii, Rhynchosinapis nivalis, Potentilla deorum, Achillea ambrosiaca* and *Festuca olympica*. The following species are also frequently found in association with *Cerastium theophrasti: Arenaria conferta, Minuartia verna* ssp. *idaea, Paronychia rechingeri, Silene saxifraga, Ranunculus brevifolius, Cardamine carnosa, Saxifraga spruneri, S. sempervivum, Euphorbia capitulata, Thymus cherlerioides, Linaria alpina, Veronica thessalica, Galium degenii, Carex laevis* and *Sesleria coerulans*.

Cerastium theophrasti flowers from the end of June to the beginning of August. Plants cultivated outdoors in Copenhagen flowered from the end of May to mid-June. The flowers are protandrous and have a faint but distinct sweet scent. Seed-setting occurs very rapidly after flowering; in the cultivated material ripe seeds developed in about three weeks. In cultivated plants all the flowers become conspicuously deflexed after anthesis (Fig. 1 B). This is less obvious in some of the collections from nature, and the flowers of 1-flowered inflorescences and the second and third flowers of 2–3-flowered inflorescences may remain more or less erect. There is some individual variation in the number of flowers per inflorescence, some individuals or populations having predominantly one-flowered, others two-flowered or occasionally three-flowered inflorescences.

Possibly related taxa

In habit there is a striking similarity with *C. uniflorum* L. and other taxa of the *C. latifolium* group. The completely different shape of the seeds appears to rule out any close relationship, however, and the similarity in habit may be due to convergent evolution imposed by the same habitat (alpine screes). In the *C. latifolium* group the seeds have a loose testa which is shallowly and irregularly rugose, whereas in *C. theophrasti* the testa is firmly attached to the rest of the seed and is densely covered with long, acute tubercles.

In our opinion the species undoubtedly belongs in the *C. alpinum* group, a complex which can by no means be regarded as fully understood. The following features seem to exclude the possibility that the Olympus plant should be conspecific with *C. alpinum* s. lat.:

(1) The chromosome number 2n = 36, which is the lowest yet recorded in the group. The most widespread chromosome number for *C. alpinum* s. lat. is 2n = 72, reported from Arctic North America, Greenland, Iceland, Scandinavia, Great Britain, the Alps, the Central Plateau, the Pyrenees and the Sierra Nevada (see Küpfer 1974 and references in Hess, Landolt & Hirzel 1967 and Fedorov 1969). 2n = 108 has been counted in material from Canada, Greenland and Scotland, and 2n = 144 has been reported from northernmost Sweden (see op. cit. and Löve & Löve 1975). The lowest number so far reported for the *C. alpinum* complex is 2n = 54 in material from Greenland (Böcher & Larsen 1950, Jørgensen et al. 1958) and Arctic Russia (Sokolovskaya & Strelkova 1960). According to Böcher (1977) the chromosome number 2n = 108 (occasionally 2n = 54) is confined to *C. arcticum* whereas *C. alpinum* s. str. has 2n = 72 (2n = 144 reported only once). Incidentally, the chromosome number 2n = 36 for *C. theophrasti* should not be taken to indicate any relationship with the *C. latifolium* group (where this number is prevalent) since 2n = 36 is the commonest chromosome number found in *Cerastium* species.

(2) The seeds which are larger than those of *C. alpinum* and have longer tubercles (see Fig. 1 F).

(3) The complete absence of long, soft, eglandular hairs which (except in completely glabrous forms) are always present in the *C. alpinum* group and are indeed a diagnostic feature for that group.

In addition, the following differences also exist, although less distinct and perhaps less important:

(4) The short petals (c. 1.4 times as long as the sepals, whereas they are about twice as long as the sepals in *C. alpinum* s. lat.).

(5) The tendency for the inflorescence to be one-flowered and without bracteoles, a feature otherwise unknown in the *C. alpinum* group.

(6) The deflexed fruiting peduncles, which at least are not a regular feature of *C. alpinum* s. lat.

There are also two rather poorly known Balkan species whose possible affinities with *C. theophrasti* should be considered.

(1) *C. runemarkii* Möschl & Rech. fil. – Described as having "seeds 0.7–0.8 mm, minutely muricate". Even if these seeds may not have been quite ripe they certainly appear to be very different from the seeds of *C. theophrasti,* which are twice as large and have long, acute tubercles. More important, perhaps, *C. runemarkii* has no glandular hairs, but has long, straight, eglandular hairs. The sepals also seem narrower and the capsule somewhat shorter and narrower. Conspecificity with *C. theophrasti* is thus ruled out, although it seems likely that *C. runemarkii* also belongs in the *C. alpinum* group s. lat. rather than in the *C. uniflorum* group. Its chromosome number, incidentally, is also 2n = 36. *C. runemarkii* is only known from the type collection from the summit area of the Aegean island of Naxos (c. 950 m).

(2) *C. hekuravense* Jáv. – According to the description this species should only have glandular hairs. If this is correct, it would constitute a similarity with the Olympus plant. In other respects, however, there seem to be great differences. The leaves of *C. hekuravense* are said to be broader (5–7 mm) and acute, the inflorescence 3–7-flowered, the bracts and bracteoles possess scarious margins, the petals are longer (13 mm!) and the seeds are smooth ("semina laevia"). If the seeds are as described, then *C. hekuravense* has no connection with *C. theophrasti* and does not belong in the *alpinum* group at all (where it was tentatively placed by Jalas in Flora Europaea). It was described from the 2500 m high limestone mountain Hekurave in Albania, and phytogeographically it would make sense to have the same species here as on Mt Olympus, but the description seems to rule out this possibility. According to information from Budapest (BP) the type is likely to have been destroyed in the Second World War.

The nearest localities to Mt Olympus for *C. alpinum* seem to be in southern Bulgaria (Pirin planina), where it is represented by ssp. *lanatum* (Lam.) Asch. & Graebn. The record "Gr" for *C. alpinum* in Flora Europaea (1: 140, 1964) may be based on the report by Stojanov & Jordanov (1938 p. 173).

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Sisyrinchium laxum Otto ex Sims found in N Greece

Arne Strid

Strid, A. 1977 12 30: Sisyrinchium laxum Otto ex Sims found in N Greece. *Bot. Notiser 130:* 473–475. Stockholm. ISSN 0006-8195.

Sisyrinchium laxum Otto ex Sims, a South American species, has been found on flats just N of Mt Olympus. Apparently this is the first record from Europe. The characteristics and affinities of the species are discussed.

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Three species of the predominantly American genus *Sisyrinchium* have been reported from Europe. *S. bermudiana* L. is a native of E North America and W Ireland, and has been introduced in England and probably elsewhere in Europe. *S. montanum* Greene, a related species originating in E North America and frequently confused with *S. bermudiana,* is widely naturalized in C Europe and appears to be spreading, the most recent records being from Romania (Rösler 1971) and Bulgaria (Kolev 1972). Concerning the taxonomy and nomenclature of these species, see Ingram (1967) and Ward (1968). A third species, *S. californicum* (Ker-Gawl.) Dryander, native of California and Oregon, is naturalized in Ireland.

The three above-mentioned species are all perennial and rather large-flowered. In 1976 a small-flowered, annual to biennial species, subsequently identified as *S. laxum* Otto ex Sims, was discovered in N Greece. The locality is: Macedonia, Nom. & Ep. Pierias, flats at N foot of Mt Olympus, 3.6 km from the village of Fotina along main road to Katerini, 140 m. Strid & Kjellsson 11313, 9.6.1976 (ATH, C, K, LD). The plants were found in a meadow in an agricultural area, chiefly at the edge of a small waterhole and by tracks left by a heavy vehicle, i.e. in places where the soil was damp to wet and the vegetation sparse.

Description

Annual to biennial, 5–15 cm tall, with thin fibrous roots. *Leaves* all or nearly all basal, linear-ensiform, 30–60 × 1.5–3 mm, with scabrid margins, not becoming dark on drying. *Stems* 2–8 per plant, ascending to suberect, much longer than the leaves, c. 0.8 mm wide, narrowly winged, with scabrid margins. Stem bearing a single, 2–4-flowered inflorescence. *Spathe-valves* subequal, herbaceous, lanceolate-ensiform, 15–25 × 2–3 mm, with scarious margins and minutely scabrid keel. *Pedicels* slender, much exceeding the spathes; flowers more or less erect, fruiting pedicel arcuate or nodding. *Flowers* c. 10 mm long and 9–15 mm in diameter; tepals subequal. Lower part of corolla urceolate, greenish yellow, sparsely villous outside; expanded part of tepals broadly elliptical, apiculate, pale blue with darker stripes, becoming dark violet blue in throat. *Filaments* connate for up to 3/4 of their length; filamentous shaft expanded and densely glandular-pubescent below, cylindrical and glabrous above. *Anthers* more or less triangular in transection, arranged as to form a yellow triangle in throat of corolla. *Style* about as long as the filaments, style branches slender, appearing inbetween the anthers. *Ovary* broadly ellipsoid to ovoid, glandular-pubescent when young. *Capsule* globose-trigonal, 3–4 mm, medium brown, smooth.

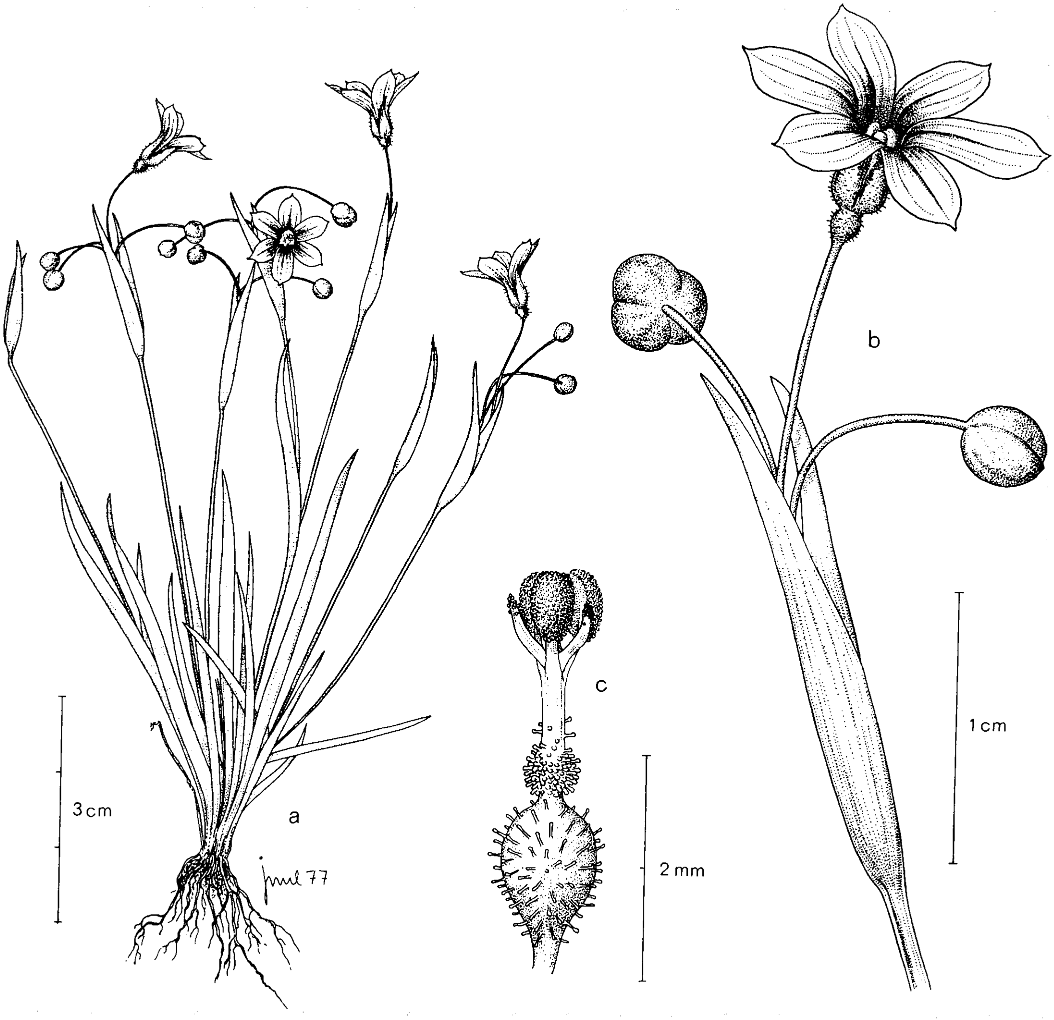

Fig. 1. *Sisyrinchium laxum,* Strid & Kjellsson 11313. Drawing based on dried material and photographs. – A: Habit. – B: Inflorescence. – C: Petals removed to show glandular-pubescent ovary, filamentous shaft with dense glandular pubescence below, anthers, and style-branches.

Seeds triquetrous, c. 0.8 mm, alveolate, black. *Chromosome number* 2n = 32.

Seeds were sown in the Copenhagen Botanical Garden on March 25, 1977. Only two germinated, after about three weeks, but the plants flowered very sparsely in the rather cool summer of 1977. Still in the end of September they have fresh green leaves; they are likely to survive a mild winter and flower in the next summer. The plants collected in nature were most probably growing as annuals, however, germinating in the early spring or possibly in the autumn, and withering in mid-summer when the site becomes completely dry.

Discussion

Our plant belongs to a taxonomically difficult group of South American species, and there is some confusion as to the application of names. According to the key in Johnson (1938) it clearly matches *S. laxum* Otto ex Sims in Curtis' Bot.

Mag. 49: tab. 2312 (1822), and there is indeed a good agreement with the original drawing and description of this species in which it is interesting to note that it is said to have "survived the last winter [in Chelsea] exposed to the open air." *S. laxum* differs from *S. micranthum* Cav., Diss. 2: 345, tab. 191 fig. 2 (1788), according to Johnson, in the larger corolla, subequal spathe-valves, glandular-pubescent ovary, in the fact that it does not darken on drying, and in the more southern, temperate distribution. The widely used name *S. iridifolium* HBK, Nov. Gen. 1: 324 (1816) apparently belongs in the synonymy of *S. micranthum* (Johnson 1938 p. 392 and Marais in litt.). Ravenna (1968 p. 286), however, regards *S. laxum* as a synonym of *S. iridifolium* ssp. *iridifolium,* and *S. micranthum* as a separate species. *S. micranthum* was described from Peru, and the original drawing is somewhat mysterious, showing a plant with a single branched, leafy stem. With the available information it seems most reasonable to follow Johnson, according to whom our plant is definitely *S. laxum*.

Johnson recorded *S. laxum* from S Brazil, Uruguay, Argentine, Paraguay and Chile, and also noted that it "occurs as an adventive species in Europe". It seems nowhere to be mentioned in the European literature, however, and it is not clear on what Johnson based this statement.

Acknowledgements. The field work in Greece was financed by a grant from the Carlsberg Foundation. The drawing was prepared by Mr P. Juul. I am indebted to Dr W. Marais at Kew for providing information helpful in the identification of the species and for checking the types of *S. micranthum* and *S. iridifolium* during a visit to Paris.

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Identification of some small species of Navicula

Hannelore Håkansson and Bjørg Stabell

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Light and electron microscopy have been used to identify some small *Navicula* species in a sediment from Halvarp bog in southern Telemark, Norway. The profile contained *N. amphipleuroides* Hust. and *N. cryptolyra* Brockmann. The relationships between *N. amphipleuroides, N. fenestrella* Hust. and *N. escorialis* Simonsen are discussed.

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A sediment profile from Halvarp bog in southern Telemark, Norway, has been investigated in order to determine former shoreline levels in this area (Stabell 1976). Specimens of small *Navicula* species are dominant in some of the samples. Correct identification of these specimens were therefore considered important both stratigraphically and ecologically.

Scanning electron microscopy showed that two species of *Navicula* were present: *N. cryptolyra* Brockmann and a species belonging to the group characterized by a large hyaline area and short marginal striae (i.a. *N. amphipleuroides* Hust., *N. fenestrella* Hust. and *N. escorialis* Simonsen). After comparison with slides at the "Friedrich Hustedt Arbeitsplatz", Bremerhaven, we managed to identify the latter species as *N. amphipleuroides*.

Phase-contrast light microscopy (LM), with a planapochromatic oil-immersion objective and scanning electron microscopy (SEM) were used. The SEM studies were made by HH in a Cambridge EM at the Zoological Institute, University of Lund.

The terminology follows Anonymous (1975).

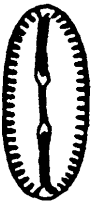
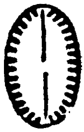
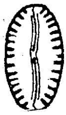
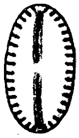
Navicula amphipleuroides and related species

Table 1 shows the main differences between *N. amphipleuroides, N. fenestrella* and *N. escorialis* as they are reported in the literature.

Hustedt (1955) described and illustrated both *N. amphipleuroides* and *N. fenestrella.* He pointed out that *N. amphipleuroides* differs from *N. fenestrella* "by the somewhat curved raphe, the distant central pores and the median rib". Simonsen (1959) gave a very brief description of *N. escorialis.* He did not mention any median rib but it is visible in the illustrations. In 1962 Hustedt provided a new description of *N. fenestrella:* "Mittelrippe sehr schmal, zuweilen an einer oder beiden Seiten von einer zarten Punktreihe begleitet". He made *N. escorialis* synonymous with *N. fenestrella.* Van Landingham (1975) considered both *N. fenestrella* and *N. escorialis* to be synonymous with *N. amphipleuroides.*

We consider that *N. fenestrella* is a distinct species, characterized by the straight raphe and the missing median rib, as stressed in the original description (Hustedt 1955). His later description (Hustedt 1962) makes the difference between *N. amphipleuroides* and *N. fenestrella* obscure. However, we know this species only from the description and illustration; we have not been able to find any material agreeing with this description in spite of careful search. In the Beaufort material no *N. fenestrella* had been especially marked. A slide from the Hustedt Collection No. N 202,13b, containing material from Snigsfjord, Norway, was examined by LM.

Table 1. Differences between some species of *Navicula* according to the literature.

Character	*amphipleuroides* (Hustedt 1955)	*fenestrella* (Hustedt 1955)	*escorialis* (Simonsen 1959)	*fenestrella* (incl. *escorialis*) (Hustedt 1962)
Median rib	strong	absent	present	narrow
Raphe	slightly curved	straight	straight, sometimes slightly curved	often curved, sometimes one or two rows of punctae
Central pores	distant	close	.	.
Length (μm)	8–12	c. 8	7.5–9	7–9
Breadth (μm)	4.5–5.5	5	4–5.5	4–5.5
Number of striae/10 μm	20–24	c. 20	18–20	c. 20
				

However, even this slide was difficult to examine, because no particular specimen had been marked. The only material referred to *N. fenestrella* by Hustedt (after the publication of the species) which we have seen, is the Hustedt Collection No. N 397,85; material from Eckernförder Bucht (15 m), collected by Dr Simonsen; in fact this is the material on which Simonsen (1959) described *N. escorialis* and, as far as can be seen in LM, it is similar to the specimen shown here (Fig. 1 B).

We also found, after examination of slides at Bremerhaven by LM, that *N. amphipleuroides* (Hustedt Collection No. N 10,38; material from Beaufort, N.C., Hafen; specimen marked with a circle, Fig. 1 A) differs from *N. escorialis* (Simonsen Collection Di 289; material from Profil Winds Grav, 5 m, grauer Feinsand mit kleinen Steinen, *Zostera,* 25.11.1955; Fig. 1 B). No extension of the striae towards the raphe was seen in *N. escorialis*. However, according to Simonsen (pers. comm.) this character shows considerable intraspecific variation. We think this depends on whether the frustule is seen from the inner or from the outer side.

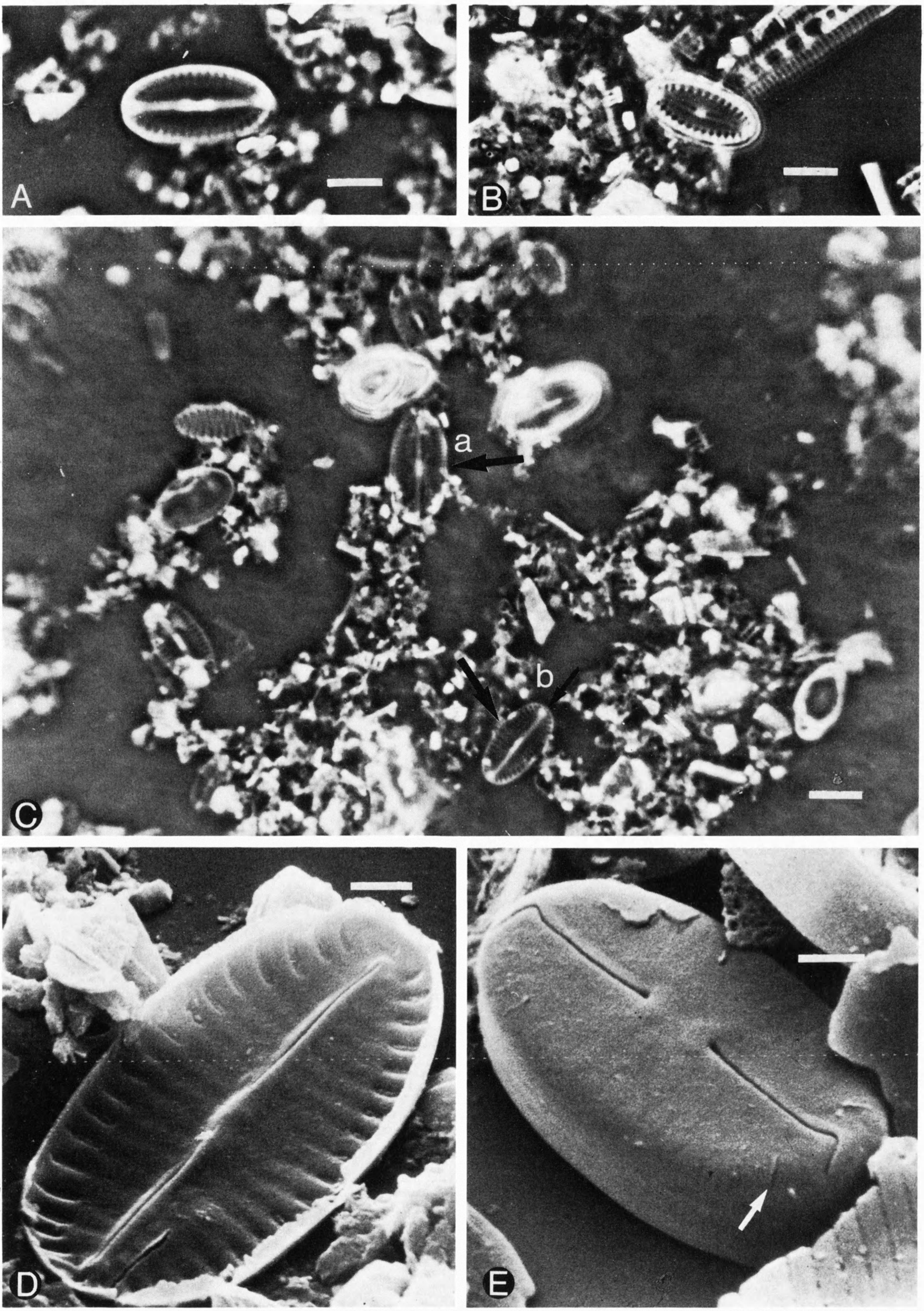
Navicula amphipleuroides Hust.

Hustedt 1955 p. 30, Pl. 5 Fig. 33, 34; Hustedt 1962 p. 175, Fig. 1308.

The *Navicula* specimens in the Halvarp samples show an extension of the striae towards the raphe and appear to have a strong median rib. We have therefore identified them as *N. amphipleuroides*. The following observations have been made on the Halvarp material (Fig. 1 C–E).

The central pores are not always far apart; the distance apart ranges from 0.8 to 1.5 μm. Both the central area and the areas at the polar ends are strongly light refractive (Fig. 1 C).

Fig. 1. A: *Navicula amphipleuroides* from the Beaufort material (Hustedt Collection No. N 10,38) (LM; photo HH). – B: *N. escorialis* from the Profil Winds Grav (Simonsen Collection Di 289) (LM; photo HH). – C: Specimens from the Halvarp bog sample (LM; photo BS). a *N. cryptolyra,* b *N. amphipleuroides* (note light-refractive areas). – D: *N. amphipleuroides*. SEM, interior view of a valve showing the somewhat thickened central nodule. – E: *N. amphipleuroides*. SEM, exterior view of a frustule showing the layer covering the marginal striae and a small split of the membrane (arrow). – Scale unit 5 μm (A–C), 1 μm (D, E).


A
B
a
b
C
D
E

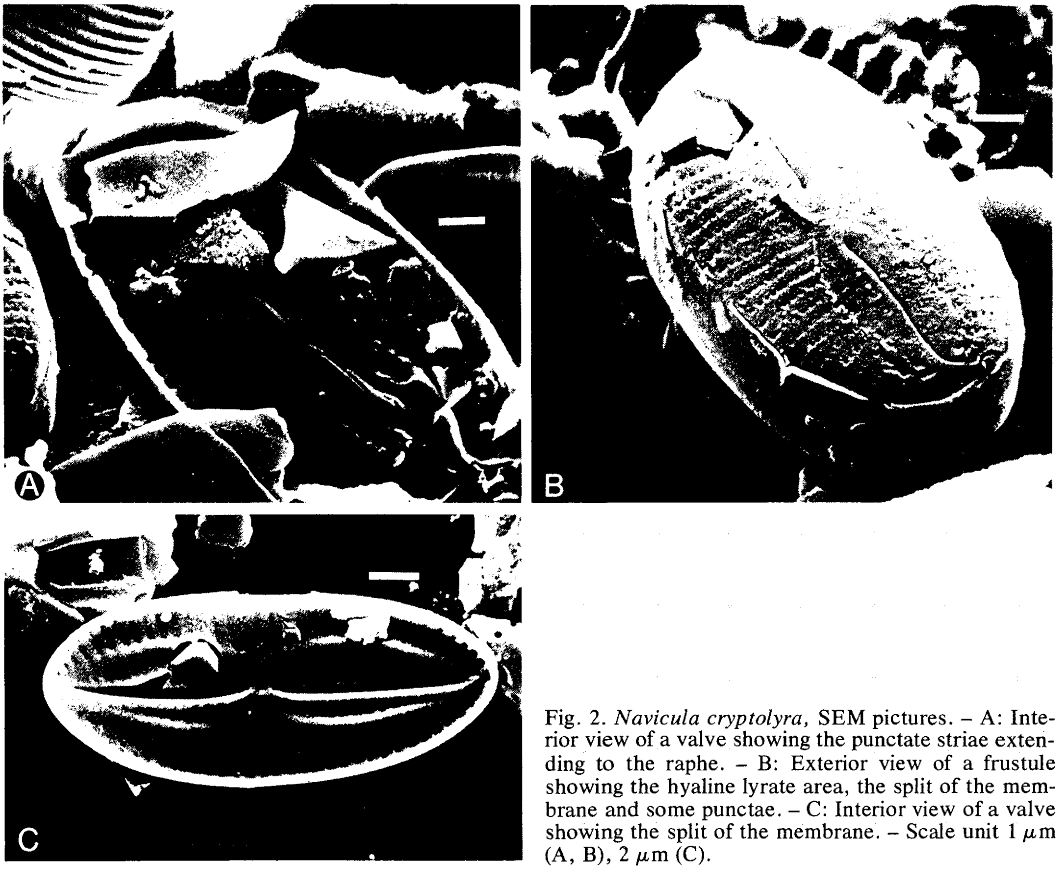


Fig. 2. *Navicula cryptolyra,* SEM pictures. – A: Interior view of a valve showing the punctate striae extending to the raphe. – B: Exterior view of a frustule showing the hyaline lyrate area, the split of the membrane and some punctae. – C: Interior view of a valve showing the split of the membrane. – Scale unit 1 μm (A, B), 2 μm (C).

The walls of the fissures seem to be fairly thick (Fig. 1 D), giving the impression of a strong longitudinal rib in LM. A weak extension of the striae (furrows) towards the raphe is clearly visible on the inner surface of the valves (Fig. 1 D). The outer surface, however, seems to have a cover which makes the striation barely visible (Fig. 1 E).

Hustedt (1962) classifies *N. amphipleuroides* as a "Meeresform". In the profile from Halvarp we have not found *N. amphipleuroides* in the lowermost samples. *N. amphipleuroides* increases at the same time as *Dimerogramma minor* (Greg.) Ralfs and *Grammatophora oceanica* (Ehr.) Grun. decrease, which may indicate that it can live in water with a low salinity. Although *Melosira sulcata* (Ehr.) Kütz. increases together with *N. amphipleuroides,* this does not indicate marine conditions since *M. sulcata* is polyhalobous and pleio-euryhaline and therefore can live in water with a salinity as low as 3–5‰.

Navicula cryptolyra Brockmann

Brockmann 1950 p. 19, Fig. 22, 23; Hustedt 1962 p. 534, Fig. 1570.

Our specimens fit very well with the description given by Brockmann (1950). It was not easy to decide whether or not this species belongs to the *Lyratae* group of *Navicula* from LM studies alone, because the lateral areas are obscure (Fig. 1 C). This fact had already been noted by Brockmann (1950). As seen in Fig. 2 A, viewed from the inner side of the valve, the punctate striae are not interrupted by the lateral areas. In Fig. 2 B, viewed from the outer side of the valve, no striae are visible between the raphe and the lateral areas. It was not possible to see whether the striae are hidden by another layer or not. Figs. 2 B, C, however, show other specimens in which the membrane has split in places, showing that there are in fact two layers. In the specimen in Fig. 2 B some punctae are visible near the raphe. Change of focus indicated that the punctation extends as far as the raphe, though sometimes interrupted by a conspicuous, hyaline, lyrate area. This feature sometimes makes identification by LM difficult.

Simonsen (1962) placed *N. cryptolyra* among the euryhaline mesohalobes, i.e. it is found in brackish water with a salinity of 0.2 to 30‰.

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Recent advances in the taxonomy of Myxomycetes

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A general survey is given of some of the results obtained and the ideas presented in taxonomic research on Myxomycetes during the last ten years. It is suggested that the Liceales, as presently circumscribed, may be an unnatural order and that *Licea variabilis* Schrad. will prove to have more in common with species of *Perichaena* Fries than with species of *Licea* s. str.

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During the past two decades increased interest has been devoted to research on the Myxomycetes and related groups of organisms. Improved culture techniques have increased our knowledge about the ultrastructure and physiology of several species. Many species, including a large number regarded as common, have resisted all attempts to get them grow and complete their life cycles under laboratory conditions. Hence, most cytological and physiological research has been restricted to a limited number of species, in the main on *Physarum polycephalum* Schw. Studies of cultures grown in moist chambers have resulted in the discovery of several types of organisms that seem to be related to Myxomycetes, but which may differ in morphological character, as well as in their life cycles. This has made the delimitation of the Myxomycetes as a taxonomic group more difficult but has led to a better understanding of the origin and phylogeny of the Myxomycetes.

Increased interest has also been focused upon Myxomycetes from a taxonomic point of view during the past two decades. A monographic treatment by Martin & Alexopoulos was published in 1969, the appearance of which has not only facilitated taxonomic studies by bringing together in one volume information from a large number of sources, but by virtue of critical discussion and emphasis on the need for further studies it has stimulated further research. Martin & Alexopoulos recognized c. 425 species, grouped into 53 genera. An additional c. 80 species and three genera have now been described (up to June 1977) as new to science. The present paper attempts to briefly survey some of the results obtained and the ideas presented in taxonomic research on Myxomycetes since the appearance of the above-mentioned monograph. However, the paper makes no claim to completeness in this respect. The endosporous orders are treated in the same sequence as in Martin & Alexopoulos (1969).

Ceratiomyxa

Although very divergent the genus *Ceratiomyxa* Schroet. has traditionally been included in monographic treatments of the Myxomycetes, so also by Martin & Alexopoulos (1969). *Ceratiomyxa* differs in having exospores, i.e. spore-like structures which are borne externally on individual stalks scattered over the surface of generally white-coloured, variously arranged, solidified plasmodial columns. All other genera produce their spores internally, in fructifications of various shapes. Also in its life cycle *Ceratiomyxa* differs in important respects from the endosporous species, e.g. reversible protoplasmic streaming, a characteristic of endosporous Myxomycetes, seems to be absent. Upon germination the exospore produces a 4-nucleate protoplast, which forms a peculiar "thread" phase (Nelson & Scheetz 1976). This structure has not been seen in any endosporous species.

The systematic affinity of *Ceratiomyxa* has been much debated. Ultrastructural studies on *C. fruticulosa* (Müll.) Macbr. have revealed similarities to, as well as differences from, endosporous Myxomycetes (Scheetz 1972). Gilbert (1935) suggested that each exospore on its stalk might be interpreted as a single sporangium, homologous with that of an endosporous species. Olive (1970, 1975), in his revised classification of the Myxomycetes and associated organisms, referred the endosporous Myxomycete genera to a subclass of their own, the Myxogastria, while *Ceratiomyxa* was included in a separate subclass, the Protostelia. The Protostelia comprises organisms with minute fruiting bodies consisting of one to several spores borne on a hollow stalk. The trophic stage varies from simple amoebae to plasmodia in which there is no shuttle movement of the protoplasm. So far about ten genera have been recognized in the Protostelia. Olive interpreted the stalked exospore of *Ceratiomyxa* as a structure homologous with the sporocarp of other protostelids. Similarities, possibly indicating phylogenetic relationships with *Ceratiomyxa*, have been observed in the protostelid genera *Ceratiomyxella* Olive & Stoianovitch (1971 b) and *Protosporangium* Olive & Stoianovitch (1972). In the latter genus the plurinucleate plasmodia may assume a worm-like shape, reminiscent of the "thread" phase formed at a certain stage in the life cycle of *Ceratiomyxa*.

The Protostelia have been regarded as primitive organisms, conceivably ancestral to the endosporous Myxomycetes as well as to *Dictyostelium* and allied genera of cellular slime moulds. Although the ultrastructure and life cycles of several protostelids are incompletely known, and no doubt many further organisms remain to be discovered, the knowledge obtained so far seems to point to an affinity of *Ceratiomyxa* with protostelids rather than with endosporous Myxomycetes. Olive's classification is interesting and deserves serious consideration.

Liceales

The order Liceales, as traditionally circumscribed, is characterized mainly by the absence of a true capillitium. The assimilative stage is either a protoplasmodium or a phaneroplasmodium (Olive 1975 p. 108), which may indicate that the group is heterogeneous and unnatural. I believe that reclassification in the future will lead to changes in the circumscription of the order as a whole, as well as in the delimitation of some of the genera.

In the three genera *Licea* Schrad., *Cribraria* Pers. and *Dictydium* Schrad. the fructifications are normally sporangia (plasmodiocarps in one or two species of *Licea*), in the remaining five genera (*Tubifera* Gmel., *Dictydiaethalium* Rost., *Lycogala* Adans., *Enteridium* Ehrenb. (=*Reticularia* Bull.) and *Lindbladia* Fries) normally aethalia or pseudoaethalia. The aethalia and pseudoaethalia possess a pseudocapillitium. Aethalia and pseudoaethalia have been suggested to have evolved by the coalescence of sporangiate fructifications, and the pseudocapillitium is generally interpreted as representing remnants of the peridium (=wall) of the coalesced sporangia. In the sporangiate genera *Cribraria* and *Dictydium* the largest part of the peridium is fugacious, but certain remnants persist in the form of parallel ribs or a reticulum. Although the term pseudocapillitium is normally not applied in this case, this structure is of course homologous with a pseudocapillitium, providing that the theory about the origin of the pseudocapillitium in aethalioid and pseudoaethalioid species is correct. *Cribraria* and *Dictydium* are closely allied and the formal merger of the two genera (Nannenga-Bremekamp 1962) is wholly defensible. However, the two genera are generally easily distinguished and most myxomycetologists keep them separate for the purposes of convenience. The monotypic and pseudoaethalioid genus *Lindbladia* is closely associated with *Cribraria* and, as repeatedly pointed out in the literature (Macbride 1922, Lister 1925, Hagelstein 1944, Martin & Alexopoulos 1969, Nannenga-Bremekamp 1974), intermediate forms connect *L. tubulina* Fries with *C. argillacea* (Pers.) Pers. The two species also have a similar ecology. Both prefer coniferous wood and may sometimes be found together (Nannenga-Bremekamp 1974). *Cribraria* is a very difficult genus taxonomically. About 30 species have been recognized. Although several species are well-defined, many taxa are highly variable and the characters of many species overlap. Alexopoulos & Sáenz Reynolds (1975) have described the taxonomic state of *Cribraria* as "well-nigh chaotic". The situation is further complicated by the fact that all attempts to grow *Cribraria* species from spore to spore-bearing stage under laboratory conditions have failed, making any study of the stability of morphological characters difficult.

In the genus *Licea,* as traditionally interpreted, the fructifications are completely devoid of both a capillitium and a pseudocapillitium. Martin & Alexopoulos (1969) recognized 19 species. At least six more species have been described up to now, viz. *L. synsporos* Nannenga-Bremekamp (1968), *L. deplanata* Kowalski (1972 a) (in the original description, Kowalski 1970 b, called *L. applanata*), *L. hepatica* Kowalski (1972 b), *L. retiformis* Nawavi (1973), *L. alexopouli* Blackwell (1974) and *L. bryophila* Nannenga-Bremekamp (1976). However, as recently pointed out by Alexopoulos (1976), the taxonomic importance of the absence or presence of a capillitium ought to be questioned in some cases. It is apparent that some species not closely related to the Liceales may also lack a capillitium, as for instance the genus *Squamuloderma* Kowalski (1972 c), but the presence of crystalline lime in the peridium and the possession of a phaneroplasmodium are characters that justify placing this taxon in the Physarales rather than in the Liceales. Five of the eight species recognized so far in the genus *Echinostelium* also lack a capillitium, but this genus differs in many important characters from the other Liceales genera and is therefore referred to a separate order.

It is well-known that the capillitium may be scantily developed in some species of *Perichaena* Fries, a genus of the Trichiales, and may even be absent in *P. corticalis* (Batsch) Rost., *P. quadrata* Macbr. and *P. syncarpon* Brooks (Keller 1971). That the capillitium may be totally absent in *Perichaena* is highly interesting from a taxonomic point of view. Alexopoulos (1976) has pointed out that *Licea retiformis* Nawavi, obviously referred to *Licea* because of the lack of a capillitium, could very well be accomodated within *Perichaena.* Nawavi (1973) also apparently had this possibility in mind when he noted the similarities of this species with members of the Trichiales. Of special interest in *L. retiformis* are the plasmodiocarpous fructifications and the type of plasmodium, described as intermediate between an aphanoplasmodium and a phaneroplasmodium. This type of plasmodium is characteristic of the Trichiales (Alexopoulos 1960), while what I would call "true" species of *Licea* have the "primitive" type of plasmodium, referred to as a protoplasmodium. Apart from *L. retiformis,* only one species in this genus forms plasmodiocarpous fructifications, namely *L. variabilis* Schrad. In my opinion this species also bears some resemblance to *Perichaena* species. Furthermore, the plasmodium of *L. variabilis,* as so far described (Sobels 1950, McManus 1966), is not a protoplasmodium but is reminiscent of that found in *Perichaena.* I suspect that *L. variabilis* will prove to have greater affinity with species of *Perichaena* than with those of *Licea* s. str.

As mentioned previously, in the Liceales, as at present circumscribed, both protoplasmodia and phaneroplasmodia occur. That phaneroplasmodia are known in some species could possibly indicate a relationship of some genera with the Physarales. Another possible indication of an affinity with the Physarales may be the presence of calcium in the dictydine granules of *Cribraria* and *Dictydium,* as demonstrated by Schoknecht (1975).

Listerella

The questioning of the taxonomic importance of the presence or absence of a capillitium, leads to interesting speculations on the affinity of the genus *Listerella* Jahn. This genus has small fructifications, generally 0.2–1 mm in diameter. The genus has been placed in the Trichiales due to the presence of a capillitium, which is often only scantily developed, however. The single species recognized, *L. paradoxa* Jahn, bears a strong resemblance to *Licea,* and even under a lens it is hardly possible to distinguish *Listerella* from species of *Licea,* subgenus *Licea.* Many authors have pointed out the great similarity in habit between the two genera. Martin & Alexopoulos (1969) write about *Listerella* that "this is essentially a *Licea* with a capillitium". Kowalski (1967, 1970 b) stressed the macroscopic similarities between *Listerella* on the one hand and *Licea minima* Fries, *L. pusilla* Schrad. and *L. deplanata* (sub nomine *L. applanata*) on the other. He recommended that *Listerella* should be referred not only to the order Liceales but even to the family Liceaceae.

On the ground that *Listerella paradoxa* has smooth peridial lobes, while *Licea minima* and *L. pusilla* have wart-like processes along the margins of the lobes, Kowalski (1967) suggested that the capillitium of *Listerella* might represent an extension of the wart-like processes in *Licea*. In this connection it should be pointed out that *Licea kleistobolus* Martin has finger-like processes which penetrate into the sporangial cavity. These processes were originally interpreted by Lippert (1894) as a rudimentary capillitium. Martin & Alexopoulos (1969) believed them to represent elongations of the tubercles. Keller & Brooks (1971), who examined numerous collections of this species, found a continuous gradation from wart-like processes to tubular outgrowths.

Kowalski (1967) also hypothesized that "the capillitium of *Listerella,* since it appears to be attached at the margins of the peridial lobes, may represent a reduced state of the pseudocapillitium of the Liceales, and that the sporangia of *Listerella* and *Licea* are not sporangia, but highly reduced aethalia". Future research may elucidate the credibility of this hypothesis. Both genera possess the primitive type of plasmodium referred to as a protoplasmodium, a character which, together with the macroscopic similarities of the fructifications, mirrors the apparently very close relationship of the two genera.

In Europe most fructifications of *Listerella paradoxa* have been found on species of the lichen genus *Cladonia*. A Californian collection on an oak leaf differs in some respects (Kowalski 1967) from typical *L. paradoxa* and may perhaps represent a second species of this genus.

Echinosteliales

The order Echinosteliales comprises species which have minute, stalked sporangia and a protoplasmodium as the assimilative stage. The order was circumscribed by Martin & Alexopoulos (1969) to comprise the single genus *Echinostelium* de Bary. Later (Alexopoulos & Brooks 1971), the genera *Barbeyella* Meylan and *Clastoderma* Blytt, in general previously regarded as members of the Stemonitales, have also been included.

In *Barbeyella* only a single species is known, *B. minutissima* Meylan. *Clastoderma* also remained monotypic for a long time, with *C. debaryanum* Blytt as the only known species. However, during the last ten years another three species have been recognized, viz. *C. pachypus* Nannenga-Bremekamp (1968), *C. microcarpa* (Meylan) Kowalski (1975 a) and *C. dictyosporum* Lakhanpal & Mukerji (1976). The second of these species had originally been regarded as a variety of *Comatricha elegans* (Racib.) G. Lister. Eight species of *Echinostelium* have been recognized up to now (June 1977). One of these, *E. lunatum* Olive & Stoianovitch (1971 a), is the smallest known Myxomycete. Its fructifications are (ex. char.) 21–44 μm tall, the sporangia are 17–30 μm in diameter and are generally 4–8-spored. The recently described species *E. arboreum* Keller & Brooks (1976 b), in contradistinction to the condition in other members of the genus, possesses a persistent peridium attached to the capillitial threads. In this respect *E. arboreum* approaches the genus *Clastoderma*.

A special interest is attached to *Echinostelium,* since it is regarded as probably the most primitive Myxomycete genus. A study of the ultrastructure of the spore wall in *E. lunatum* and in a form of *E. minutum* de Bary has revealed interesting similarities with that of the protostelid genus *Cavostelium* Olive (Hung & Olive 1972), similarities which are believed to indicate a close phylogenetic relationship between protostelids and primitive Myxomycetes. When describing *E. coelocephalum,* Keller & Brooks (1976 b) pointed out that this taxon has spores which in size and markings are strikingly similar to those of *Pocheina rosea* (Cienk.) Loebl. & Tapp., an acrasid cellular slime mold. It seems quite possible that *Echinostelium* is a primitive genus through which other endosporous Myxomycetes evolved from protostelids or related organisms (Hung & Olive 1972, Olive 1975). Of the eight species of *Echinostelium* hitherto formally recognized, five lack a capillitium. Olive & Stoianovitch (1971 a) have intimated the possibility that the non-capillitial species could be referred to the protostelids, while the species with a capillitium could be retained in the Myxomycetes. This shows how vaguely delimited the group Myxomycetes is at present.

Trichiales

The order Trichiales is characterized by fructifications with a generally well-developed capillitium, a pallid, white, brown or bright-coloured spore mass, and the absence of a columella. The assimilative stage seems to be intermediate in type between a phaneroplasmodium and an aphanoplasmodium. In *Trichia arundinariae* Rammeloo (1973) the plasmodium has been described (Rammeloo 1976 a) as intermediate in structure between a typical trichiaceous plasmodium and a phaneroplasmodium.

In modern taxonomic treatments (Martin & Alexopoulos 1969, Alexopoulos 1973, Nannenga-Bremekamp 1974, Farr 1976) the Trichiales is divided into two families, the Dianemaceae and the Trichiaceae. The main difference between the two families is that the capillitial threads are solid in the former and hollow in the latter. In the two first-mentioned taxonomic treatments, the Dianemaceae comprises the genera *Listerella, Dianema* Rex, *Minakatella* G. Lister and *Calomyxa* Nieuwl. However, as mentioned previously, Kowalski (1967) for good reasons has recommended that *Listerella,* which diverges from typical members of the Trichiales i.a. by its dark spore mass and in having a protoplasmodium as the assimilative stage, should be transferred to the Liceales, an arrangement accepted by Farr (1976). Nannenga-Bremekamp (1974) also included *Prototrichia* Rost. in the Dianemaceae. However, Kowalski (1967) demonstrated that the capillitium in this genus is basically tubular and recommended that the genus should be included in the Trichiaceae. More recently, Keller et al. (1973) have presented ultrastructural evidence that also *Minakatella* has a tubular capillitium, and they propose that this genus as well should be transferred to the Trichiaceae. Future studies may show whether the remaining two genera *Calomyxa* and *Dianema* have enough characteristics in common and are sufficiently distinct from other taxa to warrant retention of the Dianemaceae as a distinct family. Characters common to the two genera are the membranous peridium (*D. corticatum* List. being an exception in this respect, in having (ex char.) a two-layered peridium, the outer layer being cartilaginous and opaque), a solid capillitium at least partially attached to both the base of the sporangium and to the peridium, and pallid or yellowish-coloured spores under transmitted light (Kowalski 1967). Martin & Alexopoulos (1969) recognized five species of *Dianema* and one species of *Calomyxa*. Kowalski (1967) has described a further two species of *Dianema*. A second species of *Calomyxa* has been added by Farr & Kowalski (1974).

Ten genera were recognized in the Trichiaceae by Martin & Alexopoulos (1969). Although most of the genera are well-defined, many are closely related. In some genera, in which most of the species have many common characteristics and seem to comprise a natural group, one or several species may be divergent and have features in common with other genera. Several examples exist where, in important characters, one or two species narrow or even bridge the gap between established genera.

One of the most interesting genera in the Trichiaceae from a phylogenetic point of view is *Perichaena*. The genus has been monographed by Keller (1971), who recognized 13 species. The genus appears to have some clear affinities with some species of *Licea,* although the two genera are traditionally placed far apart in monographic treatments. As mentioned previously, there is evidence that the plasmodiocarpous species *Licea retiformis* and *L. variabilis* may lie closer to *Perichaena* than to the sporangiate species of *Licea*. It is interesting that *P. brevifila* Keller & Brooks (1971) may conceivably be interpreted as forming a link between the two genera. This species possesses (ex char.) an inconspicuous capillitium, consisting of short, simple to furcate, scattered threads attached to the inner sporangial wall. Keller & Brooks (1971) have suggested that this capillitium may be homologous with the finger-like processes of *L. kleistobolus* which enter the sporangial cavity.

Perichaena shares various morphological characters with several other genera and is important in any discussion of the phylogeny of the trichiaceous genera. While *Calonema* Morg. and *Oligonema* Rost. are so closely allied to *Perichaena* that they could probably be merged with it, other genera are more distinct, although single species may narrow the gaps also to such genera. Keller (1971) suggested two possibilities concerning the evolutionary standing of *Perichaena*. Either it lies close to *Licea*, thereby forming the base of one or several lines leading to other trichiaceous genera, or it is itself derived from some other trichiaceous genera or genus.

Exemples of species within the Trichiaceae that have features which intergrade with those of other genera are *Arcyria stipata* (Schw.) A. Lister (similarities with *Hemitrichia*), *Calonema luteolum* Kowalski (1969) (affinities with *Oligonema* and *Perichaena*, ex char.), *Hemitrichia karstenii* (Rost.) A. Lister (probably more correctly regarded as a variety of *Trichia contorta* (Ditmar) Rost.) and *Perichaena minor* (G. Lister) Hagelst. (approaching *Hemitrichia* in possessing spiral structures on the capillitium). Although it is possible that some of the generic distinctions in the Trichiaceae are of an artificial nature, the family as a whole appears to form a natural group. The only affinity to another order seems to be the afore-mentioned, presumed, linkage of *Perichaena* with some species of *Licea*. The lime deposition sometimes seen in the peridium of some species of *Perichaena* has been suggested as a possible affinity with the normally lime-bearing species in the Physarales. However, Schoknecht & Keller (1975, 1977) have shown by chemical tests that the lime seen in the peridium of *Perichaena* is present in the form of calcium oxalate, often mixed with crystals containing silica, while in the Physarales the peridial lime consists of calcium carbonate and possibly calcium phosphate. Schoknecht & Keller also found that calcium oxalate crystals occur between two membranous peridial layers also in phases of *Perichaena* that appear limeless.

Stemonitales

Martin & Alexopoulos (1969) recognized fifteen genera in the order Stemonitales. They included here also *Clastoderma* and *Barbeyella*. As mentioned previously, these two genera have protoplasmodia and have since been transferred by Alexopoulos & Brooks (1971) to the Echinosteliales, an arrangement adopted by Alexopoulos (1973), Nannenga-Bremekamp (1974) and Farr (1976). If these genera are removed, the Stemonitales becomes a more natural taxon. It is characterized by an aphanoplasmodium and by a special type of sporophore development, generally called epihypothallic. Because of these important characteristics, Ross (1973) and Alexopoulos (1973) assigned this group the rank of a separate subclass, juxtaposed on the one hand to the other endosporous Myxomycetes and on the other to *Ceratiomyxa*. The epihypothallic mode of sporophore development means that the hypothallus, as the sporangial primordia begin to develop, is deposited directly onto the substratum on the underside of the plasmodium, and that the stalk is formed inside the sporangial protoplast. This type of sporophore development is only known in the Stemonitales and is regarded as an important character from a phylogenetic point of view. In the Echinosteliales, Trichiales and Physarales the sporophore development is subhypothallic, i.e. the hypothallus is formed on the upper side of the plasmodium. A continuous membrane encloses the sporangial initials. The sporangial protoplast passes through the interior of the stalk. The hypothallus is laid down on the substratum as the protoplasm moves upwards within the developing stalk (Alexopoulos 1966). The two types of sporophore development have been schematised by Ross (1973) and Alexopoulos (1973). The subhypothallic type is also considered to prevail in the Liceales, but this remains to be demonstrated.

Rammeloo (1976 a) has intimated that more than one plasmodium type probably occurs in the Stemonitales, so far as this order is circumscribed by e.g. Alexopoulos (1973), and it is possible that the group may be less uniform than is often supposed. One of the most divergent genera generally referred to this order is *Diachea* Fries. Developmental studies of this genus are still incomplete, but it differs morphologically in having both stalk and columella (when present) encrusted with lime, a character often interpreted as showing an affiliation with the Physarales. In most of the recent Myxomycete surveys (Martin & Alexopoulos 1969, Alexopoulos 1973, Nannenga-Bremekamp 1974), the genus has been included in the Stemonitales, but Farr (1974, 1976) preferred placing it in the Physarales.

Although, good agreement exists on the whole concerning the delimitation of the order Stemonitales, different opinions exist regarding the circumscription of several of the genera and the order is considered to be a difficult one taxonomically. Thirteen genera were accepted by Alexopoulos (1973); quite different systems, as regards generic delimitation, have been proposed by Nannenga-Bremekamp (1967, 1974). Developmental studies are regarded as important for the discovery of the natural relationships between several genera in this order. The importance of stalk structure and capillitium development in the creation of a natural system within the Stemonitales has been emphasized by Alexopoulos (1967) and Nannenga-Bremekamp (1967). Differences in these respects separate e.g. the genera *Comatricha* Preuss and *Stemonitis* Roth.

Physarales

The order Physarales is characterized by a dark spore mass and by the presence of lime deposits. A capillitium is present in all genera except *Squamuloderma* Kowalski (1972 c). The order is well-delimited, although different opinions exist as regards the genus *Diachea*. The stemonitaceous habit of this genus and similarities with *Lamproderma* in the structure of the capillitium and peridium have led most authors to include it in the Stemonitales. Farr (1974) attached great weight to the presence of lime in the stipe and columella and considered *Diachea* to lie closer to the Physarales than to the Stemonitales. The results of a microanalysis of the calcareous deposits in *D. leucopodia* (Bull.) Rost. (Schoknecht 1975) do not contradict a placement of the genus in the Physarales.

Physarales is generally divided into two families, the Physaraceae and the Didymiaceae. The former is characterized by a calcareous capillitium, the latter by a non-calcareous capillitium. In the former the peridial lime is present in the form of non-crystalline granules, in the latter the lime is either crystalline or granular.

Martin & Alexopoulos (1969) recognized eight genera in the family Physaraceae. Most of these are well-distinguished from one another, although in some other cases the delimitation of genera may be vague. For example, *Physarum* Pers., the largest genus among the Myxomycetes with about ninety species so far described and accepted, is only vaguely, and probably unnaturally, delimited from both *Badhamia* Berk. and *Craterium* Trent. The physaroid type of capillitium (calcareous nodes connected by threads of various structure) is found in *Physarum, Craterium* and *Fuligo* Hall. The last-named genus is generally separated from the other two by normally having aethalioid fructifications; the fructifications in *Physarum* and *Craterium* are sporangiate or plasmodiocarpous. *Craterium* is separated from *Physarum* by its more or less cyathiform sporangia, often with circumscissile dehiscence. However, both these characters may be variable and it is questionable whether they warrant its retention as a separate genus. *Badhamia* is characterized by a capillitium consisting of a network of calcareous tubes. This type of capillitium is often very characteristic, but capillitia intermediate in appearance between the physaroid and the badhamioid types do occur. In a few species a continuous variation may exist, from typically badhamioid to physaroid capillitia. The border-line between these two genera has been discussed by many authors. Among recent papers in which this matter is at least partially dealt with, those by Gottsberger (1971), Carter & Nannenga-Bremekamp (1972) and Mitchell & Nannenga-Bremekamp (1976) deserve mention. One species of *Badhamia, B. ainoae* Yamashiro, has a deviant type of capillitium, consisting of calcareous columns which extend from the base of the fructification up to the peridium. This divergent species has recently been transferred to a separate genus, *Badhamiopsis* Keller & Brooks (1976 a).

In the family Didymiaceae six genera were recognized by Martin & Alexopoulos (1969), in three of which, *Wilczekia* Meylan, *Physarina* Höhn and *Diderma* Pers., the peridial lime is amorphous and granular, whereas in *Mucilago* Micheli ex Batt., *Didymium* Schrad. and *Lepidoderma* de Bary it is crystalline. The monotypic genus *Wilczekia* lies very close to *Diderma* and the single species, *W. evelinae* Meylan, has been formally transferred to *Diderma* by Kowalski (1975 a). According to Kowalski (1972 c) the genus *Squamuloderma* should also be included in the Didymiaceae. The latter genus is unique in the Physarales by its lack of a capillitium. The genus was based on material obtained from moist chamber cultivation. Before the taxon was described its life cycle was studied and completed several times in the laboratory, but the lack of a capillitium was a constant feature in all the fructifications obtained. For this reason the lack of a capillitium is believed to be a characteristic of the organism, rather than due to the environmental conditions. Kowalski (1972 c) recommended placing *Squamuloderma* in the Didymiaceae, because of the presence of crystalline lime in the peridium.

In an interesting and important paper, Schoknecht (1975) suggests that the taxonomic importance of the type of lime deposit is questionable in some cases. From laboratory cultivations it is now well-known that the environmental conditions can influence the amount of calcium secreted, and that lime may even be absent from the fructifications of normally lime-bearing species when these are grown under certain conditions. Further investigations are also needed to reveal whether species which normally produce amorphous lime could, under different environmental conditions, produce crystalline lime, or vice-versa. Farr (1974, 1976) has drawn attention to the fact that fructifications of *Diachea bulbillosa* (Berk. & Br.) A. Lister from tropical and subtropical collections contain crystalline lime, whereas in specimens from temperate zones the lime is granular. Whether this is due to climatic conditions or whether it is genetically controlled is still unknown. If it is genetically controlled, the interesting question arises as to whether or not this character alone may warrant splitting what is nowadays called *D. bulbillosa* into two species. As Farr (1974) has pointed out, this is largely a question of being consist, since in other cases great taxonomic importance has been attached to the structure of the lime deposits, e.g. it is the only character which separates the genera *Diderma* and *Didymium*.

The recently established genus *Protophysarum* Blackwell & Alexopoulos (1975) is very interesting phylogenetically. The single species so far known, *P. phloiogenum* Blackwell & Alexopoulos (1975), appeared on pieces of *Ulmus* bark placed in a moist chamber. The species was maintained in culture for many years and its life cycle and development investigated, before the genus and species were described taxonomically. Although reminiscent of a small *Lamproderma, Protophysarum* differs (ex char.) from species of the Stemonitales in certain important respects, e.g. its plasmodium, despite its small size, is a true phaneroplasmodium, and its sporangial development is subhypothallic. Blackwell & Alexopoulos (1975) accomodated *Squamuloderma* in the Physarales, family Physaraceae. It differs from the other genera of the Physarales by its apparent absence of lime deposits. However, ultrastructural studies have shown that lime is found in association with both the peridium and capillitium (ex char.). *Protophysarum* seems to be intermediate between the Echinosteliales and the Physarales and may be regarded as forming an evolutionary link between these two orders (Blackwell & Alexopoulos 1975).

Concluding remarks

Since the publication of the paper by Schoknecht & Small (1972) on scanning electron microscopy of Myxomycetes, scanning pictures have become frequent in taxonomic papers dealing with this group. These organisms are very suitable for this kind of structural investigation. Since certain structural differences may sometimes be difficult to validate taxonomically, laboratory cultivation appears necessary for a true understanding of the relationships and intraspecific variability of some species. Alexopoulos (1969) recommended that recourse to the results of experimental work should always be made in proposals for Myxomycete classification and that any revisions of genera and higher taxa, as well as descriptions of new taxa, should be preceded by experimental culture whenever possible so as to test, under differing environmental conditions, the validity of the taxonomic characters used. This recommendation is of course very sound, although at present unrealistic for genera which so far have resisted all attempts to grow them under laboratory conditions. Hitherto, c. 70 species have been cultured from spore to spore-bearing stage on agar in the laboratory. A list of these species has been compiled by Clark & Collins (1976), to which *Trichia persimilis* Karst. may now be added (Rammeloo 1976 b).

The relatively large number of Myxomycete species described during the past decade shows that much floristic work remains to be done. The Myxomycete flora on decaying wood is probably relatively well-known, but investigations of other ecological niches will, in many cases, probably yield interesting results. Good examples are provided by the newly-discovered species of snow-line Myxomycetes, i.e. species growing in the vicinity of melting snow, described by Kowalski (e.g. 1967, 1968 a, b, 1970 a, 1975 b). The bark of living trees has also been found to harbour a special Myxomycete flora (Keller & Brooks 1973, 1975, 1976 a, b, Keller et al. 1973, Brooks et al. 1977). No doubt many further species remain to be discovered. It is likely that many species now regarded as rare will subsequently prove to be much less so when their ecological demands have become better known. An example of this situation is *Barbeyella minutissima,* which, when first reported from the United States (Curtis 1968), was regarded as "exceedingly rare", but only a few years later it was designated "a common alpine Myxomycete" (Kowalski & Hinchee 1972), growing on leafy liverworts.

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The genus Peyrousea (Compositae)

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Peyrousea is a monotypic genus of the Compositae-Anthemideae from South Africa. The confused nomenclature is elucidated and the systematic position, morphology, variation and distribution of the genus are discussed.

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Peyrousea is a monotypic genus of the Compositae-Anthemideae from South Africa. The present investigation has been made in order to elucidate the nomenclature and taxonomy of the genus, especially its systematic position, morphology, variation and distribution.

Material. I have examined 82 collections from the following herbaria: BM, BOL, G, G-DC (only microfiche), K, M, NBG, P, PRE, S, SAM, UPS, UPS-THUNB (Herbarium Thunberg at UPS), W and Z (abbreviations according to Holmgren & Keuken 1974). A list of examined specimens is kept at the Museum of Natural History, Section for Botany, Stockholm.

History and nomenclature

This genus was established by Thunberg (1800 p. 163 without description, 1823 p. 700), who named it *Lapeirousia* after the French circumnavigator J. F. Galaup de La Pérouse. Thunberg had himself collected material of the plant and identified it as *Osmites calycina* Linné fil. (1781 p. 380). The new genus thus comprised the single species *Lapeirousia calycina*. However, the type specimen of *O. calycina* L. f. and, in consequence, also of *L. calycina* (L. f.) Thunb. is in the Linnaean herbarium in London, and it belongs to a species of *Relhania,* a genus entirely different from that of the plant in Thunberg's collection. This was clarified by Compton (1935 p. 71). Thunberg's unfortunate misidentification has been copied in the works of his successors. The names are typified by the *Relhania* specimen, but the descriptions cover the species of the genus treated here. Cassini (1822 p. 251), who found the epithet *calycina* inappropriate, thus changed the name to *Lapeirousia Thunbergii,* a superfluous name typified by the *Relhania* specimen. De Candolle (1838 p. 76) changed the generic name to *Peyrousea,* since Thunberg's name is a later homonym of *Lapeirousia* Pourr. (Iridaceae). He did not intend to describe a new genus, and the type species is *Peyrousea calycina* (L. f.) DC., again typified by the *Relhania* specimen. *Osmitiphyllum Kraussii* Sch. Bip. is yet another name, which belongs here although never validly published, since it was merely mentioned as a synonym for *P. calycina* (L. f.) DC. (Schultz Bipontinus 1844 p. 675).

De Candolle recognized two species within this genus. They were described from collections made by Burchell and differed in minor characters of the involucre. Later authors, including myself, have not accepted these collections as belonging to more than one species. These species were named *Peyrousea calycina,* discussed above, and *Peyrousea oxylepis* DC. The name of the latter species is a superfluous name, since in his synonymy De Candolle included *Cotula umbellata* Linné fil. (1781 p. 378), the epithet of which should have been adopted. This was realized by Fourcade (1932 p. 87), who made the combination *Peyrousea umbellata* (L. f.) Fourc.

Cotula umbellata was described by Linné fil.

from a specimen in the herbarium of Abraham Bäck, physician to the Swedish king and a friend of the elder Linnaeus. An account of this herbarium, as well as of those specimens used by Linné fil., has been given by Juel (1924) and Exell (1931), respectively. These specimens should now be in J. E. Smith's herbarium at the Linnean Society in London, but for some unknown reason the type of *Cotula umbellata* L. f. is missing. However, from the description it is obvious that it must have been based on a specimen belonging to the genus treated here. The South African plants in Bäck's herbarium were given to him by Thunberg, who certainly kept duplicates of all the species sent. *Cotula umbellata* L. f. was therefore most probably based on the same collection as that which Thunberg erroneously identified as *Osmites calycina* L. f. Specimens of this collection exist at Uppsala (UPS-THUNB) and Stockholm (S), and I have chosen one of these from the former herbarium as the lectotype.

Let us now return to the problem of the generic name. With *P. calycina* (L. f.) DC. as type species, *Peyrousea* becomes a synonym of *Relhania,* and there is no name for the genus in this treatise. This was indicated in my revision of *Relhania* (Bremer 1976 pp. 8, 27, 71). A new name could be constructed, but in my opinion the only acceptable solution is to retain the generic name *Peyrousea* by simply changing the type species to *P. umbellata* (L. f.) Fourc. Such a proposal will be put forward at the next International Botanical Congress and, consequently, I have continued to use the name *Peyrousea.*

The name of the genus has already been in danger once before. The International Botanical Congress in Cambridge in 1930 had decided that a name is illegitimate and must be rejected if it is a later homonym, even if the earlier homonym is itself illegitimate or treated as a synonym. This is precisely the case in this genus, since *Peyrousea* DC. is a later homonym for *Peyrousia* Poir., in turn a synonym of *Lapeirousia* Pourr. (Iridaceae). However, the so-called absolute homonym rule was accepted on the understanding that all well-known generic homonyms should be conserved, and *Peyrousea* DC. was one in a long list of names proposed for conservation by Rehder *et al.* (1935 p. 447). Accordingly, *Peyrousea* DC. was conserved by the Special Committee for Phanerogamae and Pteridophyta appointed by the International Botanical Congress in Amsterdam in 1935 (Green & Sprague 1940 p. 129). At that time the original collection of the type species was not examined. With *Peyrousea calycina* (L. f.) DC. as type species, the genus inevitably goes into synonymy under *Relhania,* although it is a conserved name. However, the name can still be saved by changing the type species, as explained above.

Peyrousea DC., nom. cons.

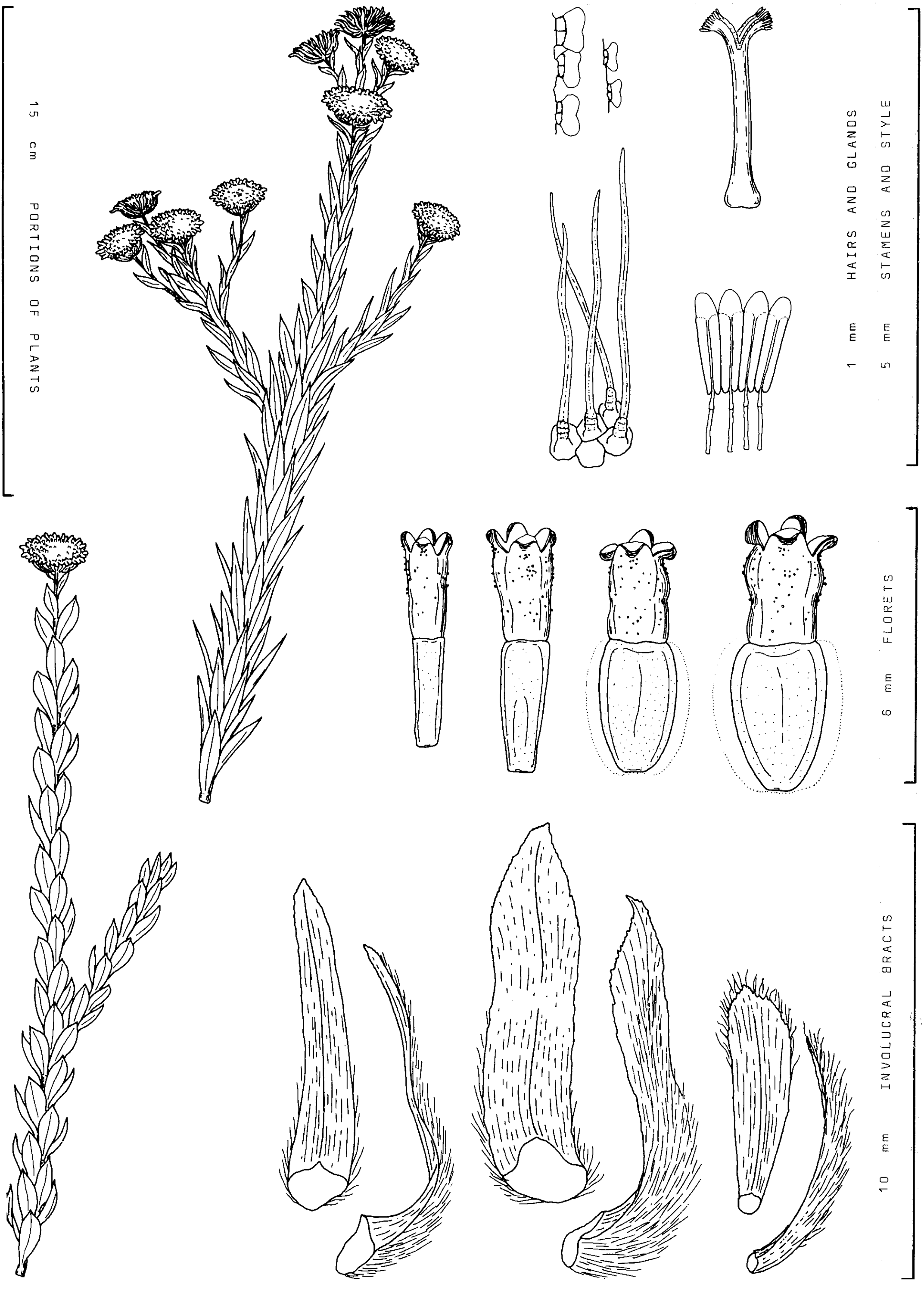
De Candolle 1838 p. 76 (non *Peyrousia* Poiret 1826 p. 363); Steudel 1841 p. 312 (*"Peurousea"*, sphalm.); Harvey 1865 p. 176; Bentham & Hooker 1873 p. 432; Hoffmann 1890 p. 283; Compton 1935 p. 71; Dyer 1975 p. 709. – Typus cons. prop.: *P. umbellata* (L. f.) Fourc. – Typus rej. prop.: *P. calycina* (L. f.) DC.

Lapeirousia auct. (non Thunberg 1800 p. 163; nec non Pourret 1788 p. 79); Cassini 1822 p. 251; Thunberg 1823 p. 700 *("Lapeyrousia");* Lessing 1832 p. 260 *("Lapeyrousia").*

The description given under the species applies to the genus, too, since only one species is accepted here.

Systematic position. There is still much work to be done on the South African genera of the Compositae-Anthemideae before we shall know anything definite about their interrelationships. With its entire leaves, *Peyrousea* looks rather anomalous in the Anthemideae, but it is generally placed in the "*Cotula*-group" of genera, characterized by compressed achenes. *Schistostephium* Less. is the most closely-related genus and it is even possible that *Peyrousea* and *Schistostephium* are sister groups, together forming a monophyletic unit. *Schistostephium* has a very similar floral morphology, especially

Fig. 1. *Peyrousea umbellata.* Features of plant parts, showing a common growth form, upper specimen (drawn from Compton 15801 in NBG), and a mountain form, lower specimen (Compton 5189 in NBG). From left to right the outer, middle and inner involucral bracts are shown in ventral and lateral views. The two left-hand florets have unripe achenes, while the two right ones have ripe, mucilaginous achenes. The hairs are drawn from a leaf; the involucral bracts have similar hairs. The smaller glands are from the achenes, while the larger ones are from the corolla. Similar glands, roughly intermediate in size, occur on the leaves and involucral bracts. (All details drawn from Compton 15801 in NBG.)


15 cm PORTIONS OF PLANTS
1 mm HAIRS AND GLANDS
5 mm STAMENS AND STYLE
6 mm FLORETS
10 mm INVOLUCRAL BRACTS

those species with homogamous capitula. Species with few, large capitula and few-lobed, almost entire leaves approach *Peyrousea* in habit. Another related genus is *Hippia* L. Thus we have here a group of three allied genera, but their mutual relationships deserve further study.

Peyrousea umbellata (L. f.) Fourc.

Fourcade 1932 p. 87; Compton 1935 p. 72. – *Cotula umbellata* Linné fil. 1781 p. 378. –*Peyrousea oxylepis* De Candolle 1838 p. 77, nom. superfl.; Harvey 1865 p. 176. – Holotypus: Thunberg, herb. Bäck, amissus? – Lectotypus: Thunberg, herb. no. 20508 (UPS-THUNB, isotypi in S).

Lapeirousia Thunbergii auct. (quoad descr., excl. syn.); Cassini 1822 p. 251. – *Lapeyrousia calycina* auct. (quoad descr., excl. syn.); Thunberg 1823 p. 700; Lessing 1832 p. 260. –*Peyrousea calycina* auct. (quoad descr., excl. syn.); De Candolle 1838 p. 77; Harvey 1865 p. 176.

Peyrousea argentea Compton 1935 p. 73. – Holotypus: Compton 4202 (BOL).

Nom. vern.: "Bels(kruie)" (Smith 1966 p. 616).

A little-branched shrub, up to 2 m high (fide coll.). *Stems* pubescent, densely leafy, gradually more sparsely upwards and thus often pedunculoid. *Leaves* alternate, erect–spreading, sessile, entire, elliptic, 8–40 mm long, 3–12 mm wide, acute and mucronate, mid-ribbed and sometimes with inconspicuous lateral veins, densely pilose with straight, appressed hairs. *Capitula* solitary or aggregated in a lax cyme at the end of the branches, homogamous. *Involucre* campanulate, 8–22 mm wide. Involucral bracts 25–70, 3–5-seriate, imbricated, firm, yellowish brown and the longest with a whitish or occasionally purplish tip, entire or serrulate apically, acute, mid-ribbed, dorsally densely pilose with straight hairs; outer bracts lanceolate, up to 8 mm long, middle bracts oblong, curved, 4.5–10 mm long, up to 2.5 mm wide, inner bracts narrowly obovate, up to 7 mm long. *Receptacle* flat–conical, nude. *Florets* 75–500, tubular, perfect. Corolla indistinctly divided into a cylindrical or somewhat compressed tube and a cyathiform–urceolate limb, 2.1–3 mm long, 0.8–1.7 mm wide, yellow, glandular, 4-lobed; lobes ovate-triangular, subcucullate. *Stamens* 4; apical anther appendage ovate; filament collar oblong, of subcubical cells. *Style* swollen at base, bifid; style-branches apically penicillate and truncate. *Achenes* obovate, strongly compressed dorsiventrally, with one distinct, somewhat winged, lateral rib on each side, 2.7–4.4 mm long, 1.7–3 mm wide, brown, minutely glandular, completely covered with myxogenic cells. *Pappus* 0.

Flowering period mainly August–November, but flowering specimens have been collected from throughout the year.

Discussion. The morphology of this plant (Fig. 1) is characterized by many reductions. The capitula are homogamous with no rays, the receptacle is epaleate, the florets are tetramerous and the achenes have no pappus. Other characteristics are the thickened, subcucullate corolla lobes and the compressed, 2-ribbed achenes, mucilaginous when soaked in water. Furthermore, *P. umbellata* should not be difficult to recognize, with its entire, pubescent leaves and rather large, discoid capitula.

The leaves and involucral bracts are covered with a rather dense pubescence of more or less straight and appressed hairs. These hairs consist of a few, small, basal cells and a long, thick-walled, terminal cell. Few-celled glands are scattered over the corolla, achenes, involucral bracts and leaves. Those on the corolla are rather conspicuous, whereas those on the achenes are much smaller and are difficult to see. The glands on leaves and involucral bracts are roughly intermediate in size, rather sparsely scattered and hidden under the indumentum.

Whereas the floral morphology of this species is constant, both habit and foliage vary. The leaves are generally 15–30 mm long and rather densely set. A few collections have smaller leaves more scattered on the stems. Some of these collections are from outlying localities W of the main distribution area, e.g. Esterhuysen 23811 from Langeberg near Montagu, Esterhuysen 24755 from Swartberg N of Ladismith and Wurts 1359 from Sandberg W of Calitzdorp. However, I cannot grant these taxonomic recognition, since there are similar small-leaved plants present within the variation range shown by the main bulk of collections from the George, Knysna and Humansdorp area.

Plants from higher altitudes have a more condensed growth habit, with fewer capitula and smaller, densely pubescent leaves, which give the foliage a silvery appearance. These plants were described by Compton (1935 p. 73) as a new species, *Peyrousea argentea* Compt., but there is a continuous variation to the habit of

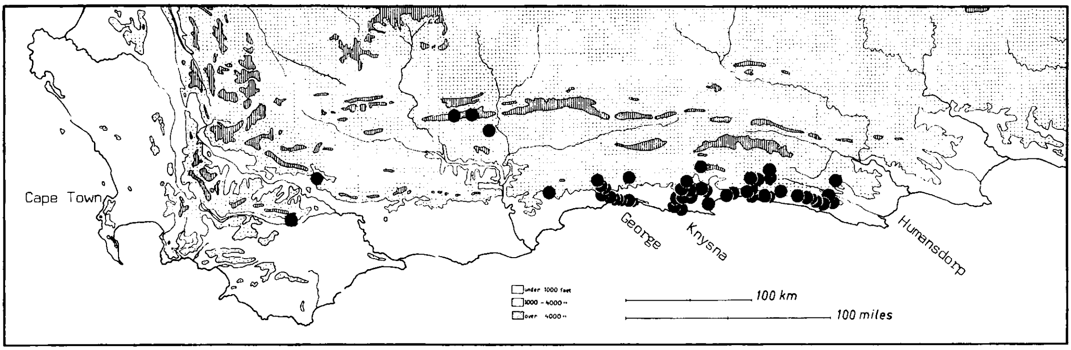


Fig. 2. Known distribution of *Peyrousea umlbellata.*

lowland plants and the distinguishing characters, as described above, are quantitative and refer to the vegetative parts only. There are no differences within the capitula. Apparently the mountain plants constitute a high altitude ecotype. Since the variation is continuous, I cannot grant it any formal taxonomic rank.

Distribution (Fig. 2). *P. umbellata* mainly occurs along the Outeniqua and Tsitsikamma mountain ranges, in the southern Cape Province between George and Humansdorp. Most of the collections are from George and Knysna divisions, where it grows all the way from the coast up into the mountains. There is also one collection from Mossel Bay and a number of collections from further east, in Uniondale, Joubertina and Humansdorp divisions. It has been collected a few times in more western localities, viz. Sandberg W of Calitzdorp (Wurts 1359), Langeberg near Montagu (Esterhuysen 23811), Swartberg N of Ladismith (Esterhuysen 13948 and 24755), and Riviersonderend (Bayliss 5793). It grows on forest margins, on cliffs and in fynbos on hillsides and on the higher mountain slopes, from sea level to above 1500 m (fide coll.).

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Botanical literature

Dixon, P. S. & Irvine, L. M. 1977: *Seaweeds of the British Isles. Volume 1, Rhodophyta. Part 1, Introduction, Nemaliales, Gigartinales.* XI + 252 pp., 90 figs. British Museum (Natural History), London. ISBN 0-565-00781-5. Price £ 10.–.

This is the first part of a marine algal flora for which it has been set as an important goal to dig to the bottom in defining the species. For the first time in a Northwest-European marine flora the type is carefully indicated for each taxon, and when the type is a specimen, this specimen has been studied. Equally great efforts have been made to provide adequate illustrative material. All species are figured, and the present first part of the flora has original drawings in all cases except for one where no type material and no later finds are known. The search behind this achievement has been very considerable and provides a firm foundation for the taxonomic treatment.

In the standing conflict between 'lumpers' and 'splitters' the authors follow the principle of not combining species where this may make future critical work more difficult. They are at variance with Söderström as regards the distinctness of *Nemalion multifidum* from *N. helminthoides,* and with Feldmann & Hamel regarding the justification of several species of *Gelidium*, and in these cases follow their personal opinion as they do not expect this to block later weighing of specific characters. In the Acrochaetiaceae, on the other hand, they undertake no combination at all, though stating about various species that "their continued independence is highly unlikely". In these cases more knowledge of the variation and ecology of the doubtful species is needed for a final settlement, and it is found that such knowledge might perhaps never be provided if the species were precociously dropped in this flora. Similarly, the authors refrain from discussing the natural grouping of all these species, they arrange them alphabetically and refer to them all by the oldest generic name, *Audouinella*. In treating the complex in this way they offer the reader all available taxonomic information but at the same time do not force any personal opinion upon him. This is scientifically ideal, but some users may find themselves rather lost when left to a personal choice in these matters.

The work on typification has entailed a few name changes. Only one affects the general botanical public, namely that *Furcellaria fastigiata* must from now on be called *F. lumbricalis* (cf. this journal Vol. 130 p. 137). Nomenclatural problems are usually summarized so that the background for debatable choices is apparent.

Users of the book will find it easy to look up the information they want. A non-taxonomic key for the genera must necessarily await publication of the remaining two parts on red algae, but those who start with an uncertain identification, from memory or obtained with the help of a smaller flora, will find in each case a comparison of the genus in question with those it is likely to be confounded with. These very consistent comparative sections will be of particular use to many botanists. The information on occurrence, biology and variation is very complete, and also characteristic parasites and some epiphytes are mentioned.

The general appearance of the new flora is pleasing. The pages are small, relatively low and broad, making it easy to keep the book open alongside one's microscope without taking up too much table space. The illustrations are all line drawings; a few might have been made with greater care, such as those of *Gelidium* sections, and several are rather coarse, as if being made for a somewhat smaller magnification, but all of them serve their purpose well.

Phycologists everywhere will look forward to the continuation of this work.

Tyge Christensen

Heywood, V. H. 1976: *Plant taxonomy.* Second edition. Studies in Biology 5. 63 pp. Edward Arnold, London. ISBN 0-7131-2609-4. Price £ 1.30.

To present plant taxonomy in a concise fashion and yet avoid a boring catalogue style is a difficult task in which Professor V. H. Heywood has succeeded admirably. The second edition of his little book, Plant Taxonomy, which has been brought entirely up to date, is an easily accessible introduction for students beginning their studies. It will certainly be a stimulus to the study of the subject in greater detail with the aid of more comprehensive textbooks. Some basic principles and a number of essential terms are explained. However, I greatly appreciate the fact that the emphasis has been placed on problems and methods rather than on descriptive text. It is a pleasure to recommend this little book to students of plant taxonomy.

Gunnar Weimarck

John, B. 1976: *Population cytogenetics.* Studies in Biology 70. 76 pp. Edward Arnold, London. ISBN 0-7131-2597-7. Price £ 1.50.

It is essential for a taxonomist to be familiar with variation and its causes at a level below that at which he is working. There is now a growing interest in population genetics among those who study taxonomy at the specific or subspecific level.

Chromosomes are doubly interesting in this context. Not only do they function as markers morphologically when they vary in number and structure, but as they contain genetic information they also play a functional part in the interplay between breeding individuals. Variation in the chromosome system may therefore affect variation in many respects at the populational level and may decisively effect the course of evolution.

Professor Bernard John is an expert on population cytogenetics and has produced a most interesting introduction to this topic. It is also of interest to the researcher. Variation in the organization, structure and number of chromosomes is intelligibly described and its effects on population structure accounted for by means of selected illustrative examples. A short section is devoted to the cytogenetics of speciation.

The number of typographic errors is, regrettably, far too high to be ignored. Some of them are disturbing, a few even ridiculous. The figure on p. 41 must surely have met with an accident. I do hope that in forthcoming editions these errors will be eliminated so that the positive impression the book makes will not be spoilt.

Gunnar Weimarck

Hilliard, O. M. 1977: *Compositae in Natal.* 659 pp., 25 figs. University of Natal Press, P O Box 375, 3201 Pietermaritzburg, South Africa. ISBN 0 86980 088 4. Price (cloth) R 24:–.

The floral richness of the Cape has led many a botanist to forget Natal, the easternmost province of South Africa. Nevertheless, with the high Drakensberg mountains on the Lesotho border and the grasslands which slope down to the coast of the Indian Ocean, Natal houses about 5000 species of flowering plants. Approximately 12 per cent of these belong to the Compositae, which is thus the largest family present. This book contains keys and descriptions for all the 640 species, distributed among 113 genera. This work represents a great step towards the completion of the Compositae volume of the 'Flora of Southern Africa', which is otherwise progressing deplorably slowly. The uninformed reader might suspect that this book is a mere compilation of results from earlier floras and revisions. On the contrary, it is the outcome of Dr Hilliard's own extensive research on this family over many years. It is obvious that the author herself is very familiar with both the living and herbarium material of the Natal Compositae.

There is a single key to all the genera as well as a key to the separate tribes, followed by keys to the genera within each tribe. Those who already have some experience of the family will generally recognize the tribes and may thus be able to go straight-away to the tribal keys. Otherwise there is the key to all the genera. However, this runs to over 13 pages in length and will inevitably be time-consuming. There are also two long generic keys to the species of *Helichrysum* and *Senecio,* with nearly 125 species each. I have tested these keys on my own collections of Natal Compositae, especially *Helichrysum.* The keys work very well and generally there is no uncertainty when deciding between the alternatives. Related species have been brought together in the key and references are given to the notes and descriptions of those species that are difficult to key out.

The descriptions are concise, yet sufficiently informative. The author's extensive field experience vouches for distinct habit descriptions. This compensates to some extent for the scarcity of illustrations. The habit of about 20 species only are illustrated. Unjustly, this lack makes the book seem dull and stodgy.

The text is offset-printed from the original typescript, with its rather uneven right-hand margin. Names and synonyms are printed in boldface and italics. With the exception of the uneven margin, I have no objections to this printing method, which I suppose will be used more and more frequently for books in the future.

Kåre Bremer

Thomas, E. & Davey, M. R. 1975: *From single cells to plants.* 171 pp. Wykeham Publications (London) Ltd, London and Winchester. ISBN 0-85109-041-9 (paper), ISBN 0-85109-520-8 (cloth). Price £ 3.25 (cloth), £ 2.50 (paper).

The Wykeham Science Series consists of textbooks at a not-too-advanced university level. A novel feature is the intentionally pedagogic approach to the subject, and for this purpose the scientific author has been assisted by an experienced schoolmaster. The present book on plant tissue culture is a good example of the fruitfulness of this approach.

The totipotency of differentiated plant cells was postulated almost one and a half century ago but experiments were not successful until the 20s, and only during the last few decades has technique developed rapidly. The historical background of problems and methods is outlined in the first chapter. The second chapter is devoted to a rather comprehensive presentation of basic materials and methods. Culture mediums and schedules are given in an appendix. The rest of the book describes the culture of plant organs, vegetative and reproductive cells and protoplasts, and morphogenesis in cell cultures. The prospects for tissue culture research are also dealt with. The system of headings and subheadings makes the book very easy to read, and the main points are clearly summarized at the end of each chapter. The illustrations are abundant and informative.

Admittedly the main applications of plant tissue culture are at present in the fields of physiology and biochemistry. However, great achievements have also been made in plant breeding, and cytogenetics, morphology and systematics certainly gain, too, from adopting suitable tissue culture techniques. Embryo culture has long been employed to facilitate the production of certain hybrids, and promising results have recently been obtained from raising plants from protoplasts hybridized in vitro. The genetic analysis of plants has in many cases been made possible through raising haploids from pollen grains. Tissue culture will probably yield much information that is otherwise difficult or impossible to obtain.

It is to be hoped that the book by Thomas and Davey will also stimulate the employment of tissue culture techniques for taxonomic purposes.

Anna Weimarck