On the genus Pyxidiophora sensu lato (Pyrenomycetes)

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The genera *Treleasia* Speg., *Mycorhynchus* sacc., *Copranophilus* Speg., *Ascolanthanus* Caill., and *Acariniola* Maj. & Wiśn. are considered congeneric with the earlier monotypic *Pyxidiophora* Bref. & Tav. *Mycorhynchidium* Mall. & Cain is transferred from the Hypocreaceae to the family Pyxidiophoraceae G. Arnold emend. Lundq., which will thus contain two accepted genera. The nomenclature of *P. asterophora* (Tul.) Lindau, the type species of *Pyxidiophora*, is analysed, and the specific name is lectotypified. The following combinations are new: *Pyxidiophora arvernensis* (Bret. & Faur.), *P. bainemensis* (Bret. & Faur.), *P. caulicola* (Hawksw. & Webst.), *P. fusco-olivacea* (G. Arnold), *P. grovei* (Hawksw. & Webst.), *P. marchalii* (Sacc. & March.), *P. microspora* (Hawksw. & Webst.), *P. moseri* (Maj. & Wiśn.), *P. petchii* (Bret. & Faur.), *P. schotterianus* (Bret. & Faur.), *P. spinuliformis* (Speg.), and *P. subbasalipunctata* (Maj. & Wiśn.). *Ascolanthanus trisporus* Caill. is considered a synonym of *P. spinuliformis*. *P. badiorostris* Lundq., on cow dung from Sweden, is new to science, and *P. arvernensis* and *P. grovei* are reported as new to northern Europe. A *Chalara* state has been found in the two latter species.

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A recent study on the pyrenomycete genus *Mycorhynchus* Sacc. by Hawksworth & Webster (1977) has inspired me to present the Swedish records of three species, material that has been filed in my herbarium since long. The known species of the genus are seldom collected and investigated because of their rarity, smallness, and the short duration of their fruit-bodies. Most of them have been described as new by Breton & Faurel (1968) and by Hawksworth & Webster (1977). These authors also discuss the generic taxonomy and came to the conclusion that *Treleasia* Speg., *Rhynchonectria* Höhn. (≡ *Eleutherosphaera* Grove), and *Ascolanthanus* Caill. are related to *Mycorhynchus*, and that *Copranophilus* Speg. should be taken as a synonym of it.

I soon became aware that also the forgotten *Pyxidiophora* Bref. & Tav., a genus not treated by the above-mentioned authors, had to be taken into consideration; it seemed hardly distinct from *Mycorhynchus* and the generic name is older than any of those relevant here. I shall comment upon these genera, but first it is necessary to discuss the nomenclature of the type species of *Pyxidiophora* and its supposed connection to *Artotrogus asterophorus* Fr. and *Asterophora* Ditm. ex Fr.

The nomenclature of Pyxidiophora asterophora

The monotypic genus *Pyxidiophora* was established by Brefeld & von Tavel (1891 p. 188) for a pyrenomycete and its phialidic conidial state parasitizing the parasitic agaric *Asterophora lycoperdoides* (Bull. ex Mérat) S. F. Gray (≡ *Nyctalis lyc.*). They called this pyrenomycete *P. nyctalidis*, but were not the first to describe it. The Tulasne brothers, to whom they referred, gave in 1865 an excellent description and illustration of it under the name *Hypomyces asterophorus* Tul. (Fig. 1). However, the Tulasnes believed that the star-like chlamydospores that are so abundant on the pileus of *Asterophora* belong to the pyrenomycete, which thus was supposed to possess two conidial states.

The Tulasnes never intended to describe a new species. They referred to their first publication

on the subject (Tulasne & Tulasne 1860), where the parasite is called "*Hypomyces asterophorus* (Fr.) Tul.", and to a species named *Artotrogus asterophorus* Fr. by Fries (1849 p. 497). *Artotrogus* Mont. was originally a monotypic genus erected for *A. hydnosporus* Mont. (Berkeley 1845), an oomycete belonging to *Pythium* and found on various dicotyledonous plants. Butler (1907 p. 100) and Middleton (1943 p. 127) have surveyed the intricate story of the discovery of this organism. The echinulate oogonia of *A. hydnosporus* apparently made Fries believe in a relationship between this species regarded as a parasite and *A. asterophorus*, after he had abandoned his earlier conviction (1829 p. 205, 1838 p. 371) that the chlamydospores were part of the agaric (or gasteromycete or whatever he considered it to be).

The status of the name *Pyxidiophora nyctalidis* depends on the typification of *A. asterophorus* and on Art. 59 of the Botanical Code of Nomenclature (Stafleu et al. 1978). Fries (1849) gave no specific diagnosis of his species, only the following references: "Asteroph. Dittm. p.p. Cord. IV. f. 24". The *Asterophora* story was given an ample account by Buller (1924) and Corner (1966), and shall not be repeated here. There has also been some discussion whether Ditmar's genus is anamorphic or teleomorphic. The generic name was validated by Fries in 1821 (not in 1829, as is generally thought), and although no species was mentioned at the time, the genus was monotypic by direct and indirect citation of pre-starting point authors, who mentioned one species only, *Agaricus lycoperdoides* Bull. All these authors described lamellae, i.e. "organs which bear basidia" (Art. 59.1), which makes *Asterophora* a teleomorphic genus. However, this conclusion has been questioned, and the two conflicting views were presented by, i.a., Donk (1964) and Singer (1975 p. 224), respectively. Examples of how the two interpretations affect the nomenclature of *A. asterophorus* are given below.

Artotrogus asterophorus Fr.

The first alternative is Singer's view, viz. that *Asterophora* is a teleomorphic genus. When Fries changed his mind in 1849 about the nature of the chlamydospores he was undoubtedly influenced by Corda (1840), whom he cited. Corda restricted *Asterophora* to the imperfect state, claiming his new species *Ast. agaricicola* to be a parasite on the agaric. He also gave the following citation: "(Asterophora agaricoides Fries l.c. [Syst. Mycol.] III. p. 205 A. lycoperdoides Dittmar l.c. Taf. 26? Nees Syst. II. Fig. 114?)". But none of these references are relevant for the typification of *Ast. agaricicola* as Corda never used parentheses for what he considered true synonyms of other species dealt with in the same work, and, besides, he questioned two of the references. Fries's citation of Corda binds *Art. asterophorus* to *Ast. agaricicola*, the only species included in the genus by this author, and his pro parte reference to Ditmar's *Asterophora* points naturally also to the chlamydosporic state.

However, Corda's account is incorrect according to Article 59, as he adopted the name of a perfect state genus for an imperfect fungus, which makes *Ast. agaricicola* a validly published but illegitimate name. Fries was thus entitled to make a new name for the chlamydosporic state, and *Art. asterophorus* must be typified by Corda's material, if such exists. From this follows, too, that all combinations based on Fries's epithet are referable to the anamorph only. It should be added that *Artotrogus*, although being a name of a teleomorphic genus, does not threaten *Art. asterophorus* as a legitimate name of an imperfect fungus, because pleomorphic oomycetes are not covered by Article 59.

If we now try the second alternative, that *Asterophora* is the name of an imperfect state genus, Article 59 is not applicable. *Ast. agaricicola* is then a legitimate but incorrect name being a younger taxonomic synonym of *Ast. lycoperdoides*. The names *Art. asterophorus* and *Ast. agaricicola* are accordingly no longer connected to each other because Fries's reference to Ditmar now takes precedence. *Art. asterophorus* becomes a superfluous name for *Ast. lycoperdoides*, and all combinations with the epithet also become illegitimate.

The conclusion of this analysis is that whichever application we give to *Asterophora*, *Art. asterophorus* is the name of an imperfect fungus. Thus a full study of the nomenclature of *Asterophora* is irrelevant here, since it has no bearing on the typification of *Hypomyces asterophorus* or *Pyxidiophora nyctalidis*. Nor have I had reason to search for the correct name of the chla-

mydosporic state. Finally, it should be mentioned that the name *Nyctalis asterophora* Fr. (Fries 1838), a superfluous name for *Ast. lycoperdoides*, has no nomenclatural connection to *Art. asterophorus* Fr. (Fries 1849).

Hypomyces asterophorus sensu Tul. — Fig. 1

We must now clarify whether *Hypomyces asterophorus* (Fr.) Tul. (Tulasne & Tulasne 1860) was published as a new combination or as the name of a new species. Plowright (1882), Lindau (1897), Maire (1911), and Müller & von Arx (1962) took it for granted that the name should be applied to the pyrenomycete and attributed to the Tulasnes, whereas Winter (1885) maintained that a new epithet should be coined, a name change actually made by Brefeld & von Tavel (1891).

We depend again upon Art. 59 (last paragraph), which means that the combination must be rejected and that the epithet *asterophorus* must be adopted for a new species with a new type and be credited to the Tulasnes alone. The inclusion in their description of the chlamydosporic state of *Asterophora* is of no importance, as the specific name in its new position is fixed to the teleomorph of the pyrenomycete. This solution had not been possible if *Art. asterophorus* were the name of a teleomorphic species, in which case the type of the name *H. asterophorus* (Fr.) Tul. would have been that of its basionym, and the pyrenomycete, accordingly, would have to be given another name.

Pyxidiophora nyctalidis Bref. & Tav. — Fig. 2

Brefeld & von Tavel (1891) had a clear concept of this fungus. They managed to grow it in culture, and proved that the phialidic anamorph with catenate conidia was beyond doubt associated with the perithecia. Brefeld (1889) had earlier confirmed by cultural work an old experiment by Krombholz (1831) showing the connection between the chlamydospores and *Asterophora*. Because of the particular conidial state, the simple structure of the perithecia, and the absence of a stroma, Brefeld & von Tavel classified the pyrenomycete in a genus of its own, a correct step in my opinion, although their descriptio generico-specifica does not quite suffice to modern standards. They also created the new name *Pyxidiophora nyctalidis* for the pyrenomycete, and deliberately excluded the chlamydosporic state. This was logical but redundant according to our present rules, as they cited the Tulasnes, and thus made *P. nyctalidis* a superfluous name for *Hypomyces asterophorus* Tul. (Art. 63).

It is possible, however, that the solution given here will not be final. Art. 59 is now debated more than ever and there is a two-alternative proposal by an I.M.A. Subcommittee (Warmelo 1979) to change the Article to the effect that any combination of names between imperfect and perfect states shall be considered validly published and legitimate. According to one model there would be, however, possibilities for exceptions when new forms are introduced with "wrong" citations. Pertinent references and indications of comb. nov. or nom. nov. would be regarded as formal errors. This model does not change the situation of *H. asterophorus* as presented here.

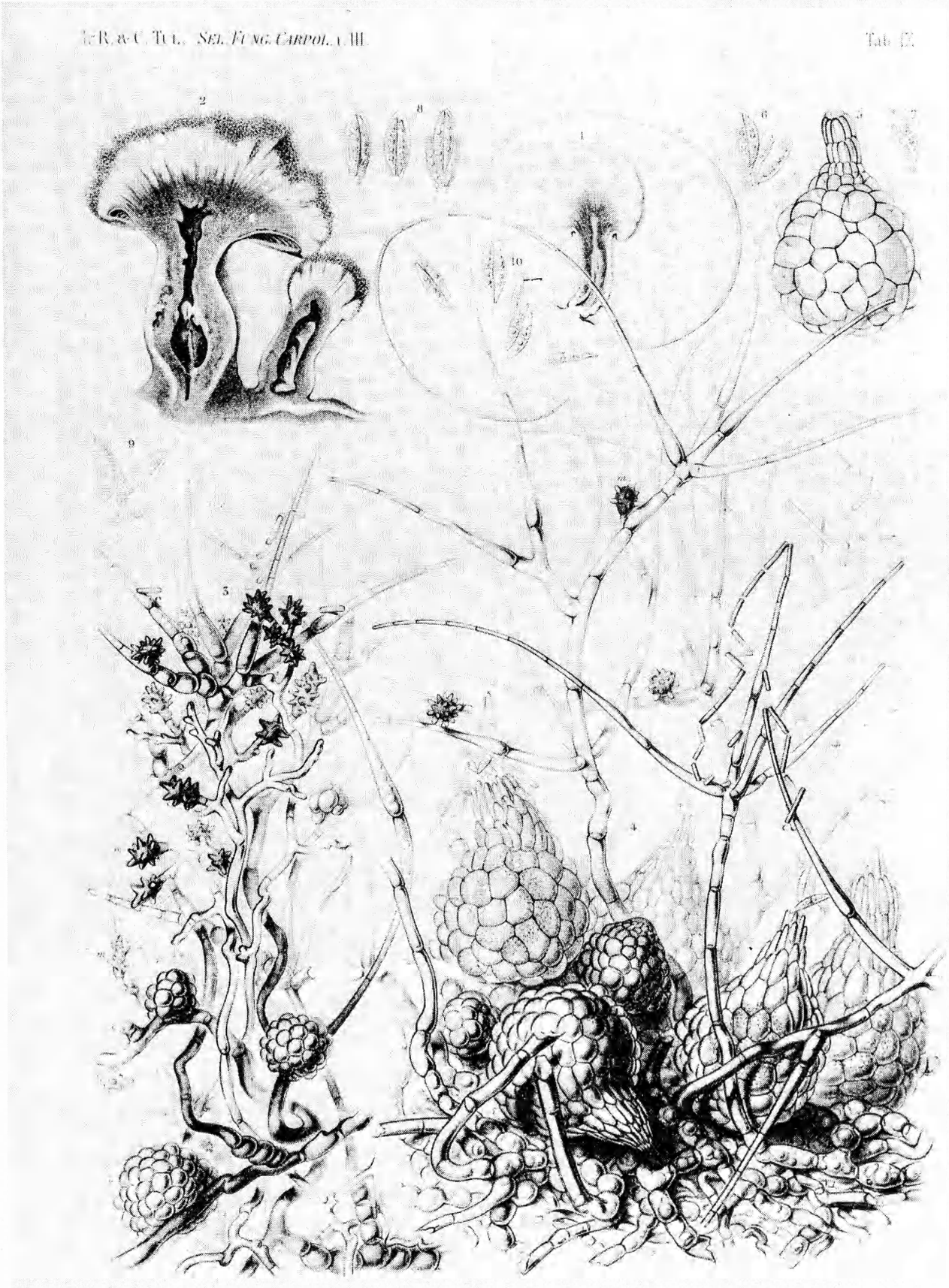
But the other alternative allows no such exceptions, and the typifications of all binomials published as combinations shall strictly follow Art. 55. If this version will be sanctioned by the XIII International Botanical Congress 1981, the name *P. nyctalidis* will become the correct name of the pyrenomycete, as Brefeld & von Tavel explicitly excluded the chlamydosporic state.

A comparison between Pyxidiophora and Mycorhynchus

It is evident already from earlier descriptions that these two genera are morphologically strikingly similar. Characters in common are the small, light-coloured, long-necked perithecia, the peridial structure with ± isodiametric cells below and elongate cells in the neck, the absence of paraphyses, the deliquescence of the asci, the low number of spores per ascus (2–6), and the hyaline, septate, ± fusiform spores usually arranged in a parallel manner. None of the authors who have studied these genera has thought of comparing them with each other, except perhaps Arnold (1972 a), who placed them in his new family Pyxidiophoraceae, but without further comment. It is possible that the parasitic habit and the presence of a conidial state in *Pyxidiophora asterophora* was considered features alien to *Mycorhynchus*.

The spores

The Tulasnes' and Brefeld's drawings of the



HYPOMYCES asterophorus Tul.

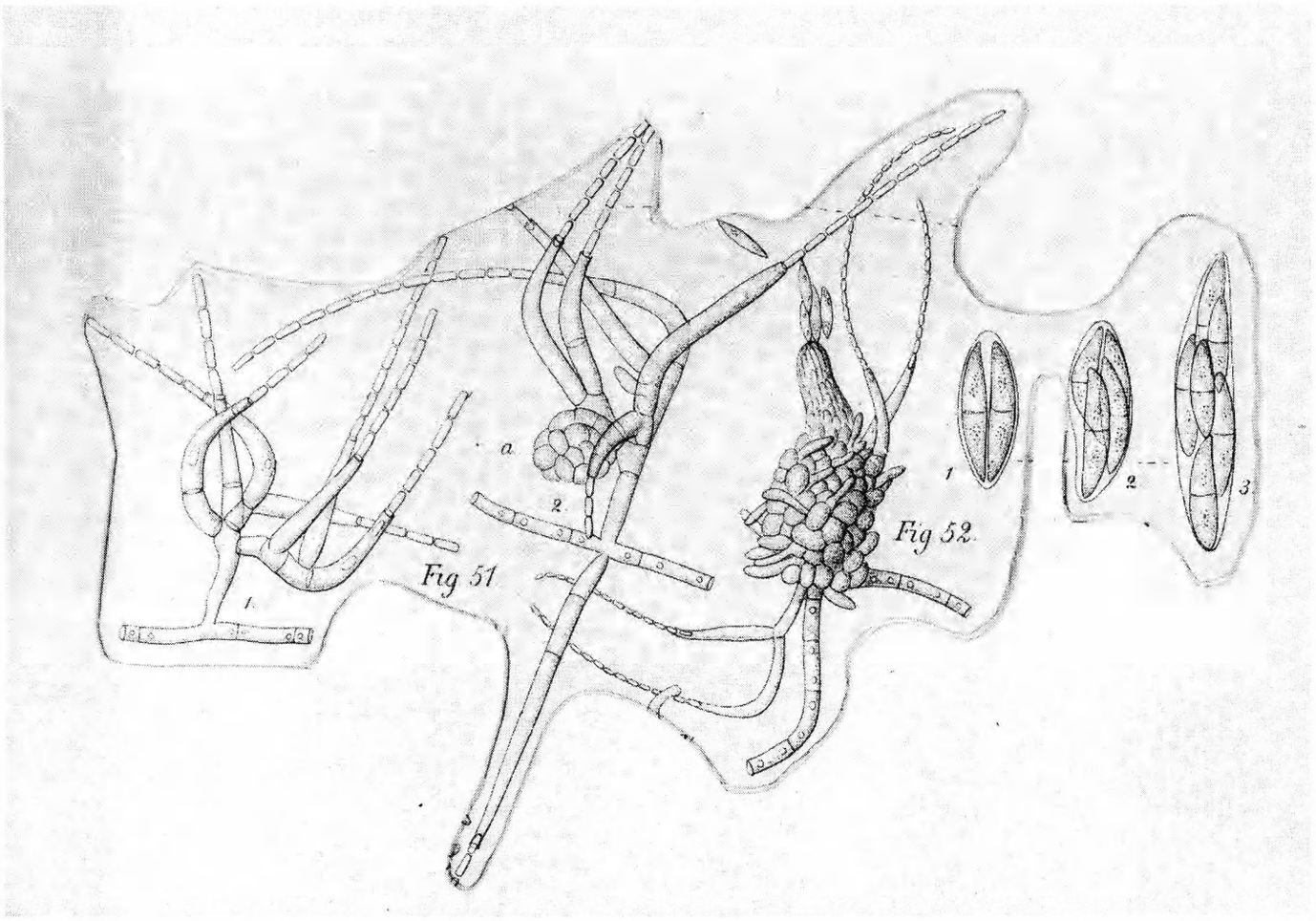
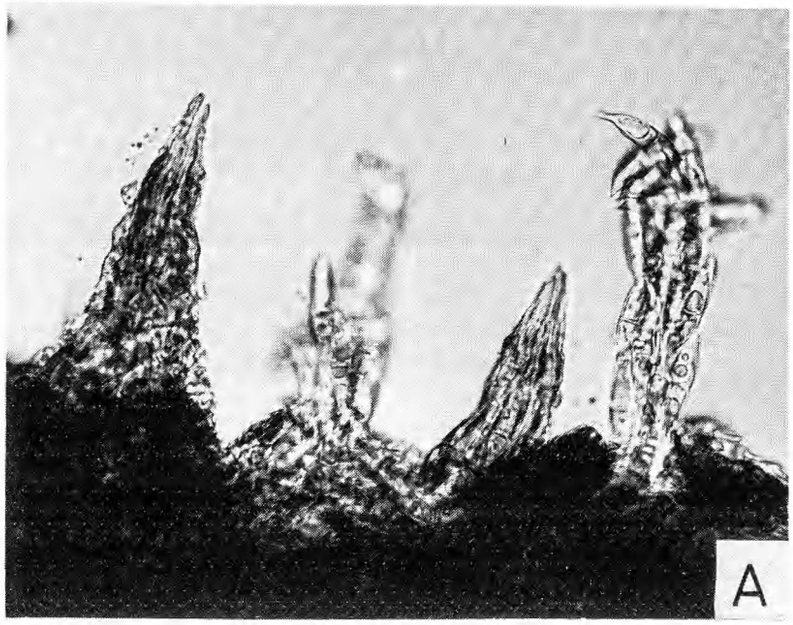


Fig. 2. *Pyxidiophora nyctalidis* (after Brefeld & von Tavel 1891) and its phialidic *Chalara* state; perithecia, asci, and ascospores to the right.

species do not show distinctly the elongate spore base characteristic of *Mycorhynchus*, although the former authors described the spores as mucronate at each end. However, it appears from the illustrations by Maire (1911) and Müller & von Arx (1962), which are founded on authentic specimens, that at least the base of the spores is drawn out. Maire's figure also shows an apical outgrowth caused by a thickening of the wall, but there is no indication that the spore wall inflates laterally as in most *Mycorhynchi*. I have examined this material in PC and ZT (see further discussion under *P. asterophora*). In the PC sample numerous loose ascospores and remnants of perithecia were found. The ZT collection contains intact perithecia and spores. In no case were asci seen.

The spores are 25–29×5–5.5 μm, ± fusiform with a pointed base and a more obtuse apex, both formed by a thickening of the wall, and staining with cotton blue; the rest of the spore wall is fairly thick, but not inflated. The shape is more asymmetric than is evident from earlier illustrations; the spores may be flat on one side and rounded on the other, sometimes bent and boomerang-like, even slightly sigmoid, but regular in ventral view. The young spores are one-celled, filled with small oil drops, then transversely septate in the middle late in their development. The protoplast is c. 15×5 μm,

Fig. 1. *Hypomyces asterophorus* (after Tulasne & Tulasne 1865). Fruit-bodies and chlamydospores of the agaric *Asterophorus lycoperdoides* to the left; perithecia, asci, ascospores, and a phialidic *Chalara* state of *H. asterophorus* to the right. both conidial states are somewhat intermingled on the figure, since the Tulasnes thought them to belong to one and the same species, the pyrenomycete.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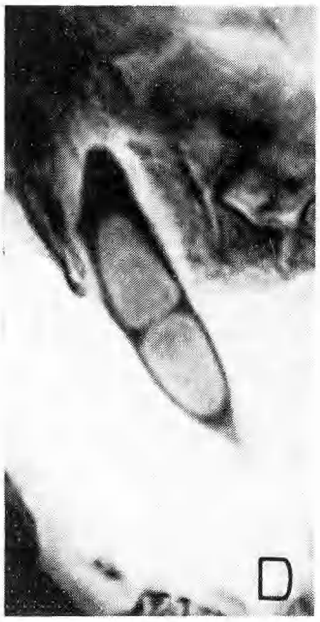
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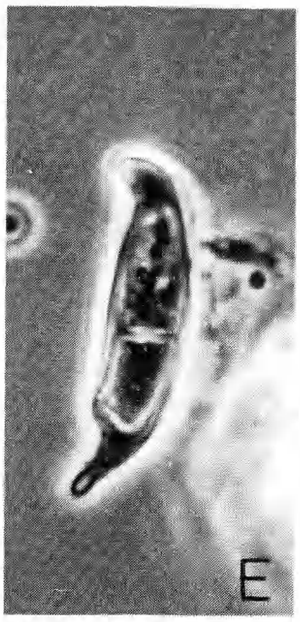
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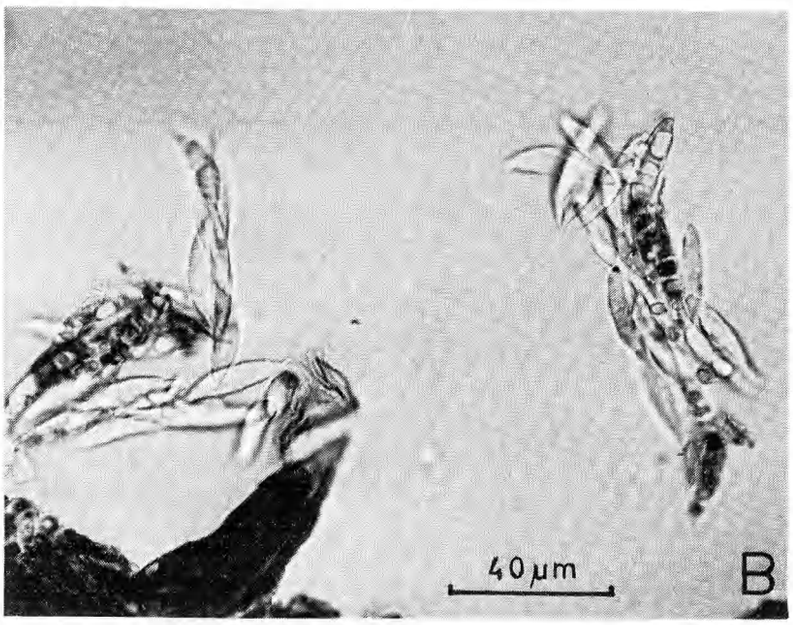
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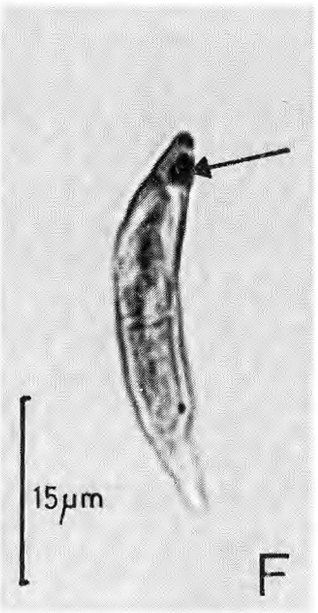
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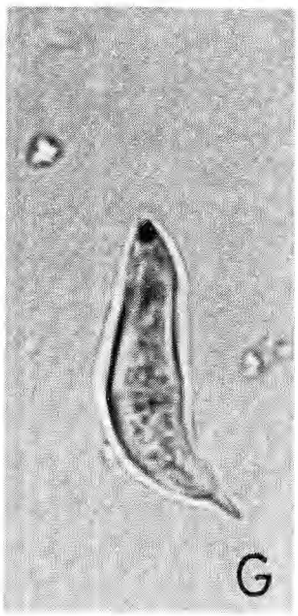
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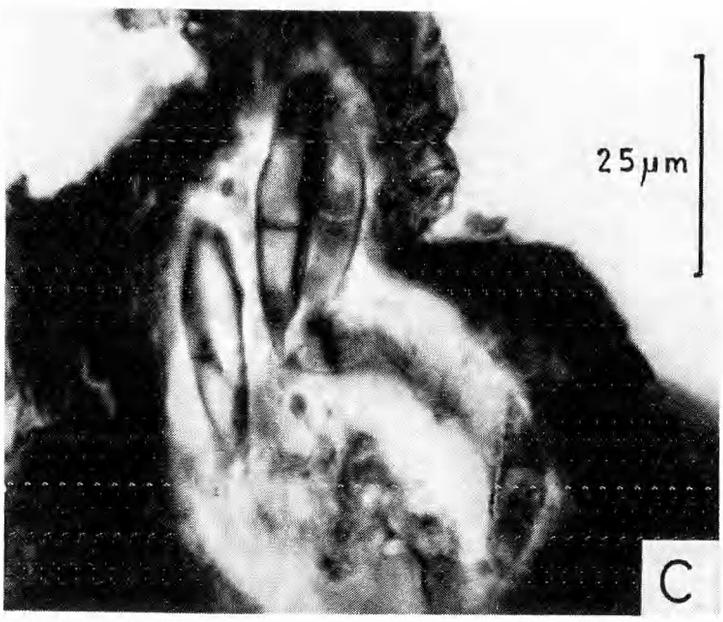
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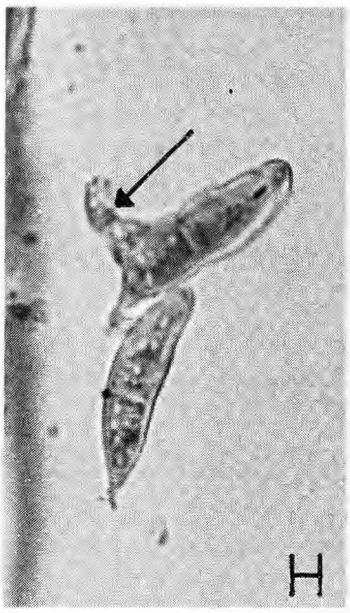
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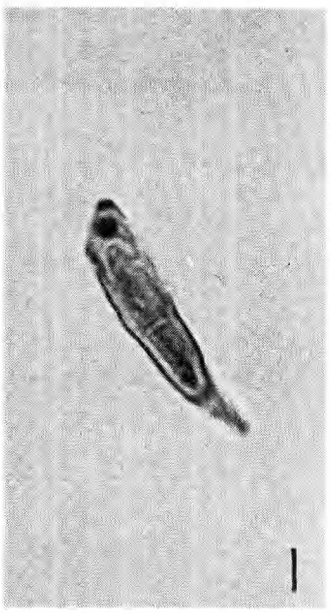

I

usually with rounded ends. Mature spores often contain a couple of large oil drops, and do not usually stain with cotton blue. The most remarkable discovery is that many spores are provided with a brown, apical or subapical spot in the wall of exactly the same kind as in *Mycorhynchus* (see below). In one spore even two spots were observed (Fig. 3).

It is difficult to find any fundamental differences in spore morphology (or perithecial structure) between *Pyxidiophora* and *Mycorhynchus*. In the latter genus the species are distinguished in the main by different size and form of the perithecia, peridial cells, and spores, form of the protoplast, occurrence of the pigmented spot in the spores, sometimes spore number, and number and position of the sporal septa. Even the pigmentation and the septation may sometimes vary *within* the species, the former feature being particularly capricious. The fact that the spore wall in *P. asterophora* does not gelatinize and swell laterally is probably of no more than specific value. This detail remains to be investigated more thoroughly on living *Mycorhynchus* spp., where in some cases a lateral inflation seems only little marked.

The asci

Both *Pyxidiophora* and *Mycorhynchus* have early deliquescing, ± ellipsoidal asci with a few spores at about the same level. An apical apparatus is not known in the *Mycorhynchi*, but Müller & von Arx (1962) and Parguey-Leduc (1977, quoting from Durand 1964) have described and illustrated a thickened, refractive apical ring with a narrow pore in *P. asterophora*. No other author seems to have noticed this ring, not even such keen observers as Brefeld and the Tulasnes. Neither have I seen it; in fact, there is not a trace of asci in the material investigated by me, which also includes sectioned perithecia full of spores. Apparently intact asci can be seen only in young, living fungi.

Oddly enough, the ZT collection, which obviously was studied by Brefeld, is the one on which Müller & von Arx discovered the ring. Dr Emil Müller in Zürich has informed me (in litt.) that the two asci on his illustration are the only ones that were found. As far as he can remember there was an apical ring, but not quite as distinct as appears from his drawing.

I have not been able to contact Miss Françoise Durand, who left science some years ago, but Dr Agnès Parguey-Leduc in Paris has kindly commented on the subject (in litt.) and also sent me some excerpts from Durand's unpublished paper (drawings and legends). Durand sectioned young, living perithecia and examined the ascus cytology on material stained with trypan blue and iron hematoxylin-eosin. She states that the apical ring is far from being constant, and when present, it is in the form of "deux masses claires, arrondies, symétriquement disposées et fixées à la paroi ascale". She did not investigate whether it was chitinoid or amyloid, but noticed that it stained more or less with trypan blue. According to Dr Parguey-Leduc, the material on Durand's microscopic slides has now totally deteriorated.

It is thus proved that *P. asterophora* at an early stage possesses some kind of non-functional ring. It seems to be indistinct and evanescent, which explains why so few mycologists have seen it. In my opinion the ephemerality of this apical apparatus disqualifies it as a generic character versus *Mycorhynchus*.

Müller & von Arx have also depicted an elongate ascus with five 2–3-seriate spores, and a similar phenomenon was illustrated by Brefeld & von Tavel (1891 Fig. 52: 3). It is possible that with a larger number of spores per ascus the asci may elongate further. When liberated from the asci, the spores adhere to one another in various numbers and combinations (Fig. 3 A, B). In Durand's material the asci are 8-nucleate, but only three spores per ascus developed and they were all arranged at the same level when full-grown.

Fig. 3. *Pyxidiophora asterophora*. A–D: *Pyxidiophora nyctalidis* from Herb. von Tavel (ZT). — E–I: *Hypomyces asterophorus* from Herb. Tulasne (PC, lectotype). Material in lactic blue and water (A). Fig. E taken in phase contrast. — A, B: Perithecia and aggregations of discharged spores. — C: Vertical section of perithecium with spores; note the orientation of the spores with their broad end directed upwards. — D–I: Spores; note the rounded ends of the protoplast in D, E, the pigmented spot in F, G, I (arrow), and the germ hypha in H (arrow). Scales: A = B; D, E, G = F; H, I = C.

Other characters

The parasitism and the presence of a conidial state in *P. asterophora* are certainly not more than specific characters. The habitat is not exclusive compared to the ecological range in *Mycorhynchus*. *Treleasia sacchari* Speg., which is reported from sugar cane leaves and belongs either in *Pyxidiophora* or *Mycorhynchus*, may be a parasite, too. *M. caulicola* Hawksw. & Webst. and *M. petchii* Bret. & Faur. are saprobes on rotten herbaceous stalks, and *M. brunneo-capitatus* Hawksw. & Webst. on polypores. "*Rhynchonectria longispora*" sensu Grove inhabits, i.a., myxomycete plasmodia, and two or three species are supposed to grow in bark beetle galleries (see discussion under *Acariniola*). The remaining species are coprophilous.

Unfortunately the anamorph was absent from the samples of *P. asterophora* studied by me. According to descriptions and illustrations it is a brownish *Chalara* with lageniform phialides and cylindrical to ellipsoidal, one-celled, hyaline conidia, 7–10×3 μm. Conidial states were thought to be missing in *Mycorhynchus*, but do exist in four other species, and are similar to that of *Pyxidiophora* (see discussion under *Ascolanthanus, Copranophilus, Pyxidiophora arvernensis*, and *P. grovei*).

Conclusion

The foregoing account shows the difficulty in separating the two genera. Admittedly, *P. asterophora* exhibits a combination of characters not observed in typical *Mycorhynchus* species, but they are not sufficient for a generic distinction.

Other supposedly related genera

The emended circumscription of *Pyxidiophora* demands a renewed scrutiny of other genera considered as related to *Mycorhynchus*. The amplest survey was given by Breton & Faurel (1968), on which some additional comments shall be made.

Treleasia Speg. 1896

Specimens of the type species, *T. sacchari* Speg., are no longer present in Spegazzini's herbarium (LPS), which has been verified by at least four mycologists. To judge from Spegazzini's original sketch of the species, published by Petrak & Sydow (1935), *Treleasia* stands very close to *Mycorhynchus* in the old sense. The spores are said to be, i.a., fusiform, straight, and uniseptate in the middle. Breton & Faurel rated the sporal differences between the genera highly, stressing the symmetry and acute ends of the *Treleasia* spores in contrast to the asymmetrical, subclaviform spores in *Mycorhynchus*. There is, however, a hitch in this comparison. One has to distinguish between the shape of the protoplast and the form of the whole spore after the swelling of the wall. Several *Pyxidiophorae* have fusiform, more or less symmetrical protoplasts very similar to the spores of *T. sacchari*. The pertinent question is whether Spegazzini's description and drawing are accurate, or if he disregarded or failed to observe a thickened spore wall. With the wide circumscription adopted for *Pyxidiophora* here, *Treleasia* falls within it, and his concept is of little importance. However, if *Pyxidiophora* and *Mycorhynchus* are kept as separate genera, it is hardly possible to tell which one is congeneric with *Treleasia* as long as *T. sacchari* has not been found and restudied. Moreover, Spegazzini's description and figure of 8-spored asci may be a misinterpretation of a discharged spore cluster (Petch 1936).

Rhynchonectria Höhn. 1902

No material is left at K of the monotype, the fungicolous *R. longispora* (Phill. & Plowr.) Höhn. (Petch 1941). The discussion on the relationship between *Rhynchonectria* and *Mycorhynchus* has been totally focussed on interpretations of the *Rhynchonectria* spores, which are said to be, i.a., fusiform, one-septate, and appendaged at both ends. Some authors merge the genera, others keep them apart (e.g. Hawksworth & Webster 1977). Further speculations on the nature of these spores are certainly fruitless until the type species has been found again and examined. Other, neglected characters may be equally important. The long and relatively narrow asci (130–150×20–25 μm) are atypical of *Pyxidiophora* s. lato. I consider *Rhynchonectria* unrelated to this genus.

Ascolanthanus Caill. 1967

The discriminating features of this genus against *Mycorhynchus* are, according to Breton & Faurel (1968 p. 257), a stroma, a conidial state, 3-spored asci, and spores with pigmented girdles and an appendage at both ends. Such criteria are not sufficient to circumscribe genera in this family (p. 133). Three-spored asci, for example, are met with also in *Pyxidiophora badiorostris* n. sp., *P. bainemensis* (Bret. & Faur.) Lundq., and *P. grovei* (Hawksw. & Webst.) Lundq., and apically attenuated spores occur in a number of species of the genus. However, the stroma and the nature of the conidial state may be characters of weight and deserve an analysis.

A. trisporus Caill., the monotype, was collected from three provinces in Spain and four in France. I have examined seven French samples (PC) representing three gatherings:

Seine-et-Oise: Carrières sur Seine. Dried specimens on straw (1), on straw in alcohol (2), and on agar in formalin (3), 20.VII.1956. Montesson. On straw in lactophenol, 31.V.1967 (4), on agar in lactophenol, 12.VI.1967 (5), and on agar in alcohol, 7 & 12.VI.1967 (6). — *Oise*: Saint Gervais near Beauvais. On straw in alcohol-formalin-acetic acid, 21.III.1961 (7). All material was obtained from horse dung.

Only the gatherings from Carrières sur Seine and Montesson belong to the protologue of *A. trisporus*. These localities are situated NW of Paris ("Region parisienne"). Nos. 1 and 2 contain stromata and the imperfect state only, whereas all the others also have perithecia. Specimens with mature, pigmented spores are present on no. 6, and this would be suitable for a possible typification (cf. p. 142).

The agar cultures are not pure, but a mixture of infected dung and agar. Thus some other species are also present, i.a., a *Pyxidiophora* species. This occurs on nos. 3 and 5, where perithecia of *A. trisporus* could not be detected, and also mixed with fruit-bodies of this species on no. 6. Its perithecia are single or aggregated, (200–)230–300×70–95 μm, neck (115–)140–190×27–36 μm, peridial cells 10–19 μm in diam., neck cells 13–33×3.5 μm, spores slender, 38–50 μm long, with a middle septum, a subapical, brown, sometimes hollow, flattened patch, a 25–33×3 μm large protoplast, and a 9–12 μm long basal appendage. Truncate, cylindrical *Chalara* conidia, 9–15×4 μm were found, but no phialides.

My first thought was that this species could be a developmental stage of *A. trisporus*. Although not proved, it is possible that pigmented spores may be produced in immature fruit-bodies. The idea must be abandoned, however, since the differences in perithecia and spores are too great. Besides, *A. trisporus* has ochraceous, large stromata, 1–12 mm in diam. (according to Cailleux), recognizable also when sterile, whereas the *Pyxidiophora* perithecia in question at most form a minute, yellowish subiculum, if any at all.

Apart from no. 6, *A. trisporus* is represented also on nos. 4 and 7 with fructifications. In the two first-mentioned collections the perithecia measure 300–630×90–215 μm with a tapering, broad-based neck, 225–380×50–135 μm, and large neck cells, 17–42×6–10 μm. The spore width is stated to be 6–7 μm, which certainly includes the inflated wall; the protoplast is only 4–5 μm broad. The Saint Gervais specimens are even taller with perithecia up to 690 μm. Cailleux gives unusually low figures for the perithecial width, 40–60 μm, and he might have included the above-mentioned *Pyxidiophora* in his measurements. Even young fruit-bodies of *A. trisporus* are wider than that.

The imperfect state

Fig. 4. The ventricose-rostrate conidiophores, up to 55 μm long, have a few basal septa and produce chains of subcylindrical to narrowly obovoid (not ellipsoidal as in Cailleux's figure), probably holoblastic conidia, 11–17×4–5.5 μm, with conspicuous, mostly deciduous connectives.

The situation is complicated by the occurrence of typical *Chalara* phialides. They grow in fewer numbers on the stromata, mixed with the other kind of conidiophores, and are about the same size, but more regular in form with a cylindrical collarette. The conidia are of a size similar to those mentioned above, strictly cylindrical with truncate ends lacking connectives. Whether this *Chalara* is connected with the *Pyxidiophora* in question or whether *A. trisporus* has two anamorphs, I am unable to decide. Perhaps none of the two imperfects is associated with *A. trisporus*. The non-phialidic anamorph has recently turned up on badger dung from Harparbol, Almunge par., Uppland, Sweden (1.X.1979, Lqt 12415-d, UPS), and it is worth noting that neither

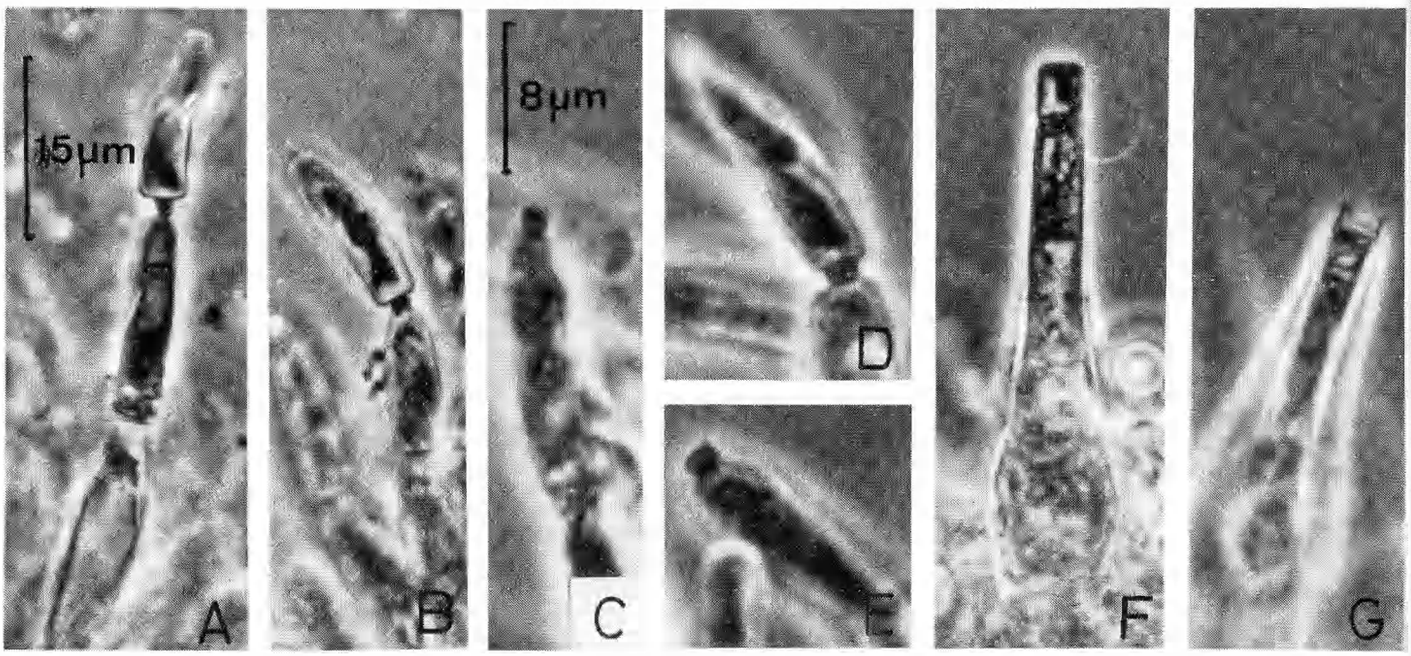


Fig. 4. *Ascolanthanus trisporus* from Carrières sur Seine, France, leg. Cailleux 20.VII.1956 (PC); formalin-preserved specimens on straw. Phase contrast. — A–E: Catenate conidia with tapering apex and distinct connectives; part of conidiophore visible in A. — F, G: *Chalara* phialides with cylindrical, truncate conidia without connectives found mixed with the afore-mentioned state; possibly not belonging to *A. trisporus*. Scales: B, G = A; D, E = C.

Chalara nor any *Pyxidiophora* perithecia could be detected on the material. Single-spore cultures have not yet been made.

When comparing *A. trisporus* with species of *Mycorhynchus, M. spinuliformis* (Speg.) Bret. & Faur. (≡ *Copranophilus s.*) is the first one to be discussed.

Copranophilus Speg. 1909

The generic name has usually been placed in synonymy with *Mycorhynchus*. In 1964 I examined the type collection of *C. spinuliformis* Speg., the monotype (on cow dung from La Plata, XII.1908, LPS 1761), but failed to find any perithecia. Breton & Faurel (1968 p. 232) also searched in vain. Fortunately the description, illustration, and original drawing give a fairly good clue to the morphology of the species. Important information in the protologue seems to have been neglected: "Acervuli subglobosi parvi albo-cinerelli, spinuloso-hirti" and "Acervuli superficiales subglobosi tenelli (3–4 mm diam.); perithecia stromate centrali subgossypinulo dense constipata ...".

These phrases state, in fact, that the species has a 3–4 mm large, whitish, spiny-hairy stroma and that the perithecia are densely aggregated on this stroma. Also Spegazzini's illustration (copied by Breton & Faurel) shows this distinctly. All these features suggest *Ascolanthanus*. On the dried collection of *A. trisporus* mentioned, the masses of conidia form a whitish powder on the stroma, which could correspond to what Spegazzini called "albo-cinerelli". The spinose-hairy surface may allude to the mat of erect conidiophores. There are on the whole very few characters, if any, to separate the two fungi. All measurements correspond roughly to one another in the two descriptions, except that the neck cells in *C. spinuliformis* are somewhat longer, 30–60 µm, the perithecia are said to be "fuscidula" (apart from the hyaline ostiolum), and some peridial cells are "sinuoso-parenchymatico".

A phenomenon emphasized greatly by Breton & Faurel is the upside-down position of the spores in the ascus. As in the *Treleasia* case, I rather believe, as did Petch (1936), that Spegazzini never saw asci. The supposed ascus wall could be the aggregated inflated walls of the outer spores. Besides, when spores have been observed protruding from the perithecial ostiolum in other *Mycorhynchi* (or *Pyxidiophorae*), the broad and/or pigmented end always comes

first (cf. Fig. 3 C). Only one other species has been described with supposedly broad-based spores (Arnold 1972 a), viz. *M. fusco-olivaceus* G. Arnold, but the author is certainly mistaken about the orientation of these spores, as he neither discovered asci nor even mentioned this characteristic when comparing his species with others in the genus.

An intriguing detail on Spegazzini's drawing still remains to be explained: four, one-celled, elongate, hyaline bodies with a tapering end. They were called "éléments indéterminés" by Breton & Faurel, and were not mentioned by Spegazzini, not even in the legend. However, on the sketch kept in LPS 1761 the size is given to 12–15×3 μm. I do not hesitate to interpret these bodies as conidia. They have the same form and size as those of *A. trisporus*. Spegazzini was obviously uncertain about the origin of these conidia, and preferred to ignore them.

The taxonomic value of the stroma is limited as some *Mycorhynchus* spp. are more or less stromatic too. Thus the perithecia of *M. schotterianus* are said to be partly sunk in a soft, parenchymatous stroma. The caulicolous *M. petchii* (= *M. marchalii* sensu Petch) is described to have perithecia "clustered, superficially on, or partly embedded in, a delicate parenchymatous, pale brown stroma, forming subglobose tufts up to 0.5 mm diameter, or smaller and confluent in extended patches" (Petch 1936). Nevertheless, neither of these three authors nor Hawksworth & Webster, who also studied Petch's original specimens, have had any objections to range this fungus among the non-stromatic species of *Mycorhynchus*. In some cases the occurrence of a stroma is not even constant as a specific property (cf. *Pyxidiophora grovei*).

Conclusions

Ascolanthanus and *Copranophilus* are undoubtedly congeneric. Probably also their type species are conspecific, although no pigmentation was found in the spores of *C. spinuliformis*. If the stroma be accepted as a generic character, *Copranophilus* must be maintained for the stromatic species with *Ascolanthanus* as a synonym. In my opinion this is not taxonomically motivated and the genus can be merged with *Mycorhynchus*, i.e. *Pyxidiophora* s. lato. Nor is the peculiar conidial state in *Copranophilus* a convincing argument for generic separation of the perfect state.

Acariniola Maj. & Wiśn. 1978 a—Fig. 5

This genus was established for two Polish species, *A. basalipunctata* Maj. & Wiśn. and *A. subbasalipunctata* Maj. & Wiśn. (the holotype), supposed to be parasites on mites in bark beetle galleries. In the same paper the similar *Thaxteriola moseri* Maj. & Wiśn. is described, also from Poland and with the same ecology. The latter fungus has also been recorded on mites in Louisiana, U.S.A. (Majewski & Wiśniewski 1978 b). All three species were thought to be organisms of unknown taxonomic position, and were placed in the "*Thaxteriolae* group", a name used by Thaxter (1920) for external arthropod parasites resembling Laboulbeniomycetes, and characterized by an elongate, septate, apically tapering thallus with a black foot-cell and by formation of spores in the apical cell.

Majewski & Wiśniewski found that none of the species was confined to any particular host species or sex, or to any special part of the body of the mites, but they were most common on the legs. The thallus is said to be attached to the host by a dark foot, which in *T. moseri* possesses a "penetration pore". In the *Acariniola* species this pore is located near the middle of the thallus in the same cell.

When I saw the illustrations of these fungi I was struck by their extreme similarity to *Pyxidiophora* ascospores. By the courtesy of Dr T. Majewski in Warsaw (WA) I could examine five slides (incl. six paratypes) of the species, and my first impression was confirmed. The hoof-like, dark "foot" of *T. moseri* is a parallel of the pigmented body found in *Ascolanthanus trisporus* (= *Pyxidiophora spinuliformis*) and *Mycorhynchus subspinuliformis* Bret. & Faur. The "penetration pore", whatever function it may have, is present in *P. grovei* too (Fig. 10). A pigmentation in the middle part of the "thallus" is met with in *Mycorhynchus brunneocapitatus* Hawksw. & Webst. as well. The "thalli" often adhere to one another in bundles and with the same orientation as in discharged *Pyxidiophora* spores. The form of the protoplast is similar. The pointed "tip" of the "thalli" does not differ in outline from the basal elongation of the *Pyxidio-*

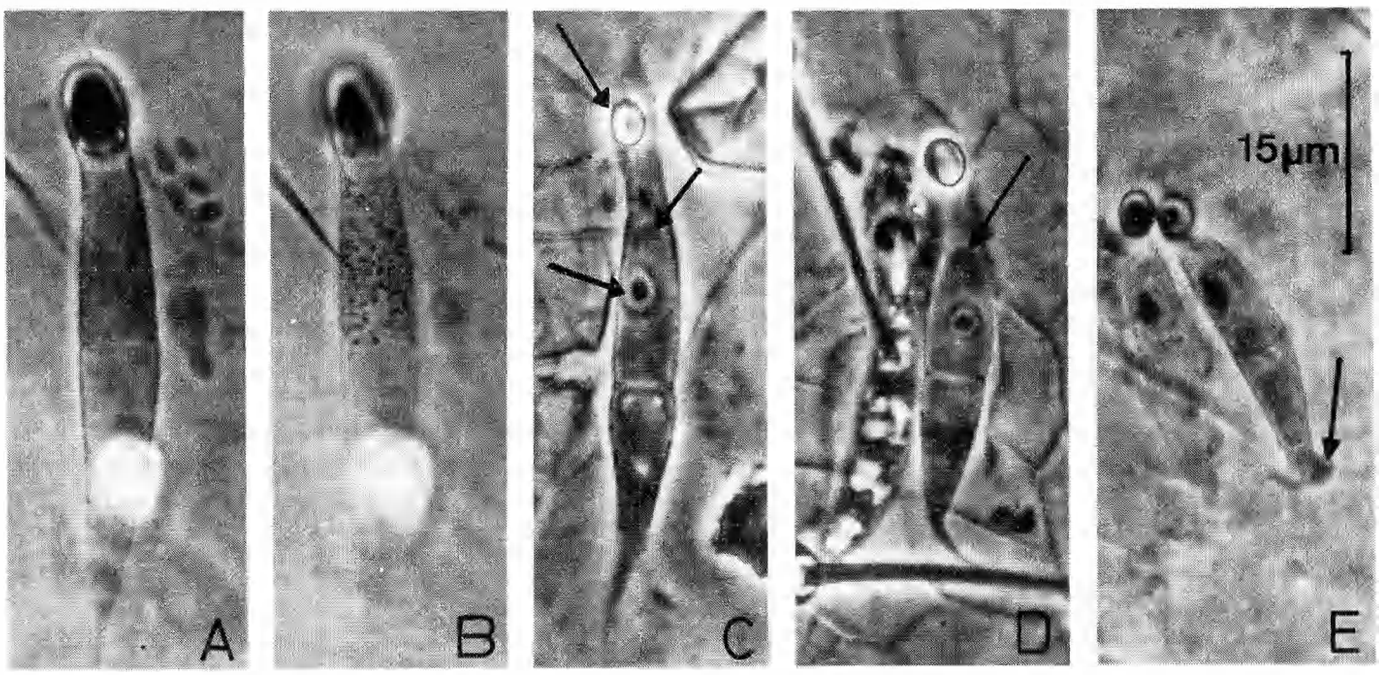


Fig. 5. Spores of *Acariniola* and *"Thaxteriola"* on mites from Zielonka Forest, Poland, leg. Pawlik (WR); specimens in polyvinyl-lactophenol. Phase contrast. — A, B: *"Thaxteriola" moseri* (slide 708); different focussations; the white spot is an artifact. — C, D: *Acariniola subbasalipunctata* (328); note the pigmented spots and the upper limit of the protoplast (arrows). — E: *A. basalipunctata* (140); germ hypha at arrow. Scale: A–D = E.

phora spore. A germinating spore was observed on slide 140 of *A. basalipunctata* (Fig. 5 E) and it looked exactly like the germ hypha illustrated on Fig. 3 H (*P. asterophora*) and Fig. 6 D, 7 (*P. arvernensis* (Bret. & Faur.) Lundq.). The authors' Fig. 3 C (left spore) may show the same phenomenon.

Majewski & Wiśniewski illustrate "thalli" with broken "tips" with diffuse, cytoplasmic globules inside, and postulate that the latter could be spores, but they have not seen such spores with certainty. The small, hyaline, ellipsoidal spores observed here and there on the mites are probably conidia of *Graphium* or ascospores of *Ceratocystis* species that also inhabit bark beetle galleries. The material is not very easy to study because of its treatment for several days in 50°C lactophenol and mounting in polyvinyl lactophenol; some finer details might have disappeared. Thus, a strongly inflated wall, like in most *Pyxidiophora* spores, could not be seen, nor the upper contour of the protoplast in *T. moseri*, not even by phase contrast.

These species apparently form fruit-bodies in the bark beetle galleries. Their slimy spores aggregate at the ostiolum, and become transported by passing mites, probably also by beetles. Such an adaptation explains the higher concentration of spores on the legs of the vectors.

Majewski & Wiśniewski considered the septation an important character, and restricted the three-celled spores to *T. moseri* and the two-celled spores to the *Acariniola* species. Such features are not of generic status in *Pyxidiophora*. A couple of spores of *A. basalipunctata* were even found to have an extra septum near the base. However, *T. moseri* is clearly distinct from the other two by its peculiar, hoof-like, pigmented body (8×5.5 µm) with a pore. The total spore size is 45–50×5.5–6.5 µm (41–54×4.5–6 µm; orig. diagnosis), and the basal elongation c. 5–6 µm. The upper part of the spore is verruculose.

The *Acariniola* species are separated only with difficulty. Their spores have about the same size (*A. basalipunctata*: 34–51×4.5–8 µm; *A. subbasalipunctata*: 24–53×3–7 µm; orig. measurements), a flattened, brown, pore-less, subapical body (4×3×1.5–2 µm; my meas.), and a small, brown ring (2–2.5 µm; my meas.) above the septum. Their basal elongation is 5–11 µm long and their protoplasts resemble each other with the rounded upper tip far below the pigmented body. In *A. basalipunctata* the upper [sic!] cell and in

A. subbasalipunctata the lower [sic!] cell is verruculose, but the other cell may also be partly roughened. The material seen by me is too scarce to allow definite conclusions as to the taxonomy of the *Acariniolae*, particularly as their fruit-bodies are unknown. The two fungi may be conspecific. The names *A. subbasalipunctata* and *T. moseri* are here combined into *Pyxidiophora*, whereas a transfer of *A. basalipunctata* should be postponed pending further studies.

It shall be added that *Thaxteriola* (Spegazzini 1918) is a genus quite unrelated to *Pyxidiophora*.

Dr T. Majewski (in litt.) now shares my opinion about the nature of his species, but prefers not jo join me in the new combinations.

Specimens examined. The WA material was collected by C. Pawlik from the Zielonka Forest near Poznan, Poland, on vectors of *Dendrolaelaps* and *Proctolaelaps* in galleries of *Hylurgus ligniperda* (Fbr.) and *Myelophilus piniperda* (L.) on *Pinus silvestris*. — *A. basalipunctata*: 3.III.1974 (slide 140), 6.IV.1974 (241, on *Dendrolaelaps*; not publ.), 13.V.1974 (364). — *A. subbasalipunctata*: 6.IV.1974 (241), 5.V.1974 (328), 13.V.1974 (364). — *T. moseri*: 13.V.1974 (364), 9.III.1975 (708).

Synopsis

Pyxidiophoraceae G. Arnold 1972 a emend. Lundq.

Pyxidiophora s. lato and its synonyms were referred by earlier authors to either pycnidial fungi or to the Hypocreaceae s. lato. Müller & von Arx (1962), however, placed *Pyxidiophora* s. str. in the Hypomycetaceae, and *Mycorhynchus* in the Hypocreaceae s. str. How these families should be defined will not be treated here. Information on their history and various circumscriptions is given in Rogerson (1970), who accepted only one family in the order, viz. Hypocreaceae. His approach was adopted by Müller & von Arx (1973). A contrasting standpoint was taken by Arnold (1968, 1972 b), who maintained the Hypomycetaceae in a very narrow sense (3–4 genera) and excluded *Pyxidiophora* s. str.

That this genus has been placed in one or other of these families is understandable. The resemblance, particularly to *Hypomyces*, is obvious as regards perithecial colour, spore morphology, habitat, and lack of paraphyses. But the ascal form and structure and manner of spore discharge are different, and the two genera are probably not akin. Even more far-fetched is to place *Pyxidiophora* s. str. among the *Nectriae*, as proposed by Clements & Shear (1931).

The first to realize the exclusiveness of *Pyxidiophora* s. lato was Spegazzini (1909) in a comment on *Copranophilus*: "Genus eximium cum *Treleasia* familiolam *Nectriaceis* nonnihil aberrantem certe constituens". Arnold (1972 a) arrived at the same conclusion, and erected the new family Pyxidiophoraceae for *Pyxidiophora* s. str. and *Mycorhynchus*. He considered it related to the Melanosporaceae because of its deliquescent asci. If this theory be correct, the Pyxidiophoraceae may not even belong to the Hypocreales, as Rogerson (1970) did not include the Melanosporaceae in this order.

Whether the imperfect states could contribute to the family classification here is uncertain. *Chalara* is found in *Pyxidiophora* and one species of *Hypomyces*, but does not seem to occur in *Melanospora* (Tubaki 1958). On the other hand, authorities such as Nag Raj & Kendrick (1975) and Arnold (1972 b) do not mention any connection between *Chalara* and *Hypomyces*. The latter author lists 11 imperfect genera for the Hypomycetaceae and 7 for *Hypomyces*, and claims that the conidial states in question characterize the species only.

As far as is known only two genera constitute the family Pyxidiophoraceae: the type genus in a wide sense and the monotypic *Mycorhynchidium* Mall. & Cain (Malloch & Cain 1971). The latter taxon, which was originally placed in the Hypocreaceae, differs merely by its cleistocarpic state. This feature is given little taxonomic weight by some modern authors, but a generalization is not defendable. In this case I regard the cleistocarpic state as being a good generic criterion. A minor emendation of the family limits is thus necessary:

Non-stromatic or stromatic; ascocarps ostiolate and long-necked or closed, ± light-coloured, membranaceous. Paraphyses lacking. Asci unitunicate, non-amyloid, soon deliquescing. Spores fusiform to clavate to cylindrical, usually basally elongate, with one or a few transverse septa, rarely one-celled, mature hyaline but often ultimately with limited, brown pigmentation, particularly in the upper part. Conidial state hyphomycetous, phialidic and holoblastic (?).

Saprophytic, especially coprophilous, rarely parasitic.

Pyxidiophora Bref. & Tav. emend. Lundq.

Brefeld & von Tavel 1891 p. 188. — Orig. monotype: *P. asterophora* (Tul.) Lindau.

Rhynchomyces Sacc. & March. in March. 1885 p. 60, nom. illeg.; non *Rhynchomyces* Willk. 1866. — *Mycorhynchus* Sacc. in Sacc. & D. Sacc. 1906 p. 418. — Orig. monotype: *R. marchalii* Sacc.

Treleasia Speg. 1896 p. 236. — Orig. monotype: *T. sacchari* Speg.

Copranophilus Speg. 1909 p. 410. — Monotype: *C. spinuliformis* Speg.

Ascolanthanus Caill. 1967 p. 1473. — Monotype: *A. trisporus* Caill. nom. illeg. (not typified) = *Pyxidiophora spinuliformis* (Speg.) Lundq.

Acariniola Maj. & Wiśn. 1978 a p. 7. — Holotype: *A. subbasalipunctata* Maj. & Wiśn.

Perithecia free or partly sunk in a soft, light-coloured stroma or subiculum, hyaline to ochraceous, rarely partly brown, long-necked. *Peridium* pseudoparenchymatous, membranaceous, two-layered, with an outer layer of isodiametric cells below and elongate, cylindrical cells in the neck. *Paraphyses* absent. *Asci*, where observed, subclavate to ellipsoidal, unitunicate, rapidly dissolving, without or rarely with a non-functional apical ring, non-amyloid, 2–3–4(–8?)-spored. *Spores* parallel to one another in the ascus, at maturity aggregating in slimy masses on the ostiolum, subclavate to fusiform or cylindrical, attenuated particularly at the base, 0–4-septate at a late stage, usually with a gelatinized and swelling, smooth or verruculose wall, mature hyaline but often finally with an apical ur subapical, lateral, brown body or with smaller pigmented spots or girdles. Conidial states, where known, phialidic (*Chalara*) and holoblastic (?). — Coprophilous or saprophytic on other substrates, rarely mycoparasitic.

Particular attention should be drawn to the pigmented body of the spores, since it has been allotted a diagnostic value at the specific level (Hawksworth & Webster 1977). The taxonomic importance of this phenomenon seems exaggerated. There may be species in the genus that are unable to develop such a stage, but certainly others that regularly or only sporadically do it. A pigmentation is known in ten or eleven species of *Pyxidiophora*. Its protective function must be practically nil, nor is it connected with the physiological maturation of the spores. It may be an evolutionary whim.

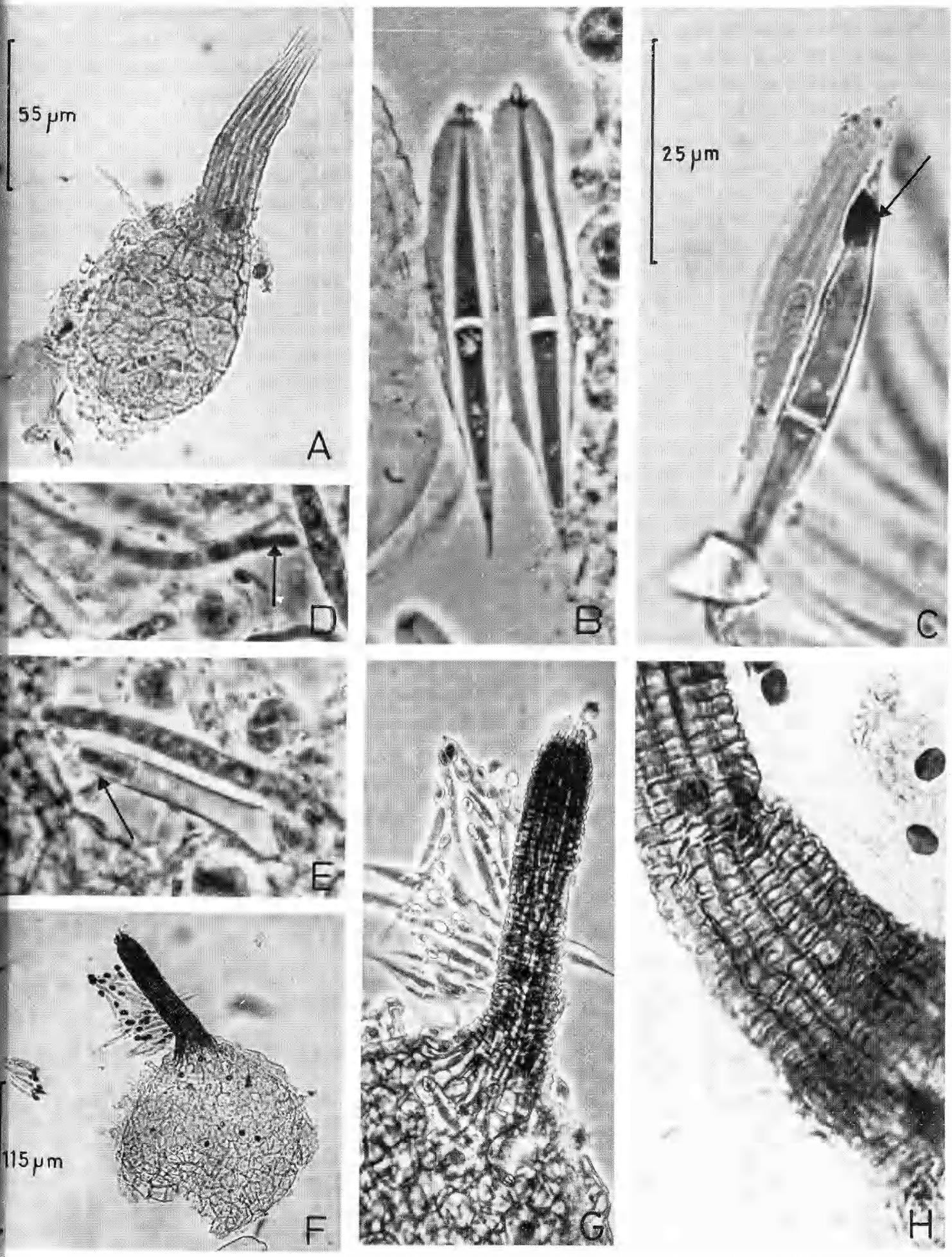
Hawksworth and Webster accepted 12 species in *Mycorhynchus* including *Copranophilus*. With the addition of *Pyxidiophora* s. str., *P. badiorostris* n. sp., *Treleasia, Ascolanthanus*, and *Acariniola* the number increases to 20, but 5–7 of these species have a dubious status. It has not been my ambition to revise them all, as they have been given good treatments by other authors. Apart from those already analysed, only the three Swedish species shall be fully described.

Pyxidiophora arvernensis (Bret. & Faur.) Lundq. comb. nov.—Figs. 6 A–E, 7

Mycorhynchus arvernensis Bret. & Faur. 1968 p. 249.

Non-stromatic; perithecia yellowish, glabrous or with a few thick, septate, hyaline hairs, narrowly pyriform, 130–170×45–65 μm, long-necked; neck tapering, 65–105×20–30 μm, composed of elongate, cylindrical cells, 10–18×3–4.5 μm, which are drawn out into pointed beaks around the ostiolum; peridial cells rounded to angular, 7–18 μm in diam. *Paraphyses* lacking. *Asci* not seen. *Spores* clavate-fusiform, 48–57×5–7 μm, swelling to 10 μm in width, hyaline; protoplast at first fusiform, often truncate at base, then rounding up at the ends, 38–48×3.5–4 μm, with a septum in or just below the middle; the inflated wall contracted above into a point, often slightly constricted below the apex, and basally elongated into a whip-like, 6–10 μm long appendage. At maturity a flattened, rounded or angular, brown body, 5–6×4×1.5–2.5 μm, occasionally develops in the spore wall laterally below the apex.

Fig. 6. A–E: *Pyxidiophora arvernensis*. Lqt 3429-b (UPS). — F–H: *Pyxidiophora badiorostris* n. sp., Lqt 2776-e (UPS). Material in lactic blue. Figs. B, D, E, G taken in phase contrast. — A: Perithecium. — B: Spores showing the inflated wall and the shape of the protoplast. — C: Spores; note the pigmented spot (arrow). — D: Germinating spore (arrow). — E: *Chalara* phialide with conidium (arrow). — F: Crushed perithecium and spores. — G, H: Perithecial neck. Scales: B, D, E, H = C; G = A.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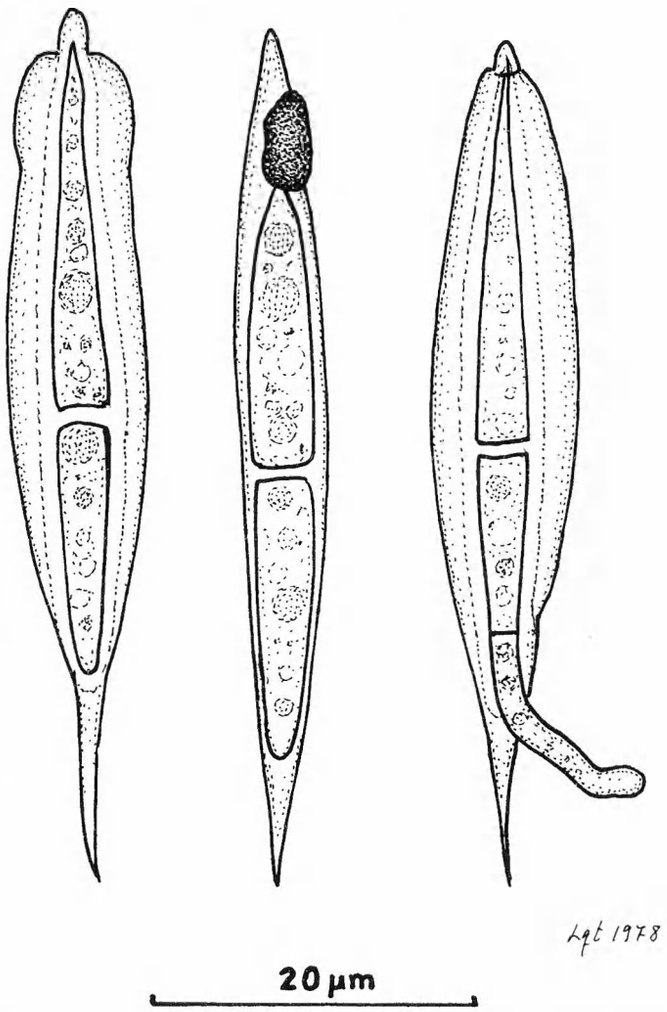


Fig. 7. *Pyxidiophora arvernensis*. Lqt 3429-b (UPS). Spores; one with a germ hypha.

Specimens examined. Sweden: *Jämtland*, Åre par., Storlien, in subalpine region, on reindeer dung, 17.VI.1962, Lqt 3429-b (UPS). — *Uppland*, Rasbokil par., NW of Lake Lafssjön, on roe deer dung, 25.X.1964, O. Eriksson 2510 (UPS). — *Finland*: *Kuusamo*, Kuusamo par., SSW of Liikasenvaara near Oulankajoki River, on hare dung, 24.VIII.1978, Lqt 11679-a (UPS, slide). New to Northern Europe.

All specimens are developed in moist chamber cultures. The species was hitherto known only on cow and horse dung from Clermont-Ferrand in France. Breton & Faurel did not observe any pigmentation in the spores, nor the strong inflation of the spore wall. They also stated that the length of the cells hardly exceed 10 µm, and that the "pseudosporophore"—i.e. the basal elongation without protoplast—is absent (p. 256). I consider all these differences versus the Nordic specimens to be either within the normal variation of the species or be founded on incomplete observations (cf. comment under *Pyxidiophora* and *P. grovei*). The pseudosporophore could be difficult to distinguish from the protoplast in young spores. A new study of authentic specimens may be needed to settle these questions.

The type of *P. arvernensis* (leg. Breton 3.X.1965) is said to be placed in Paris (PC), but "is not available" there (J. Mouchacca in litt.). Nor has Dr André Breton (Clermont-Ferrand) any material in his possession, since he left all of it to the late L. Faurel (Breton in litt.). It is possible that collections of this species and other *Pyxidiophorae* are still among Faurel's mycological remains, and have not yet been filed in PC. Dr Breton also took the trouble to send me fresh horse dung from the type locality, the Cournon Bridge at Allier River, but *P. arvernensis* did unfortunately not develop in my moist chamber cultures.

The imperfect state. Fig. 5 E. A hyaline *Chalara* is present on Lqt 3429-b, growing mixed with the perithecia. Both states seem to originate from the same hyphae, but the connection remains to be proved by single-spore cultures. The phialides are lageniform, 25–38 µm long, with a 5.5–8 µm wide venter and a 3–4 µm wide, cylindrical collarette. The conidia are 6–19×3–3.5 µm, cylindrical, truncate, one-celled, hyaline.

Pyxidiophora asterophora (Tul.) Lindau—Figs. 1–3

Lindau 1897 p. 351.

Hypomyces asterophorus Tul. in Tul. & Tul. 1860 p. 14; non *H. asterophorus* (Fr.) Tul., ibid. ≡ *Asterophora lycoperdoides* (Bull. ex Mérat) S. F. Gray, stat. con. — *Pyxidiophora Nyctalidis* Bref. & Tav. 1891 p. 189, nom. superfl. for *H. asterophorus* Tul. — Lectotype selected here on *A. lycoperdoides* from Héricy, France, Herb. L. R. Tulasne (PC).

Imperfect state: *Chalara brefeldii* Lindau nom. nov. in Rabenh. 1906 p. 750. — *Polyscytalum fungorum* Sacc. 1886 p. 336; non *Chalara fungorum* (Sacc.) Sacc. 1877. – Orig. coll. from Hockering Wood, England, IX.1880, leg. C. B. Plowright and J. M. Du Port (not seen).

Illustrations. Tulasne & Tulasne 1865 Pl. IX: 4–10. — Plowright 1881 Pl. 147: c–h (partly after the Tulasnes). — Brefeld & von Tavel 1891 Pl. V: 51, 52. — Maire 1911 Pl. XVI: 1. — Müller & von Arx 1962 Fig. 317. — Parguey-Leduc 1977 Fig. 1 d. Copied illustrations are excluded here.

Specimens examined. France: *Seine-et-Marne*, Héricy, "In Ag. adusto et Nyctali superposita", VIII–IX.1858, leg. L. R. Tulasne as *Hypomyces asterophorus* and *Nectria microscopica* Tul. in sched.

(PC, lectotype). — *Germany*: *Westfalen*, Münster, Hiltrup, near the railway station, "auf Nyctalis asterophora auf Russula adusta", IX.1889, leg.?, Herb. F. von Tavel as *Pyxidiophora Nyctalidis* nob. (ZT).

I have examined all material of *Asterophora lycoperdoides* in Herb. Tulasne, but found the pyrenomycete on the collection from Héricy only. Four samples originate from Chaville in Seine-et-Oise (25.VII.1860; end of July, 1860; VII–VIII.1860; VIII.1860), and one from Meudon in Seine-et-Oise (25.X.1857). One is without a locality and date. The Tulasnes (1865) stated that they saw the chlamydosporic fungus "hundreds of times .... in the neighbourhood of Versailles [close to Chaville], Compiègne etc.", but only rarely the ascophorus state, which was first discovered "around Fontainebleau in August 1858". This place alludes to Héricy, which is situated close to Fontainebleau. In 1860 the authors reported the species as a whole on both *Asterophora lycoperdoides* and *A. parasitica* (Bull. ex Fr.) Sing. from "Fontebellaqueo .... agri versaliensis, Modoni nempe, Cavillae, etc.".

As regards Brefeld's herbarium, it is not mentioned in Lanjouw & Stafleu's index of collectors (1954) and is said to be unknown (Stafleu & Cowan 1976). I have received negative answers from Munich (M), Münster (MSTR), and also from the Botanical Garden in Münster, of which Brefeld was the director in the 1880's. But Dr I. Friederichsen in Hamburg (HBG) has kindly informed me that in 1935–36 all the cryptogamic collections of the Botanical Institute in Münster were sent by Prof. Mevius to the Berlin Museum. The unopened boxes were kept in the cellar during the war and escaped the destruction on March 1, 1943. In an institutional report in Willdenowia 2, p. 783, 1961, Brefeld's herbarium is stated to be accessible, but this does not accord with information received from Dr B. Hein, Curator of the Berlin Herbarium. He has searched in vain for *P. nyctalidis* and other Brefeldian collections.

Fortunately there is an authentic sample of *P. nyctalidis* in Zürich (ZT). This syntype can be used for lectotypification if one of the proposals to change Art. 59 be accepted (p. 122). In such a case also the Tulasnes' material of the species will receive syntype status as part of the protologue of *P. nyctalidis*.

Distribution. *P. asterophora* is undoubtedly rare. Apart from France and Germany it is reported only from England (Plowright 1882) and U.S.A. (Berkeley 1875). Saccardo (1883) listed also Finland (Karsten 1873) and Italy, but the Italian collection in Herb. Saccardo (PAD) and the Uppsala copy of Karsten's Fungi Fenn. Exs. No. 512 do not exhibit the pyrenomycete. The same is certainly true for the Crouans' (1867) records from Brittany, as there is no indication that perithecia were seen. Further information on the bibliography of the species is given by Arnold (1976).

The imperfect state. Figs. 1, 2. This was placed in *Polyscytalum* by Saccardo (1886), in *Chalara* by Lindau (1906), in *Paecilomyces* by Tubaki (1958 p. 206), and again in *Chalara* by Nag Raj & Kendrick (1975) in their monograph of this genus. There is still some uncertainty about the correct epithet of the anamorph. The latter authors rejected the name *Chalara brefeldii* as a nomen dubium, as they had not been able to locate and examine the type. Nor could they get enough information from the description. They obviously allude to Brefeld & von Tavel's publication, but overlooked that *C. brefeldii* and *Polyscytalum fungorum* are both founded on Plowright's English material. This type collection, if it exists, has apparently not been restudied.

Pyxidiophora badiorostris Lundq. sp. nov. —Figs. 6 F–H, 8

From Latin *badius*, chesnut-brown, and *-rostris*, beaked, referring to the brown perithecial neck.

Nonstromatica; perithecia semi-immersa, vulgo dispersa, 230–295×105–140 μm, globosa, longicollia, ± glabra; collum 95–145×21–28 μm, sursum decrescens, apice conico, valde transverse rugosum, badium. *Peridium* membranaceum, semipellucidum, flavidum, cellulis externis angulatis vel rotundatis, 10–23 μm diam.; cellulae externae colli elongatae, 10–20×4.5 μm, circa ostiolum longe acutae, cristis crassis, badiis, transversis, anastomosantibus obtectae. *Paraphyses* carentes. *Asci* trispori, 45–50×10–20 μm, subclavati, inamyloidei, cito deliquescentes. *Sporae* 38–52× 4.5–5.5 μm, longe clavato-fusiformes, basim versus attenuatae, hyalinae; protoplastus 27–38×3–3.5 μm, utrinque acutus tum rotundatus, infra medium 1(–2)-septatus; paries sporarum praesertim apicaliter tumescens, appendicem basalem, 14–18 μm longam formans, maturitate corpore brunneo, applanato, rotundato, subapicali, 5–6×4.5×2 μm, instructus. Species coprophila.

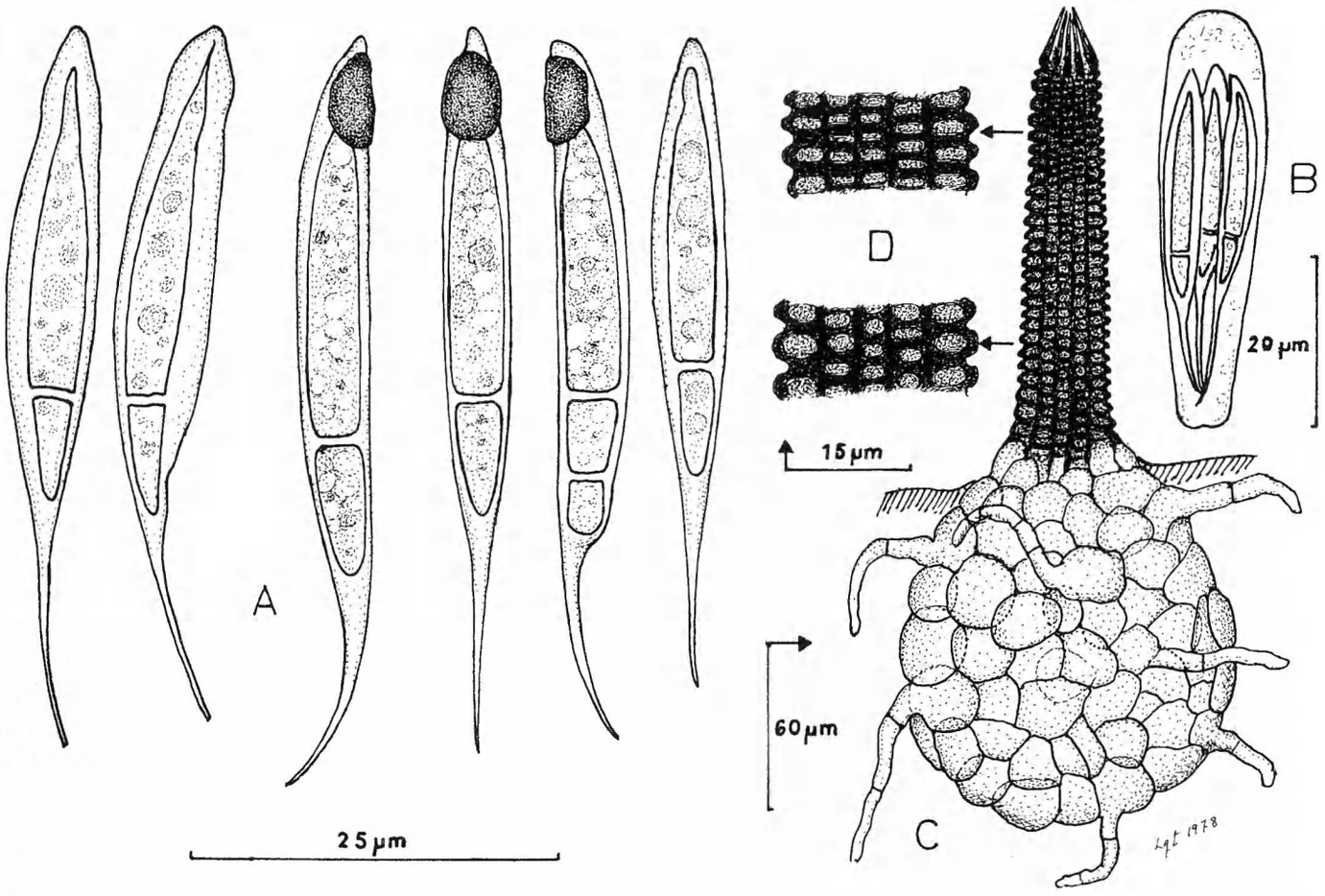


Fig. 8. *Pyxidiophora badiorostris* n. sp. A, B: Lqt 3165 (UPS, holotype). C, D: Lqt 2776-e (UPS). — A: Spores at hyaline and pigmented stages. — B: Young, three-spored ascus. — C: Perithecium. — D: Detail of the perithecial neck.

Non-stromatic; *perithecia* scattered or aggregated, 230–295×105–140 µm, rounded, long-necked, glabrous or with a few thick, hyaline hairs; neck 95–145 µm long, 21–28 µm wide below, 13–15 µm wide above, conical at the tip, rugose, chestnut-brown. *Peridium* membranaceous, semi-transparent, yellowish, with thin-walled, angular to rounded, 10–23 µm large outer cells; neck cells cylindrical, 10–20×4.5 µm, forming 5–6 visible longitudinal rows, pointed around the ostiolum, covered with brown, thickened, transverse, anastomosing ridges and plates. *Paraphyses* lacking. *Asci* unitunicate, 3-spored, 45–50×10–12 µm, subclavate, non-amyloid, without apical apparatus, deliquescing. *Spores* gathering around the ostiolum in slimy masses, 38–52×4.5–5.5 µm, hyaline, elongate, clavate-fusiform, with a drawn-out base; protoplast 27–38×3–3.5 µm, with acute, later rounded ends, 1(–2)-septate below the middle; outer spore wall swelling, particularly in the upper part of the spore, giving it an obtuse although tapering profile, often slightly constricted below the apex, and forming a 14–18 µm long basal elongation. At maturity a brown, flattened, rounded body, 5.5–6×4.5×2 µm, is laid down subapically and laterally in the spore wall. Coprophilous.

Specimens examined. Sweden: *Ångermanland*, Ytterlännäs par., Västertorp, on cow dung, 20.VIII.1961, Lqt 3165-e (UPS, holotype); isotypes in K, S, TRTC. — *Jämtland*, Hammerdal par., Fyrås, on cow dung, 14.VIII.1960, Lqt 2776-e (UPS).

The specimens appeared after 23–28 days in moist chamber cultures. *P. badiorostris* i easily distinguished from all other *Pyxidiophorae* by its brown, rugose perithecial neck. No distinct stroma has been observed, nor any conidial state.

Pyxidiophora bainemensis (Bret. & Faur.) Lundq. comb. nov.

Mycorhynchus bainemensis Bret. & Faur. 1968 p. 246.

Acariniola basalipunctata Maj. & Wiśn. 1978 a p. 9

This may be a synonym of *Pyxidiophora subbasalipunctata* (Maj. & Wiśn.) Lundq.; see comment under *Acariniola*.

Mycorhynchus brunneo-capitatus Hawksw. & Webst. 1977 p. 331

This species could be the same as *Pyxidiophora microspora* (Hawksw. & Webst.) Lundq.; see comment under that name.

Pyxidiophora caulicola (Hawksw. & Webst.) Lundq. comb. nov.

Mycorhynchus caulicola Hawksw. & Webst. 1977 p. 331.

Pyxidiophora fusco-olivacea (G. Arnold) Lundq. comb. nov.

Mycorhynchus fusco-olivaceus G. Arnold 1972 a p. 190.

Pyxidiophora grovei (Hawksw. & Webst.) Lundq. comb. nov.—Figs. 9, 10.

Mycorhynchus grovei Hawksw. & Webst. 1977 p. 333.

Perithecia free or gregarious on a stroma, yellowish, glabrous or with a few thick, hyaline hairs, globose, long-necked, 200–290×70–95 μm; neck cylindrical to tapering, pointed, 100–190 μm long, 20–28 μm wide below, c. 14 μm wide above, composed of cylindrical cells, 15–31×3–4 μm, ending in narrow beaks around the ostiolum; outer peridial cells rounded to angular, 9–18(–23) μm in diam. *Paraphyses* absent. *Asci* 3-spored, c. 55×20 μm, ellipsoidal, evanescent. *Spores* clavate-fusiform, (43–)48–58×4.5–6 μm, swelling up to 8 μm in width, hyaline to yellowish; protoplast at first fusiform, often truncate at base, then rounding up at the ends, 38–45×3–4.5 μm, with a transverse septum in or just below the middle; the inflated wall forms an acute apex and a 13–16 μm long, whip-like, basal elongation. At maturity a subapical, flattened, round or angular, brown body, 4–5×3–4×1.5–2.5 μm, occasionally with a central pore, is formed laterally in the spore wall.

Specimens examined. *Sweden*: *Uppland*, Forsmark par., Rönngrund, on fresh sheep dung, 26.IX.1962, Lqt 3788-a (IMI, PC, S, UPS). Haga par., Åtorpet, on fresh elk dung, 18.XI.1979, Gunnerbeck 3477-d (UPS). Uppsala, Marieberg, on sheep dung, 23.VII.1964, Lqt 4302-c (UPS). New to northern Europe.

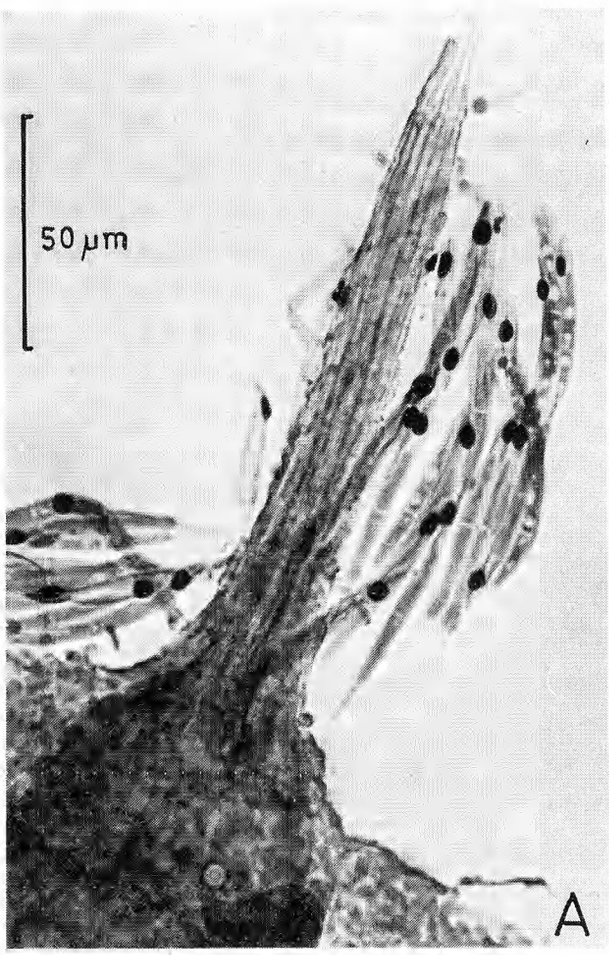
The only find hitherto known is on horse dung from Liverpool, England (Grove 1932 as *Mycorhynchus marchalii*; Hawksworth & Webster 1977). The Swedish specimens appeared after 11–12 days in moist chamber. They are accompanied by a *Chalara* state (Fig. 8 F), indistinguishable from that found together with *P. arvernensis*. Neither in this case has the connection been proved.

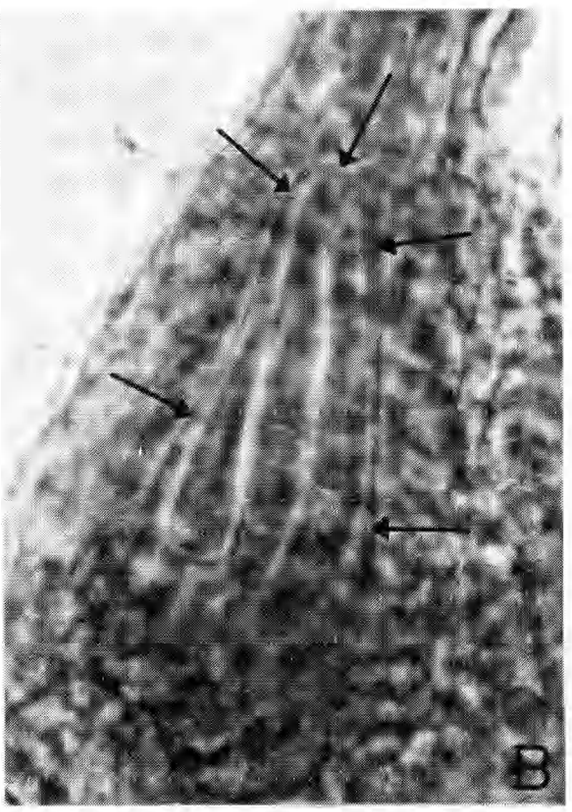
According to the original description, *P. grovei* deviates from my specimens by smaller neck cells (10×3 μm), slightly longer spores (53–65 μm), and absence of a pigmented stage and a stroma. However, Dr David Hawksworth (Kew) has told me (in litt.) that he has re-examined the type collection of *P. grovei* and discovered three pigmented spores, and found that the neck cells could be up to 32 μm long. He also remarks that the tendency to form a stroma seems to be general in the genus, and he does not attach much taxonomic importance to it.

The related *Pyxidiophora petchii* (Bret. & Faur.) Lundq. (= *Mycorhynchus marchalii* sensu Petch 1941) matches Swedish material in some respects too, for example as regards the occurrence of a stroma and the size of the neck cells. On studying the original slides (in BM), Breton & Faurel (1968) also detected two pigmented spores. On the other hand, *P. petchii* is caulicolous and its peridial cells are much too small, only 7–10 μm in diam. Furthermore, Petch's spore measurements are unreliable in this case. They were stated to be 40–63×6–7 μm, but both Breton & Faurel and Hawksworth & Webster (1977), who investgated dried material in Kew, could not find spores exceeding 53 μm in length. Dr Hawksworth has kindly compared material of my 4302-c with both *P. grovei* and *P. petchii*, and found it to accord with the former species. Particularly the longer and slender spores and the larger peridial cells distinguish *P. grovei* from *P. petchii*.

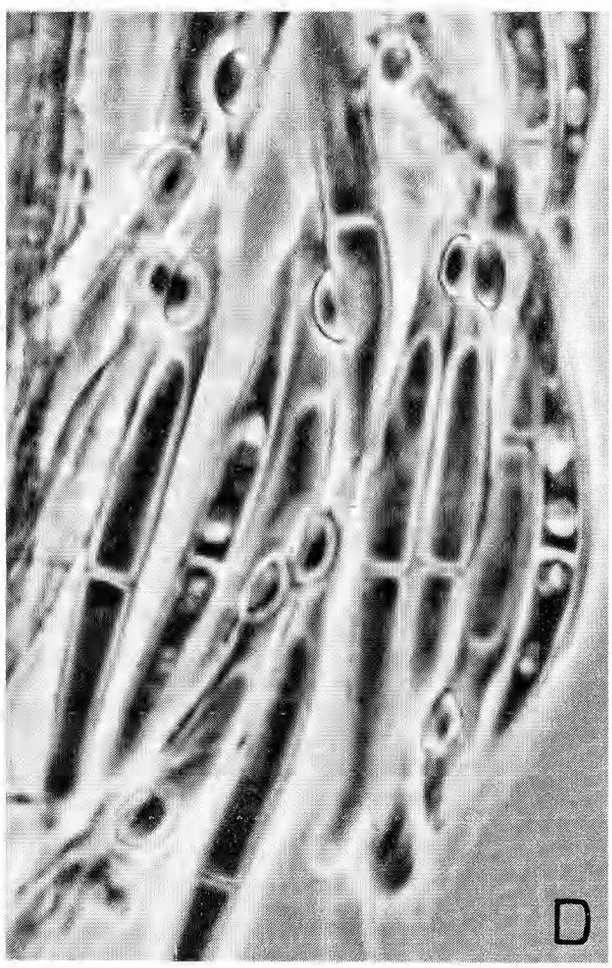
Pyxidiophora marchalii (Sacc.) Lundq. comb. nov.

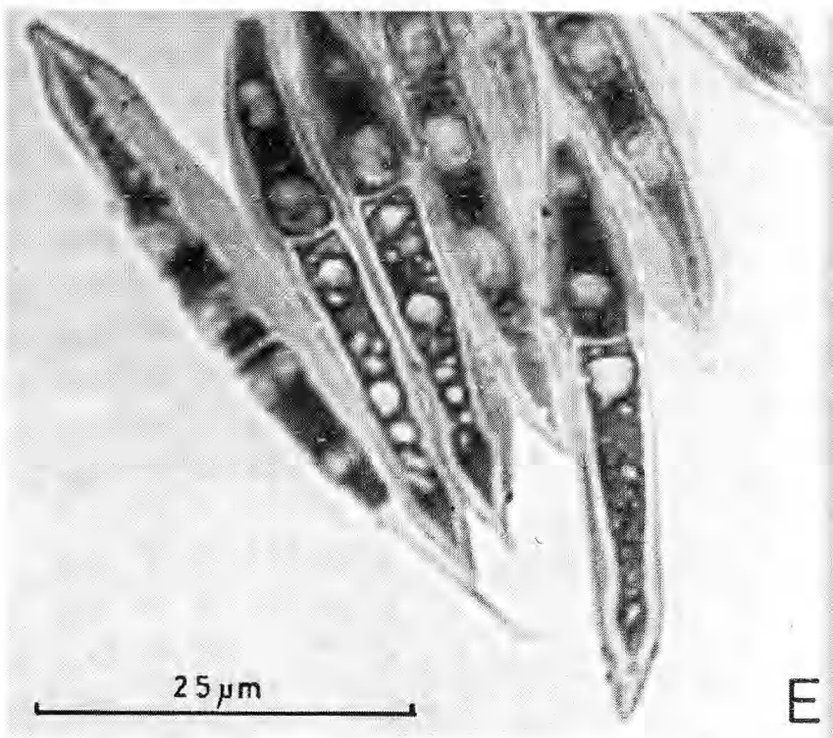
Rhynchomyces marchalii Sacc. in March. 1885 p. 60.

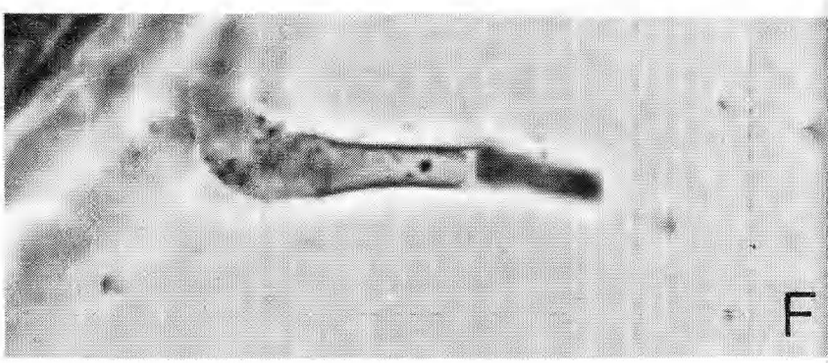

50 µm
A


B


C


D


25 µm
E


F

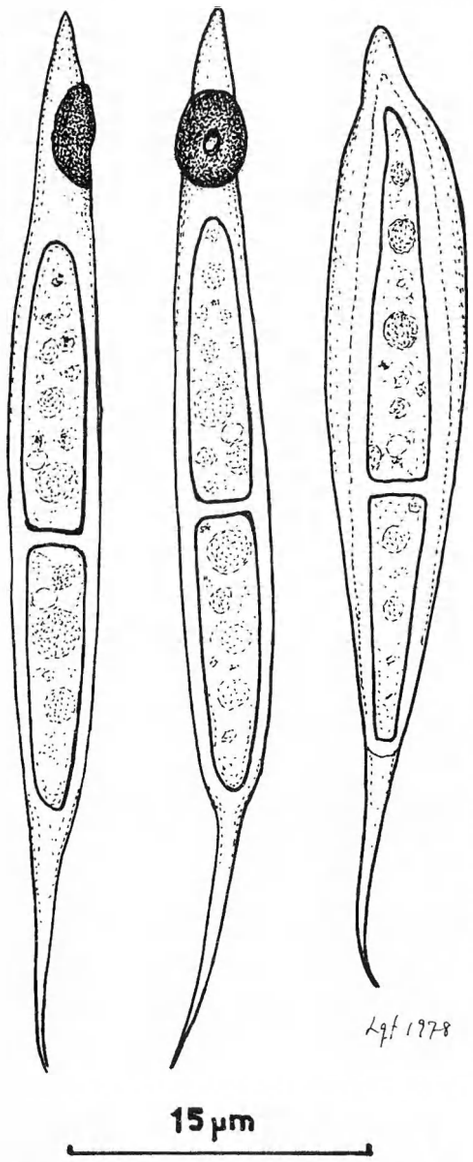


Fig. 10. *Pyxidiophora grovei*. Lqt 4302-c (UPS). Spores at pigmented and hyaline stages.

Pyxidiophora microspora (Hawksw. & Webst.) Lundq. comb. nov.

Mycorhynchus microsporus Hawksw. & Webster. 1977 p. 336.

Mycorhynchus brunneocapitatus Hawksw. & Webst. (1977 p. 331) may be a synonym. The only tangible difference between the two is the pigmented spores in *M. brunneocapitatus*. Dr Hawksworth reports (in litt.) that he has investigated a rich material of *P. microspora* without finding any pigmentation, whereas such occurred regularly in mature spores of *M. brunneocapitatus*. I am not fully convinced that this difference is constant. Dr Hawksworth suggests that if the species be united, *microsporus* is the epithet to be preferred.

Pyxidiophora moseri (Maj. & Wiśn.) Lundq. comb. nov.

Acariniola moseri Maj. & Wiśn. 1978 a p. 5. The species is discussed under *Acariniola*.

Pyxidiophora petchii (Bret. & Faur.) Lundq. comb. nov.

Mycorhynchus petchii Bret. & Faur. 1968 p. 244. See comment under *P. grovei*.

Pyxidiophora schotteriana (Bret. & Faur.) Lundq. comb. nov.

Mycorhynchus schotterianus Bret. & Faur. 1968 p. 250.

Pyxidiophora spinuliformis (Speg.) Lundq. comb. nov.

Copranophilus spinuliformis Speg. 1909 p. 410. See comment under *Copranophilus*.

Pyxidiophora subbasalipunctata (Maj. & Wiśn.) Lundq. comb. nov.

Acariniola subbasalipunctata Maj. & Wiśn. 1978 a p. 7. See comment under *Acariniola*.

Mycorhynchus subspinuliformis Bret. & Faur. 1968 p. 252.

The status of this species is doubtful. Although lacking(?) a stroma and a conidial state, it is very close to *Pyxidiophora spinuliformis* (incl. *Ascolanthanus trisporus*) in certain perithecial and sporal characters. It has, to mention one, the same kind of two-capped pigmentation of the spores. The species should be studied anew.

Fig. 9. *Pyxidiophora grovei*. A, B, D–F: Lqt 4302-c (UPS). C: Lqt 3799-a (UPS). Material in lactic blue. Figs. B–D, F taken in phase contrast. — A: Perithecium with pigmented spores. — B: Perithecium with a young, three-spored ascus visible through the wall (arrows mark the outline of the ascus). — C–E: Spores; compare the form of the ends of the protoplasts in the pigmented and the hyaline spores. — F: *Chalara* phialide with a conidium. Scale: B–D, F = E.

Ascolanthanus trisporus Caill. 1967 p. 1474; not validly published.

As has been elucidated earlier in the present paper, the differences between this species and *Copranophilus spinuliformis* Speg. are insignificant. If the former is to be accepted as an independant species, its name must first be validated by a typification. Cailleux (1967, 1973) mentioned but did not specify the type. Since a valid publication of a name requires an indication of the type (Article 37), one must require that at least some clue to it shall be *published*, irrespective of whether the type is marked in the herbarium or not. This is also the interpretation of Hawksworth (1974 p. 156), who cites an example directly applicable here.

Dubious names

Hypomyces fusisporus Tul. in Tul. & Tul. 1865 p. 55

The perithecia are said to be whitish to dingy, elongate, 150–200×50–60 μm, the asci broadly obovoid, 4-spored, and the spores obovoid-fusiform, 50×10 μm, with a cuspidate base.

The type collection is from Chaville in Seine-et-Oise, France, 3.VII.1860, Herb. Tulasne (PC). It has the text "perexigua, Sphaeronematis aemula, in Ag. adusto nyctalifero" and a poor drawing of a spore that is hyaline, claviform with a mucronate apex and a longitudinal row of three oil drops(?) in the middle.

M. Cornu (XI.1887), Maire (1911), and Arnold (6.I.1965) studied the material without finding any pyrenomycete, and they all treated *H. fusisporus* as a synonym of *H. asterophorus* Tul. (≡ *Pyxidiophora a.*). I can verify that the species is no longer present on the scarce substrate, which is *Asterophora parasitica* (Bull. ex Fr.) Sing.

The smooth-walled chlamydospores typical of this agaric are also found here. The Tulasnes were acquainted with these spores, which they naturally thought to be parasitic and specifically distinct from *H. asterophorus*. They consequently established a new species, *Hypomyces baryanus*, solely for these chlamydospores, but the name is illegitimate according to Art. 59.3 (Tulasne & Tulasne 1860 p. 13).

Treleasia? musicola Speg. 1909 p. 411

Authentic specimens are lacking according to Breton & Faurel's (1968 p. 232) and my own examination of the type collection (on banana leaves, La Plata, 30.IX.1906, C. Spegazzini, LPS 1752). Only nine empty leaf fragments are left, and an enclosed drawing almost identical to the published illustration. The species looks like a member of *Pyxidiophora*, except that the asci have a short, narrow stipe and a tapering tip. If this is correctly interpreted, *T. musicola* may not belong in *Pyxidiophora*, but Spegazzini may also have made a mistake (cf. *T. sacchari*).

Treleasia sacchari Speg. 1896 p. 235

This species is discussed under *Treleasia*. It is certainly a representative of *Pyxidiophora* s. lato. No type specimens exist.

Excluded species

Mycorhynchus betae (Hollr.) Sacc. & D. Sacc. 1906 p. 418

Sphaeronaema betae Hollr. 1904 p. 202. This is a coelomycete.

Mycorhynchus exilis (Höhn.) Sacc. & D. Sacc. 1906 p. 418

Rhynchomyces exilis Höhn. 1902 p. 1021. This is a coelomycete.

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Floristic report from the island of Psathura (Greece)

SVEN SNOGERUP, ROLAND von BOTHMER and MATS GUSTAFSSON

Snogerup, S., Bothmer, R von & Gustafsson, M. 1980 06 16: Floristic report from the island of Psathura (Greece). *Bot. Notiser 133:* 145–148. Stockholm. ISSN 0006-8195.

All vascular plants known from the island are listed with comments on a few finds such as *Pilularia minuta* A. Braun, *Taraxacum* sect. *Palustria, Callitriche brutia* Petagna and *Ranunculus baudotii* Godr. The new combination *Aphanes minutiflora* (Azn.) Snog. et al. is made.

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Psathura, the northernmost island in the Northern Sporades, is situated 7 km N of Giura and c. 50 km S of the Chalkidiki peninsulas (Fig. 1). It is 0.8 km² in area. Most of the island is only c. 10 m high above sea level, the highest point being only 17 m. It is mainly covered by open scrub in which the shrubs *Pistacia lentiscus, Sarcopoterium spinosum, Olea europaea* var. *sylvestris, Rosa canina, Myrtus communis* and *Vitex agnus-castus* have been observed. *Ferula communis* was also abundant. The flattest parts are presumably flooded during the winter and in 1972 at least one pool remained in the south at the end of April. Outcrops of tertiary lava occur in the north and south. The soil cover is shallow consisting of fresh products of erosion with very little humus. In the south is a small area of mobile sand.

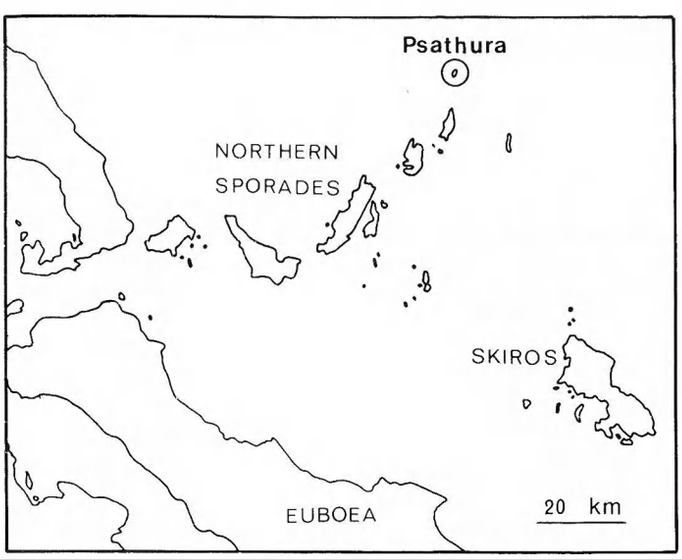

Fig. 1. The geographical position of Psathura.

As even the highest parts of Psathura must have been little above sea level when the water reached its highest level during postglacial times most of the flora must have reinvaded during this comparatively short time. This may explain why 6 of the c. 130 species hitherto known from Psathura have not been recorded or observed by us on the other islands of the Northern Sporades, viz. *Pilularia minuta, Callitriche brutia, Ranunculus baudotii, Taraxacum* sect. *Palustria, Lythrum borysthenicum* and *Elatine sp.* The semi-aquatic habitats must have been under-populated in terms of species number for long periods and represented a challange to long distance dispersal.

The area is grazed by only a few sheep, but grazing may previously have been heavier. There is a lighthouse on the island, and during its construction in particular some species may have been introduced. Probable introductions by man are *Solanum nigrum, Bromus madritensis, Urtica urens, U. pilulifera, Silene vulgaris, Cardaria draba, Capsella rubella* and *Malva parviflora*, etc.

Though Psathura is not truly maritime the composition of its vegetation shows some traits reminding of maritime islets, as the unusually high frequency of some individual species such as *Ferula communis* (cf. Runemark 1969).

The few previous mentions of plants from Psathura are cited in our list of species according to Phitos (1967) and marked "lit". The island was visited by Bothmer and Gustafsson on the 25th April, 1972. In all, 80 collections and field notes on some common species were made. The collections are kept at LD. The list also includes a few collections and observations made by Runemark and Nordenstam in 1960, marked "R & N". A full-scale floristic investigation of the Northern Sporades is being carried out in cooperation with D. Phitos, Patras, see Gustafsson and Snogerup (1974).

Aphanes minutiflora (Azn.) Snog. & al., comb. nov.

Alchemilla minutiflora Aznavour, Bull. Soc. Bot. Fr. 46: 141–142 (1899).

The species is distinct in habit as well as in the size of hypanthia and we cannot accept it as a synonym of *A. microcarpa* (Boiss. & Reut.) Rothm. We found these two species growing mixed on Peristeri, N Sporades, but no intermediates (Snogerup & Bothmer 43820 and 43821, LD). *A. minutiflora* has also been found on Skiros (Snogerup & Gustafsson 44289, LD) but not in the intensely investgated area of the Kikladhes. *A. minutiflora* differs from *A. microcarpa* in having hypanthia only 0.5–0.6 mm long. Under favourable conditions it reaches a height of up to 12 cm, with internodes up to 15 mm, the leaves, however, being only 5–8 mm. It is also more yellowish than *A. microcarpa* and the less similar *A. arvensis* L.

Comments on some other finds

Pilularia minuta Dur. ex A. Braun has previously been recorded only from some widely scattered W Mediterranean localities as shown in Jalas & Suominen (1972) and Meusel & al. (1965). It occurred in the pool in the south and had ripe spores. The mud was full of the hardened sporocarps of previous years. The leaves were only 5–12 mm long and the rhizome was very thin like the leaves. The sporocarps were 1.0–2.2 mm in diameter, with long hairs. The spores resembled those of W Mediterranean material.

This is an easily overlooked species, and it was in fact found in this locality only because a sample of the mud was collected for later inspection. *Pilularia minuta* may therefore have a much more continuous distribution than is indicated by the comparatively few localities observed. Irregular and widely disjunct occurrences are, however, known for other semiaquatic species in the E Mediterranean, as those reported by Gradstein and Smittenberg (1977).

Taraxacum sect. Palustria. Most of the species of this section are more northerly and occur at higher altitudes. The leaves of the Psathura material are more deeply divided than is usual in this section. This may be a new species but the material has been left undertermined pending revision by a specialist.

Callitriche brutia Petagna is stated by Schotsman (1972) to occur only in W and S Europe reaching Italy. Chamberlain (1972), however, records it from the Istanbul area, from Zonguldak in N Turkey and from the E Aegean island of Lesvos. Our find confirms that it occurs in the E Mediterranean.

Lythrum borysthenicum (Schrank) Litv. is rare in the Balkan Peninsula. In the Aegean area it is previously known from near Istanbul and from Crete.

Ranunculus baudotii Godr. is reported only doubtfully from Greece (Cook 1964). Our material is small-flowered but otherwise quite typical. Equally small-flowered forms are found, for example in Scandinavian material.

Anthemis spp. The mainly maritime species of *Anthemis* in the Aegean are still imperfectly understood. We leave the two species from Psathura undetermined.

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List of species

Pteridophyta

43464 *Pilularia minuta* Dur. ex A. Braun

Angiospermae

obs *Parietaria cretica* L.
obs *Urtica pilulifera* L.
43475 *U. urens* L.
43474 *Polygonum maritimum* L.
43420 *Rumex pulcher* L.
obs *Salsola kali* L.
obs *Cerastium glomeratum* Thuill.
43439 *Moenchia erecta* (L.) P. Gaertn.
43457 *Petrorhagia velutina* (Guss.) P. W. Ball & Heyw.
43467 *Polycarpon diphyllum* Cav.
43461, 43463 *Sagina apetala* Ard., different forms
obs *Silene gallica* L.
43476 *S. vulgaris* (Moench) Garcke, weedy form
obs *Clematis cirrhosa* L.
43466 *Ranunculus baudotii* Godr.
43485 *R. chius* DC.
43493 *Fumaria judaica* Boiss.
43443 *Papaver pinnatifidum* Moris
obs *Capparis spinosa* L.
obs *Arabidopsis thaliana* (L.) Heynh.
obs *Cakile maritima* Scop.
43488 *Capsella rubella* Reut.
43482 *Cardaria draba* (L.) Desv.
43445 *Malcolmia flexuosa* (S. & S.) S. & S. ssp. *naxensis* (Rech. fil.) A. Stork
43468 *Crassula tillaea* Lest.-Garl.
43444 *Sedum litoreum* Guss.
43469 *Umbilicus horizontalis* (Guss.) DC.
43432 *Aphanes minutiflora* (Azn.) Snog. & al.
43480 *Rosa canina* L.
lit. *R. pouzini* Tratt.
obs *Sarcopoterium spinosum* (L.) Spach
R & N obs *Anthyllis hermanniae* L.
43490 *Hymenocarpus circinnatus* (L.) Savi
43471 *Lotus angustissimus* L.
43455 *L. conimbricensis* Brot.
lit. *L. cytisoides* L.
43483 *Medicago littoralis* Lois.
43437 *M. truncatula* Gaertn.
lit. *Trifolium arvense* L.
43422 *T. campestre* Schreb.
43453 *T. glomeratum* L.
43433 *T. suffocatum* L.
43478 *Erodium cicutarium* (L.) L'Hér. ssp. *cicutarium*
43462 *E. moschatum* (L.) L'Hér.
obs *Geranium rotundifolium* L.
obs *Linum trigynum* L.
43419 *Euphorbia exigua* L.
43479 *E. paralias* L.
R & N obs *E. peplis* L.
43460 *E. peplus* L.
obs *Mercurialis annua* L.
obs *Pistacia lentiscus* L.
43497 *Malva parviflora* L.
43489 *Hypericum rumeliacum* Boiss.
43426 *Lythrum borysthenicum* (Schrank) Litv.
obs *Myrtus communis* L.
43421 *Crithmum maritimum* L.
obs *Eryngium campestre* L.
obs *E. maritimum* L.
43486 *Ferula communis* L. ssp. *communis*
lit. *Ferulago nodosa* (L.) Boiss.
obs *Lagoecia cuminoides* L.
43470 *Tordylium apulum* L.
43441 *Torilis nodosa* (L.) Gaertn.
obs *Anagallis arvensis* L.
obs *Asterolinon linum-stellatum* (L.) Duby
obs *Olea europaea* L. var. *sylvestris* Brot.
43472 *Centaurium maritimum* (L.) Fritsch
43473 *C. erythraea* Rafn ssp. *rhodense* (Boiss. & Reuter) Melderis
43435 *Galium murale* (L.) All.
43495 *Echium arenarium* Guss.
43446 *Lithospermum apulum* (L.) Vahl.
43423 *Myosotis incrassata* Guss. var. *pontica* (David) Grau
43484 *Vitex agnus-castus* L.
43465 *Callitriche brutia* Petagna
obs *Prasium majus* L.
obs *Salvia verbenaca* L.
obs *Teucrium divaricatum* Heldr.
43494 *Solanum nigrum* L. ssp. *nigrum*
43438 *Linaria pelisseriana* (L.) Mill.
43430 *Plantago bellardi* All.
obs *P. coronopus* L. s.l.
43429 *P. lanceolata* L.
43477 *Lonicera implexa* Ait.
43418 *Valerianella microcarpa* Lois.
obs *Aetheorhiza bulbosa* (L.) Cass.
R & N 16871 *Asteriscus aquaticus* (L.) Less.
obs *Bellis annua* L.
obs *Calendula arvensis* L.
R & N obs *Carlina corymbosa* L.
R & N obs *Centaurea spinosa* L.
43454 *Crepis hellenica* Kamari ssp. *hellenica*
43436 *Filago eriocephala* Guss.
43434 *F. pygmaea* L.
43459 *Hedypnois rhagadioloides* (L.) F. W. Schmidt ssp. *tubaeformis* (Ten.) Heyek
43456 *Hypochoeris glabra* L.
obs *Inula viscosa* (L.) Ait.
lit. *Otanthus maritimus* (L.) Hoffm. & Link.
obs *Pallenis spinosa* (L.) Cass.
43442 *Sonchus oleraceus* L.
43431 *Taraxacum* sect. *Palustria*

obs *Pancratium maritimum* L.
43424 *Juncus bufonius* L.
43427 *J. capitatus* Weig.

43491 *Carex divisa* Huds.
43492 *C. divulsa* Good.
obs *Aira elegantissima* Schur.
43451 *Bromus madritensis* L.
43450 *B. scoparius* L.
43440 *Catapodium marinum* (L.) Hubb.
obs *C. rigidum* (L.) Dony
obs *Dactylis glomerata* L. ssp. *hispanica* (Roth) Nym.
obs *Hordeum murinum* L. s.l.
obs *Lagurus ovatus* L.
43481 *Lolium rigidum* Gaudin ssp. *lepturoides* (Boiss.) Senn. & Maur.
obs *Lophochloa cristata* (L.) Hyl.
obs *Oryzopsis miliacea* (L.) Asch. & Schweinf.
43428 *Parapholis incurva* (L.) Hubb.
R & N 16869 *Phalaris aquatica* L.
43417 *P. minor* Retz.
obs *P. australis* (Cav.) Steud.
obs *Psilurus incurvus* (Gouan) Schinz & Thell.
43448 *Vulpia muralis* (Kunth) Nees
43449 *V. myurus* (L.) Gmel.
obs *Arisarum vulgare* O. Targ.-Tozz.

Because of insufficient material the following collections are left undetermined:
43425 *Elatine* sp.
43447 *Limonium* cf. *oleifolium* Mill.
43458 *Anthemis* cf. *scopulorum* Rech. fil.
43496 *A.* cf. *flexicaulis* Rech. fil.

A new species of Elaphomyces Nees ex Fr. subgen. Malacoderma Vitt.

LARS E. KERS

Kers, L. E. 1980 06 16: A new species of Elaphomyces Nees ex Fr. subgen. Malacoderma Vitt. *Bot. Notiser 133:* 149–153. Stockholm. ISSN 0006-8195.

Elaphomyces striatosporus Kers sp. nov. (*Ascomycetes, Plectascales*) is described from southern Norway. The species is recognized by its small ascocarps (0.3–1.2 cm in diam.), the persistent and whitish mycelial crust, the black, horny (dry) peridium and by the spores which are unusually large among the *Malacodermei*, viz. (10–)14–16(–18) μm in diameter and which have a reticulate to striate ornamentation. Only found once, under *Corylus avellana*. The new species is compared with those species with which it may be confused.

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Elaphomyces striatosporus sp. nov. (subgen. Malacoderma Vitt.) — Figs. 1–3

Holotypus: Norvegia. Regio Osloensis: Aker. Prope locum Gaustad nominatum. 22.IX.1952. Leg. F.-E. Eckblad s.n. (0).

Species haec a speciebus aliis subgeneris *Malacodermatis* Vitt. facile distinguitur his notis: crusta mycelialis terrestris persistens e hyphis copiosis albis vel dilute ochraceis composita, cortex mollis laevis sepiaceus vel ater, 30–40 μm crassus, peridium 0,5–1,5 mm crassum, madefactum elasticum gelatinosum atrumque, in siccitate corneum et olivaceo-brunneum, ascosporae atro-brunneae (10–)14–16(–18) μm diametro, ornamento variantes, eodem aliquantum irregulariter asperulatis vel reticulatis vulgo autem subtiliter rugosis vel striatis. Species hypogaea adhuc semel sub *Corylo avellana*, ubi ascocarpia gregaria vel dense aggregata creverunt, inventa est.

Ascocarps small, globose, spherical or usually somewhat depressed, without regular depressions (foveae), elastic and soft in moist condition, drying very hard, not brittle. Surface smooth, somewhat wrinkled in dry material, dark sepia to almost black, dull. Smallest and largest mature specimen 0.3×0.4 cm and 0.8×1.2 cm in diameter respectively. Crust conspicuous, firmly adhering to the ascocarp surface, persistent, composed of a white to pale ochraceous tinged mycelium mixed with soil particles. Mycelium of the crust flocculent, of loosely tangled hyphae, hypheal elements richly branched, with few septa, rigid, hyaline under the microscope, smooth, unequally thick, generally 1.5–3.0 μm in diameter but with local swellings up to 6–10 μm in diameter, wall c. 0.3 μm thick. Adjacent hyphae often anastomosing by small papillae. Roots of vascular plants sparsely present in the crust, some roots found in intimate contact with the cortical wall but not penetrating into the peridium. *Cortex* up to 30–40 μm thick, soft-textured, pseudoparenchymatic, dark sepia to black in section, weakly differentiated from the peridium. Exterior surface of cortex smooth, dull, densely and inconspicuously reticulate by minute, dark sepia coloured patches separated by very narrow meshes in a pale brown colour. The reticulation is only visible on cleaned, moistened material studied under high magnification. Cortex composed of diffusely separated groups of opaque cells. The groups are broadly conical to flattened–elongate in vertical section, up to 50–70 μm broad at base and 30–40 μm high, cells 3–10 μm in diameter, mostly isodiametric, forming a textura angulosa, walls variously thickened up to 2.5 μm. Cortical groups more or less confluent at their bases, laterally connected and sometimes also covered by a compact system of tangentially oriented hyphae with cells isodiametric to elongate, pale brown to hyaline and smooth. *Peridium* much thicker than the cortex, 0.5–1.5 mm thick, fleshy

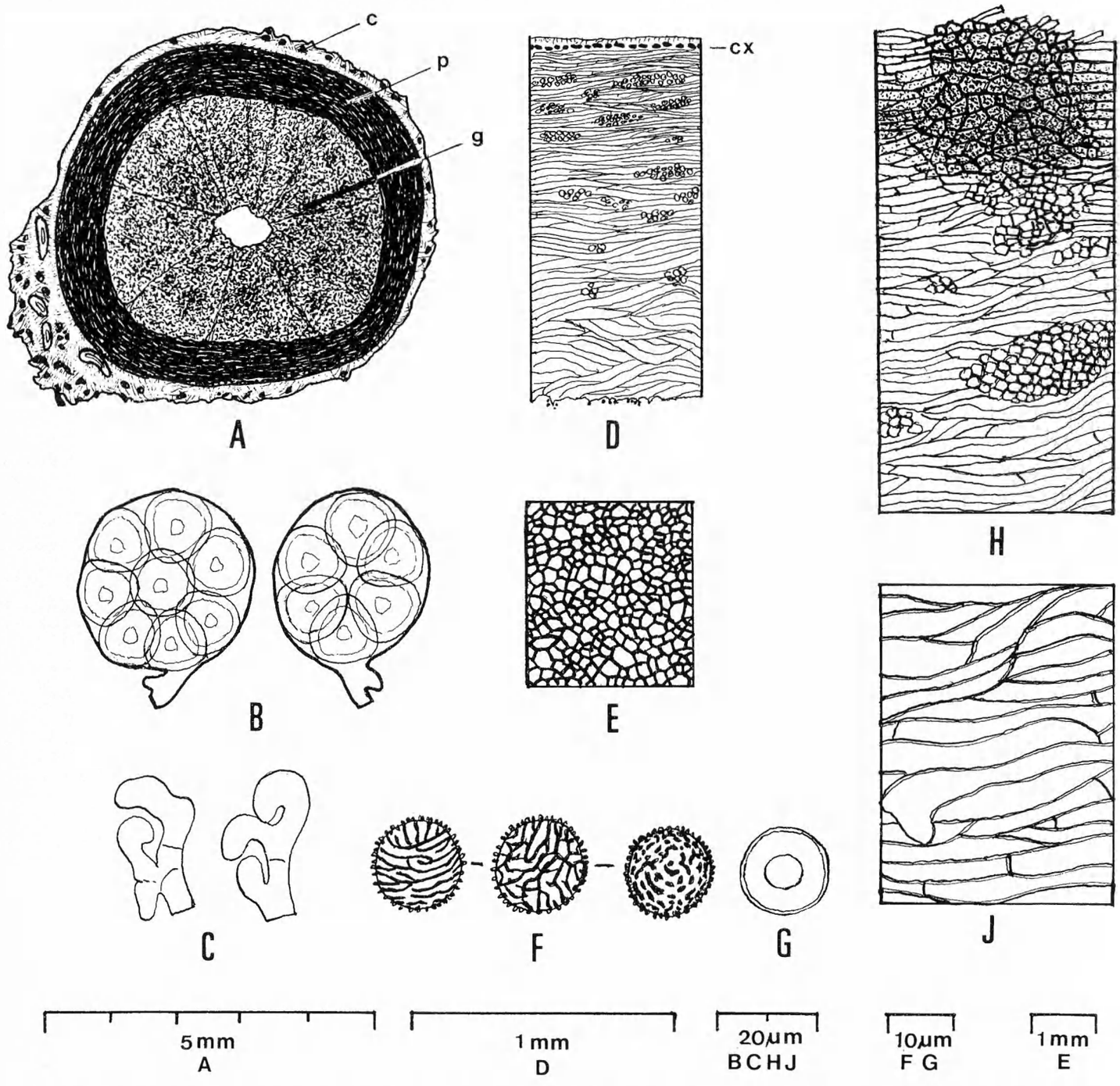

Fig. 1. *Elaphomyces striatosporus* Kers sp. nov. — A: Mature ascocarp in median, vertical section, c=crust, p=peridium, g=gleba. — B: Two asci with immature ascospores. — C: Apical portions of ascogene hyphae with ascus primordia. — D: Cortex and peridium in vertical section, cx=cortex. — E: Surface of ascocarp showing a plane, reticulate pattern. — F: Three mature ascospores showing variable ornamentation (light microscope). — G: Unripe ascospore. — H: Cortex and outer portion of the peridium in vertical section, cx=cortex. — J: Innermost portion of the peridium in vertical section. (Drawn from the holotype).

elastic when moist, of a horny context when dry, dull black in moist condition. Newly cut sections of dry material glossy dark olivaceous brown, concolourous or usually faintly striated by a few diffusely marked tangential lines of a paler colour than the rest. Sections of dry peridium with a faint bluish tinge when studied with the naked eye. Peridium compact, non-lacunose, composed of mainly parallel, tangentially oriented hyphae. Bundles of hyphae running cross-wise with the ordinary system more frequently present in the outer portion of the peridium. Hyphae gradually broader towards the interior, 2–3 μm in diameter near the cortex whereas reaching 5–8

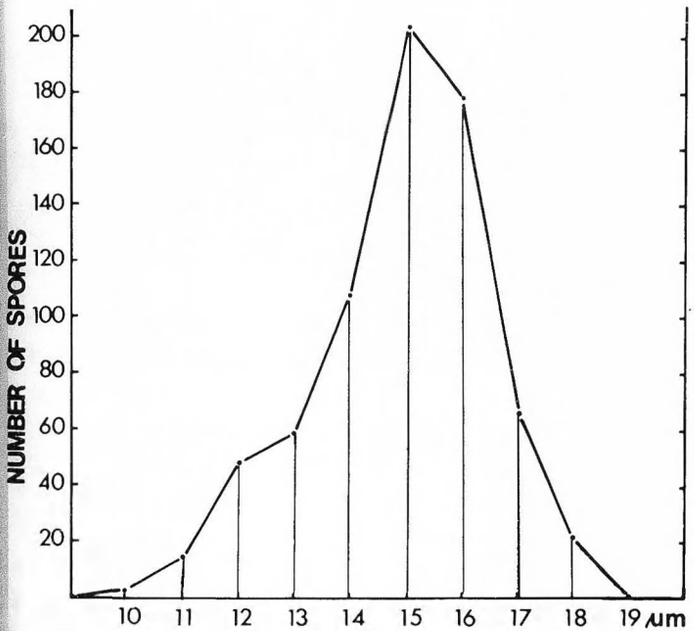

Fig. 2. Diagram showing variation in ascospore size in *Elaphomyces striatosporus*. Ornamentation included. The measurements based on spores from four ascocarps. (From the holotype).

µm in diameter near the gleba, walls 1.0–1.5 µm thick, slightly gelified. *Gleba* dark sepia when mature, sharply set off from the peridium; dissepiments white, evanescent, spurious or lacking in mature ascocarps; capillitium abundant, hyphae smooth, ashy grey in mass, 1.5–2.5 µm in diameter, strongly coiled and twisted, with few septa, sparsely branched, thin-walled. *Asci* (4–6-)8-spored, spherical to obovate in outline, (25–)30–35 µm in diameter when 8-spored, 25–30 µm in diameter when 4–6-spored, stipe c. 5 µm long, the size of the spores shows little if any variation within the individual asci. *Ascospores* spherical, often with long remaining (tetrad) facets in youth, (10–)14–16(–18) µm in diameter inclusively ornamentation 1.0–1.5 µm high. Immature spores hyaline to pale yellowish brown, smooth to faintly warted, exospore c. 1.0 µm thick, cytoplasm enclosing a large oil drop. Mature spores dark sepia to almost black in mass, small spores opaque, larger spores with a semi-transparent endospore wall and an opaque exospore ornamentation. Ornamentation variously shaped, irregularly tuberculate to incompletely reticulate in some spores whereas minutely rugose to striated in most spores.

Holotype: Norway. Oslo District: Aker. Near Gaustad. Under *Corylus avellana*. 22.IX.1952. Leg. F.-E. Eckblad s.n. (O).

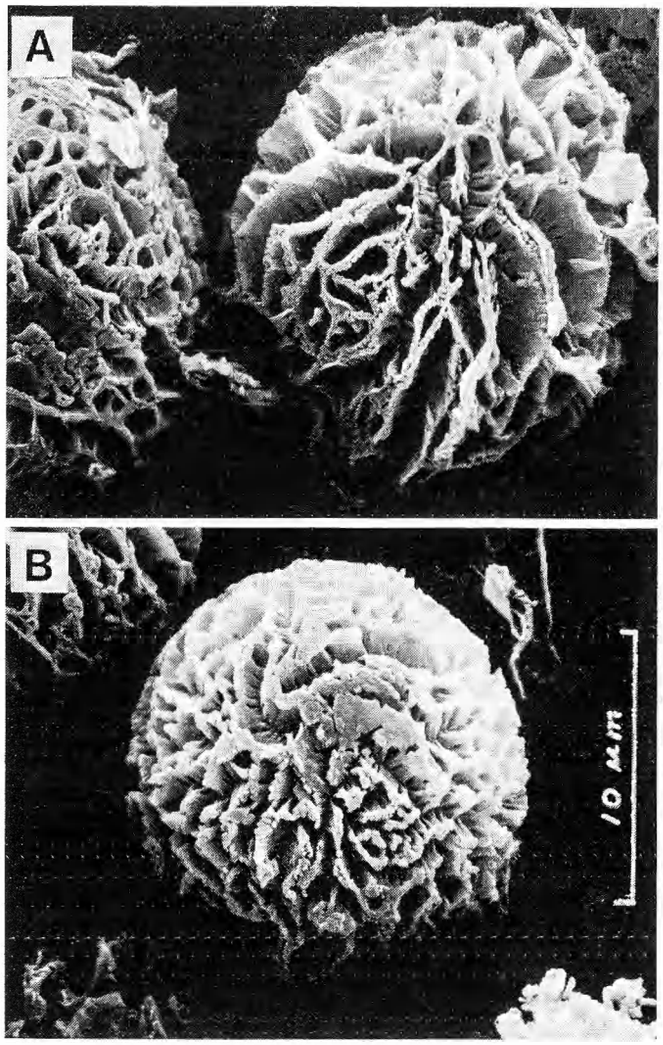

Fig. 3. Mature ascospores of *Elaphomyces striatosporus*, showing variable ornamentation. A = the common type. B = uncommon type with a dense ornamentation. SEM-pictures. (From the holotype).

Comments

The material has previously been classified tentatively as *Elaphomyces leveillei* Tul. (Eckblad 1962 p. 208, 1971, pp. 15, 17). The new species is, however, easily distinguished from that species e.g. by its much smaller ascocarps, whitish mycelial crust, the very thin and smooth cortex, the horny and black peridium, the smaller spores and by the exospore ornamentation. Whereas *E. leveillei* has the brittle and carbonaceous cortex characteristic of the subgenus *Scleroderma* Vitt., the new species is the first Scandinavian representative of the subgenus *Malacoderma* Vitt. This subgenus has been characterized by a very thin and fleshy cortex. The surface of the ascocarps therefore generally becomes more or less wrinkled in drying. Besides, the spores are

comparatively small for the genus, viz. less than 15 μm in previously known species. Although *E. striatosporus* shows the cortical features which distinguish the *Malacoderma*-group, the spores are somewhat larger than would be typical for the subgenus.

A comparison has been made with other species of the *Malacoderma*-group. The following species are known from Europe: *E. atropurpureus* Vitt., *E. citrinus* Vitt., *E. immutabilis* Speg., *E. mutabilis* Vitt., *E. papillatus* Vitt., *E. sulphureo-pallidus* Vacek. From northern America *A. appalachensis* Linder seems to be the only species which can be clearly referred to this species group (cp. Fischer 1897, Dodge 1929, Vacek 1949, Ceruti 1960, Szemere 1965, Linder 1939).

I can not find *E. striatosporus* to be closely allied to any of the aforementioned species. The new species may, however, be compared with *E. mutabilis* and *E. papillatus*. *E. mutabilis* is fairly variable and it has a persisting, thick crust suggesting that found in *E. striatosporus* (cp. Tulasne & Tulasne 1851 p. 105 & Tab. 3: 1, Hesse 1894, p. 65, Fischer 1897 pp. 84, 85, Ceruti 1960 Tab. 2). *E. mutabilis* differs from *E. striatosporus* in the soft-textured, pale coloured peridium, the smaller spores and in the exospore ornamentation. *E. immutabilis* is generally considered to be merely a form of *E. mutabilis* (Fischer 1897 p. 85). It differs in the same features as does *E. mutabilis*.

Szemere has reported 10–19(–26) μm large spores in some specimens which he refers to *E. papillatus* (Szemere 1965 p. 92). The new species is certainly distinct from *E. papillatus* s. str. which differs in the weakly organized crust, the yellowish brown and papillated cortex, loose-textured, lacunose and purplish peridium, generally 4-spored asci, and in the smaller spores and their ornamentation (cp. Hesse 1894 p. 67, Dodge 1929 p. 163, Ceruti 1960 Tab. 3: 2).

Elaphomyces striatosporus may also be confused with *E. cyanosporus* Tul. although this species belongs to a quite different species group, viz. the subgenus *Scleroderma* subsection *Phlyctospora* (Zobel) Dodge. The representatives of this subsection are characterized by a rooting, sterile base. This feature may, however, be weakly developed and even lacking in some specimens. It is not always a reliable characteristic. *Elaphomyces cyanosporus* shows a superficial resemblance to *E. striatosporus* due to the thick, blackish coloured and hard peridium, the slightly wrinkled surface and the generally small ascocarps. It differs from *E. striatosporus* in the much thicker cortex, the context of the peridium and in the large spores with a regular, dense reticulum (cp. Dodge 1929 p. 181 ff, Ceruti 1960 Tab. 10 & 11).

The new species is easily identified by the usually striate spores. A comparable, though not identical ornamentation is found in two other species, viz. *E. virgatosporus* Hollós and *E. carbonaceus* Corner & Hawker (Ceruti 1960 Tab. 10: 2, Corner & Hawker 1953 Fig. 2 G).

The development of the spore ornamentation seems to follow a general scheme in all species studied. Minute, vertical rods are formed into a smooth, gelatinous exospore. As the matrix dries these rods glue to each other. They do this to a variable extent and in different ways so as to form blocks, warts, spines, plates etc. (Hawker 1968). Most spores of *E. striatosporus* appear striate under the light microscope. In these spores the rods coalesce into narrow plates with few anastomoses or branches (Fig. 3 A). In extreme cases some plates extend uninterrupted and simple from pole to pole. If the plates are broken up at short intervals the spores appear minutely and irregularly reticulate under the light microscope (Fig. 3 B).

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Crocus in Greece: new taxa and chromosome numbers

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80 populations of 10 taxa of *Crocus* from N Greece have been studied in cultivation. Two new taxa are described, viz. *C. stridii* and *C. chrysanthus* ssp. *multifolius*. New localities for all taxa studied are presented. Mt Grammos, Mt Ossa, Mt Varnous and Mt Voras are new localities for *C. cvijicii* Kosanin, previously only known from Mt Vermion. *C. sieberi* Gay is widespread in N Greece. The somatic chromosome numbers were established in 56 populations. They deviate from previous reports in some cases, as in *C. veluchensis* Herbert (2n=24, 25), *C. chrysanthus* Herbert (2n=18, 19), *C. olivieri* Gay (2n=6+1B), *C. pulchellus* Herbert (2n=10), *C. sieberi* (2n=24) and *C. cvijicii* (2n=19, 20).

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The authors have been studying the genus *Crocus* in N Greece since 1976. This article is based only on material collected by ourselves. We have made collections all over Greece, but mainly from the central and northern parts. In this paper 80 populations representing 10 taxa, mainly from N Greece, are included. 56 of them were examined cytologically. Further details on chromosome morphology, distribution and variation will be presented later.

A large number of chromosome counts have been published by Brighton et al. (1973). They have started a cyto-taxonomic study of the genus based on some 700 collections kept in cultivation at Kew.

Material and methods

The material has been cultivated either in a private garden in Thessaloniki or in the experimental field of the Copenhagen University Botanical Garden. We generally collected 20 individuals from each population, 10 for drying and 10 for cultivation. Only one corm was kept in each pot so that individual chromosome numbers could be established.

The first set of our collections is kept at the Herbarium of the Institute of Systematic Botany and Phytogeography, Thessaloniki, Greece (H.Th.). Less complete sets are at Kew (K) and Copenhagen (C).

Cytological investigation was limited to mitotic studies using a root tip squash technique. The best results were obtained when the root tips were collected immediately after a frost night and then pretreated in alpha-bromonaphtalene for five hours in a refrigerator at a temperature of c. +4°C. They were then fixed in Carnoy (3:1), hydrolyzed in 1-N HCl at 60°C for 8 minutes, stained in Feulgen for c. two hours and treated in a solution of 5 % pectinase before squashing in 45 % acetic acid. The squash technique used was as in Östergren & Heneen (1962). We counted the chromosome number of at least 10 good metaphase plates of each individual.

Unless otherwise stated the nomenclature is according to Hayek (1933).

The following abbreviations are used: ZE Evgenia Zacharof, PA Kostas Papanicolaou, N. Dramas, N. Kavalas etc. refer to the administrative departments (Nomos) of Greece.

Crocus cvijicii Kosanin

Collections: N. Pellis: Mt Voras, 2 km N of Notia, opening in beech forest, 1500 m, PA 3213 (H.Th., C) — N. Florinis: Mt Varnous, c. 3 km before Pisoderi, 1550 m, ZE 601 (H,Th., C) — N. Imathias: Mt Vermion, along the path from the refuge of Tria Pigadia to the peak of Tsanaktsis, 1600 m, ZE 838 (H.Th.); same path, 1900 m, ZE 538 (H.Th., C); above Koutsoufliani, around the church of Agios Pavlos, 1200 m, ZE 536 (K, H.Th., C); above Ano Grammatiko, along the road to Magoula, 1250 m, ZE 539 (K, H.Th.); summit area, E of the peak of Tsanaktsis, 1800 m, ZE 541 (K, H.Th.)

— N. Ioanninon: Mt Grammos, 10 km N of Plikati, Koukouli, 1820 m, ZE 542 (H.Th., C) — N. Larisis: Mt Ossa, snow-patches in summit area, ZE 603 (H.Th., C).

New to Mt Voras, Varnous, Grammos and Ossa. In Greece *C. cvijicii* was previously known from a single locality on Mt Vermion (Mathew 1976 a). Outside Greece it is present in SW Jugoslavia and SE Albania.

C. cvijicii is a spring species with finely fibrous, reticulate corm-tunics, 2–4 leaves and pale cream to deep orange-yellow flowers with pubescent throat. It has been found at snow-patches at 1800–2300 m, flowering in May and June (Mathew 1976 a). We have, however, also collected it in beech forest, flowering in March (PA 3213, ZE 601, 536, 539).

The species is morphologically and cytologically variable. Variation was observed in flower colour, shape and size of tepals, number of sheathing leaves, and length of perianth-tube.

Chromosome number: 2n=18, 19, 20, In the populations ZE 541 and 536 it was found to be 2n=18 and 19, respectively. In PA 3213 and ZE 601 both 2n=18 and 2n=20 was found; finally ZE 542 had 2n=18 except for one individual which had 2n=20. The numbers 2n=19 and 20 are reported for the first time, the previously known number being 2n=18 (Brighton et al. 1973). Chromosome number variation within populations has also been observed in *C. scardicus* Kosanin (Sopova 1972), which is a close ally of *C. cvijicii* occurring in the mountains W of Skopje, Jugoslavia; it has 2n=32, 34, 35 and 36. Further investigations will be carried out on *C. cvijicii*.

Crocus pulchellus Herbert

Collections: N. Chalkidikis: Peninsula of Agion Oros, main massif of Mt Athos, S side, rocky place, 1850 m, PA 3005 (H.Th., C); above Karyes, chestnut forest, 550 m, PA 3006 (H.Th.); Peninsula of Sithonia, hill of Dragoudeli, Agios Ilias, 750 m, PA 3004 (H.Th., C); peninsula of Kassandra, c. 500 m NW of Nea Skioni, by the road, PA 3073 (H.Th.). — N. Kavalas: Mt Pangaeon, central part of summit area, Tsekour Madra, 1550 m, PA 626 (H.Th.) — N. Imathias: Mt Vermion, c. 3 km N of Koumaria, Ornofolies, 800 m, ZE 581 (H.Th.) — N. Serron: Ipsomata Lachana, on road from Serre to Thessaloniki, PA 3062 (H.Th.).

C. pulchellus is flowering from the beginning of September to the end of October. The corm-tunics are smooth and papery, splitting into rings at the base, the leaves are absent at anthesis, and the flowers are lilac-blue. It occurs in the SE part of the Balkan peninsula; in Greece it is rather common in the north.

It is found in open woods but we also collected it in the summit areas of Mt Athos and Mt Pangaeon. The plants from Mt Athos were reported by Grisebach (1844 p. 374) as *C. speciosus* Bieb.; the latter in fact occurs only in SE Bulgaria and the Crimea. The Athos material may have been mistaken for *C. speciosus* because of its strongly veined tepals, but differs in the following characters: Flowers never speckled externally; throat of perianth deep yellow; filaments yellow and densely pubescent, anthers 0.9–1.4 cm, white.

Chromosome number: 2n=10, 12. All populations mentioned above, except for PA 3006, have been studied. In all plants examined the chromosome number was found to be 2n=12 except for two individuals of PA 3005 which had 2n=10; this number is new for the species which otherwise seems to have uniformly 2n=12 (Brighton et al. 1973, Šopova 1972).

Crocus cancellatus Herbert s.lat.

Collections: N. Pierias: Mt Olimbos, just N of Litochoron, Mili, 350 m, PA 3078 (H.Th.) — N. Kavalas: Mt Pangaeon, NNW side, above the monastery of Thia Analipsis, rocky place, PA 912 (H.Th.) — N. Imathias: Mt Vermion, N of Koumaria, Ornofolies, ZE 511 (H.Th.) — N. Chalkidikis: Peninsula of Agion Oros, main massif of Mt Athos, around the church of Panagia, rocky place, 1550 m, PA 3010 (K, H.Th.).

C. cancellatus is flowering from the beginning of September to the middle of November. Its main characteristics are: Corm-tunics strongly fibrous, coarsely reticulate; leaves absent at anthesis; flowers white to deep blue-purple. It occurs in Greece and S Jugoslavia. The record from the peninsula of Agion Oros is a new one; within this relatively small area there are no less than 5 species of *Crocus*.

Chromosome number: 2n=16, 16+1B. B chromosomes have been reported previously (Brighton et al. 1973). We found 2n=16+1B in all plants of PA 3078 from Mt Olimbos which agrees with the report by Mathew from the same area. All the other populations cited above had 2n=16.

Crocus olivieri Gay

Collections: N. Chalkidikis: Peninsula of Agion Oros, along the path or the summit area, mixed forest, 1250 m, PA 3013 (K, H.Th.) – N. Thessalonikis: Mt Chortiatis, E side, c. 1 km S of the village of Peristera, ZE 519 (K, H.Th.).

For a description, see Mathew (1976 b). Our material fits subsp. *olivieri* exactly. In both our populations the filaments are minutely pubescent but only those of ZE 519 have a purple spot at the apex.

Chromosome number: 2n=6+1B. One accessory chromosome was found in all plants examined of both populations. Previous reports indicate 2n=6 (Mather 1932, Pathak 1940, Šopova 1972, Brighton et al. 1973), 6+2B (Brighton et al. 1973).

Crocus flavus Weston

Collections: N. Ioanninon: Mt Grammos, around Drosopigi, 800 m, ZE 544 (K, H.Th.) — N. Pierias: Mt Olimbos, E side, S of Litochoron, 500 m E of the church of Agios Ioannis, mixed with *C. chrysanthus*, PA 3014 (K, H.Th.).

C. flavus belongs to the *C. olivieri* group. For a characterization, see Mathew (1976 b). PA 3014 fits subsp. *flavus* exactly, while ZE 544 seems to be subsp. *dissectus* Baytop & Mathew, which has several slender style branches; it has been considered an endemic of W Turkey.

Chromosome number: 2n=8, counted in both populations. Brighton (1976) found 2n=8 and 8+11B. No accessory chromosomes were observed by us.

Crocus chrysanthus Herbert

Crocus chrysanthus belongs to the *C. biflorus* group (see under *C. stridii*). *C. chrysanthus* is distributed on the Balkan Peninsula and in E Romania. It is variable cytologically (Šopova 1972, Brighton et al. 1973) and morphologically. It is rather common in Greece. We found the somatic chromosome numbers 2n=8, 12, 18, 19, 20. Our material with 2n=8 differs morphologically and therefore we describe it here as a new subspecies.

C. chrysanthus subsp. **multifolius** Papanicolaou & Zacharof, ssp. nov. — Fig. 1 A

Orig. coll.: N. Larisis: 3 km E of Skotousa, Aigiannis, 400 m, 24.2.1976, Papanicolaou 3015 (C holotypus, K et Herb. Univ. Thessaloniki isotypi).

Folia (4–)5–6, flores superantia. *Filamenta* papillosa; lobi antherarum colorati atropurpurei. *Chromosomatorum somaticum* numerus 2n=8.

Other collections: N. Magnisias: Above Velestinon, around the church of Panagia, 500 m, PA 3039 (H. Th.) — N. Pellis: Mt Voras (Kajmakčalan), along the forest road to the highest point, opening in beech forest, 1350–1500 m, 1976 PA (C).

Leaves usually 5–6, much exceeding the flowers. *Filaments* papillose; basal lobes of anthers with a blackish-purple spot at the tip. *Chromosome number* 2n=8.

2n=8 was counted in all three collections mentioned. The cytotype with 2n=8 occurs in S Jugoslavia as well. (Šopova 1972), but nothing is mentioned about morphological features of the Jugoslavian plants. Known distribution in Greece, see Fig. 2.

C. chrysanthus subsp. **chrysanthus** — Fig. 1 B

Collections: N. Kastorias: Mt Vitsi, 3 km after Oxia on forest road from Kastoria to the peak, opening in beech forest, 1200–1300 m, ZE 527 (K, H.Th., C); along the road from Kastoria to Amideon, on the cross to Klissoura, ZE 513 (K, H.Th.) — N. Kozanis: Mt Voion, 5 km before Pentalofos, on road from Konitsa to Kozani, opening in beech forest, 1500–1550 m, ZE 526 (K, H.Th., C); Mt Askion, c. 5 km from Vlasti on road to Ptolemaida, beech forest, 1300 m, ZE 528 (K, H.Th., C) — N. Larisis: Mt Ossa, 2 km N of Spillia, opening in oak forest, 900–950 m, ZE 525 (K, H.Th., C); c. 3 km from Elason on road to Larisa, ZE 530 (K, H.Th., C) — N. Ioanninon: 5 km before Metsovon on road from Trikala to Ioannina, opening in beech forest, 1500 m, ZE 524 (H.Th., C); Mt Grammos, 5 km N of Plikati, opening in beech forest, 1300 m, 1978, ZE (K, H.Th., C) — N. Pierias: Mt Olimbos, Litochoron, around the church of Agios Ioannis, PA 3012 (K, H.Th., C) — N. Serron: Ipsomata Lachana, on road from Serre to Thessaloniki, ZE 533 (K, H.Th., C); Mt Kerkini (Belles), 3 km N of Ano Porojia, 700 m, ZE 523 (K, H.Th., C); Mt Menikion, Mousnitsa, c. 20 km from Serre along the forest road to the peak, 900 m, ZE 520 (K, H.Th., C); 11 km N of Serre, close to Chrisopigi, 800 m, ZE 516 (K, H.Th., C) — N. Dramas: Mt Rodhopi, along the forest road from Drama to Karadere, 1100 m, ZE 532 (H.Th., C); Mt Falakron, E side, beside Nestos river, Tulubari, c. 850 m, ZE 531 (K, H.Th., C) — N. Kilkis: c. 3 km from Kilkis on road to Thessaloniki, ZE 522 (H.Th., C); 3 km from Polikastron on road to Kilkis, ZE 823 (H.Th., C) — N. Thessalonikis: Mt Chortiatis, above Chortiatis, along the forest road to the peak, opening in beech forest, 850 m, ZE 521 (K, H.Th., C); outside Asvestochorion, Kouri, oak forest, PA 3040 (H.Th.) — N. Chalkidikis: Peninsula of Kas-

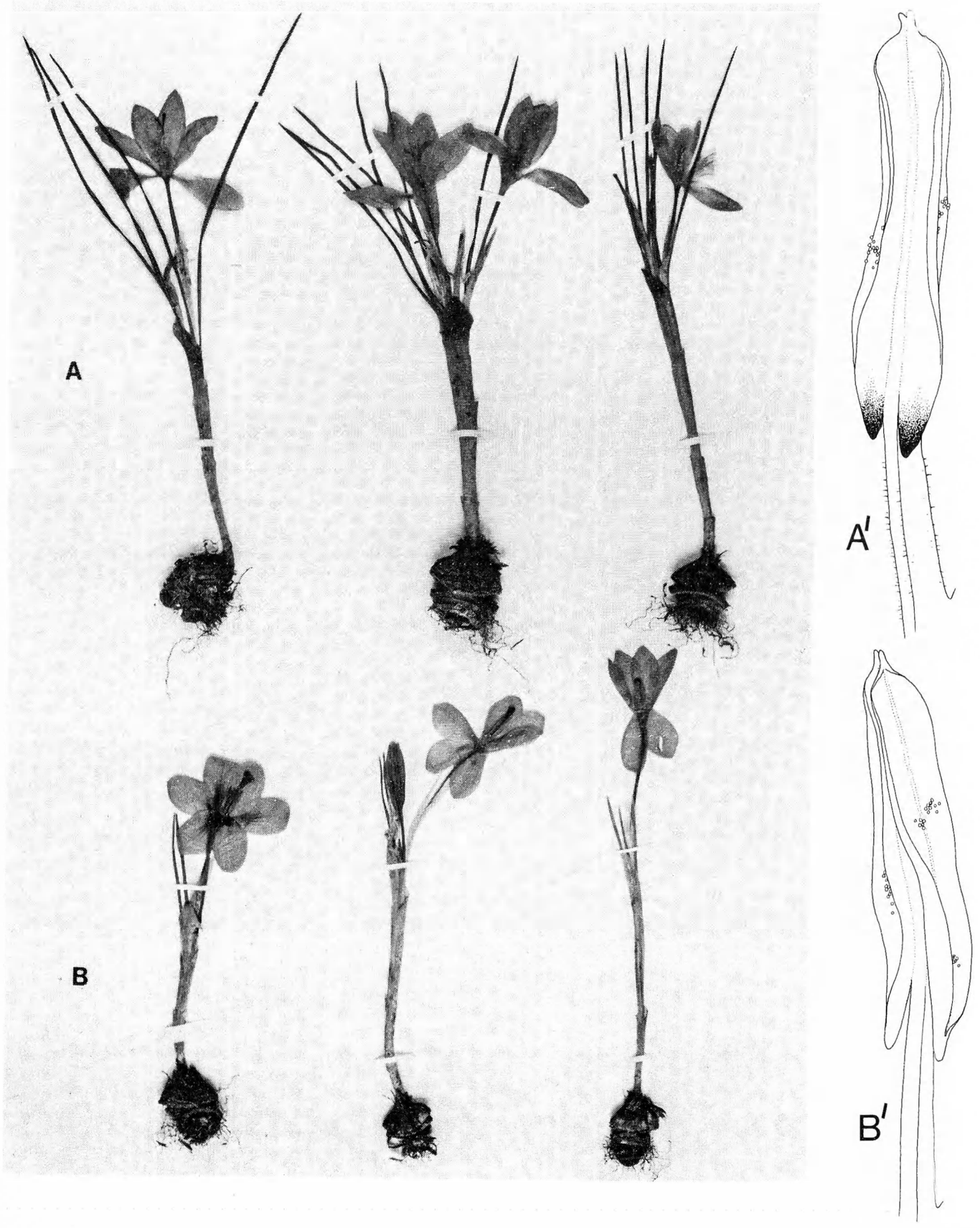

Fig. 1. *Crocus chrysanthus*, habit (×0.5) and stamen (×5.7). — A: subsp. *multifolius* (PA 3015), note papillose filament and blackish spot at tips of anther lobes. — B: subsp. *chrysanthus* (ZE 531).

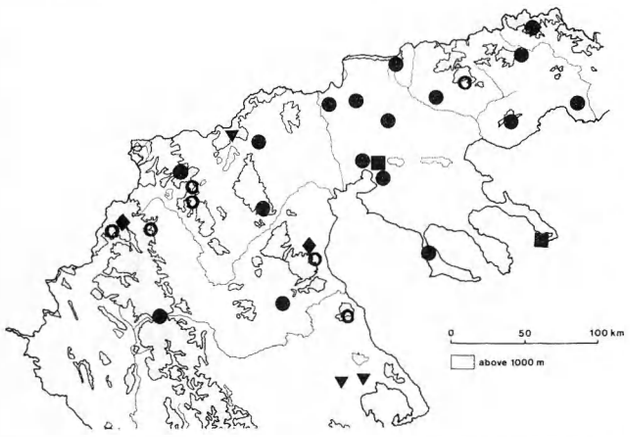

Fig. 2. Localities for cultivated material of ● *C. chrysanthus* ssp. *chrysanthus* (open circles: not cytologically studied. — ■ *C. olivieri*. — ◆ *C. flavus*. — ▼ *C. chrysanthus* ssp. *multifolius*.

sandra, c. 5 km N of Kalandra, ZE 518 (K, H.Th., C) — N. Kavalas: Mt Pangaeon, S–SE side, along the forest road from Akrovounion to the peak of Pilaf Tepe, opening in beech forest, 1400 m, ZE 517 (K, H.Th., C); E of Kavala, near Podolivadon, ZE 514 (K, H.Th., C) — N. Imathias: Mt Vermion, along the road from Veria to Kozani, close to Panagia Soumela, 1300 m, ZE 515 (K, H.Th., C) — N. Pellis: c. 4 km from Edessa on road to Florina, PA 3011 (K, H.Th.).

Leaves 3–4, shorter than the flowers; basal lobes of anthers with or without a blackish-purple spot; filaments usually glabrous.

Chromosome number: 2n=12, 18, 19, 20. The number 2n=18 is new for the species, found in three plants of ZE 515 while the rest had 2n=20; the number 2n=19 is also new, found in two plants of ZE 523, while the rest had 2n=20. 2n=12 was known previously (Brighton et al. 1973); in out material it occurs in ZE 528 and ZE 516. In all the other populations examined (ZE 527, ZE 530, ZE 524, ZE 533, ZE 532, ZE 531, ZE 522, ZE 823, ZE 521, PA 3040, ZE 512, ZE 517, ZE 514, PA 3011) 2n=20 was found. The geographical origin of our material is shown in Fig. 2.

Crocus sieberi Gay

Collections: N. Pellis: Mt Voras (Kajmakčalan), S side, NE of Panagitsa, along the forest road from Patima to Kalivia Giannakoula, 1350–1500 m, 1976, PA (C) — N. Ioanninon: 5 km from Metsovon on road to Trikala, Profitis Ilias, beech forest, 1500 m, ZE 512 (K, H.Th.) — N. Serron: Mt Menikion, 23rd km on road from Serre to Eripia Lailia, opening in beech forest, 1300–1350 m, ZE 508 (K, H. Th.) — N. Imathias: Mt Vermion, between Kastanea and Zoodochos Pigi, beech forest, 1250–1350 m, ZE 500 (K, H.Th.) — N. Kozanis: Mt Askion, just outside Vlasti on road to Ptolemaida, beech forest, 1300 m, ZE 504 (K, H.Th.) — N. Thessalonikis: Mt Vertiskos, above Ossa, along the path to the peak, beech and oak forest, 800 m, PA 202 (H.Th.) — N. Kastorias: Mt Voion, above Kotili, 1200–1300 m, PA 201 (H.Th.) — N. Pierias: Mt Pieria, W of Elatochorion, 850–950 m, PA 209 (H.Th.).

C. sieberi is a spring species with reticulate corm-tunics but without a basal spathe. The flowers are pale lilac to deep lilac-purple or combinations with white; there are 2–7 leaves, 1.5–6 mm wide, present at anthesis.

The species was previously regarded as endemic to Greece but occurs in Jugoslavia as well (B. Mathew, pers. comm.). It is morphologically very variable (Fig. 3). *C. nivalis* Bory & Chaub. from NW Greece and *C. atticus* Orph. from Attica are possibly conspecific. ZE 512 (Fig. 3 D) fits more or less *C. nivalis* (Hayek 1933) by having a deep yellow, pubescent throat and 7–10 mm long anthers. Plants intermediate to *C. sieberi* s.str. are found in other populations, however.

ZE 508 (Fig. 3 A) is deviant and we are not sure whether it belongs to *C. sieberi* or to *C. veluchensis* Herb. or is a hybrid between these two; some individuals have a white, pubescent throat and white filaments, features, occurring in *C. veluchensis*, whereas other plants in the same population have yellow, glabrous throat and yellow filaments. *C. sieberi* and *C. veluchensis* are very close and possibly not distinct species.

Chromosome number: 2n=22, 24. The chromosome number was found to be 2n=22 in ZE 500, ZE 504, PA 201, PA 1976 and 2n=24 in ZE 508 (only two plants were examined cytologically); this may be a hybrid between *C. sieberi* with 2n=22 and *C. veluchensis* with 2n=26, but further studies are needed since intraspecific aneuploidy is common in *Crocus*.

Crocus veluchensis Herbert

Collections: N. Pierias: Mt Olimbos, E side, S of Litochoron, 500 m E of the church of Agios Ioannis, PA 3000 (K, H.Th.) — N. Dramas: Mt W. Rodhopi, along the forest road from Drama to the peak of Karadere, Bozovo, mixed forest, 1400 m, ZE 500 (K, H.Th.); Mt Falakron, E of Pirgi, alpine region, snow-patches, 1700 m, ZE 552 (H.Th.); Central Rodhopi, N of Prasinada, peak of Spilia, 1100 m, ZE 557 (H.Th.) — N. Florinis: Mt Varnous, 3 km from Pisoderi on road to Florina, 1500 m, ZE 506 (K, H.Th.); Mt Varnous, 8 km E of Agios Germanos, ZE 507 (K, H.Th.) — N. Imathias:

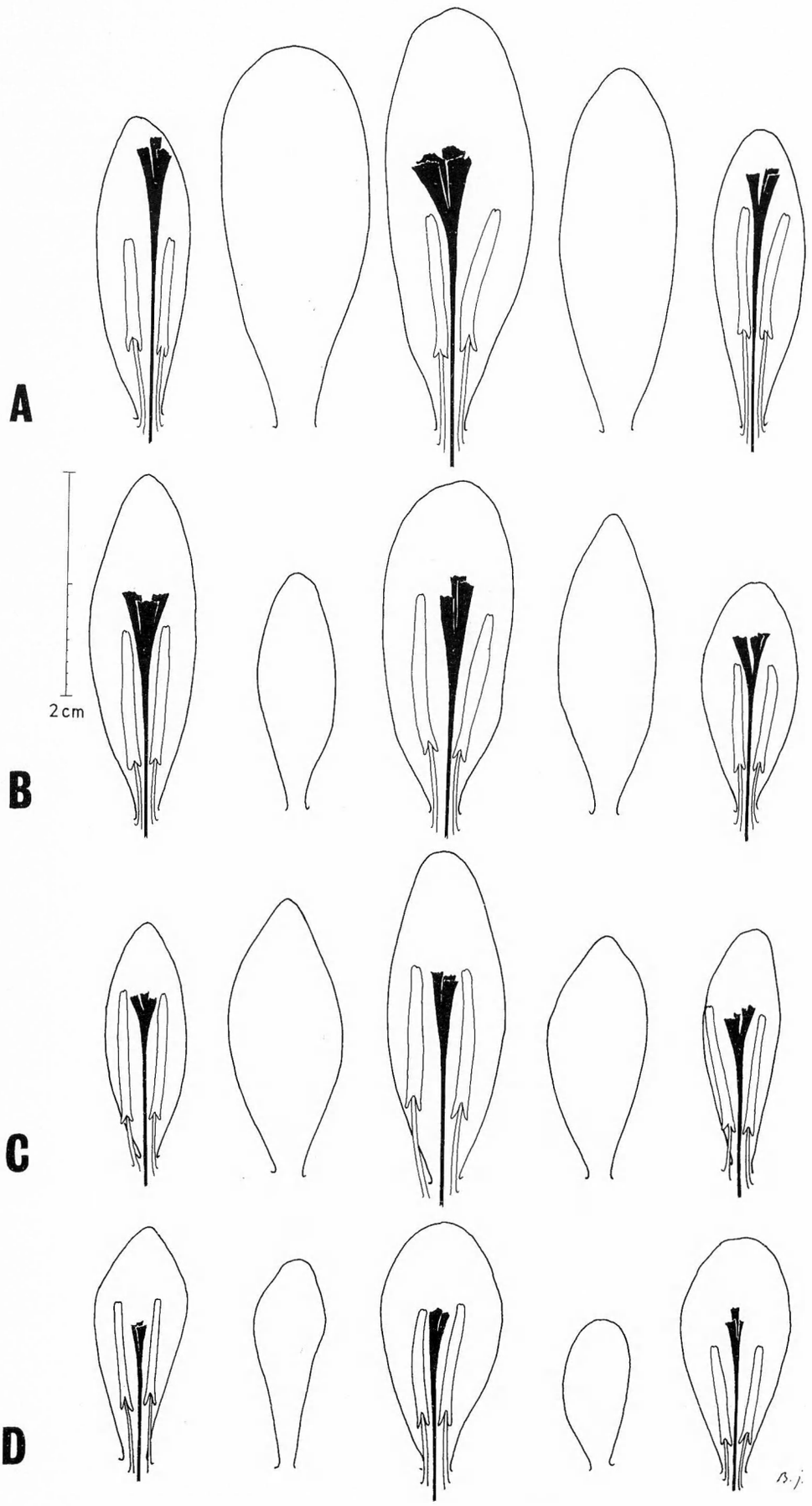

Fig. 3. *Crocus sieberi*, tepals from five different individuals from four populations. — A: ZE 508. — B: ZE 504. — C: ZE 505. — D: ZE 512.

Mt Vermion, above Agios Pavlos, 1700 m, PA 261 (H.Th.) — N. Magnisias: Mt Pilion, just above Chania, beech forest, PA 3002 (K, H.Th.) — N. Kavalas: Mt Pangaeon, S side, along the road from Akrovounion to the peak of Pilaf Tepe, opening in beech forest, 1200 m, ZE 503 (K, H.Th.); Mt Pangaeon, central part of summit area, Tzitzova, snow-patches, 1700–1750 m, ZE 509 (K, H.Th.) — N. Larisis: Mt Ossa, alpine area, snow-patches, PA 3001 (K, H.Th.) — N. Chalkidikis: Mt Cholomon, above Arnea, beech forest, 650 m, ZE 501 (K, H.Th.) — N. Serron: Mt Kerkini (Belles), above Ano Porojia, 900 m, ZE 551 (H.Th.) — N. Xanthis: Mt Rodhopi, W of Dimarion, opening in beech forest, ZE 602 (H.Th.) — N. Pellis: Mt Paikon, W of Kromni, 1300 m, ZE 553 (H.Th.); Mt Voras (Kajmakčalan), W of Ano Garefion, 1100 m, PA 3021 (H.Th.) — N. Kilkis: Mt Disoron (Krousia), above Ano Theodorakion, 600 m, PA 3022 (H.Th.) — N. Ioanninon: Mt Grammos, N of Plikation, 1200 m, ZE 555 (H.Th.).

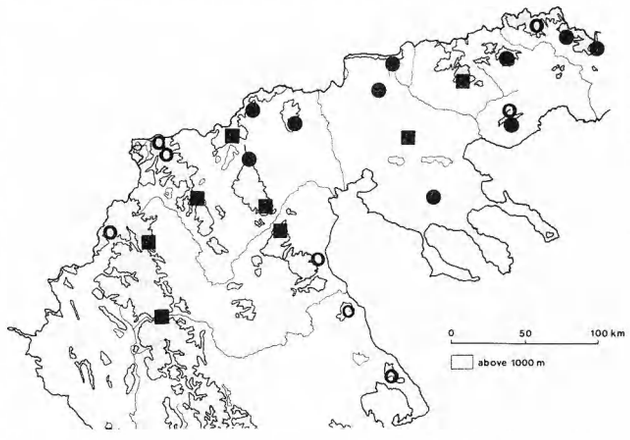

Fig. 4. Localities for cultivated material of ● *C. veluchensis* (open circles: not cytologically studied). — ■ *C. sieberi* (total distribution in N Greece).

C. veluchensis belongs to the spring-flowering group with reticulate corm-tunics which is also represented in Greece by *C. cvijicii* and *C. sieberi*; the flowers are pale to deep lilac-blue with a white, pubescent throat. It is distributed on the S part of the Balkan peninsula.

According to Hayek (1933), *C. veluchensis* has entirely white or violet flowers with a hairy throat, while *C. sieberi* has white and violet or pure white tepals, while the throat is yellow and glabrous. The only reliable character in our material of *C. veluchensis* seems to be the white throat, however. The species overlap in distribution (Fig. 4) and ecology.

Chromosome number: 2n=24, 25, 26. 2n=26 was found in all populations studied (ZE 500, ZE 557, PA261, ZE 503, ZE 501, ZE 551, ZE 553, PA 3021, PA 3022) except in ZE 552 which had 2n=24 and 25. Previous reports are 2n=20 (Šopova 1972), 2n=26 (Brighton et al. 1973), 2n=46 (Popova 1972).

Crocus stridii Papanicolaou & Zacharof, sp. nov. — Fig. 5

Orig. coll.: NE Greece, N. Thessalonikis, Mt Chortiatis, above Chortiatis, 800 m, 14.2.1977, Zacharof 543 (C holotypus, Herb. Univ. Thessaloniki isotypus). In meadow, by a stream, together with *C. chrysanthus*.

Cormus ovoideus, 1,5–2 cm diam.; *tunicae* papyraceae, inferne in annulos concentricos horizontaliter circumscissos secedentes; *Folia vaginantia* 4–6, albida; *folia* 5–8, synanthia, 1–1,2 mm lata, ciliata, flores superantia; *bracteae* binae, albidae, 6–8 cm longae. *Flores* 1–3, hiemales; *perianthii tubus* 5–10 cm longus, extus 6-vittatus, fauce puberulus; *perianthii segmenta* oblanceolata, acuta, 2,5–3,5×0,7–1 cm magna, extus 3-vittata vel alba, basi aurantiaca. *Filamenta* aurantiaca, papillosa vel puberula, 5–6 mm longa; *antherae* atropurpureae vel luteae, 11–14 mm longae, sagittatae, lobis basalibus 2–2,5 mm longis; pollen pallide flavum; *stigma* antheris brevius vel plus minusve aequans; *stylus* aurantiacus, rami stigmatici 3. *Capsula* ellipsoidea, 9–11×4,5–5,5 mm.

Corm ovoid–globose, 1.5–2 cm in diameter; tunics smooth, the innermost coriaceous, the outer papery, splitting into rings at the base, the rings toothed, constricted at the top into a short toothed sheath. *Sheathing leaves* (proper spathes) 4–6, whitish. *Leaves* 5–8, present at anthesis, slender, acuminate, much exceeding the flowers, upper surface with a distinct white line covering as much as c. 2/3 of leaf-width, distinctly or sparsely ciliate. *Bracts* (bracteoles) 2, whitish, 6–8 cm. *Flowers* 1–3, appearing in winter; perianth-tube very slender, white with 6 purple stripes, 5–10 cm long, c. 1.1 mm in diameter; *segments* oblong-lanceolate, more or less acute, 2.5–3.5×0.7–1 cm, the outer mostly white with three purple stripes on the back or entirely white, the inner white and not striped; *throat* deep yellow to orange, puberulent. *Filaments* orange, papillose or puberulent, 5–6 mm long; *anthers* mostly purple (some individuals with yellow anthers), 11–14×c. 0.5 mm, c. 2.5 times as long as the filaments, sagittate, with basal lobes 2–2.5 mm long; pollen grains pale yellow. *Style* orange-red, divided into 3 slender branches, shorter than or equal to the anthers. *Capsule* elliptical, 9–11×4.5–5.5 mm. Chromosome number 2n=10.

Crocus stridii is a winter species belonging to the *C. biflorus* complex, characterized by smooth,

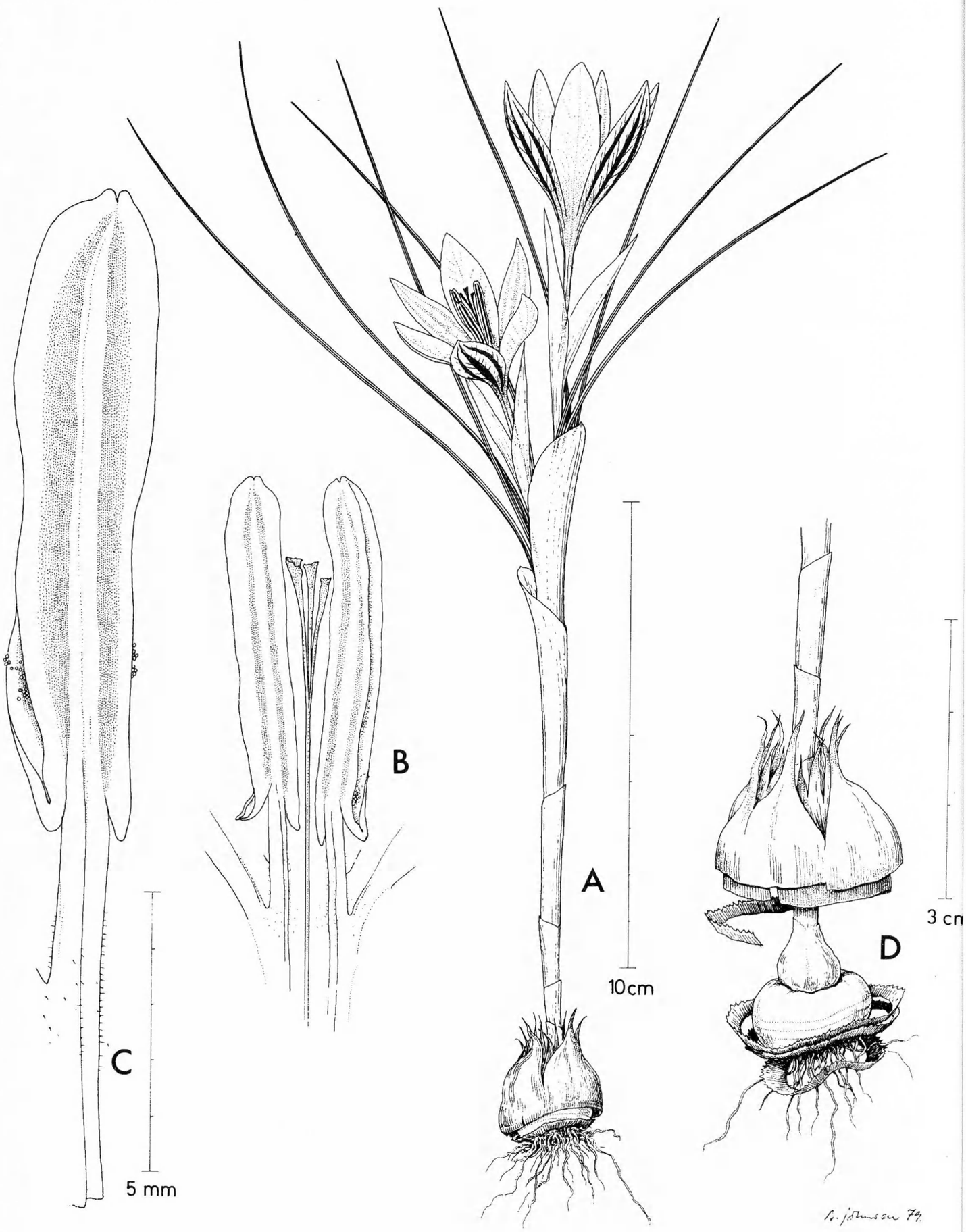

Fig. 5. *Crocus stridii*, type collection. — A: Habit. — B: Part of throat, stamens and style. — C: Stamen (note papillose filament). — D: Corm (note tunics splitting off at base).

Table 1. Differences between *Crocus stridii* and related species. Information on *C. biflorus* and *C. crewei* is taken from Hayek (1933) and Hooker (1845) respectively.

Species	No. of sheathing leaves	No. of leaves	Pubescence of throat and filaments	Anthers	
				Colour	Length (mm)
C. biflorus	2	3–5	glabrous	yellow	6–11
C. crewei	2	2	glabrous	purple	5–6
C. stridii	3–6	5–8	puberulent or papillose	purple or yellow	11–14

papery corm-tunics splitting into rings at the base. The complex comprises *C. pestalozzae* Boiss. and *C. danfordiae* Maw (both extra-European), *C. chrysanthus, C. biflorus* Mill. and *C. crewei* Hook. fil. (Mathew & Baytop 1976). *C. stridii* is most similar to the two last mentioned, but can be easily separated on the higher number of leaves and sheathing leaves, the longer anthers and the puberulent throat (Table 1). There is another plant described from W Turkey which comes into consideration, *C. biflorus* var. *nubigena* (Herbert) Bak., which also belongs to the above mentioned complex (Mathew & Baytop 1976) and has purple anthers but differs constantly from *C. stridii* in having anther length 6–7 mm (B. Mathew, pers. comm.).

Acknowledgements. We would like to thank Professors Arne Strid and G. Lavrentiades for their encouragement and advice in this work and in the preparation of the paper, and also Dr Brian Mathew who confirmed some of our determinations. The drawings were made by Mr B. Johnsen and the Latin diagnosis were checked by Dr T. Christensen.

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Inheritance of dissected leaflets in Vicia grandiflora Scop.

KOSTAS PAPANICOLAOU

Papanicolaou, K. 1980 06 16: Inheritance of dissected leaflets in Vicia grandiflora Scop. *Bot. Notiser 133:* 165–167. Stockholm. ISSN 0006-8195.

Entire versus dissected leaflets in *Vicia grandiflora* Scop. is controlled by a single pair of genes, the former showing incomplete dominance. Individuals with the three types of leaflet shape (entire, intermediate and dissected) may be found in the same population and are not worthy of taxonomic recognition. All three forms have 2n=14 and 97–99 per cent pollen fertility.

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Vicia grandiflora Scop. is a yellow-flowered annual which may be distinguished from the superficially similar *V. lutea* L. and *V. hybrida* L. on the glabrous standard, subequal calyx-teeth and relatively large number of seeds per legume (c. 15). It is widespread in the east Mediterranean area extending westwards to Italy and Sicily (Ball 1968) and eastwards to S Russia, the Crimea, N and NW Iraq and Afghanistan (Davis 1969).

V. grandiflora is a variable species, especially as far as leaflet characters are concerned (Boissier 1872, Halácsy 1901, Hayek 1927, Davis 1969). Plants with dissected leaflets have been recognized as *V. grandiflora* var. *dissecta* Boiss. (Boissier 1872) or as *V. serrata* Pantoc. (Pantocsek 1873); the latter has been recombined as *V. grandiflora* var. *serrata* (Pantoc.) Rohl. (Rohlena 1905) or *V. grandiflora* subsp. *rotundata* (Ser.) Janch. var. *serrata* (Pantoc.) Rohl. (Hayek 1927).

Materials and methods

Variation in leaflet shape was observed in a collection (Papanicolaou 127) from Mt Pangaion (Pangaeon) in NE Greece. Seeds taken from herbarium specimens gave rise to five individuals with entire leaflets, four with dissected leaflets and two with an intermediate type of leaflets.

Reciprocal crossings were made between individuals with entire and dissected leaflets. Nearly all the flowers of three individuals with entire leaflets and two individuals with dissected leaflets were emasculated to be used as female parents. The anthers were removed by means of a forceps prior to pollen shedding, an excessive amount of foreign pollen was immediately put on the stigma, and the inflorescences were isolated in bags. Pollination was repeated after 6–7 days. After 10 days the bags were removed to facilitate the ripening of the pods.

All the inflorescences of one individual with entire leaflets, one with dissected leaflets and two with the intermediate type of leaflets were isolated in bags without emasculation to be self-pollinated.

Seeds of all the above plants were harvested in the end of June, 1978, and sown in December of the same year.

To establish the chromosome numbers the plants were kept overnight at c. 5°C; root tips were fixed in the Svalöv modification of the Navashin-Karpechenko fixative, sectioned with a microtome and stained with crystal violet. At least ten good metaphase plates were examined in each slide.

Pollen fertility was established by using "cotton blue" (10 g phenol, 10 ml glycerine, 10 ml lactic acid, 10 ml water, 0.5 g cotton blue). A small amount of pollen was mixed in a droplet of the above solution on a slide and covered with a plastic cover slip. The percentage of stained pollen grains was calculated (between 250 and 300 pollen grains were counted in each slide).

Results and discussion

Crossings between individuals with entire and dissected leaflets produced hybrids with the intermediate type of leaflets regardless whether plants with dissected leaflets were used as male or female parent (15 hybrids were produced in

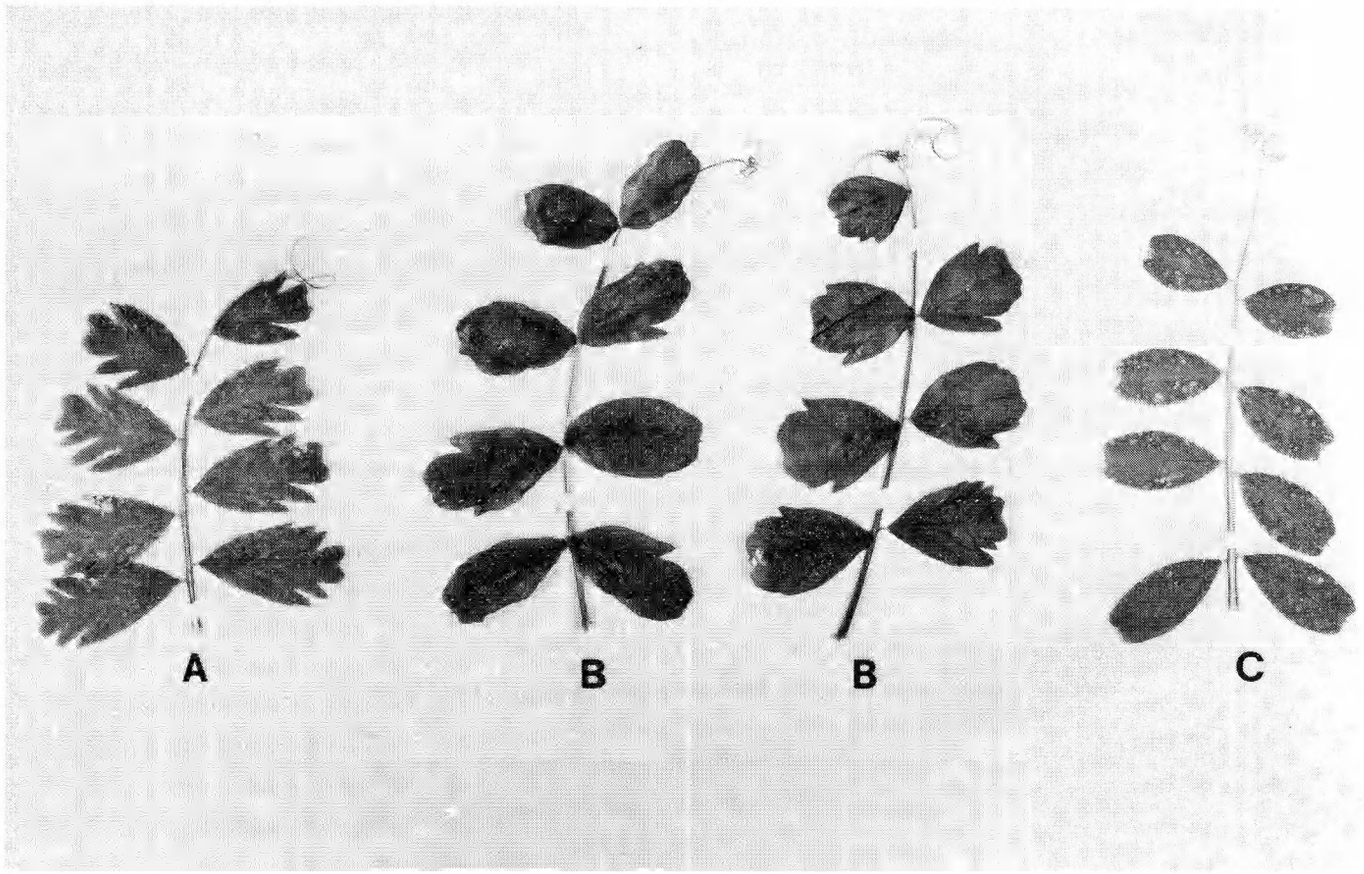

Fig. 1. Leaves (70 % of natural size) of *Vicia grandiflora*. — A & C: Dissected, and entire leaflets respectively. — B: Intermediate leaflets of a hybrid between A and C.

one case, 20 in the other). Pollen fertility of parents as well as hybrids was found to be 97–99 per cent.

Ten seeds of two legumes, obtained from two isolated (self-pollinated) flowers of a plant with entire leaflets produced ten individuals which had the same leaflet shape as the parent.

Fifteen seeds of three pods, obtained from three isolated (self-pollinated) flowers of a plant with dissected leaflets produced fifteen individuals which had the same leaflet shape as the parent.

From the two individuals with an intermediate type of leaflets 46 seeds were obtained after isolation (self-pollination) of six flowers. These seeds gave rise to eleven individuals with entire leaflets, 23 with an intermediate type of leaflets and 12 with dissected leaflets, i.e. very close to a 1:2:1 ratio.

The results agree with the assumption that the observed variation in leaflet shape is controlled by a single pair of genes, the factor for entire leaflets showing incomplete dominance. Presumably this applies also to the forms with dissected leaflets which have previously been recognized as a separate variety or even species. Given the simple genetic background and the fact that mixed populations occur, plants with dissected leaflets should not be recognized as a separate taxonomic entity.

Leaflet shape may be used as a genetic marker by plant breeders. It is important for identifying hybrids in highly self-pollinating species such as many in the genus *Vicia*. Donnelly (1958, 1962) and Moriya (1961) have used the flower colour or the absence of tendril, respectively, as an aid in identification of varieties, in seed certification, in weeding out off-type plants resulting from chance crossing or mechanical mixing, and in genetic studies of other characteristics.

The chromosome number was counted in four individuals (two with entire and two with dissected leaflets). It was found to be $2n=14$ in all cases. This agrees with the number reported by others from other areas (Yamamoto 1973, Donnelly 1962, etc.).

Acknowledgements. The study was suggested by Professor Arne Strid who also read the manuscript. The photograph was taken by Mr. Flemming Sarup.

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Taxonomic significance of septal ultrastructure in the genus Onnia Karsten (Polyporineae/Hymenochaetaceae)

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Moore, R. T. 1980 06 16: Taxonomic significance of septal ultrastructure in the genus Onnia Karsten (Polyporineae/Hymenochaetaceae). *Bot. Notiser 133:* 169–175. Stockholm. ISSN 0006-8195.

Septal ultrastructure of *Onnia* spp. and a selected number of other polypore type species indicates that there is an anomalous group of genera in the Hymenochaetaceae with nonperforate parenthesomes. These are *O. circinata, O. leporina, O. tomentosa, Inonotus hispidus,* and *Phellinus torulosus.* The species found to have regularly perforate parenthesomes were *Coltricia perennis, Fomes fomentarius, Phaeolus schweinitzii* and *Polyporus tuberaster.* The possible taxonomic significance of these observations is discussed.

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The several patterns of septal ultrastructure are of critical importance in the taxonomy of higher fungi (Moore 1978, 1979, 1980). Within the Basidiomycota there occur several fundamental variations of the characteristic dolipore/parenthesome septum: most species of the superclass Homobasidiomycia have regularly perforate parenthesomes (Patton and Marchant 1978), while the jelly fungi (Heterobasidiomycia), with the exception of the Tremellineae, have nonperforate parenthesomes. An exception to this distribution was reported by Setliff et al. (1972) when they showed nonperforate parenthesomes in *Polyporus tomentosus.* Although this assignment of this species is accepted by, e.g., Overholts (1953), Harrison (in Petersen 1971), and Miller (1972), an inquiring letter to Dr. D. N. Pegler elicited the response that this species "... has no connection with the genus *Polyporus* (Mich.) Fr. nor indeed with the family Polyporaceae (Fr.) Fr. It is a xanthochroic species belonging to the Hymenochaetaceae Donk, in the genus *Onnia* Karst. ..."

The following study was therefore undertaken to determine if the septal morphology of this species was an isolated example or whether, perhaps, it was part of a larger anomaly.

Materials and methods

Mycelium from cultures of the following fungi was fixed for 1 h in 3 % acrolein in 0.2M sodium cacodylate buffer (pH 7.2), washed for 1 h in the buffer, postfixed for 1 h in 1 % buffered OsO_4, rinsed in the buffer (two changes in 10 min.), dehydrated in an acetone series (interrupted by overnight staining in 1 % uranyl nitrate in 70 % acetone) transferred to propylene oxide, and embedded in Epon 812. Epon resin was prepared by mixing exactly 10 ml of Epon 812 with 8.9 ml of MNA (methylnadicanhydride) and then adding and mixing 0.28 ml DMP-30 (2,4,6-tri [dimethylaminomethyl] phenol). Material from propylene oxide was processed through a graded series of 2:1, 1:1, 1:2 propylene oxide:Epon resin mixture (15 min per step), and then through three changes of 100 % Epon over a day. Specimens were then placed in flat embedding moulds and caused to harden by being placed in a 60°C oven for 48 hours.

Sections cut with a diamond knife on a Cambridge-Huxley ultramicrotome were picked up on uncoated grids and stained for about 30 seconds with Reynolds' lead stain (1.33 g lead nitrate + 1.76 g sodium citrate dissolved in 30 ml distilled water; shake for 30 min, add 8 ml 1N NaOH and dilute to 50 ml with distilled water). After a thorough rinsing the grids were examined in an AEI EM-6G electron microscope.

Coltricia perennis (Fr.) Murrill. Centraal Bureau voor Schimmelcultures, CBS 372.52.
Fomes fomentarius (L. ex Fr.) Kickx. Forest Products Research Laboratory, Aylesbury, England, FPRL 50E.

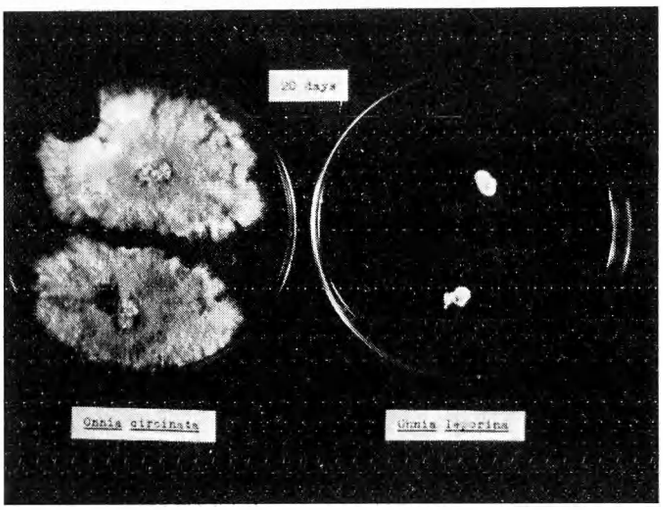


Fig. 1. Difference in growth rates on malt agar between, left, *Onnia circinata* (CBS 246.30) and, right, *O. leporina* (CBS 420.48).

Inonotus hispidus (Fr.) Karsten. CBS 386.61.
Onnia circinata (Fr.) Karsten. CBS 246.30.
Onnia leporina (Fr.) Jahn. CBS 420.48.
Onnia tomentosa (Fr.) Karsten. DAOM 52894.
Phaeolus schweinitzii (Fr.) Patouillard. CBS 326-29.
Phellinus torulosus (Pers.) Bourd. & Galz. FPRL 222.
Polyporus tuberaster Fries. Eastern Forest Products Laboratory of Canada, Ottawa, S-61.

Results and discussion

The first of Karsten's two species, *Onnia circinata,* was designated as the type by Murrill in 1903 (Donk 1960). This species and *Polyporus dualis* Peck have been placed in synonomy with *O. leporina* (Jahn 1978). In culture CBS 420.48 grows much slower than CBS 246.30 (Fig. 1). In the 1972 CBS catalogue the first number is listed as *P. circinatus* var. *dualis* and the second is listed as *P. circinatus* Fries. The parenthesomes of both isolates are nonperforate (Fig. 3). Those of CBS 246.30 are unusual in that in median section they frequently display a circumflex profile with a clear spot in the central 'bend' (Fig. 3 A). There is a suggestion in Fig. 2 B that the parenthesomes of *O. tomentosa* may have similar central inclusions. Although the parenthesomes of these two isolates are comparable, the marked differences in their growth rates may indicate that *O. leporina* and *O. circinata* are, in fact, distinct species. But it must be emphasised that these observed cultural differences are between just two isolates—one that has been in culture since 1948, the other since 1930 (last two digits of the CBS numbers). Their significance, if any, can be verified only by extensive studies of more, preferably recently collected, isolates. (There is, of course, the added *caveat* of all mycological studies based on cultures, that the results are no better than the correct identity of the isolates being used).

Karsten's second species, *Onnia tomentosa,* was transferred to *Coltricia* by Murrill in 1904; it is treated in this genus by Ryvarden (1978), although he also includes it in his key to the species of *Onnia;* Lowe (1942) treats the species as a synonym of *Polyporus circinatus.* In *Coltricia, C. tomentosa* is the only species with setae. The type species of *Coltricia* is *C. perennis,* a species that has perforate parenthesomes (Fig. 5 A, C), while *C./O. tomentosa* has nonperforate parenthesomes (Fig. 2 B, C) and in which a central clear inclusion may occasionally be seen (Fig. 2 B). The ultrastructural evidence, therefore, supports Karsten's original interpretation and Jahn's (1978) present inclusion of this species in *Onnia.*

There is another species of *Onnia, O. triqueter* (Lentz) Imaz., but material of this species has not been available. The characters of this and the other two recognised species are also discussed by Černý (1974).

Jahn (1978) remarks in his summary that *Onnia* is close to *Inonotus,* another Karsten genus segregated from *Polyporus* Fr. and typified by *I. hispidus.* The septa of this species have nonperforate parenthesomes (Fig. 3 D). The difference in septal micromorphology between *C. perennis* and *I. hispidus* could be a critical diagnostic character for separating *Coltricia* and *Inonotus,* genera whose borderline is "somewhat troublesome" (Ryvarden 1978).

Pegler in the aforementioned correspondence also suggested that *Phaeolus schweinitzii* and *Phellinus* spp. might also be related to *Onnia.* These genera, like *Coltricia, Onnia,* and *Inonotus,* are in the Hymenochaetaceae. The type species of *Phellinus, P. torulosus,* does have nonperforate parenthesomes (Fig. 2 A), but those of *Phaeolus schweinitzii,* type species of this genus, prove to be perforate (Fig. 5 B, E). Because many species of *Phellinus* have been previously referred to *Fomes* (s. lat.) and the other species examined here to *Polyporus,* it was deemed desirable to determine the ultrastructure of *F. fomentarius* and *Polyporus tuberosus,* their respective type species. Both of these species

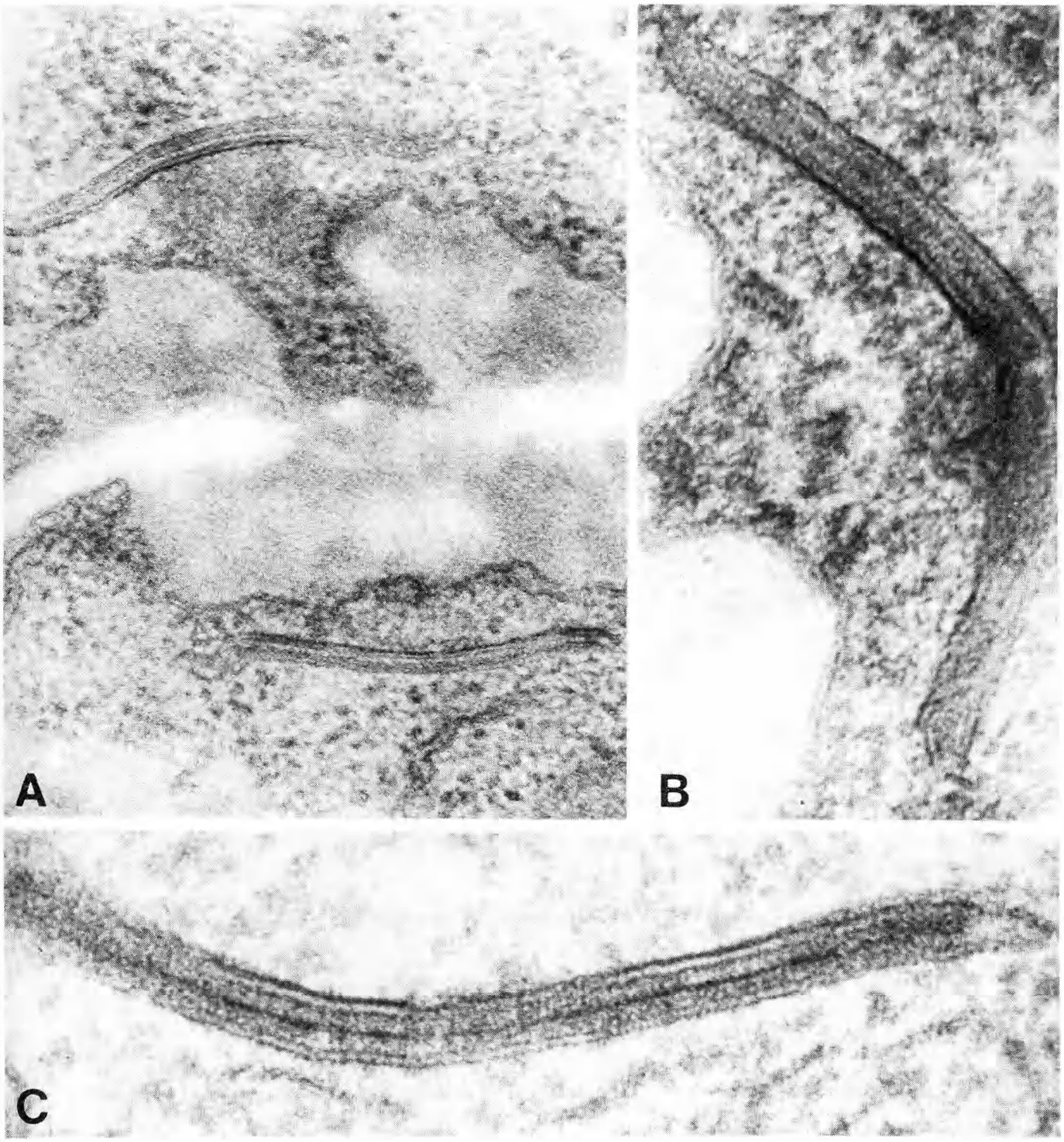
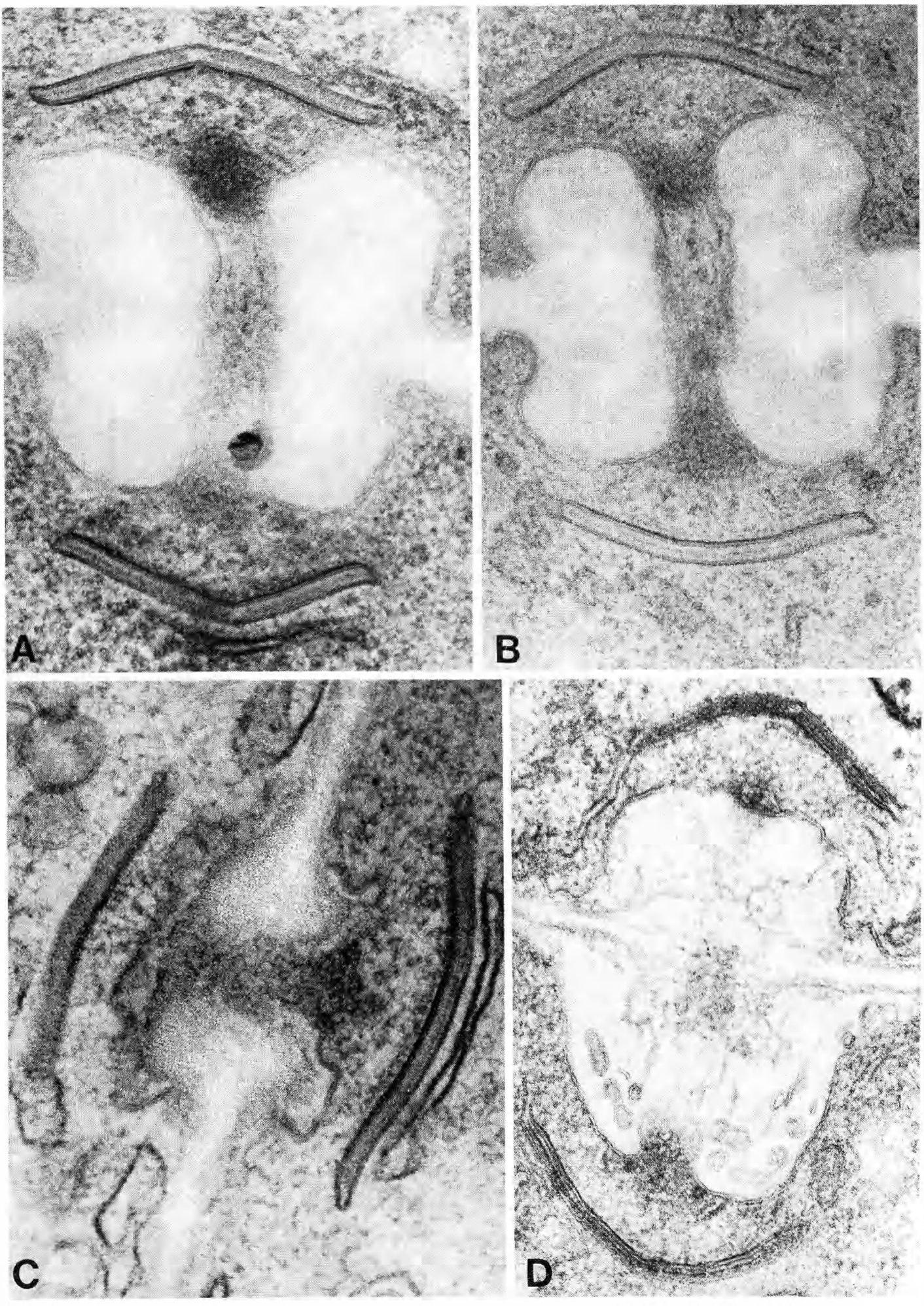


Fig. 2. Parenthesome morphology. — A: Slightly oblique section of a *Phellinus torulosus* dolipore septum showing both of the nonperforate parenthesomes (×100,000). — B–C: *Onnia tomentosa* parenthesomes (×250,000). — B: A parenthesome with a median clear spot similar to those of *O. circinata* (Fig. 3 A); the rim of the dolipore is discernible on the left. — C: Median parenthesome section showing the structural characteristics: a pair of bounding membranes that frequently are observed to be continuous with the endoplasmic reticulum (see Fig. 3 D & Moore 1975), a central interposed line or membrane (see Moore & Patton 1975), and a dark matrix material.

have the anticipated perforate parenthesomes (Figs. 4, 5 D).

The taxonomy of the 'polypores' is very complex and in a state of flux. A number of the postfriesian genera proposed in the last century and early in this one are only now gaining general recognition, largely through close attention to the mitic system (Pegler 1973 a, b). But, as Donk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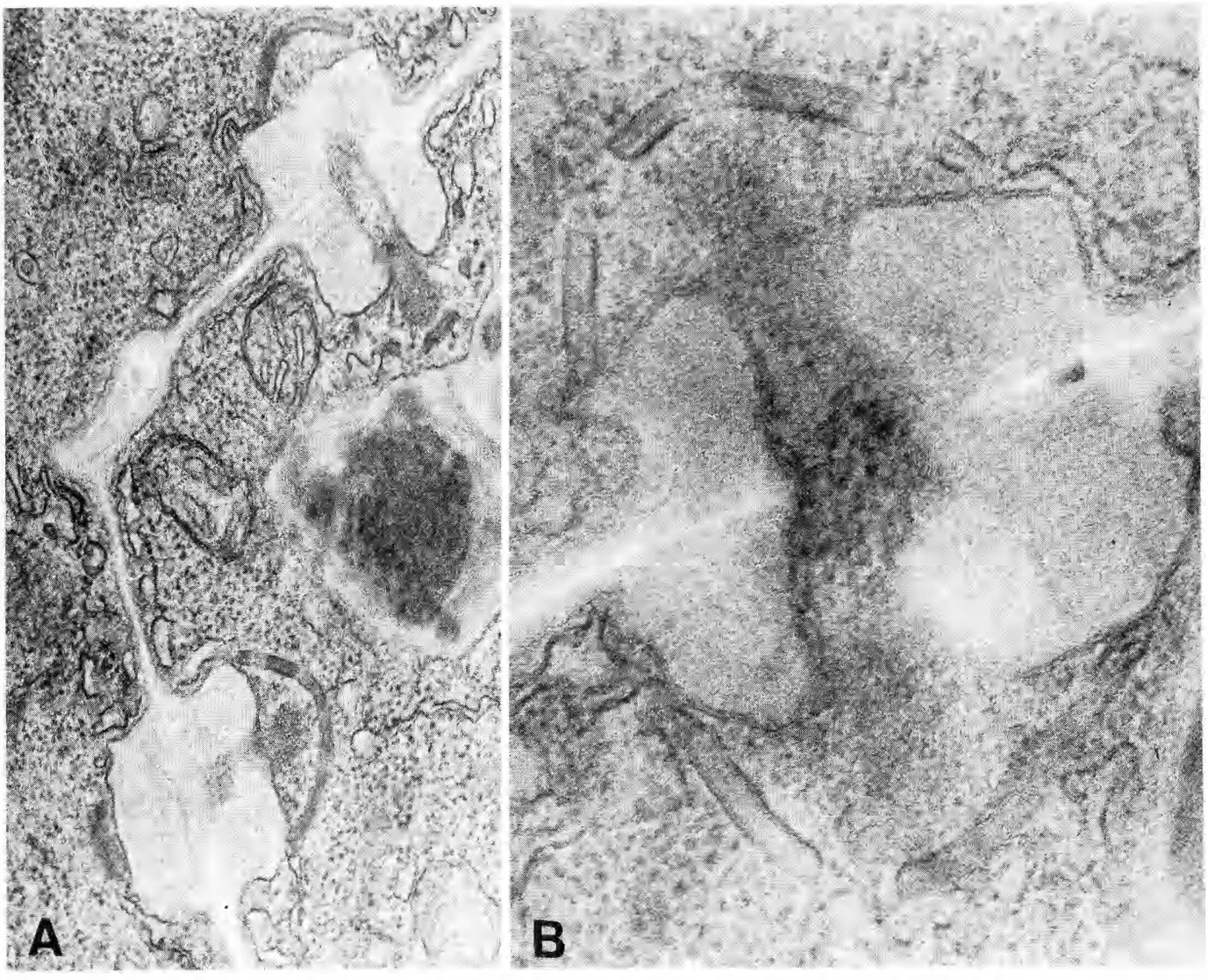
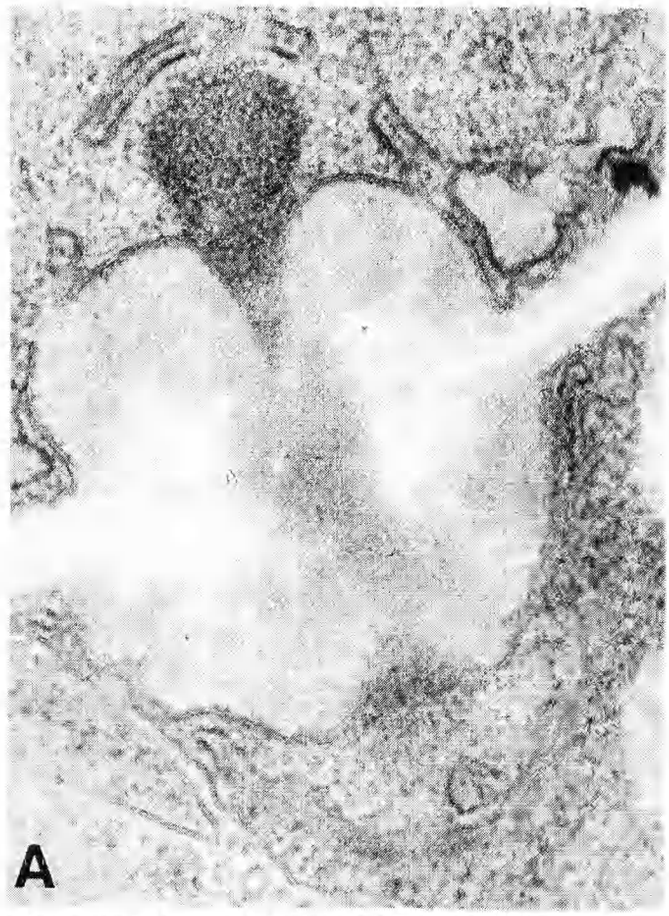


Fig. 4. Septa of *Fomes fomentarius*. — A: 1.s. through a clamp connection showing both dolipores and perforate parenthesomes (×50,000). — B: Median 1.s. of a septum at higher magnification showing the perforate nature of both parenthesomes (×100,000).

(1964) points out, improvements in the classification of these fungi requires "... an increasingly bigger repertoire of characters from which to draw." The importance of cultural, developmental, and histochemical studies is well established (Petersen 1971, Part 2), but the significance of subcellular characters discernible only by transmission electron microscopy still remains largely unappreciated. In the present limited sampling of the Hymenochaetaceae there is the prospectus of an aggregate of species with nonperforate parenthesomes. Those examined here represent only the polyporoid genera of the subfamily Hymenochaetoideae and appear in the group at the end of Donk's (1964, p. 276) key. This group also includes *Aurificaria, Cyclomyces, Coltriciella, Flaviporellus, Phylloporia,* and *Xanthoporia*. To determine the extent of the distribution of this exceptional trait will require the examination of not only material from spe-

Fig. 3. Dolipore septa with nonperforate parenthesomes (×100,000). — A–B: *Onnia circinata*. — A: A near median section in which each parenthesome has a circumflex profile and displays a clear spot in its 'bend' (compare with Fig. 2 B of *O. tomentosa*); a characteristic darkly staining occlusion is observable in the upper orifice of the dolipore. — B: Median dolipore section showing both occlusions and typical parenthesomes. C: *Onnia leporina*. — D: *Inonotus hispidus*.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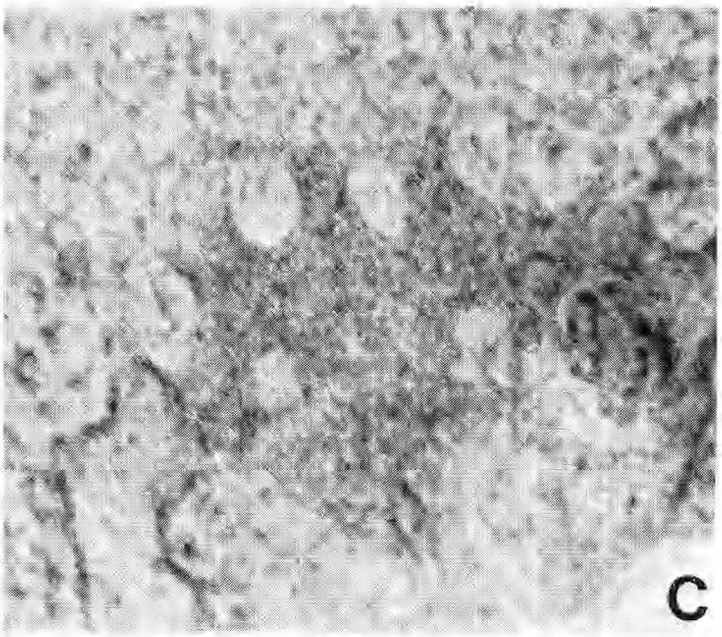
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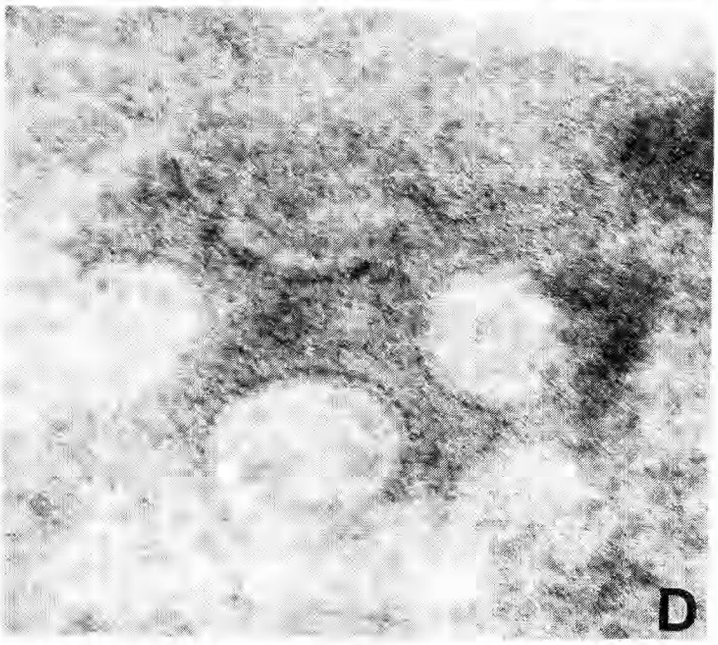
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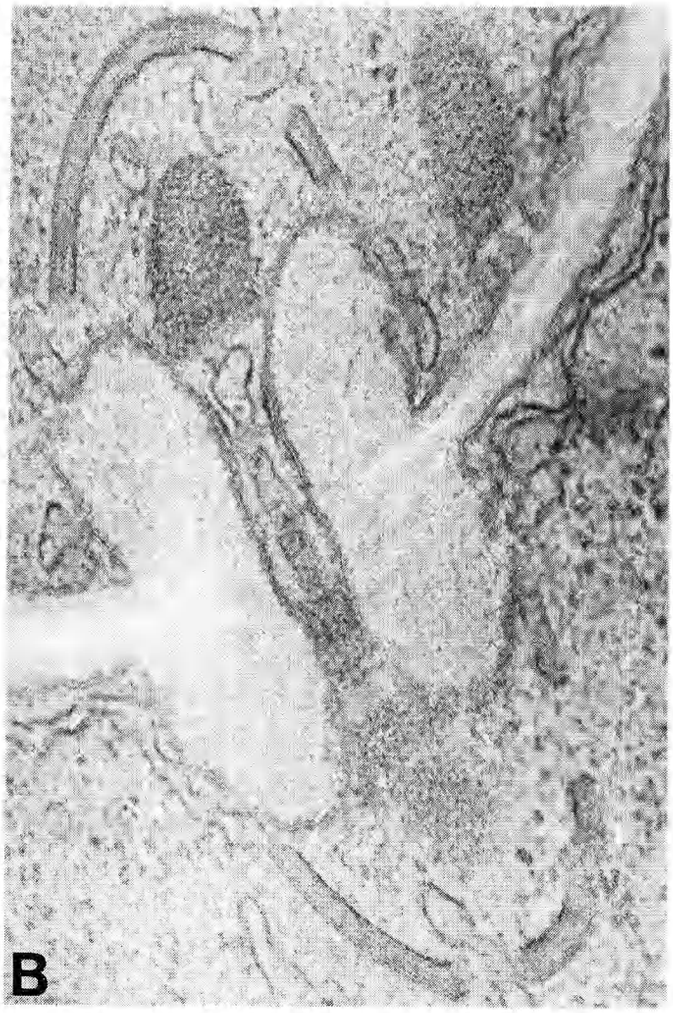
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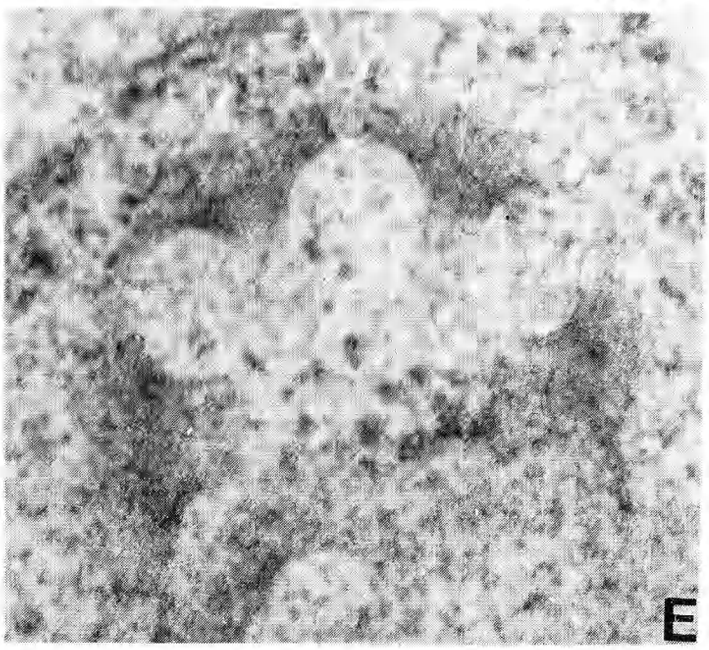
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cies of these and other genera in the family, but also material of additional species of the genera examined here. Most such material is not available in the major culture collections. The elucidation of this information requires, therefore, that authorities who know and have access to living material of these species (field or culture) arrange for its electron microscopical analysis.

I remain convinced that septal ultrastructure is basically a conservative character and that exceptions to general patterns can be of great taxonomic importance. Thus species of *Inonotus, Onnia* and *Phellinus* with nonperforate parenthesomes are novel within the Homobasidiomycia, while species of *Coltricia* and *Phaeolus* with perforate parenthesomes appear to be counter-exceptional, but whether just within this group of genera or within a larger segment of the subfamily or family remains to be determined.

Acknowledgements. It is a pleasure to recognise the esteemed assistance of Dr. S. F. Lowry for his help with the electron microscopy and photography. The very helpful correspondence of Dr. D. N. Pegler is also gratefully acknowledged.

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Fig. 5. Septa with perforate parenthesomes. — A–B: l.s. of septa (×100,000) — A: *Coltricia perennis.* — B: *Phaeolus schweinitzii.* — C–E: glancing parenthesome sections showing differences in pore size and distribution (×150,000); such variation may have taxonomic significance (Patton & Marchant 1978). — C: *C. perennis.* — D: *Polyporus tuberosa.* — E: *P. schweinitzii.*

The pollen morphology of the tribe Calenduleae with reference to taxonomy

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Pollen morphological studies of the representatives of all the 8 genera of the tribe Calenduleae were made by light and transmission electron microscope. The tribe is rather stenopalynous and five pollen types reliable to the genera of the tribe are recognizable. The pollen morphological data confirm the current generic boundaries of the tribe and indicate a reassessment of the taxonomic status of *Dipterocome,* which does not fit in the tribe Calenduleae. Structural exine characteristics in this tribe support a consanguinity with the Heliantheae and Senecioneae.

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The Calenduleae currently comprise eight genera including the strongly deviating, monotypic genus *Dipterocome* which has to be considered more as a "satellite" genus of the tribe. The tribe Calenduleae consists of 113 species and a large number of subspecies (Norlindh 1978).

The Calenduleae occur throughout Africa. They are also found in south and central Europe and in west and southwest Asia, but seem to be concentrated in the Mediterranean area and South Africa.

Palynologically, the tribe is rather stenopalynous. However, certain pollen morphological features, recorded in the genera and species of the tribe, are undoubtedly interesting for taxonomic purposes.

The most important pollen morphological studies of the taxa included in the Calenduleae were previously made by Stix (1960), Dimon (1971), Praglowski (in Norlindh 1978) and Skvarla et al. (1978). However, in these publications, the Calenduleae are treated in a larger context and a pollen morphological monograph on the Calenduleae still does not exist. Therefore, the authors felt that a brief palynological investigation of the tribe Calenduleae would be useful.

The aim of the study is to present a general survey of the pollen morphological data of the 37 representatives of the entire tribe investigated hitherto and to establish the pollen types. It is also hoped that the results obtained will be useful for further taxonomic work on the tribe Calenduleae.

Material and methods

Dried polliniferous material from S was used along with one specimen of *Gibbaria scabra* and one of *Castalis tragus* received from GB and LD, respectively. All the specimens were selected and identified by Prof. T. Norlindh.

Material for light microscopic studies was acetolyzed and embedded in glycerin-jelly. The slides were sealed with paraffin and about 20 pollen grains were measured and examined the day after the preparation of slides. The light microscope observations are incorporated in the text and summarized in Table 1. Photomicrographs were taken with a Leitz Ortholux microscope equipped with ×100, N.A. 1.32, oil immersion objective using Ilford sheet film SP 348. The material for electron-microscopy was not acetolyzed. Whole anthers were treated for about 50 hours in TAG solution (Rodewald & Karnovsky 1974). Subsequently, the pollen grains were treated with 0.1 % OsO_4 solution, dehydrated, and embedded in Spurr. Ultra-thin sections, about 600 Å thick, were sectioned on

Table 1. Pollen morphological data of selected species of the tribe Calenduleae. Measurements in μm. Collections, see Appendix.

Taxon	polar axis	eq. diam.	ora lalongate	lolongate	distinctly pointed ends at equator	slightly constricted	not constricted	colpi distinct	comparatively distinct	almost indistinct	w w th 2
Calendula											
C. officinalis	42	44		8×4			+			+	
C. arvensis	46	47		10×5			+		+		
C. echinata	37	38		8×6		(+)	+		+		
C. fulgida	39	43		7×3			+	+			
C. maritima Ross 347	38	40		7×5			+	+			
C. suffruticosa	39	42		8×5			+		+		
Osteospermum											
O. spinosum var. *spinosum*	32	34	4×10		+	+	(+)	+			
O. spinosum var. *runcinatum*	28	30	3×8		+	+			+		
O. polygaloides	27	28	2×6		+	(+)	+		+		
O. sanctae-helenae	32	33		6×4		+	+	+			2-
O. thodei	33	35		8×6		(+)			+		2-
O. calendulaceum	27	29	3×6				+		+		
O. dentatum Acock 650	30	31	4×7	5×3		(+)		+			
O. dentatum Lindeberg s.n.	34	36		4×7			+	+			2-
O. connatum	29	30		7×3			+		+		
O. amplectens	27	28		5×4			+	+			
O. fruticosum	33	34	2×8		+		+		+		
O. acutifolium	32	33	4×10		+	+				+	
O. caulescens	36	38	5×10		+	+		+			
O. ecklonis	29	31	3×8		+	+	(+)		+		
Chrysanthemoides											
C. incana	30	31		5×3			+			+	
C. monilifera	31	32	3×7				+			+	
Dimorphoteca											
D. pluvialis	25	26	2×6			+			+	+	
D. chrysanthemifolia	34	36	3×9		+	+	+		+		
D. cuneata	31	32	4×11			+			+		
D. montana var. *montana*	29	31	3×12		+	+	+	+			2-
D. montana var. *venusta*	36	37	6×11			+		+			2-
D. polyptera	25	24		3×2			+		+		
D. sinuata (n=9)	26	27	3×7				+		+		
D. sinnuata (2n=18)	Diameter =37 μm		5×9				+		+	+	
Castalis											
C. tragus	30	32	3×9		+		+		+		
C. nudicaulis	31	33	5×10	6×5	+	+	+		+		5-
C. spectabilis	36	38	5×14		+	+			+		
Gibbaria											
G. scabra	30	31	3×6	(5×3)			+			+	
G. ilicifolia T. Norlindh 5595	26	27	(3×5)	4×3			+		+		
G. ilicifolia Hafström s.n.	25	28	(3×4)	4×3			+		+		
Garuleum											
G. pinnatifidum	34	35		6×4			+		+		2-
G. latifolium	32	33		5×3			+			+	
G. bipinnatum	33	35		6×4			+		+		2-
Dipterocome											
D. pusilla	32	30		6×3			+	+			

distance between apices	height of solid zone	height of basal zone	with one hole	with two-holes	with conical confines	cavae maximal height	thick-ness of exine (polar view, mesocolpia)	remarks
7.0	5.0	1.5				2.0	13.0	pollen often irregular in size and shape (genetic disturbances)
10.0	4.5	1.5				4.0	13.0	caveae comparatively high
7.0	3.0	1.0				2.5	9.5	ora often with minute, pointed, lateral incisions
7.0	4.0	1.0				3.0	10.5	ora often with minute, pointed, lateral incisions
7.0	3.5	2.0	+		(+)	3.5	13.0	hole in spines distinct, circular ora occur
8.0	4.0	1.0				5.0	13.0	caveae comparatively high
6.5	2.0	2.5	+			1.0	7.5	
6.0	1.5	2.0	+			1.0	6.5	
5.5	1.5	2.0	+			1.5	7.5	
8.0	2.5	2.5	+	+		<1.0	8.0	ora often rectangular in shape
7.5	2.5	2.5		+	+	2.5	9.0	conical confines in the solid zone of spines are encountered
5.5	2.0	3.0	+			1.0	6.5	
5.5	2.0	2.5	+			1.5	8.0	
8.5	2.0	3.0	+		+	1.0	9.0	comparatively large, oval ora, conical confines in the solid zone of spines are encountered
6.0	2.0	2.5	+		(+)	1.0	8.0	slightly constricted ora occasionally occur, conical confines in the solid zone of spines are encountered
5.5	2.0	2.0	+			1.0	6.5	circular ora occur
6.0	1.5	2.5	+			1.5	7.0	
7.0	2.0	3.0	+			1.0	8.0	
7.5	2.0	3.0	+			1.5	8.5	
5.5	1.5	2.5	+			2.0	7.0	
5.5	2.5	2.0	+			<1.0	6.5	caveae thin, spinules comparatively densely distributed
5.5	2.0	2.0	+			<1.0	6.5	caveae thin, spinules comparatively densely distributed
6.0	2.0	2.0	+			1.0	6.5	pollen comparatively small, caveae distinct, spines slender
8.0	2.0	3.0	+			<1.0	9.0	ora varying in size
6.0	1.7	1.8	+			1.0	6.0	
6.0	2.0	2.3	+			1.2	7.5	ora distinct, often constricted, caveae thin
9.0	2.0	3.0	+	+		2.5	9.0	ora broad, caveae high, spines often with two holes
5.0	1.0	2.0	+			1.0	5.5	pollen comparatively small, spinules with short solid zone
5.5	1.0	2.0	+			1.5	5.5	pollen comparatively small, spinules with short solid zone
8.0	1.0	2.0	+			1.0	7.0	tetraploid species, pollen comparatively large, asymmetric, often with more than 3 apertures
6.0	1.5	2.0	+			1.2	7.0	
7.0	2.0	2.0	+			<1.0	6.5	
7.5	1.5	2.5	+			<1.0	8.0	
5.0	1.5	2.0		+		1.5	6.0	spines usually with one hole
5.0	1.5	1.5	+	+		1.0	6.0	pollen and spinules comparatively small, two holes in spines often occur
5.0	1.5	1.5	+	+		1.5	6.0	pollen and spinules comparatively small, two holes in spines often occur
5.5	3.0	2.0		+		<1.0	7.0	caveae thin, spinules densely distributed
5.5	3.0	3.0	+	+		<1.0	8.5	caveae thin, spinules densely distributed
5.5	3.0	2.0		+		<1.0	7.0	caveae thin, spinules densely distributed
6.0							6.5	very different type of pollen, lacking caveae, with distinct infratectal bacula and minute spinules on the tectum

an LKB 4801 A ultratome with a diamond knife and post stained with aqueous uranyl acetate and lead citrate. Sections were examined with a Zeiss 10 transmission electronmicroscope.

Generic description (excluding Dipterocome)

The pollen grains are radially symmetrical, usually oblate-spheroidal, polar axis 24–48 μm, equatorial diameter 24–49 μm, 3-colporate, tectate, caveate.

The exine sculpture is spinose or less frequently spinulose. The exine structure consists of a comparatively thick tectum complex, lacking infratectal bacula.

The tectum complex (corresponding to the exine structure, Fig. 3, inkdrawing), increases in thickness under the supratectal processes. It is composed of three layers differing considerably in thickness. The outermost, relatively thin (c. 0.2 μm), continuous compact layer with tectal perforations (Fig. 2 G, arrow t) has a smooth surface and progresses to the base of the solid part of the spines where it amalgamates with the latter. The thickest, median layer (Fig. 2 G, bracket) consisting of intratectal bacula or other elements of the exine usually radially oriented and often irregular in shape, is rather airy. The innermost layer of the tectum complex (Fig. 1 C, arrow B) usually twice as thick as the outermost one, is thinner than the median, bacular layer. The innermost layer, "Stützschicht" (Stix 1960), appears to consist of thickened basal segments of intratectal bacula, which fuse almost entirely into a relatively compact layer with distinct, channel-like confines in it. As a rule, the inner surface of the innermost layer of the tectum complex consists of bacula-like or other irregularly shaped processes protruding into the *caveae* or fusing with the underlying foot layer. In all the layers of the tectum complex, except the solid supratectal part of processes, there are minute internal foramina varying in size and shape.

The foot layer occurs universally. In *Calendula* it is vestigial or partially lacking. The foot layer is continuous, compact, and approximately as thick as the outermost layer of the tectum complex. The internal foramina are not encountered in the foot layer.

The endexine, present as a rule, is often slightly lamellate, continuous or occasionally disrupted in non-apertural parts 0.5–1.0 μm thick, and considerably thicker in *Calendula*. In this genus the endexine is approximately as thick as the innermost, compact layer of the tectum complex in non-apertural parts. The distal surface is usually smooth, the proximal mostly uneven, often with processes.

Generic description of Dipterocome

The pollen grains are radially symmetrical, prolate spheroidal, polar axis 31 μm, equatorial diameter 20 μm, 3-colporate, tectate, caveae lacking.

The exine sculpture is spinulose, consists of minute, supratectal solid spinules less than 0.5 μm high.

The exine structure consists of tectum perforatum containing a thin layer of intratectal bacula and distinct, comparatively thick infratectal bacula reaching 3.0 μm in length.

The nexine is approximately 2.0 μm thick.

Description of pollen types

The tribe Calenduleae, as circumscribed in the present paper, exhibits certain pollen morphological features which are useful for the establishment of five pollen types encountered within the tribe. The pollen types are named after the genera *Osteospermum, Calendula, Gibbaria, Garuleum* and *Dipterocome*.

Osteospermum-type Fig. 1 A–C

Pollen grains with usually lalongate, often large, slightly constricted ora, having pointed ends. The total number of spines or spinules is 65–80. The spines consist of an upper solid and an underlying structured zone. The solid zone usually contains one minute hole.

Calendula-type Fig. 1 D–I

Pollen grains relatively large (equatorial diameter to 50 μm), with large distinct, lolongate, unconstricted ora and a large number of slender spines consisting mainly of a long solid zone. The spines are numerous (100–130).

Gibbaria-type Fig. 3 A

Pollen grains with usually lolongate, uncon-

stricted ora. The total number of spines c. 70. The spines consist of an upper solid and an underlying structured zone. The solid zone contains one or two minute holes.

Garuleum-type Fig. 3 C–E

Pollen grains with 100–120 spines, consisting of an upper solid and an underlying structured zone. As a rule, the solid zone contains one or two minute holes. The individual spines are situated rather closely at the base. Ora lolongate, thin (less than 1.0 μm high).

Dipterocome-type Fig. 3 F–H

Pollen grains with minute supratectal solid spinules (less than 0.5 high), distinct infratectal bacula and comparatively thick nexine. (c. 2.0 μm). Caveae lacking entirely. Ora lolongate.

Key to pollen types

1. Infratectal bacula always present, well developed, caveae lacking ..... *Dipterocome*-type
– Infratectal bacula lacking, caveae present as a rule 2
2. Ora usually lalongate ..... *Osteospermum*-type
– Ora lolongate 3
3. Approximately 70 spines in one pollen grain ..... *Gibbaria*-type
– 100–130 spines in one pollen grain 4
4. Equatorial diameter more than 38 μm, distance between the apices of spines 7–10 μm ..... *Calendula*-type
– Equatorial diameter 35 μm or less, distance between the apices of spines c. 5 μm ..... *Garuleum*-type

Remarks on pollen morphology

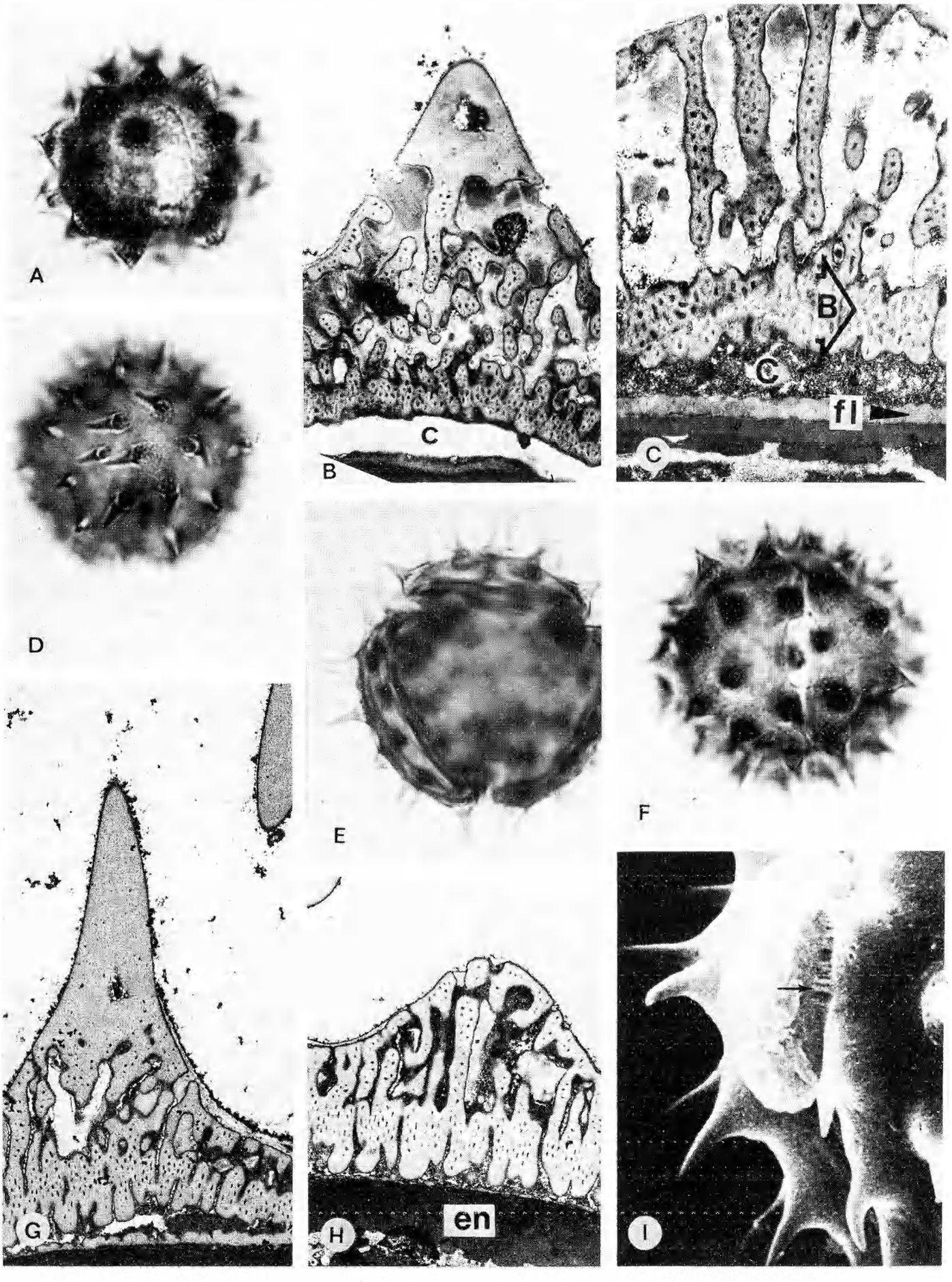
According to the definition of sculpture (Praglowski 1975, Praglowski & Raj 1978), in Calenduleae only the supratectal solid part of spinules or spines should be included in the exine sculpture. The underlying, non-solid part of processes transgressing into the tectum complex and protruding over the circular contour of pollen grains integrates with the former apical part. The lower non-solid part of processes also forms part of the tectum complex structurally, and consequently belongs to the exine structure. In agreement with the evidence encountered in the investigation, the spiny processes are interpreted as consisting of two different parts, which were measured separately.

In Calenduleae, as well as in several other taxa of the Compositae, one process is composed of a sculptural supratectal solid part and of a structured, tectal part, both of which forming one morphologically indivisible unit, the spine (Fig. 3 I).

The pollen grains in the Calenduleae are characterized by the presence of distinct caveae (Figs. 1 B "C", 2 E "C") which are found in all the genera with the exception of *Dipterocome*. The caveae have been discussed or exhibited previously by, e.g., Stix (1960), Skvarla & Turner (1966), Skvarla et al. (1978) and Horner & Pearson (1978). There exists, however, a certain degree of confusion concerning the stratigraphic settlement of the caveae. In the present paper, the caveae are said to be situated over the unsplit foot layer.

In fact, there is no pollen morphological or fine structural evidence which supports splitting the foot layer. In the Calenduleae the foot layer is continuous, compact and homogeneous and does not contain internal foramina. The internal organization of the remaining tectal part of the ectexine exhibits, as a rule, internal foramina, which are also found in the basal zone of the tectum (Fig. 1 H) corresponding to "Stützschicht" (Stix 1960) and to the "foot layer 1" (Horner & Pearson 1978).

The pollen grains of all the genera in the Calenduleae except for *Dipterocome* have spines or spinules in which the supratectal solid part usually contains only one hole (Fig. 2 E). Processes with two holes or conical confines are also found, but are rare. Stix (1960) describes and illustrates similar results in the pollen types of Calenduleae with the exception of the *Osteospermum*-type, which according to her, should be void of intraspinular holes. In fact, these holes are encountered in all species of *Osteospermum* investigated in this work (cf. *Osteospermum spinosum* var. *spinosum*, Fig. 1 B). The omission of this feature in *Osteospermum* by Stix (1960) probably depends on the fact that her excellent study was performed by light microscope exclusively. For the same reason, the authors can hardly agree with Stix (1960) regarding the presence of infrategillar bacula in the *Calendula*- and *Castalis*-types. The elements in these two pollen types considered by Stix as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short, infrategillar bacula, finestructurally belong to the lowest layer of the tectum complex ("Stützschicht").

Comments with reference to taxonomy

The pollen grains of *Calendula* (the type-genus for the tribe), possess some morphological features characteristic of this genus only. These features include size of pollen grains, which are the largest within the tribe (equatorial diameter up to 50 μm), the presence of particularly large, lolongate ora, high caveae (up to 5 μm), an inner organization of long, solid slender spines, an almost total absence of the foot layer and the presence of compartively thick endexine. *Calendula* represents a characteristic, pollen morphologically well delimited and easily recognizable group, which can hardly be confused with any other representative of the tribe.

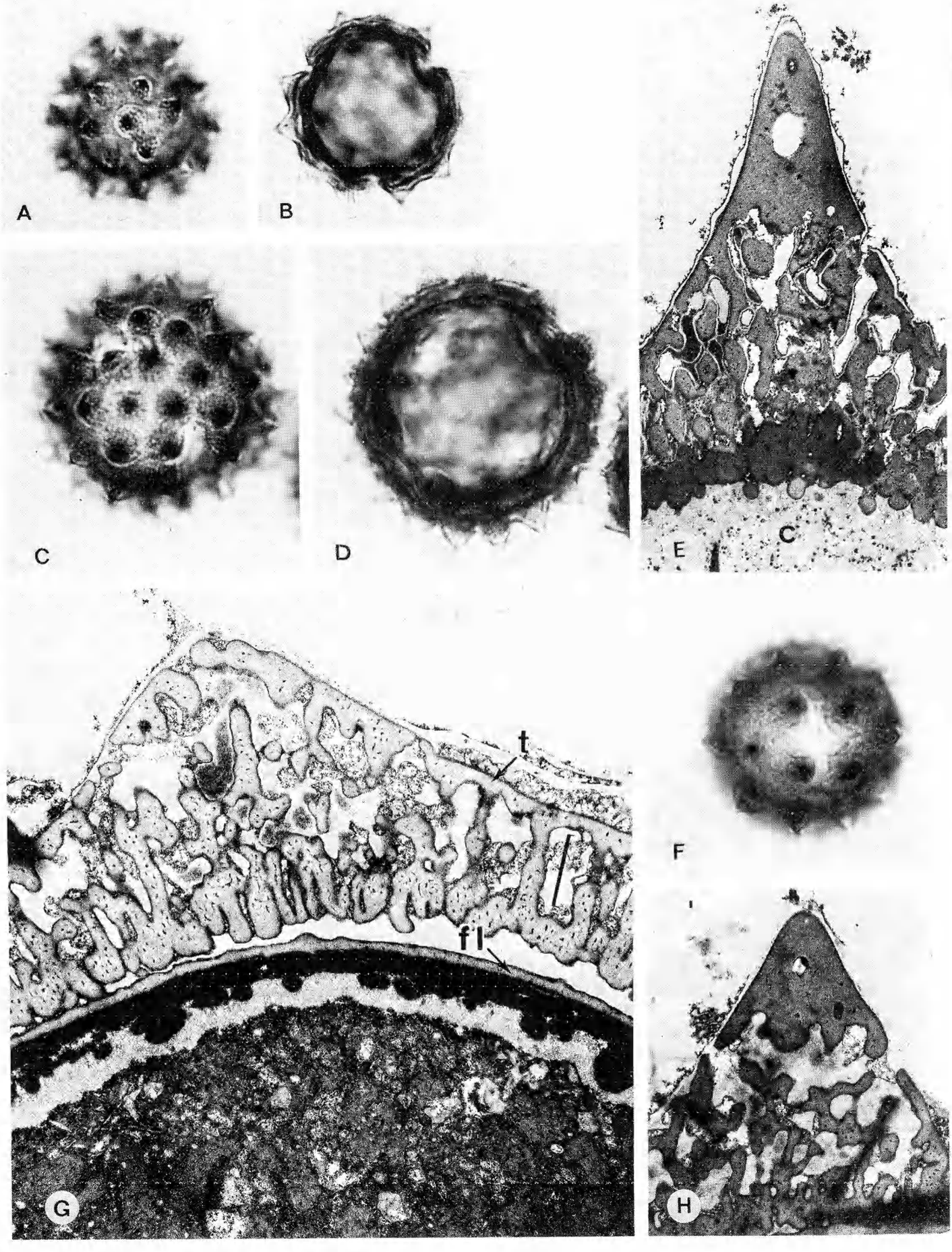
The *Osteospermum* pollen type includes the largest genus *Osteospermum* (c.70 species) and some other small genera, *Dimorphotheca, Castalis* and *Chrysanthemoides*. It is, however, rather difficult to record clear pollen morphologic criteria useful for a good generic segregation within this group of taxa. Possibly, the pollen grains of the genus *Chrysanthemoides* could be separated from the rest because of the slightly larger number of spines, but this feature alone is insufficient for the segregation. The type-species of the subgenus *Osteospermum O. spinosum* and that of subgenus *Tripteris O. dentatum* are easily distinguishable on pollen morphological criteria. The pollen of *O. dentatum* differs from that of *O. spinosum* by having large oval ora, wide colpi and thick exine. Conical confines in the solid zone of spines occur rather frequently.

The pollen morphological affinity between the genera *Dimorphotheca* and *Osteospermum* is obvious. The pollen grains of *Osteospermum fruticosum,* the type-species of the section *Blaxium* (formerly genus), have more morphological features in common with *O. spinosum* than with *Dimorphotheca pluvialis,* type-species of the genus *Dimorphotheca.*

Usually lolongate ora and spinules having one or two holes distinguish the pollen grains of the small genus *Gibbaria* (two species) from the *Osteospermum-Dimorphotheca-Castalis* complex. The pollen morphological profile of the genus *Gibbaria,* however, is less prominent than that of the genera discussed previously. Nevertheless, in spite of the differences mentioned above, pollen morphologically *Gibbaria* seems to fit best in the complex *Osteospermum-Dimorphotheca-Castalis*. To a certain extent, the pollen grains of *Gibbaria scabra* differ from those of *Gibbaria ilicifolia* in size, the character of the ora, and the number of holes in the solid part of the spines.

The pollen grains of *Garuleum* are characterized by the presence of a comparatively large number of spines, lolongate ora, comparatively wide colpi and particularly thin caveae. The spines in pollen grains of *Garuleum* stand much closer to each other than those in *Calendula* and the caveae in *Garuleum,* in contradistinction to *Calendula,* are particularly thin. Pollen morphologically, *Garuleum* stands rather far from *Osteospermum* and *Dimorphotheca* and the present

Fig. 1. A: *Osteospermum dentatum*, equatorial view, os large, lolongate. — B–C Fragments of sections through spine-bearing exine. — B: The spine and tectum, supratectal solid part of the spine lacks the internal foramina which are found only in the tectal strata, "C" empty cavea. — C: Infraspinal tectum, sectioned near the spine centre (the spine not visible). The internal foramina (dark dots) distinct. Comparatively long bacular elements of the median zone and the basal, rather compact zone of the tectum arrow "B" overlying the cavea "C", filled with delicate, granular material. The foot layer arrow "fl" is compact comparatively thin and continuous. The endexine under the foot layer, partially disrupted at the inner surface. — D–E *Calendula fulgida,* pollen grain in polar view. — D: high focus. — E: Optical cross-section, showing high caveae and long, slender spines. — F: *Calendula arvensis,* equatorial view exhibiting large lolongate os and distinct colpus. — G–H *Calendula suffruticosa,* an almost perfectly radial section through the spines and the infraspinal exine. — G: Solid, supratectal part of the long spine, approximately as long as the remaining ectexine. Vestigal foot layer present. — H: Section through the exine along the border of one of the colpi in the area where the tectum anastomoses or is very close to the endexine. The section shows a bulging part of tectum in the vicinity of the spine centre. Cavea reduced. The internal foramina are found in all layers of the tectum. The foot layer is lacking. The endexine "en" dark stained, thick, as thick or slightly thicker than the basal zone of the tectum. — I. *Calendula maritima* SEM×4300. Slender spines and the area of the aperture with operculum-like lid, which is connected with the exine surrounding the os by means of delicate radial elements, arrow. — All light micrographs × 1080, transmission electron micrographs × 13,000.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study can hardly provide arguments in favour of a closer taxonomic affinity between *Garuleum* and the latter two genera.

The pollen grains of *Dipterocome* differ essentially from the remaining representatives of the Calenduleae by the absence of caveae and by supratectal spines which are reduced to minute solid spinules, less than 0.5 μm high. The occurrence of distinct infratectal bacula, as well as comparatively thick nexine is also typical for this genus only. Pollen morphologically, *Dipterocome* does not fit at all in the tribe Calenduleae and in this respect exhibits affinities with the Cynareae and the Anthemideae. Other characteristics in *Dipterocome* deviating from those in the tribe Calenduleae include sub-bilabiate marginal flowers, anthers muticous at the base, and connate filaments (Norlindh 1978, p. 962). Taking into account the above features and pollen morphology, the taxonomic status of the monotypic genus *Dipterocome* undoubtedly deserves reconsideration. The geographical distribution of *Dipterocome,* extending from Palestine eastwards as far as Afghanistan, also show considerable displacement from the main distribution area of the tribe Calenduleae. Only one species of the tribe Calenduleae, *Calendula persica* C. A. Mey., has a similar, though probably not as extensive, distribution as *Dipterocome*.

The pollen grains of the endemic species *Osteospermum sanctae-helenae,* a relict species from the Tertiary (Norlindh 1978 p. 969), are easily distinguishable from remaining taxa of the tribe through comparatively high caveae, distinct, rather large ora and the presence of conical confines in spinules. The peculiar geographical isolation of this species is also reflected in the pollen morphology.

The pollen grains of the tetraploid specimen of *Dimorphotheca sinuata* show some morphological differences and aberrations having to do mainly with the size, symmetry, and number of spines.

Pollen of Calenduleae show affinity with those of the Astereae, Senecioneae, and Heliantheae. The latter tribe was considered by several authors to exhibit the most primitive characters in the Compositae (Bessey 1915, Hutchinson 1916, Wodehouse 1928 b, Tomb 1975).

The occurrence of internal foramina in the ectexine, encountered only in Heliantheae, Senecioneae, and Calenduleae as well as in one species of the Cichorieae, seems to be a primitive feature and agrees with the phylogenetic status of the three tribes mentioned above.

The consanguinity of the Calenduleae with the Senecioneae, as expressed by Small (1919), Norlindh (1946), Cronquist (1955 b), and other authors, is in harmony with the pollen morphological data and perhaps the Calenduleae should be considered an offshoot of the Senecioneae rather than a direct derivative of the Heliantheae.

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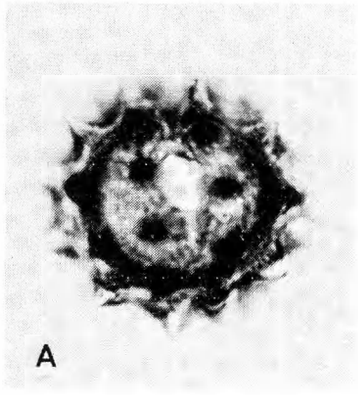
Fig. 2. A–D *Dimorphotheca sinuata*. — A–B polar view. — A: comparatively high focus. — B: optical cross-section. — C–D large pollen grain from a tetraploid specimen (2n=18) in two, successive foci. — C: relatively high focus showing two of the large asymmetrically distributed apertures. — D: optical cross-section, the number of spines at least twice those in the grain from the diploid specimen (A–B). — E: *Dimorphotheca chrysanthemifolia*. Fragment of the section showing the spine, the tectum and high cavea "C" beneath the tectum. The upper, solid part of the spine contains one hole. — F–H *Castalis tragus*. — F: pollen grain in equatorial view exhibiting a large lalongate os with pointed ends and a distinct colpus. — G: Section showing the structure of the exine. The tectum consists of an outer perforated thin layer, a median zone with bacula-like elements and at the base, an innermost, rather compact zone facing the cavea. All three layers of the tectum contain the internal foramina (small black dots). The foot layer "fl" comparatively thin, continuous, lacking the internal foramina. The endexine dark, continuous, its innermost surface with globular excrescences intruding into the intine. The intine approximately as thick as the endexine. — H: Section through the spine with one hole and the underlying, structured part. — All light micrographs × 1080, transmission electron micrographs × 13,000.



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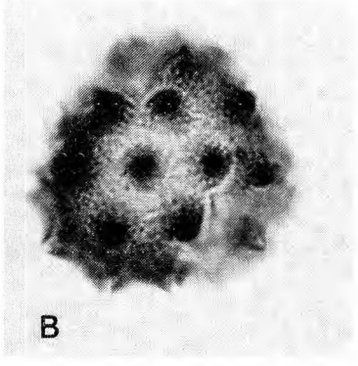

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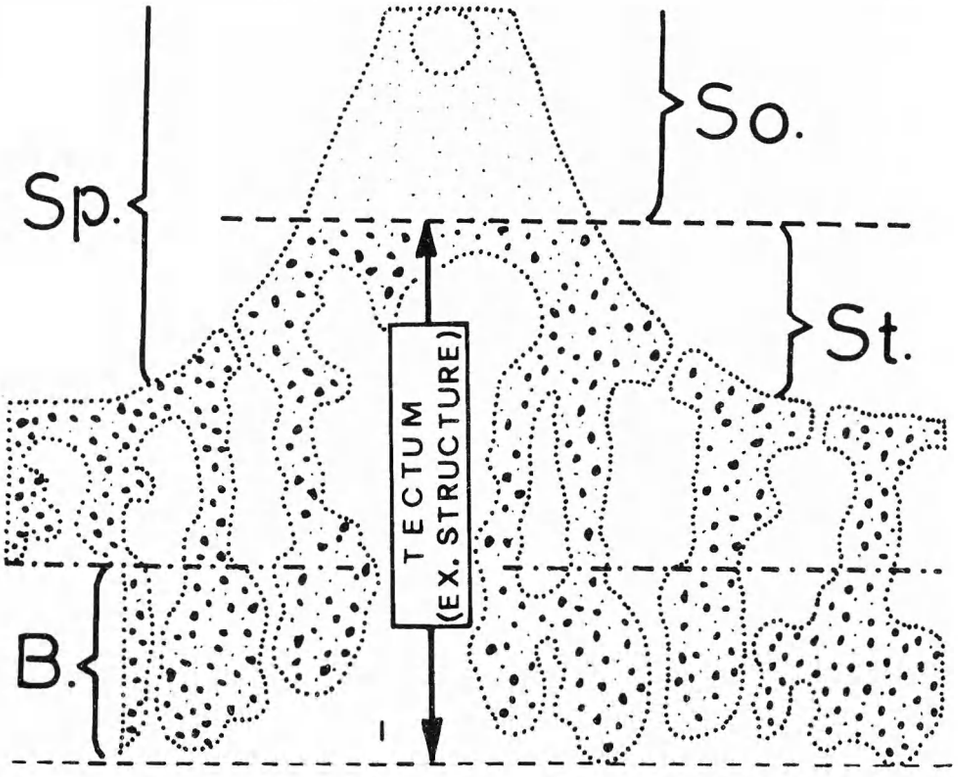

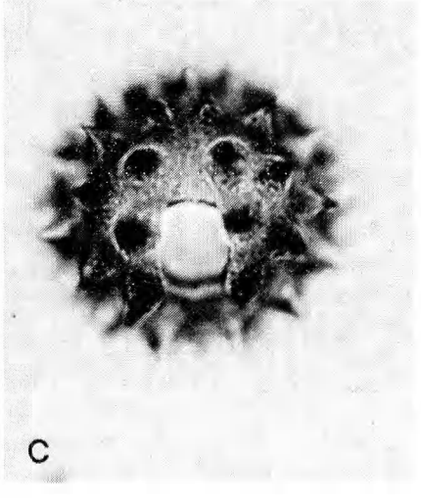

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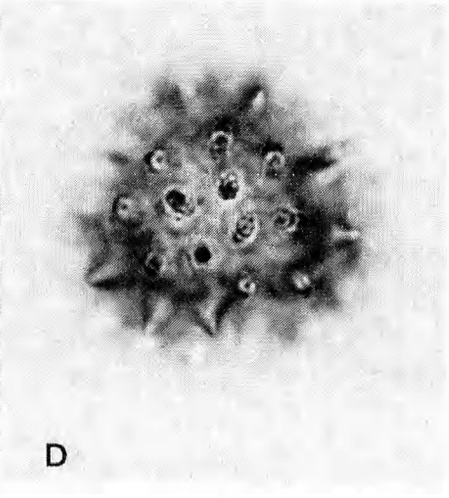

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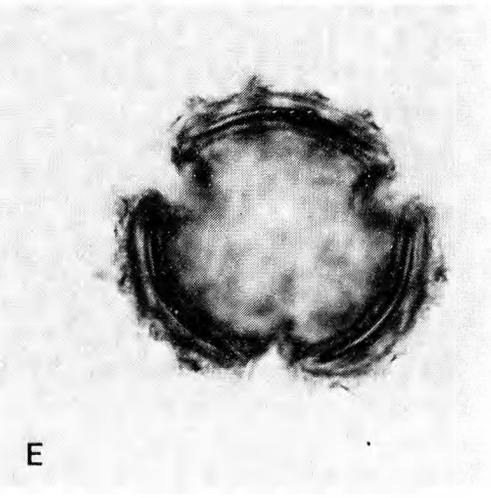

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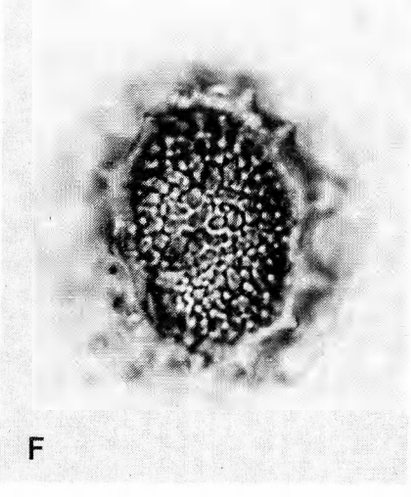

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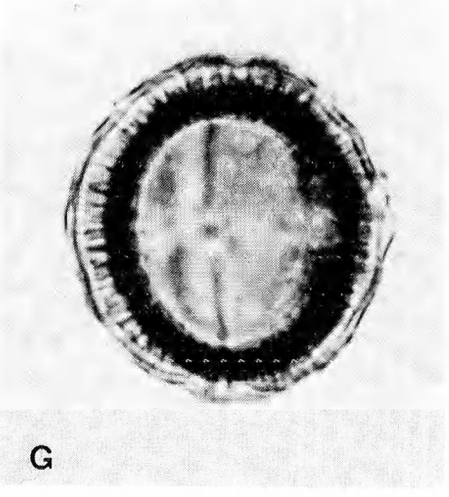

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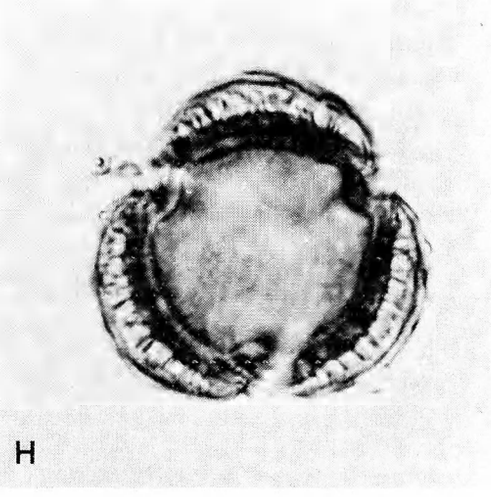

H

Appendix. Collections investigated

* Species exhibited in Figs. 1–3.

Calenduleae Cass. Type-genus **Calendula** L.

Calendula L. Type-species *C. officinalis* L.

C. officinalis L. Iran, Aschabad. Sintenis 403
C. arvensis L. Sicily, Palermo. Lanza s.n.*
C. echinata DC. Morocco. Agadir. Maire s.n.
C. fulgida Raf. Sicily, Palermo. Todaro 619*
C. maritima Guss. Sweden, cult. Hort. Bergianus. Norlindh s.n.* — Sicily, Trapani. Ross 347
C. suffruticosa Vahl. Tunisia, Mountain Kalaa-El-Harrat. Murbeck s.n.*

Osteospermum L. Type-species *O. spinosum* L.

Subgen. *Osteospermum* (L.) T. Norl. Type-species *O. spinosum* L.

Sect. I. *Oppositifolia* DC.–XI. *Spinosa* T. Norl.
O. spinosum L. var. *spinosum*. South Africa, Cape Province. Nordenstam 33
O. spinosum L. var. *runcinatum* Berg. South Africa, Cape Province. Norlindh 5621
O. polygaloides L. South Africa, Caledon Div. Hafström & Lindeberg s.n.
O. sanctae-helenae T. Norl. S:t Helena. Norman 10
O. thodei Mark. South Africa, Bergville Distr. Barclay & Gentry 988

Sect. XII. *Blaxium* (Cass.) T. Norl. Type-species *Osteospermum fruticosum* (L.) T. Norl. A revision of *Blaxium* is now in progress by Norlindh (1978, p. 977) who thinks it might be possible to re-establish this old Cassinian genus.
O. fruticosum (L.) T. Norl. South Africa, Cape Province. Norlindh 5543
O. acutifolium (J. Hutch.) T. Norl. South Africa, Caledon Div. Wall s.n.
O. caulescens Harv. Cult. Hort. Bergianus, Stockholm. Norlindh s.n.
O. ecklonis (DC.) T. Norl. Cult. Stockholm, Univ. Bot. Garden. Norlindh s.n.

Subgen. *Tripteris* (Less.) T. Norl. Type-species *Osteospermum dentatum* Burm. fil.

Sect. XIII. *Trifenestrata* T. Norl. — XV. *Efenestrata* T. Norl.
O. dentatum Burm. fil. South Africa, Milnerton. Lindeberg s.n.* — South Africa, Cape Province. Acock 650
O. connatum DC. South Africa, Cape Province. Ecklon & Zeyher 154
O. amplectens (Harv.) T. Norl. Cult. Hort. Bergianus, Stockholm. Norlindh s.n.

Sect. XVI. Oligocarpus (Less.) T. Norl. Monotypic.
O. calendulaceum L. fil. (Transitional species between the subgenera *Osteospermum and Tripteris*.) Norlindh 1943, p. 346. Cult. Hort. Bergianus, Stockholm. Norlindh 5830

Chrysanthemoides Tourn. ex Fabr. Type-species *C. incana* (Burm. fil.) T. Norl.

C. incana (Burm. fil.) T. Norl. South Africa, Cape Province. Hafström s.n.
C. monilifera (L.) T. Norl. ssp. *monilifera*. South Africa, Stellenbosch Distr. Acock 453*

Dimorphotheca Vaill. ex Mnch. Type-species *D. pluvialis* (L.) Mnch.

D. pluvialis (L.) Mnch. South Africa, Cape Province. Norlindh 5515
D. chrysanthemifolia (Vent.) DC. Sweden, cult. Hort. Bergianus. Norlindh s.n.*
D. cuneata (Thunb.) Less. South Africa, Cape Province. Wall s.n.
D. montana T. Norl. var. *montana*. South Africa, Cape Province. Norlindh 5925
D. montana T. Norl. var. *venusta*. South Africa, Cape Province. Esterhuysen 11340
D. polyptera DC. South Africa, Kuiseb River Region. Kers 1284
D. sinuata DC. Sweden, cult. Hort. Bot. Lundensis. Norlindh s.n.*
D. sinuata DC. (tetraploid specimen). Sweden, cult. Hort. Bergianus. Norlindh s.n.*

Castalis Cass. Type-species *C. tragus* (Ait.) T. Norl.

C. tragus (Ait.) T. Norl. South Africa, Calvinia Div. Lewis 65253*. LD.
C. nudicaulis (L.) T. Norl. var. *graminifolia* South Africa, Cape Province. Norlindh 5537
C. spectabilis (Schltr.) T. Norl. South Africa, Transvaal. Hafström & Acock 1542

Fig. 3. A: *Gibbaria ilicifolia*, equatorial view, os large, lolongate. — B: *Chrysanthemoides monilifera*, polar view. — C–E *Garuleum pinnatifidum*. — C: equatorial view, os large, lolongate, colpus wide. — D–E polar view. — D: pollen grain in comparatively high focus, showing a rather large number of spines. — E: optical cross-section, thin white lines between the tectum and nexine are the caveae. — F–H *Dipterocome pusilla*. F–G equatorial view. — F: pollen grain in low focus exhibiting the apical parts of thick, infratectal, partially branched bacula. — G: optical cross-section, showing a thin layer with intratectal bacula, thick infratectal bacula and thick nexine (dark layer). — H: polar view, optical cross-section. — I: Schematic representation of the tectum complex and the spine in the Calenduleae (*Dipterocome* excluded). Sp. the spine. So. the solid, supratectal part of the spine with one hole, lacking the internal foramina. St. the structured, wide part of the spine included in the tectum complex. The latter complex corresponds to the exine structure and contains the internal foramina (thick, dark dots). B. the compact zone at the base of the tectum complex (Stützschicht according to Stix 1960). — All light micrographs × 1080.

Gibbaria Cass. Type-species *G. scabra* (Thunb.) T. Norl.

G. scabra (Thunb.) T. Norl. South Africa, Willowmore Distr. Dahlstrand 1334. GB.
G. ilicifolia (L.) T. Norl. South Africa, Cape Province. Norlindh 5595*
G. ilicifolia (L.) T. Norl. South Africa, Cape Province. Hafström s.n.

Garuleum Cass. Type-species *G. pinnatifidum* (L'Herit.) DC.

Subgen. *Garuleum*. Type-species *G. pinnatifidum*

G. pinnatifidum. (L'Herit.) DC. South Africa, Sneeuwbergen. Drège s.n.*
G. latifolium Harv. South Africa, Natal. Rudatis 1864.

Subgen. *Rutidocarpaea* (DC.) T. Norl. (monotypic)

G. bipinnatum (Thunb.) Less. South Africa, Albany Distr. Wall s.n.

Dipterocome Fisch. & Mey. A monotypic "satellite" genus in the tribe.

D. pusilla. Fisch. & Mey. Afghanistan, Nachitshevan. Grossheim & Gurvitsh s.n.*

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Anatomy of the phylloclades of Phyllocladus hypophyllus

BRITT BERGGREN

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The anatomy of the mature phylloclades of *Phyllocladus hypophyllus* Hook. fil. has been studied with the aid of light microscopy and scanning and transmission electron microscopy. The ontogeny of the phylloclades has been examined by light microscopy of cleared material and by scanning electron microscopy of transversal and longitudinal sections. The similarity with the anatomy of coniferous leaves is striking and includes the presence of transfusion tissue. Transfusion tissue in stems is here apparently reported for the first time. The cortex of the phylloclades contains several thin-walled, large cells, previously described as "sclereids". Their structure and ontogeny indicate, however, that they are in fact accessory transfusion tracheids. Resin ducts are well differentiated in juvenile organs implying that resin production has an important role, perhaps in protection of the plant.

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Phyllocladus hypophyllus Hook. fil. is a conifer growing in moist forests in mountain regions on Borneo and New Guinea. It has some remarkable properties, e.g., the organization of the reproductive as well as the assimilating organs. The leaves are small and scaly and fall off early, while flattened leaf-like stems, so-called phylloclades or cladodes, assume assimilating properties. This kind of feature has evolved independently in several angiosperm families, and is described for instance in Cactaceae and the genera *Ruscus* and *Asparagus* (Velenovsky 1903), but seems to be limited to *Phyllocladus* among the gymnosperms.

The genus *Phyllocladus* is now generally regarded as a member of the family Podocarpaceae (de Laubenfels 1969), but was earlier placed in Taxaceae (Pilger 1903). Several investigators have considered the genus as being intermediate between Podocarpaceae and Taxaceae, among them Robertson (1906), who has found a few Podocarpacean features, while the occurrence in *P. alpinus* of lateral bundles of centripetal xylem is belived to be due to relationship with Taxaceae. She finds it especially notable that the secondary walls of the centripetal xylem show a combination of bordered pits and spiral or scalariform thickenings.

Keng (1963, 1974, 1977) has studied the anatomy of *P. hypophyllus* and described the vascular tissues at different levels of the stem and in the phylloclades (Keng 1977). The pinnate phylloclades is composed of 5–10 segments. Immediately below each segment, the vascular tissue of the stem forms a cylinder of xylem and phloem and in addition two small traces, which enter the segment, and one leaf-trace of a scaly leaf. Sections cut through the phylloclade segments perpendicular to the vascular bundles show them to be composed of a number of leaf- and branch-traces arranged in one plane. Each vascular bundle is accompanied by a resin duct external to the phloem. Keng regards the phylloclade as an ancient structure, in which the distinction between leaf and branch has not been sharply developed, and after emphasizing the relationship to Podocarpaceae as well as Taxaceae has proposed the establishment of the new family Phyllocladaceae.

Hida (1951) studied the assimilating organs of some conifers and found the phylloclades of *P. hypophyllus* Hook. fil. ("*P. protractus* (Warb.) Pilger") to develope palisade chlorenchyma on the "adaxial" side. Most conspicuous in his pictures is however the occurrence of large, relatively thin-walled cells in the cortex. Those cells were interpreted as sclereids.

A characteristic feature of coniferous leaves is

the transfusion tissue, composed of tracheids and often in addition parenchyma cells. It is associated with the vascular bundles (Foster & Gifford 1973, Napp-Zinn 1966). The origin and function of the transfusion tissue has not been satisfactorily determined, but the tissue is commonly assumed to be concerned with translocation between the vascular bundle and the mesophyll. The distribution of transfusion tissue varies between different families and genera. In Podocarpaceae it occurs as a wing-like process on each side of the vascular bundle, as described by Griffith (1957) in a study on anatomy and ontogeny of transfusion tissue in *Podocarpus macrophyllus*. Adjacent to the phloem there occur specialized thin-walled, elongated transfusion parenchyma cells, viz. Strasburger cells (albuminous cells). The transfusion tracheids are of different size and shape, varying from isodiametric to elongated with the same length as xylem tracheids. The lignified walls are scalariform, scalariform-reticulate or have circular bordered pits. Accessory transfusion tissue in *Podocarpus macrophyllus* occurs as two wing-like extensions of the transfusion tissue and consists of tracheids and parenchyma cells. Most of the cells are elongated at right angles to the veins. As Griffith (1957) has pointed out, the lignified elements of the accessory transfusion tissue have been described by different authors as tracheids, sclereids, and osteosclereids. Due to the presence of bordered pits, characteristic for elements of the xylem, she finds the designation as tracheids justified. The transfusion tissue of *Pinus* needles completely surrounds the two vascular bundles and is bounded on the outside by an endodermis. It consists of relatively thin-walled tracheids with bordered pit-pairs and large parenchymatous cells (Walles et al. 1973). On the abaxial side of each vascular bundle there are also albuminous cells adjacent to the phloem. The albuminous cells have local wall thickenings, characteristic of transfer cell activity, as described for *Pinus* by Parameswaran and Liese (1970) and Walles et al. (1973). The albuminous cells in gymnosperms are considered to be functionally comparable to the companion cells in angiosperm phloem (Esau 1969).

The purpose of this investigation was to use contemporary techniques to study the structural adaptations of the stem structures of *P. hypophyllus* as assimilating organs, and to use this information for comparison of their anatomy with that of conifer leaves. An investigation of the ontogeny of the phylloclades was made to obtain further insight into the organization of the tissues and the nature of different cell types.

Material and methods

Segments of phylloclades from *P. hypophyllum* were sampled from a plant collected on Mount Kinabalu, Borneo, by H. Erdtman and grown in the green-house of the Institute of Botany, University of Stockholm.

Material to be examined by light microscopy (LM) was cut into relatively large pieces, c. 25 mm^2, and fixed in FAA for at least 24 hours, dehydrated in an ethanol series, embedded in Paraplast, cut into 8–10 μm thick sections, and stained with safranin-fast green. Segments of 3, 5, 18 and 29 mm length were studied by clearing. After fixation the material was cleared by treatment with 5 % NaOH for 3 days at 37°C and then with a saturated solution of chloral hydrate for 3 days at 37°C. The cleared tissues were stained with safranin.

For scanning electron microscopy (SEM) the material was fixed and embedded as for light microscopy. It was cut into thick sections (c. 30 μm), deparaffinated with xylene, transferred to ethanol, critical point dried from CO_2, sputter coated with Au-Pd, and observed with a Cambridge Stereoscan 600.

For transmission electron microscopy (TEM), phylloclade segments were cut into small pieces (1–2 mm^2) and fixed in glutaraldehyde solutions. The specimen in Fig. 3 B was fixed in 2 % glutaraldehyde in 0.1 M phosphate buffer (pH c. 7.0). The material used for the remaining TEM pictures was fixed with 2 % glutaraldehyde in 0.1 M cacodylate buffer. After osmication with 1 % OsO_4 in 0.1 M phosphate buffer the specimens were embedded in Epon-Araldite (Mixture No. 1, Mollenhauer 1964) or Spurr resin (Spurr 1969). They were cut with a diamond knife. The sections were stained with uranyl acetate and lead citrate and examined with a Zeiss EM 10 A.

Observations

Mature phylloclades

The mature segments are 60–70 mm long.

The epidermis is covered with a thick cuticle, and SEM pictures (Fig. 1 B) show an almost smooth surface interrupted only by scattered stomata, which occur on both sides of the phylloclade. Cleared material demonstrates that the size and shape of the epidermal cells is very irregular. TEM pictures reveal that the cuticle and the cell walls contain numerous minute crystals (Fig. 2 A). Both outer walls and anticlinal walls are thickened (Figs. 1 A, 2 A), and the presence of a heavily stained nucleus shows that

the epidermal cells have living protoplasts. In TEM micrographs epidermal cells have a thin peripherial cytoplast and a large vacuole, sometimes containing tannin as dense granules (Fig. 2 A).

The stomata are somewhat sunken below the surface and overarched by subsidiary cells. Adjacent to the stomatal opening part of the subsidiary cells is raised to form a protecting rim (Figs. 1 B, 2 A, B). The guard cells shown in Fig. 2 A are not centrally cut, but it is apparent that the walls between the two guard cells are relatively thick. Even the walls in contact with the subsidiary cells are thickened. In the guard cell shown in Fig. 2 A there are several mitochondria, chloroplasts, many ER profiles, several vacuoles, and darkly stained bodies (presumably lipids). The subsidiary cells (Fig. 2 A) also have thickened walls, and contain a nucleus, chloroplasts, mitochondria, and tannin in the vacuoles. There is no hypodermis in the phylloclades (Figs. 1 A, 3 C).

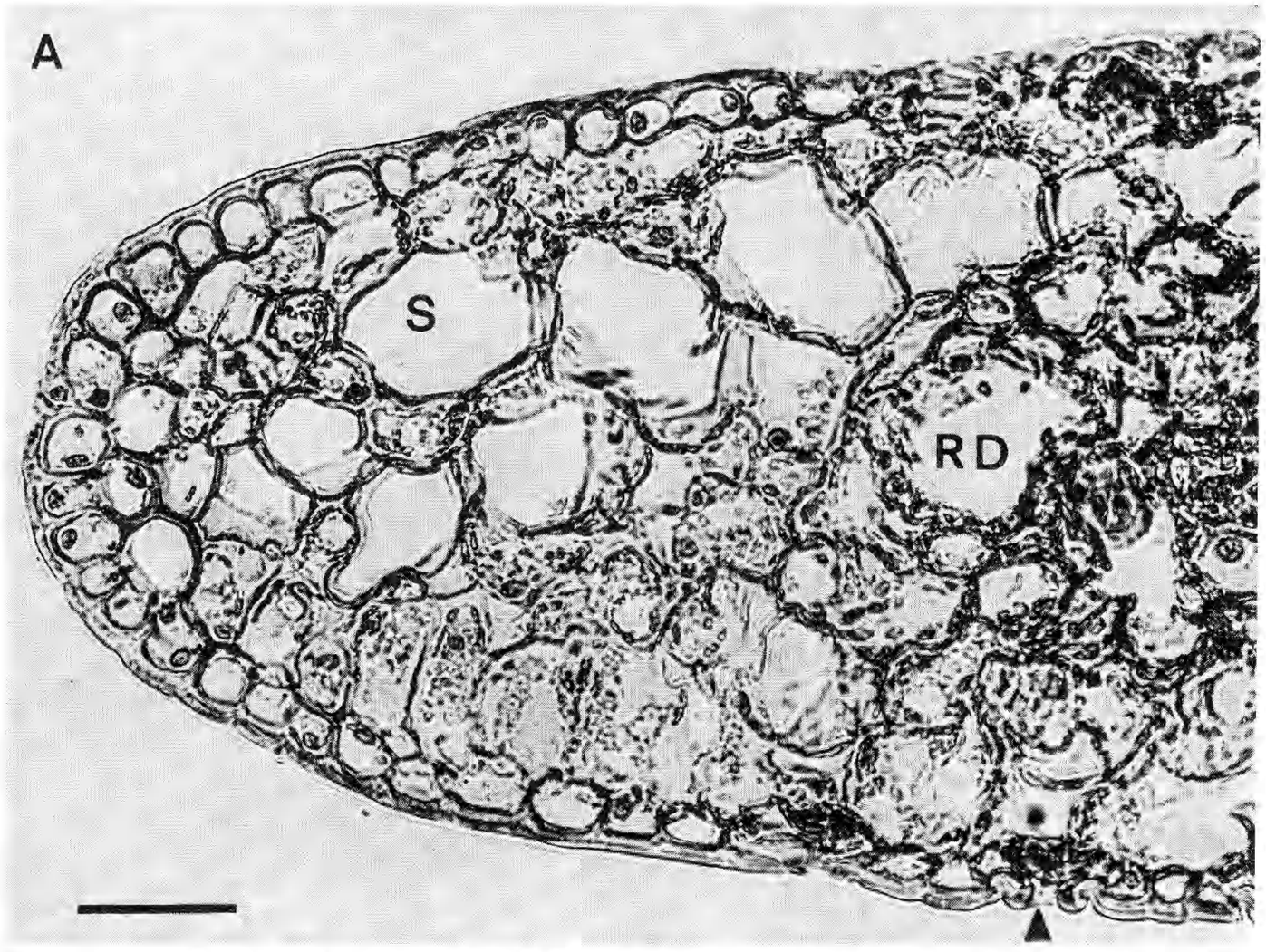
The cortex is primarily composed of chlorenchyma cells and large, empty cells which have been interpreted as sclereids (Hida 1951). Chlorenchyma cells form a palisade layer on the adaxial side of the phylloclade and have a large central vacuole and many chloroplasts (Fig. 3 A, B). The chloroplasts have many grana and often contain a large starch grain and several plastoglobuli. Mitochondria, ER, ribosomes, and tannin globules are also found in chlorenchyma cells.

The large cells lack protoplasts and have relatively thin, lignified secondary walls as seen in LM and are somewhat elongated at right angles to the vascular bundles. They have elongated pores and wall thickenings (Figs. 2 B, 3 A, B). These cells appear to be accessory transfusion tracheids and will be referred to as tracheids. These tracheids are relatively evenly distributed throughout the cortex, and are quite apparent due to their greater size (Figs. 1 A, 3 A, C) as compared with the chlorenchyma cells. For instance, the tracheid shown in Fig. 3 A has a diameter of c. 65 μm and a length of c. 130 μm, and some tracheids are larger than this. Many intercellular spaces are formed between the accessory transfusion tracheids and the spongy chlorenchyma (Fig. 3 A, C).

Near the phloem of each vascular bundle there is one schizogenous resin duct, whose epitelial cells are surrounded by a sheath of relatively thin-walled parenchyma cells (Fig. 3 C).

The vascular tissue and the transfusion tissue. The arrangement of the vascular bundles in transversal sections can be seen in Fig. 5. The metaxylem is composed of tracheids with thick lignified walls, and rows of parenchyma cells (Figs. 3 C, 4, 6 A). The protoxylem tracheids with spiral or scalariform wall thickenings (Fig. 6 A) are compressed, while the metaxylem tracheids are arranged in regular rows and have very thick walls with bordered pits (Fig. 6 A). On the walls towards parenchyma cells the pits are simple, as expected (Fig. 6 A). In TEM pictures the secondary wall of the metaxylem tracheids appears to be composed of at least three layers. The parenchyma cells contain ER, mitochondria and other organelles and have vacuoles of varying size, sometimes with a content dense to electrons. The walls have primary pit-fields. Xylem and phloem are separated by 1–2 rows of cambial cells. The phloem can be regarded as abaxial in the flattened branches, of which the segments of the phylloclades are composed. It consists of somewhat compressed, relatively thin-walled sieve-cells (Figs. 4, 6 A) and some parenchyma cells. Just outside the phloem there are some fibers with extremely thick secondary walls (Fig. 5). Cells with many vacuoles and wall ingrowths like those in transfer cells have been observed in the rows of parenchyma in the phloem (Fig. 4). These transfer cells have thin layers of protoplasm with amoeboidal chloroplasts, containing starch grains.

Surrounding the vascular strand there is a sheath of two kinds of cells, all very large, some of them thin-walled and parenchymatic and others empty with thicker walls, which in transverse section look like having spiral thickenings and bordered pits like tracheids. The thick-walled cells are elongated in the same direction as the veins. These cells are much wider than the xylem tracheids but not as large as the earlier mentioned accessory transfusion tracheids. The bundle "sheath" is supposed to be a transfusion tissue with parenchyma cells and tracheids. The living transfusion cells have a dense content, but localized wall thickenings in combination with a dense protoplast, characteristic of albuminous cells, have not been found. Even in the transfu-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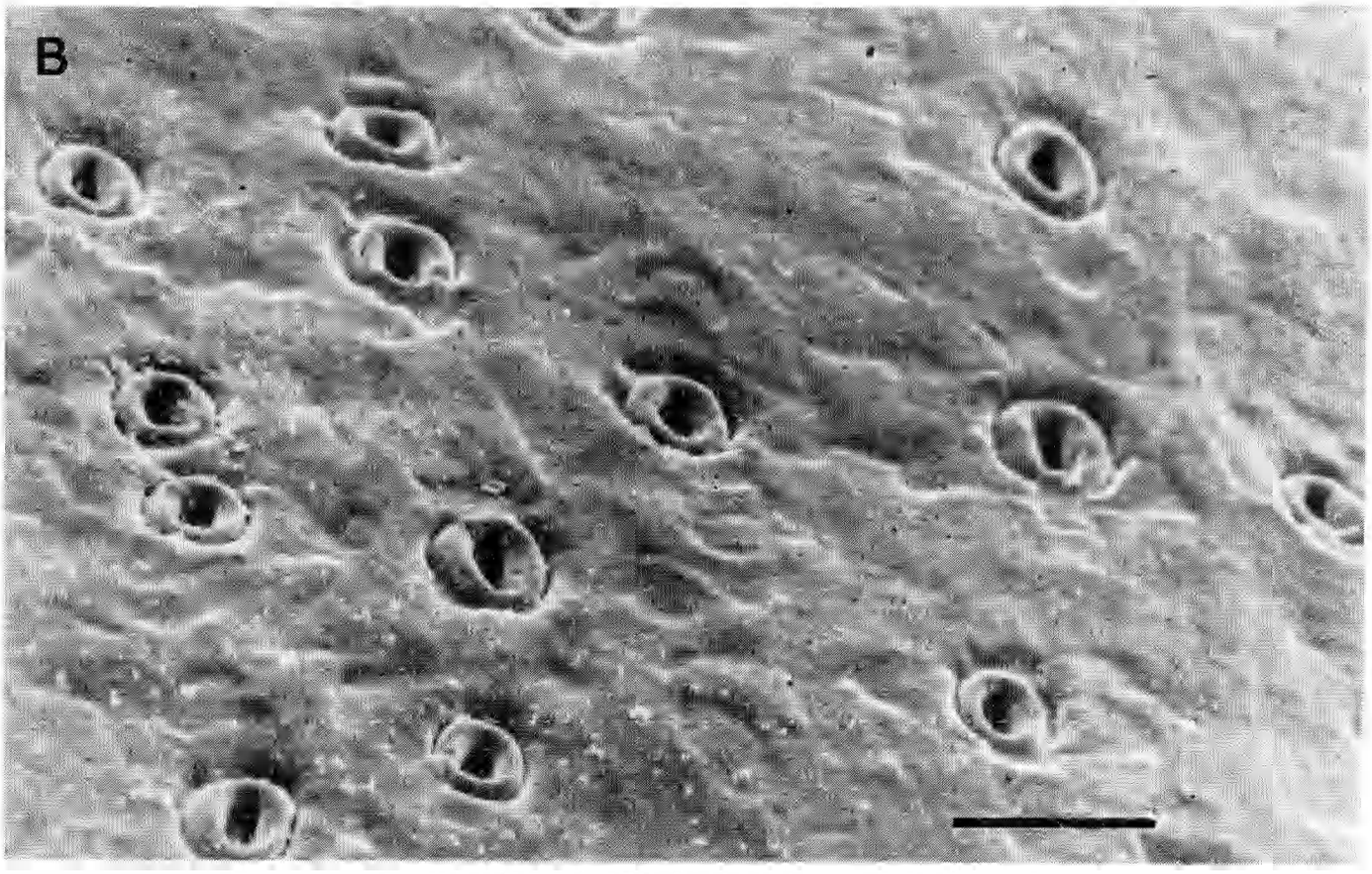
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sion tissue, transfer cells with wall thickenings are seen in TEM pictures (Fig. 6 B) and in LM of semithin sections of Spurr embedded material, stained by the method of Gunning and Pate (1969).

Ontogeny of the phylloclades

The epidermis. In the phylloclade segments of 3–5 mm length, the epidermal cells are arranged in relatively regular rows. The anticlinal walls have no secondary thickenings. The segments seem to be composed of branching stems as well as rudimentary leaves (cf. Velenovsky 1903). Stomata have differentiated only in what might be regarded as immature leaves (cf. Fig. 7 B). Thickened secondary anticlinal walls of the epidermis cells can be seen in phylloclade segments of 18 mm length. The cells are more irregular than at the earlier stages of development. Stomata occur on all surfaces of the phylloclade.

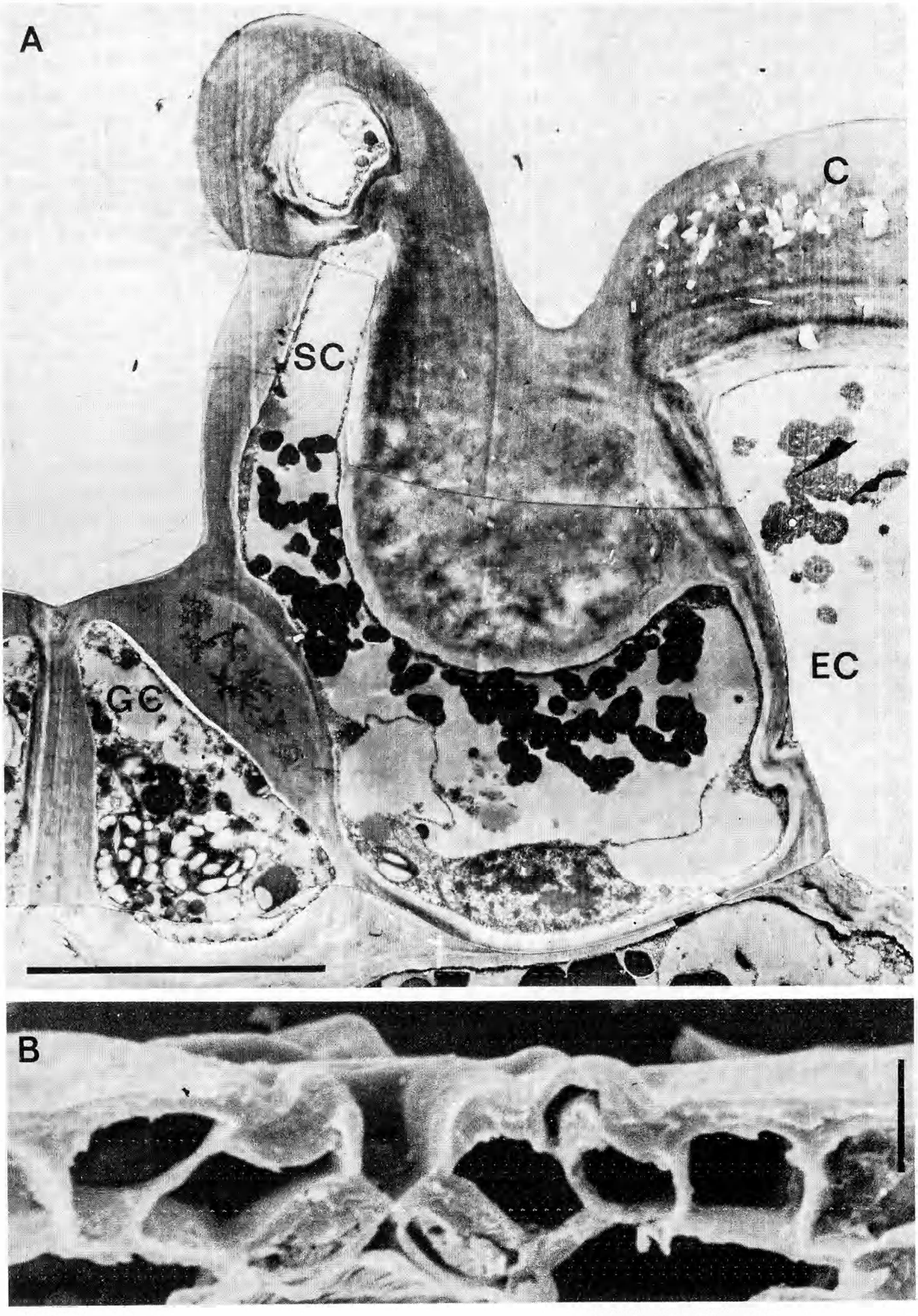
The cortex. The accessory transfusion tracheids differentiate slowly. In segments of 3–5 mm length, tracheid initials can be seen as cells, which are somewhat elongated at right angles to the veins. When the phylloclade is c. 18 mm long, the accessory transfusion tracheids have assumed their irregular shape. Development of the characteristic secondary wall of the accessory transfusion tracheids (Fig. 3 A) is not present in segments of 18 mm length but is found in the segment when it is 29 mm long. Resin ducts on the other hand can be observed in segments that are only 5 mm in length.

The vascular tissue and the transfusion tissue. There are protoxylem tracheids with spiral wall thickenings in phylloclade segments that are no more than 3 mm in length. They have developed acropetally, but have not in these immature segments reached the leaf apex (Fig. 7 A). Near the leaf apex a few relatively large cells have developed (Fig. 7 A) which at this stage show spiral wall thickenings and probably are transfusion tracheids. When the phylloclade segment is 5 mm long, each leaf trace of the phylloclade (Fig. 7 B) has two or more rows of xylem tracheids. The tracheids have differentiated almost to the leaf apex and are surrounded by many transfusion tracheids, which develop basipetally from near the leaf apex (Fig. 7 C). The development of the cauline bundles of the phylloclade still lags behind, as can be seen in Fig. 7 C, but nevertheless they have a few transfusion tracheids (Fig. 8 A, C). Some of the transfusion tracheids have already developed bordered pits (Fig. 8 B).

Fig. 1. — A: Transverse section of lateral part of phylloclade. Epidermis cells with nuclei and thick cuticle, chlorenchyma cells, and large accessory transfusion tracheids with lignified walls. One stoma, centrally cut, is also seen (arrow). LM. — B: Cuticle with scattered stomata; subsidiary cells form a slightly elevated, protecting ring. SEM. — Scale line equals 50 μm. — Key to labelling in Figs. 1–8: C cuticle, CA cambium, CC chlorenchyma cell, CP chloroplast, EC epidermal cell, GC guard cell, MX metaxylem, PF phloem fiber, PH phloem, PX protoxylem, R ray, RD resin duct, S accessory transfusion tracheid, SC subsidiary cell, TP transfusion parenchyma, TT transfusion tracheid.

Fig. 2. — A: Composite figure of transverse sections that include a guard cell and a subsidiary cell. In the guard cell chloroplasts with several starch grains and vacuoles with globules of tannin can be seen. In the subsidiary cell the nucleus and a vacuole with tannin are seen. TEM. — B: Transverse section of a stoma with guard cells, overarched by subsidiary cells, which are partly raised above the surface. A thin-walled accessory transfusion tracheid forms the bottom of a substomatal cavity. SEM. — Scale lines equals 10 μm. — Labelling, see Fig. 1. (See p. 194.)

Fig. 3. — A: Section through a number of thin-walled accessory transfusion tracheids, devoid of contents and with many pit-fields in their walls. One chlorenchyma cell is also seen. Its protoplasm forms a netlike structure and contains several chloroplasts. SEM. Scale line equals 20 μm. — B: The secondary wall of an accessory transfusion tracheid shows unsymmetrical distribution of the pits, which are more numerous on the walls in contact with chlorenchyma cells. The chlorenchyma cell contains chloroplasts with starch grains and large tannin globules in the vacuole. TEM. Scale line equals 10 μm. — C: Transverse section of a phylloclade shows epidermis with a stoma, large accessory transfusion tracheids, vascular bundle with xylem and phloem, and a sheath of thin-walled parenchyma cells. Outside the phloem is a resin duct with thin-walled secretory cells. SEM. Scale line equals 50 μm. — Labelling, see Fig. 1. (See p. 195.)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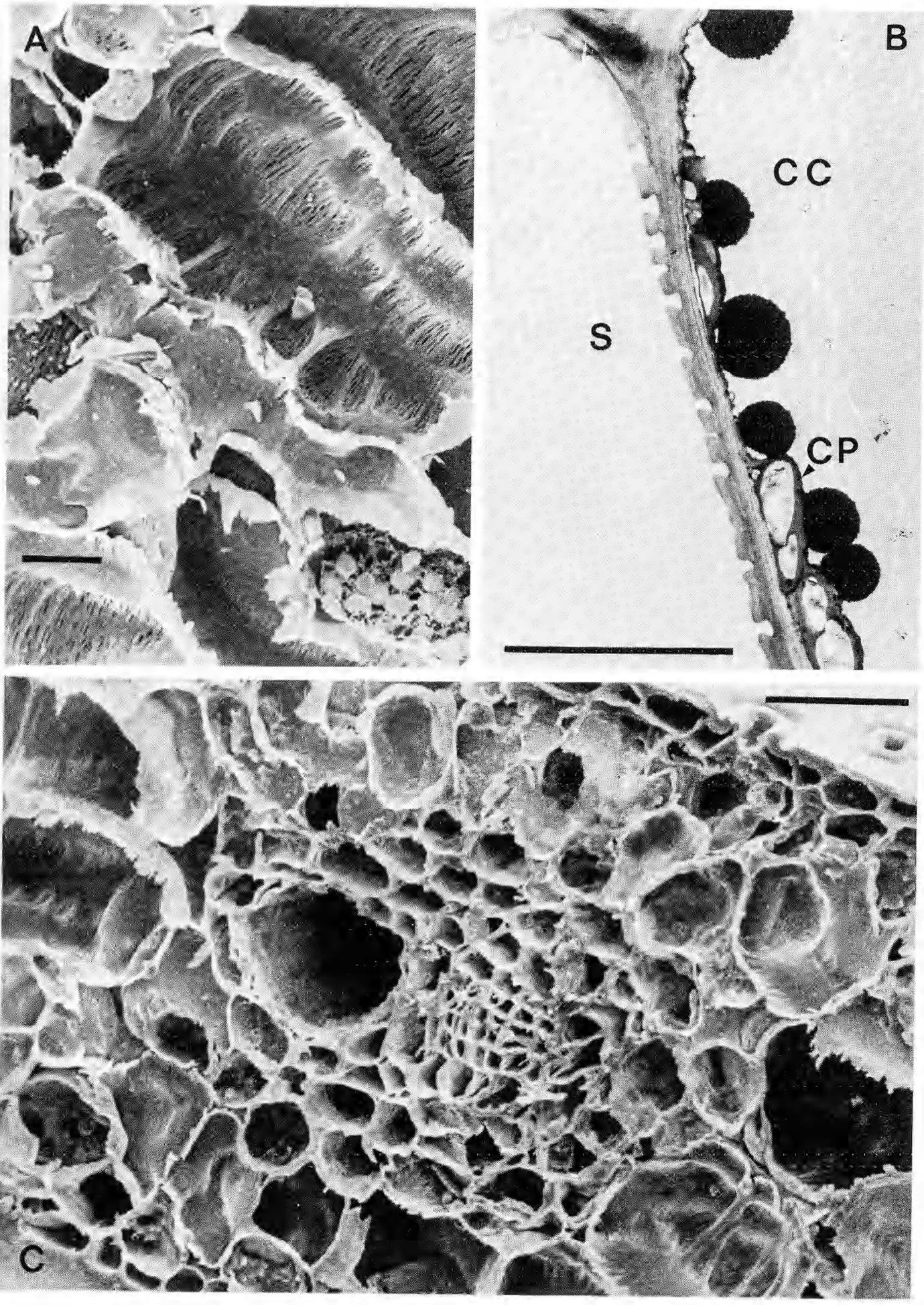
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Discussion

Apart from the arrangement of the vascular bundles, the phylloclades of *Phyllocladus hypophyllus* show striking similarities with coniferous leaves. The thick cuticle and the thickened outer and anticlinal walls of the epidermal cells are found both in needles of *Pinus* and phylloclades of *Phyllocladus*. *Phyllocladus* has living epidermal cells and lacks a hypodermis, in contrast to the needles of *Pinus*. These distinctions may be due to the evolution of *Phyllocladus* in a less dry climate than *Pinus*.

The cortex of the phylloclades is composed of two types of cells, chlorenchyma and thin-walled non-living cells. These latter cells, which are extremely variable in shape (Fig. 3 A, B) seem to me to correspond to the accessory transfusion cells, which Griffith (1957) has described in *Podocarpus*. The accessory transfusion tracheids in the leaves of *Podocarpus* are isodiametric or elongated at right angles to the veins, sometimes with a wavy outline. Their pores are gathered in groups in the parts of walls that are in contact with other cells. The cells with lignified secondary walls in the phylloclades of *Phyllocladus* differentiate quite late like the accessory transfusion tracheids of *Podocarpus*. Similar cells are found in the leaves of *Araucaria*, and Lederer (1955) has suggested that they might be homologous to the accessory transfusion tissue of *Cycas*.

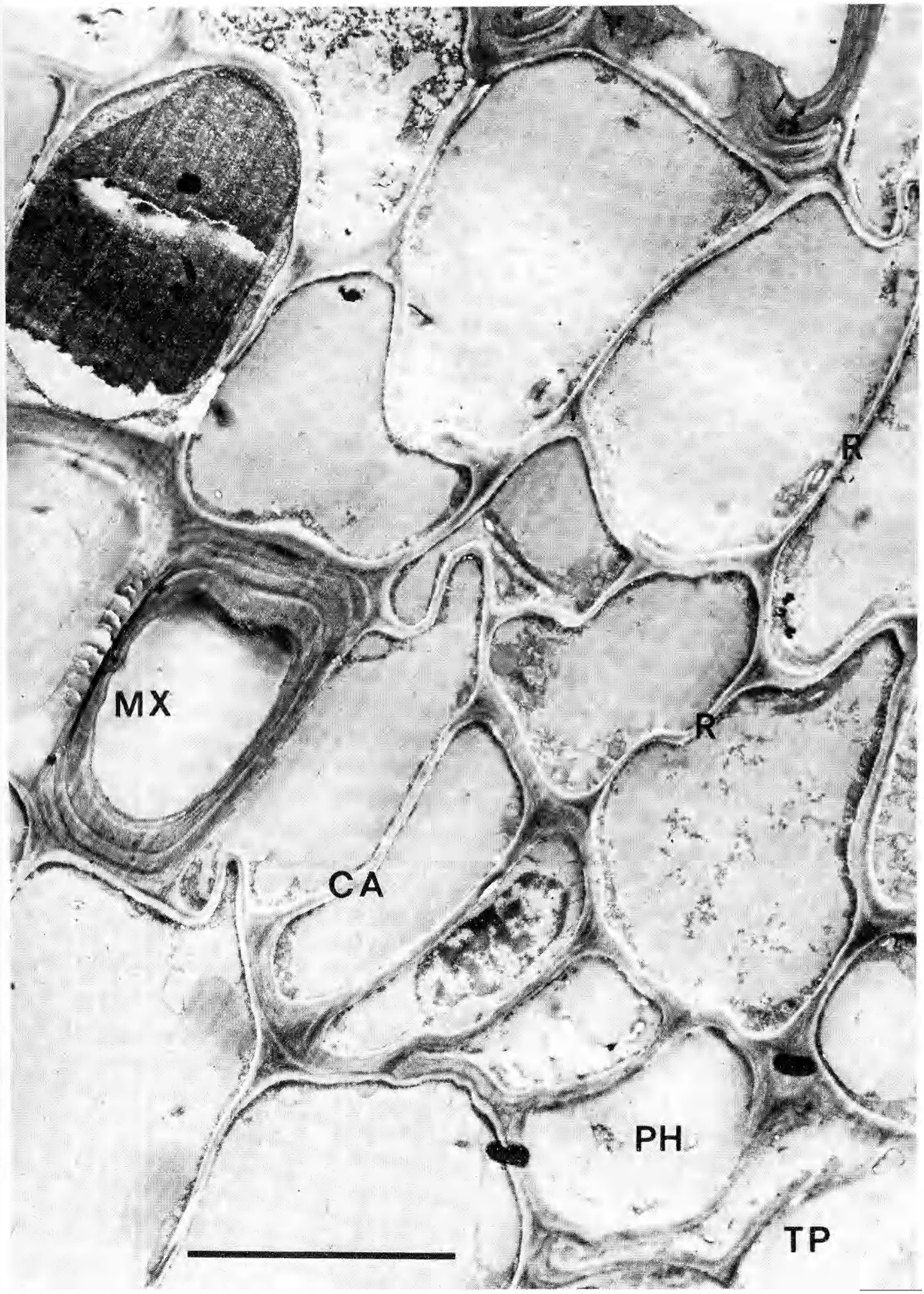
In contrast to the accessory transfusion tracheids, the transfusion tracheids of *Podocarpus* differentiate basipetally, very early during ontogenesis. The same phenomenon has been noted in the case of the bundle sheath tracheids of *Phyllocladus* (Fig. 7 C). Those cells seem to be identical to the tracheids in what Robertson (1906) has called centripetal xylem. Because of the mode of development (basipetally) I prefer to consider them as transfusion tracheids (cf. Napp-Zinn 1966 p. 27). The early development of transfusion tracheids in pine neddles has been described by Campbell (1972), who like Walles et al. (1973), found these cells to have relatively thin, secondary walls with bordered pits and to be devoid of protoplasts, features which are also common to the transfusion tracheids of *Phyllocladus* (Fig. 6 A). Lederer (1955) in his study of gymnosperm leaves has included *Taxus* among those gymnosperms whose transfusion tracheids have scalariform wall thickenings and bordered pits. The transfusion parenchyma cells of *Taxus* leaves are found below compressed phloem cells and above and between the transfusion tracheids. The transfusion parenchyma cells of *Pinus* needles have a large vacuole with tannin deposits and a very thin lining of cytoplasm (Campbell 1972); similar cells are observed in *Phyllocladus* (Fig. 6 B).

In *Pinus* needles, as well as in some other coniferous leaves, the transfusion tissue is bordered by an endodermis, but *Podocarpus* leaves lack this delimitation of the transfusion tissue. Lederer (1955) makes a distinction between the pinacean type with a well developed endodermis, and the *Taxus* type with only a "parenchymatic sheath" and transfusion tracheids and transfusion parenchyma gathered into more or less compact complexes. Lederer considered the *Taxus* type to be the more primitive. *Podocarpus* obviously belongs to this *Taxus* type and the same seems to be the case with *Phyllocladus*

Fig. 4. Transverse section of part of a vascular bundle. The xylem tracheids have thick, secondary walls with bordered pits; on the walls adjacent to parenchyma cells only half-pits. The parenchyma of the xylem has only a thin layer of protoplasm, and a large vacuole, sometimes filled with granular material. The cambium cells are irregular, containing several amoeboidal plastids. Some of the sieve cells have relatively thick walls. TEM. — Scale line equals 10 μm. — Labelling, see Fig. 1.

Fig. 5. Transverse section of phylloclade, showing the orientation of vascular bundles in the centre of a mature phylloclade. — A: Edge of section. LM. — B: Middle part of section. LM. — Scale line equals 50 μm. — Labelling, see Fig. 1. (See p. 198.)

Fig. 6. — A: Transverse section of a vascular bundle with phloem, metaxylem, protoxylem, transfusion tracheids, and transfusion parenchyma. The protoxylem elements are slightly deformed, while phloem and metaxylem form regular rows. SEM. Scale line equals 10 μm. — B: Part of a transfusion parenchyma cell with wall thickenings traversed by plasmodesmata (arrows). This cell is interpreted as a transfer cell. TEM. Scale line equals 1 μm. — Labelling, see Fig. 1. (See p. 199.)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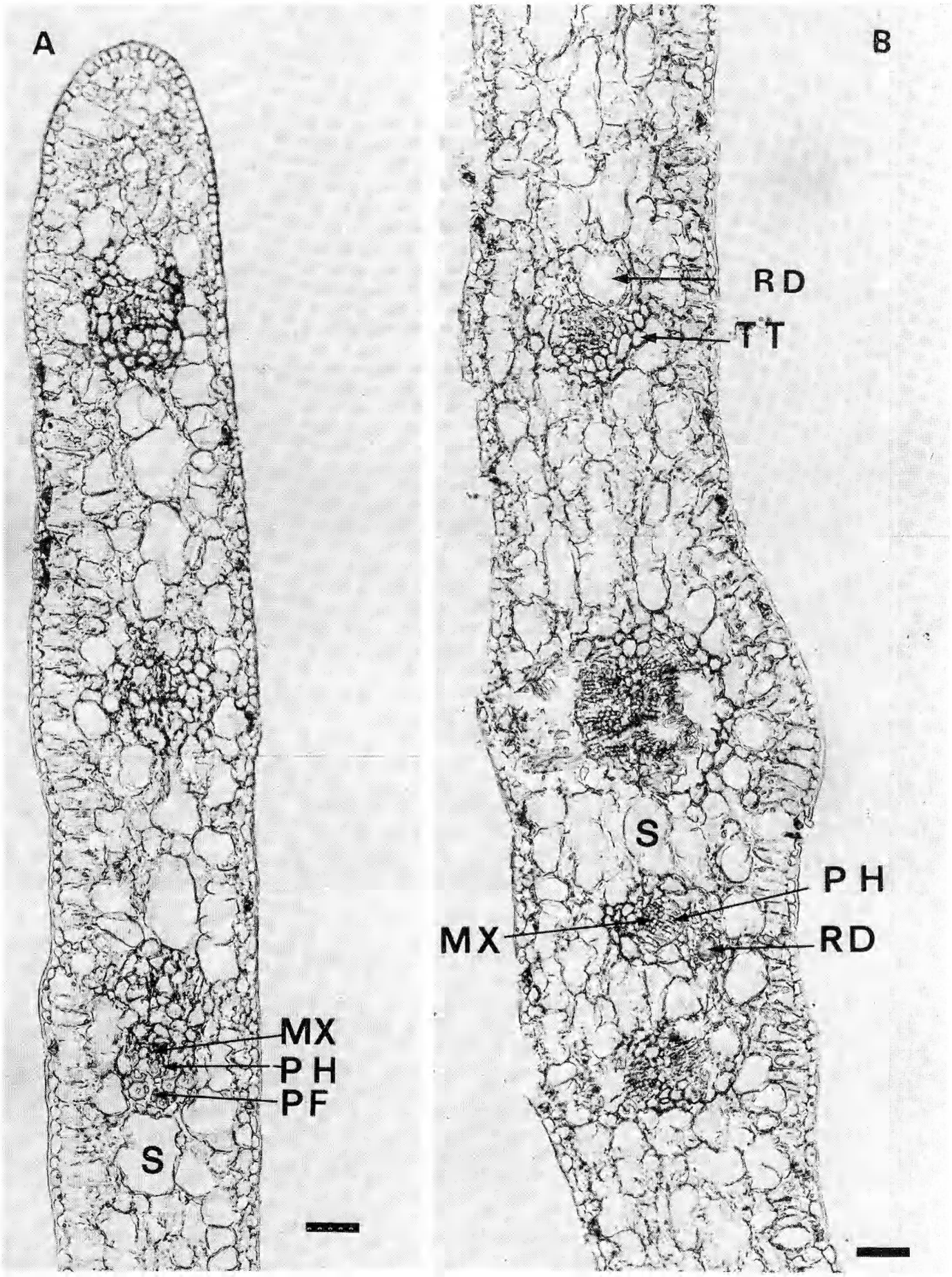
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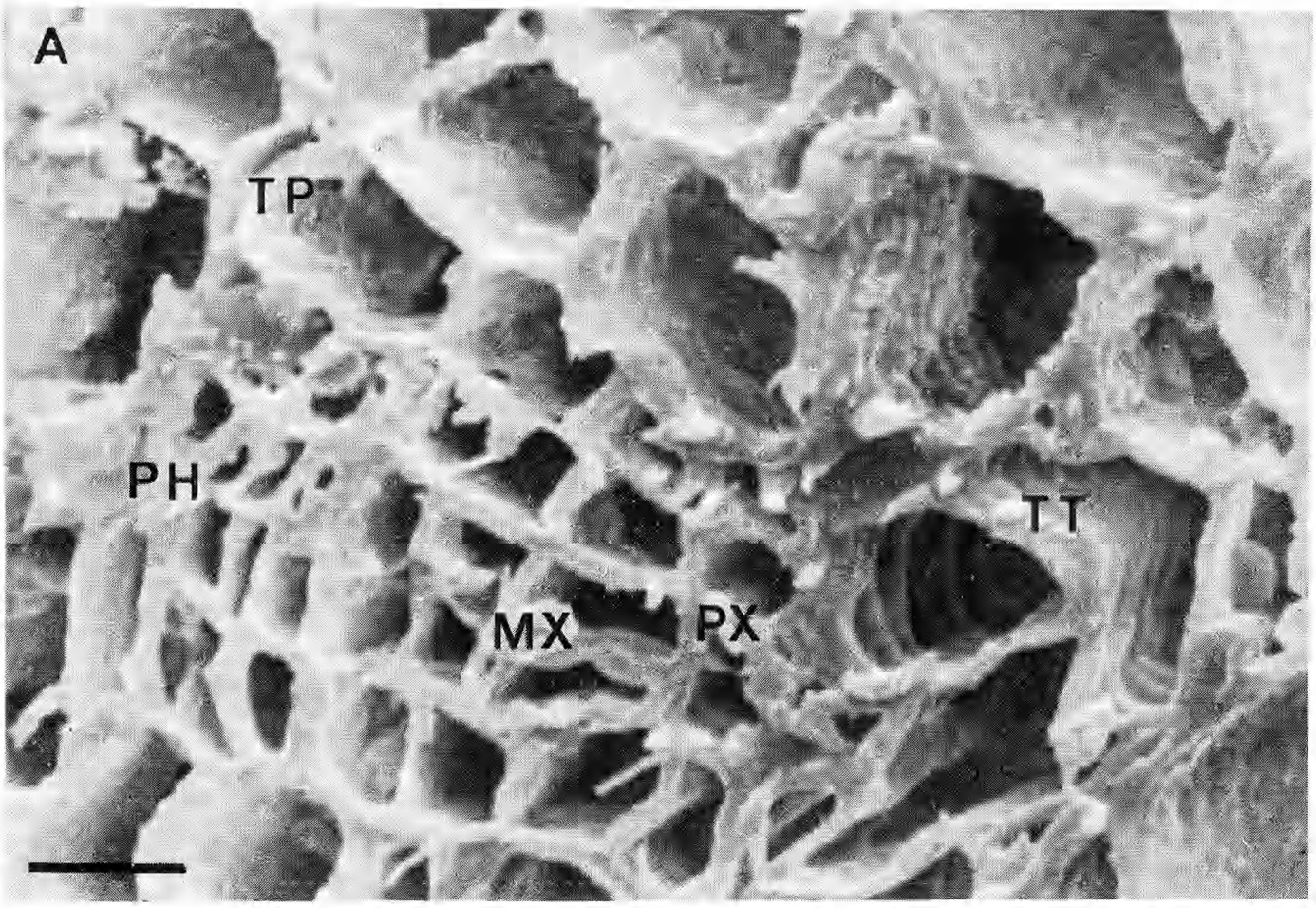
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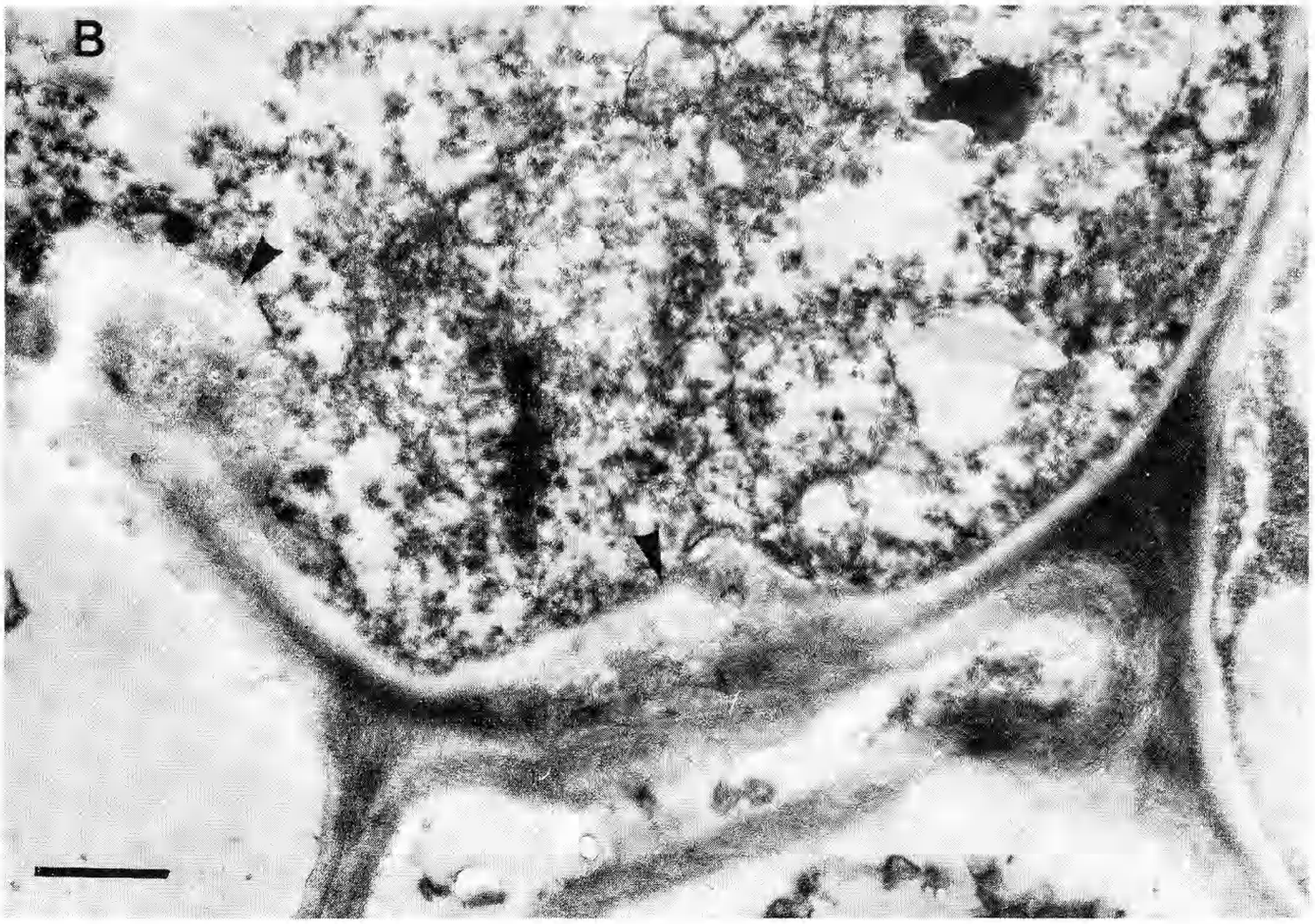
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cladodes (Figs. 3 C, 8 C). Just outside the vascular strands there are thin-walled parenchyma cells with many chloroplasts and globules of tannin, alternating with the thin-walled cells with lignified walls which I suggest are transfusion tracheids.

The development of the phloem has not been studied in the present investigation. In cleared segments, however, the phloem cells can be seen as several parallel lines of elongated cells, even when the segment is only 3 mm long. Only one line of protoxylem can be seen in the cleared material, while SEM pictures of a cross section show this line to be composed of 3–4 rows of protoxylem tracheid elements (Fig. 8 C). At that early stage the phloem can hardly be distinguished from the cortex. The sieve cells mature relatively late, after elongation is completed, as Campbell (1972) and Neuberger & Evert (1974) described for pine needles. That interpretation can be compared with the report of relatively rapid sieve cell differentiation in the hypocotyl of *Pinus resinosa* (Neuberger & Evert 1974); in this case the cambial activity is reported to begin soon after completion of elongation of the hypocotyl.

There have been numerous speculations as to the function of the many ergastic substances found in plants. Some have been regarded as end products of metabolism, that are not utilizable metabolically, e.g. tannins, terpenes, and resins (Esau 1977). Resin ducts, however, differentiate very early in the ontogeny of leaves (Napp-Zinn 1966) and resin ducts are reported even in young shoots, 1 mm thick (Kucera & Butterfield 1977), of *Phyllocladus* species. I have found schizogenous resin ducts in cross sections of 5 mm long phylloclade segments and the younger segments smell strongly of resin when cut. Thus I want to suggest that resin production offers protection against predators, that is no longer needed when the organ is mature and contains many fibers and other cells with stiff walls. My suggestion is consistant with Campbell's (1972) observation of the frequent degeneration of the resin canals of mature pine needles.

Acknowledgements. I would like to thank Professor B. Walles, Institute of Botany, University of Stockholm, for valuable advice and never-failing interest. I am also very grateful to Dr J. Rowley for teaching me the techniques of TEM, for all other aid given me and for reading the manuscript. For teaching me the techniques of SEM and light microscopy and for valuable advice I wish to thank FK Eva Kronestedt. I would also like to thank Miss Inger Eriksson and Mrs Edel Alsterborg for technical advice.

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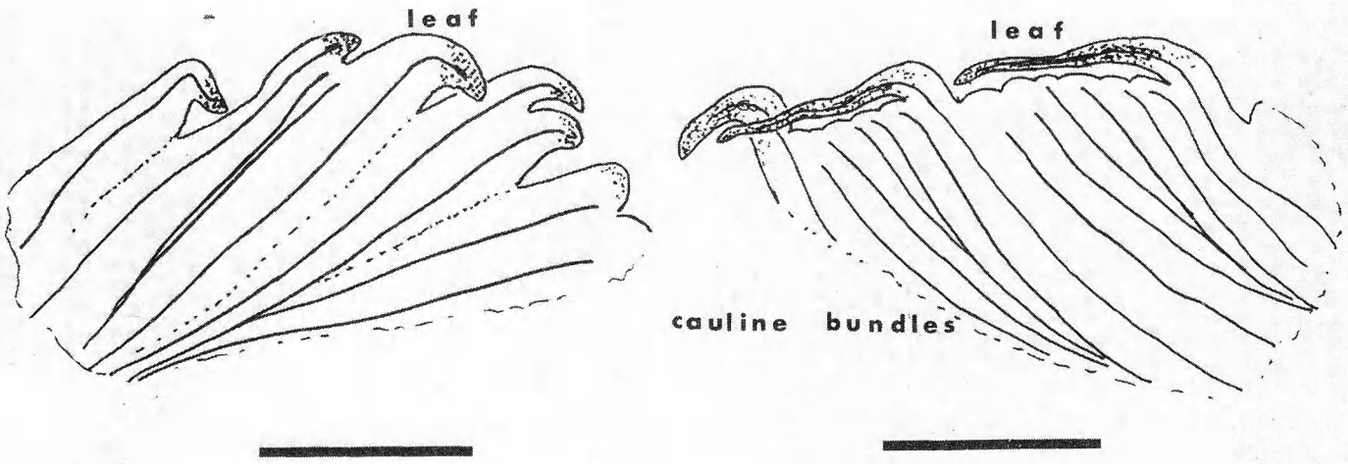
Fig. 7. — A: Drawing of part of an immature phylloclade segment, totally 3 mm long. — B: Drawing of part of an immature phylloclade segment, totally 5 mm long. A clear difference between what can be regarded as leaf traces and cauline bundles can be seen. Scale line equals 1 mm. — C: Cleared part of 5 mm long segment; leaf trace and cauline bundle. Leaf trace with xylem and transfusion tracheids and cauline bundle with one line of protoxylem and further out in the apex one transfusion tracheid. LM of cleared preparation. Scale line equals 50 μm. — Labelling, see Fig. 1.

Fig. 8. — A: Transverse section of a 5 mm long segment. A few cells of protoxylem and parenchyma are seen. SEM. Scale line equals 5 μm. — B: Longitudinal section of a 5 mm long segment; leaf trace with differentiating transfusion tracheids having bordered pits. SEM. — C: Transverse section of a 5 mm long segment. Cauline bundle with protoxylem and a few transfusion tracheids. SEM. — Scale line equals 10 μm. — Labelling, see Fig. 1. (See p. 202.)



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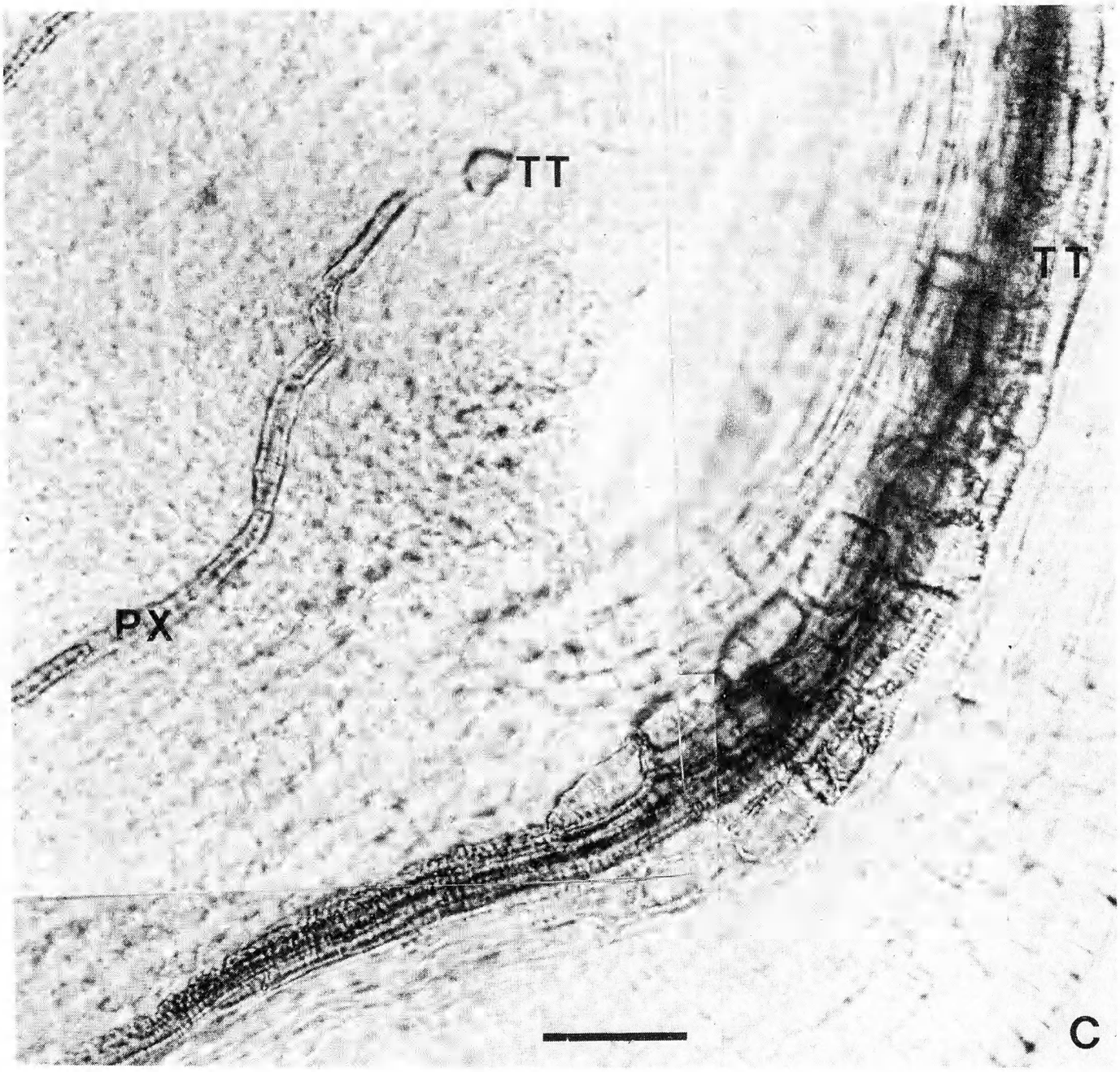

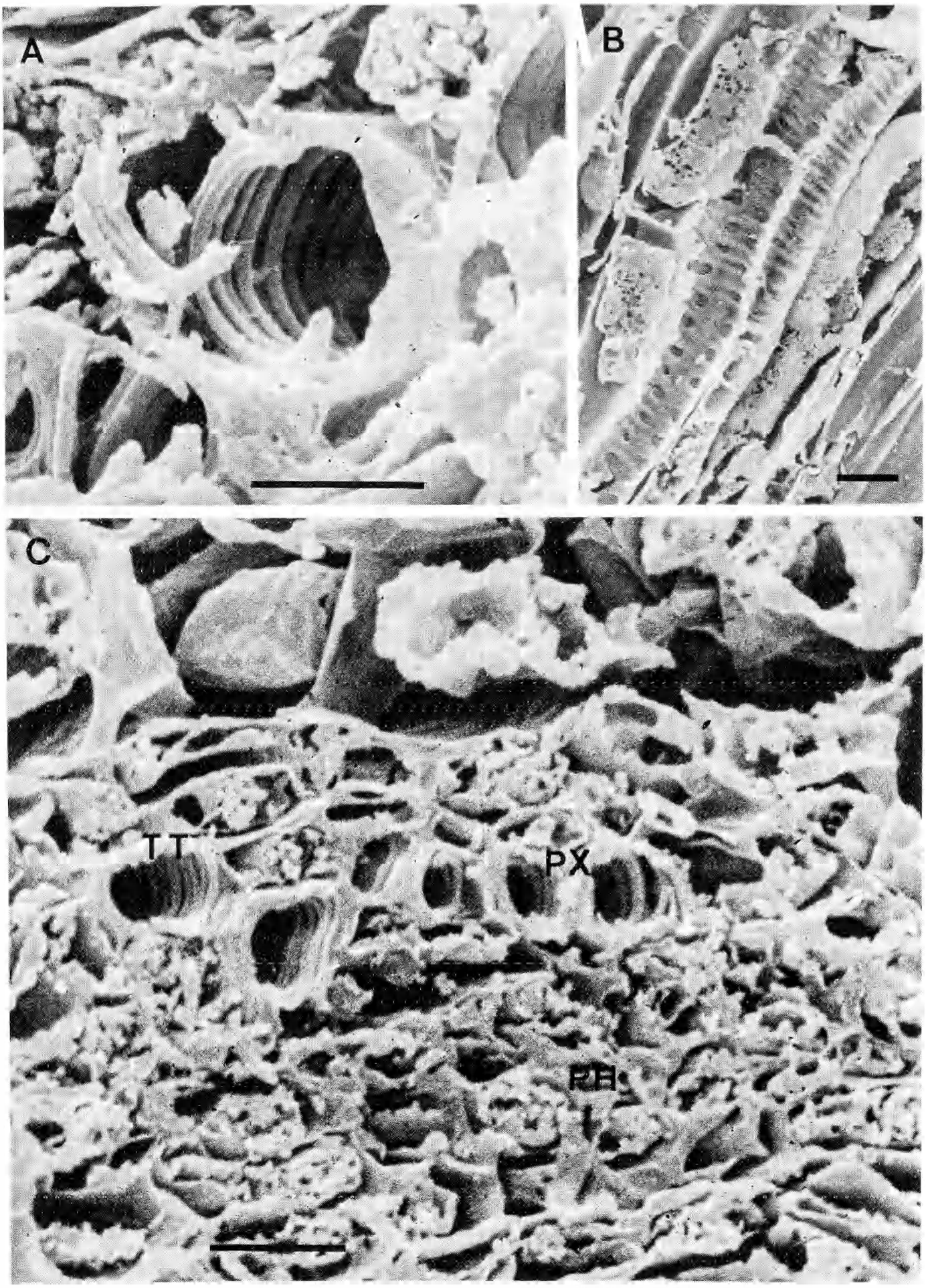
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The Bartsia abyssinica-group (Scrophulariaceae) in Tropical Africa

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Detailed morphological studies of a comprehensive herbarium material of Tropical African *Bartsia* with rotate white to pink corolla necessitated reduction of two of the five species previously recognized (*B. mannii* Hemsl. and *B. elgonensis* R. E. Fr.) to synonyms of *B. abyssinica* Benth., while two others, viz. *B. petitiana* (A. Rich.) Hemsl. and *B. nyikensis* R. E. Fr., are reduced to varieties of the same species. The distribution of *B. abyssinica* s.lat. is mapped and its variation pattern described.

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The Tropical African species of *Bartsia* with white to pink corolla have long been problematical to taxonomists. Of the two earliest species described, *B. abyssinica* Benth, and *B. petitiana* (A. Rich.) Hemsl., both from Ethiopia, the latter was regarded by Engler (1892 p. 384) as synonymous with the former. In the revision by Fries (1924) they were maintained as separate species together with the later described *B. mannii* Hemsl. from West Africa (Hemsley 1906 p. 459), and two more new species, *B. elgonensis* R. E. Fr. from Mt Elgon and *B. nyikensis* R. E. Fr. from Malawi. The numbers of collections seen by Fries for the five species recognized by him were only 2, 9, 1, 1 and 1, respectively, so he had little chance to appreciate the variation within each of his taxa. In most herbaria the naming of material of this group has been so haphazard that a thorough revision was needed (cp. Hedberg 1957 p. 325).

This investigation was performed as a team work during a postgraduate course in systematic botany at the University of Uppsala under the supervision of the senior author. The participants in this course (P.-E. Holmlund, R. L. A. Mahunnah, B. Mhoro, W. R. Mziray and A.-C. Nordenhed) all took part in the handling of herbarium material, measurements and tabulation, diagram construction, etc., as well as in the drawing of taxonomic conclusions and drafting the manuscript. The evolutionary discussion and the final wording were contributed by the senior author.

Material and methods

This study was based on herbarium material, obtained on loan from BM, BR, EA, K, P, S and UPS (abbreviations according to Holmgren & Keuken 1974). Altogether some 330 sheets were inspected, representing 270 collections. From this material we selected for detailed scrutiny all collections containing reasonably good flowers, fruits and leaves, altogether 215. All features deemed to be of potential taxonomic interest were measured or recorded. Leaves, flowers and fruits were measured with an ordinary hand rule to the nearest mm. The pubescence of styles and stems was studied under a stereomicroscope with up to 50 × magnification. Pollen morphology was studied partly on acetolyzed grains under an ordinary light microscope (oil immersion), and partly with a scanning electron microscope (Jeol JSM 35). Seed morphology was studied under a stereomicroscope and is illustrated with SEM photographs (Fig. 4). The results of measurements of maximum leaf width and of the length/width ratio of the fruits are shown in histograms (Figs. 2, 3) and the combined variation in maximum leaf width and fruit shape ratio is illustrated in a pictorialized scatter diagram, in which symbols for other variables are also entered (Fig. 5). Each numerical value used represents the mean of 3 measurements. The altitudinal preference of the three varieties recognized by us is given in a histogram (Fig. 1) and the geographical distribution of the taxa recognized is shown on distribution maps (Figs. 6, 7).

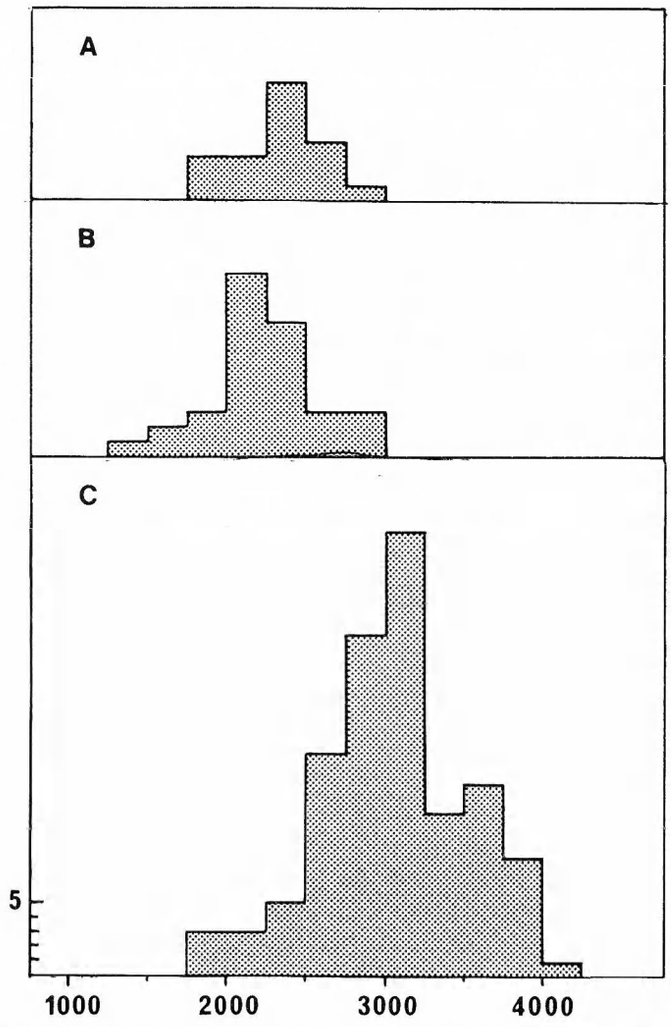


Fig. 1. Histograms comparing the altitudinal distribution of *Bartsia abyssinica* var. *nyikensis* (A), var. *abyssinica* (B), and var. *petitiana* (C). The horizontal axis gives the altitude in m, the vertical axis the number of collections recorded for each altitude interval of 250 m.

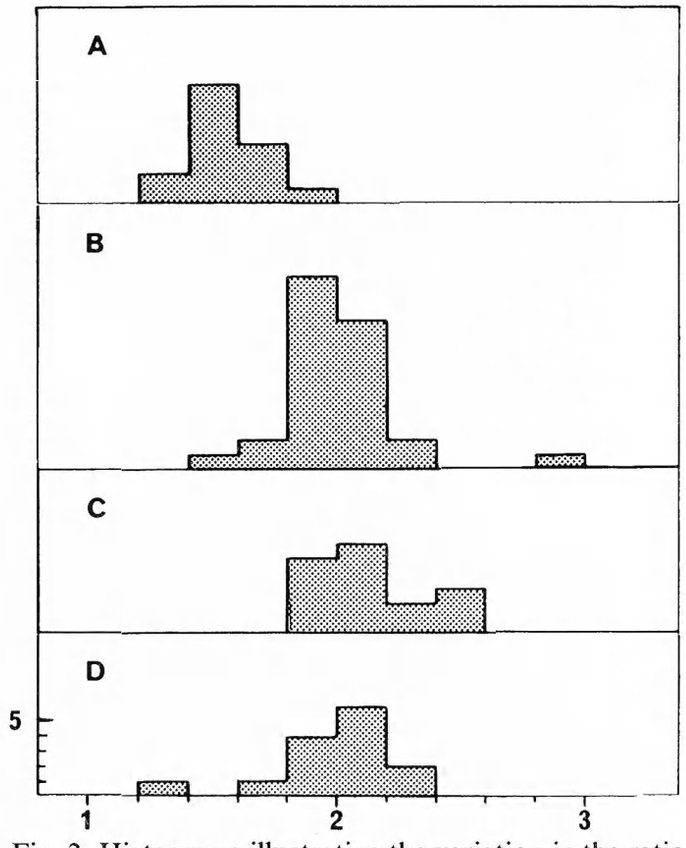


Fig. 2. Histograms illustrating the variation in the ratio of fruit length to fruit width (horizontal axis) in the material studied of *Bartsia abyssinica* var. *nyikensis* (A), var. *abyssinica* (B), var. *petitiana* (C), and the intermediate specimens (D).

Morphological variation and taxonomic conclusions

The main distinctive criteria employed by Fries (1924 p. 65) within this group were whether or not the inflorescence is branched, whether the bracts are longer than the flowers, and whether or not the leaves are petiolate. He also quoted differences in the shapes of inflorescence branches, fruit apex, and calyx lobes. However, none of these criteria resulted in a clear distinction in the larger material available to us. It is true that most of the specimens labelled *B. petitiana* have an unbranched inflorescence—although their stems are often branched at the base (cp. e.g. Fries 1924 Pl. 2:1). But intermediate specimens with 1–2 branches do occur. It is also worth recording that the specimens with unbranched inflorescence, var. *petitiana*, ascend to much higher levels than those more richly branched, vars. *abyssinica* and *nyikensis* (Fig. 1). The reduced branching of the inflorescence at high level may of course be suspected to represent only an altitudinal modification, but since this feature is mostly coupled with glabrous styles and many-ridged seeds it is more likely to represent a genetically conditioned adaptation. Climatical vicissitudes at a high level are known to have caused adaptive reductions in height and branching in many afroalpine taxa, e.g. *Dipsacus pinnatifidus* Stend. ex A. Rich. (Hedberg & Hedberg 1977).

Whether or not the bracts are longer than the flowers seems to be of little taxonomic significance—no discontinuous variation could be found in our material. The same applies to the attachment of the leaves. A short petiole can sometimes be found on larger leaves, but most of them are sessile. The shape of the fruit apex depends too much upon the degree of ripening and the manner of pressing to be of much use, but the general shape of the fruit (length/width

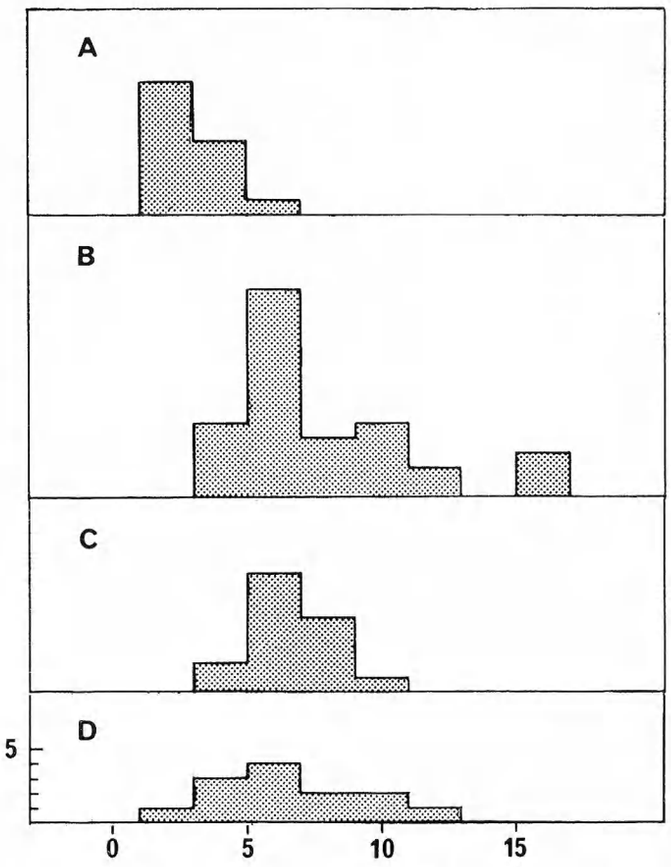


Fig. 3. Histograms illustrating the variation in maximum leaf width (horizontal axis, mm) in the material studied of var. *nyikensis* (A), var. *abyssinica* (B), var. *petitiana* (C), and the intermediate specimens (D).

ratio) proved more useful (Fig. 2). As regards the appearance of the inflorescence there is a tendency for specimens called *B. nyikensis* to have thinner and more curved inflorescence branches, but there is no definite distinction. Another rather striking feature in most *nyikensis*-specimens is the narrow leaves (Fig. 3). Nevertheless intermediates also occur in this character.

A previously neglected morphological character was found in the seeds. In typical "*B. nyikensis*" these have more than ten comparatively low longitudinal ridges, whereas in the rest of the material the ridges are fewer (usually 6–9), higher, and more translucent. But intermediate seeds do occur (Fig. 4 A–C), and this character is not definitely linked with the other features characterizing "*B. nyikensis*". Yet another interesting criterion was found in the pubescence of the styles, which tend to be glabrous in the *nyikensis* material, glabrous or weakly pubescent in the *petitiana* material, and pubescent in the remaining collections.

The pollen morphology was studied in a few representative collections. The pollen grains are tricolpate or occasionally tetracolpate with a rather variable P/E ratio and show the same characteristic reticulum with *Croton* pattern as occurs in the yellow-flowered Bartsias from the same region (Hedberg et al. 1979 p. 6).

The combined variation in the features mentioned is illustrated in a pictorialized scatter diagram (Fig. 5). The weak correlation demonstrated between the different features studied makes it impossible to maintain any interspecific boundary within this material. We have therefore decided to divide it into three varieties: var. *abyssinica,* var. *petitiana,* and var. *nyikensis,* between which fall a number of intermediate specimens. The material from West Africa, previously called *B. mannii,* and represented in the scatter diagram by special symbols, differs in no significant way from var. *abyssinica.* The type collection of *B. elgonensis* clearly falls within the variation range of var. *petitiana.*

Synopsis

Bartsia abyssinica Benth.

Bentham 1846 p. 545; Engler 1892 p. 384; Hemsley & Skan 1906 p. 460; R. E. Fries 1924 p. 67; Robyns 1947 p. 245; Agnew 1974 p. 567.

Alectra abyssinica (Benth.) A. Richard 1851 p. 118. — *Glossostylis abyssinica* Hochst. ex A. Richard 1851 p. 118, pro syn. — Orig. coll.: Ethiopia, Mt. Scholoda, Schimper I: 356 (BM, BR, K lectotype, selected here, P, S).

Perennial suffrutescent herb up to 3 m high. Stems erect or ascending, sometimes rambling, terete, usually ± densely pubescent with straight or hooked, patent or retrorse hairs. Leaves elliptic to lanceolate, sessile or subsessile, thick and rigid, with rounded or cuneate base and obtuse or acute apex, crenate. Inflorescence an open spike-like raceme, branched or unbranched. Corolla obliquely campanulate with curved tube, shorter than the limb, white to pink. Style about 6 (5.5–7) mm long, glabrous or pubescent. Capsule ovoid to almost globular. Seeds about 0.9–1.2 mm long, slightly curved, provided with 6–14 longitudinal ridges (Fig. 4 A–C). Pollen grains spheroidal, c. 29 μm in diameter, tricolpate, exine with distinct *Croton* pattern resembling that in *Bartsia longiflora* (cp. Hedberg et al. 1979 Figs. 8–9).

Three varieties are recognized.

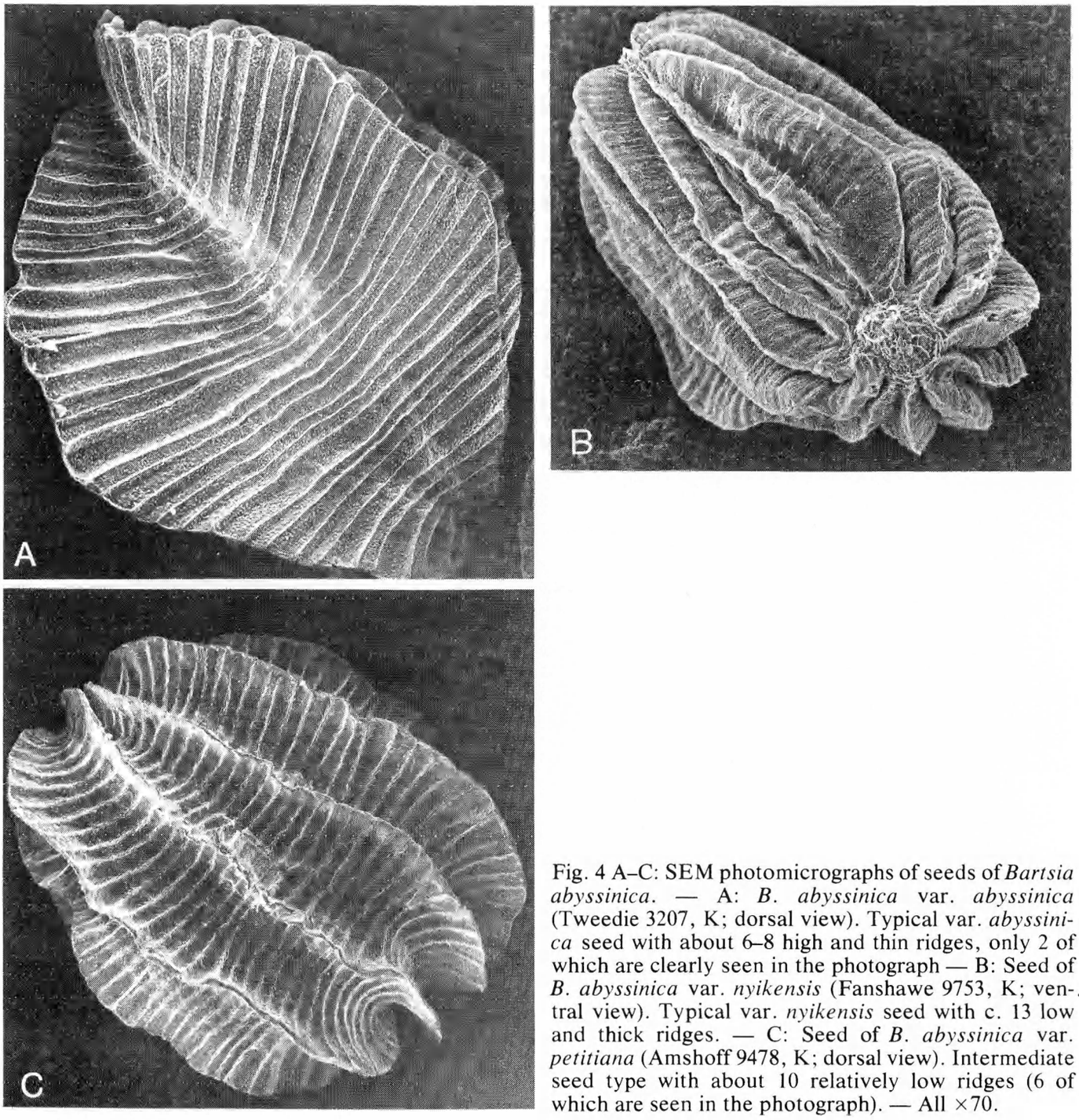
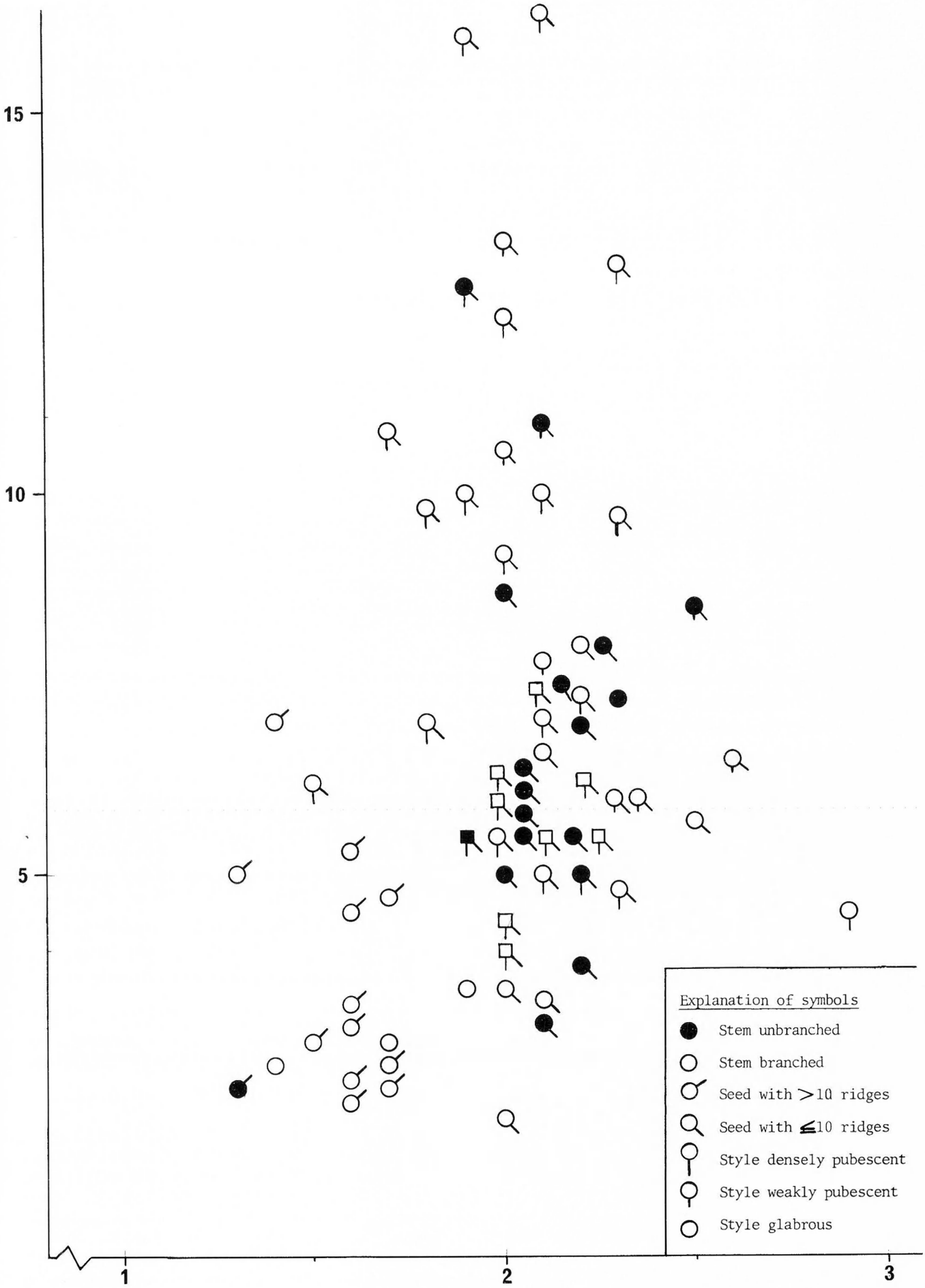


Fig. 4 A–C: SEM photomicrographs of seeds of *Bartsia abyssinica*. — A: *B. abyssinica* var. *abyssinica* (Tweedie 3207, K; dorsal view). Typical var. *abyssinica* seed with about 6–8 high and thin ridges, only 2 of which are clearly seen in the photograph — B: Seed of *B. abyssinica* var. *nyikensis* (Fanshawe 9753, K; ventral view). Typical var. *nyikensis* seed with c. 13 low and thick ridges. — C: Seed of *B. abyssinica* var. *petitiana* (Amshoff 9478, K; dorsal view). Intermediate seed type with about 10 relatively low ridges (6 of which are seen in the photograph). — All ×70.

Fig. 5. Pictorialized scatter diagram illustrating the combined variation in the ratio of fruit length to fruit width (horizontal axis) and maximum leaf width (vertical axis). Specimens from West Africa are represented by square symbols, those from East Africa by filled or unfilled circles.


15
10
5
1
2
3
Explanation of symbols
Stem unbranched
Stem branched
Seed with >10 ridges
Seed with ≤10 ridges
Style densely pubescent
Style weakly pubescent
Style glabrous

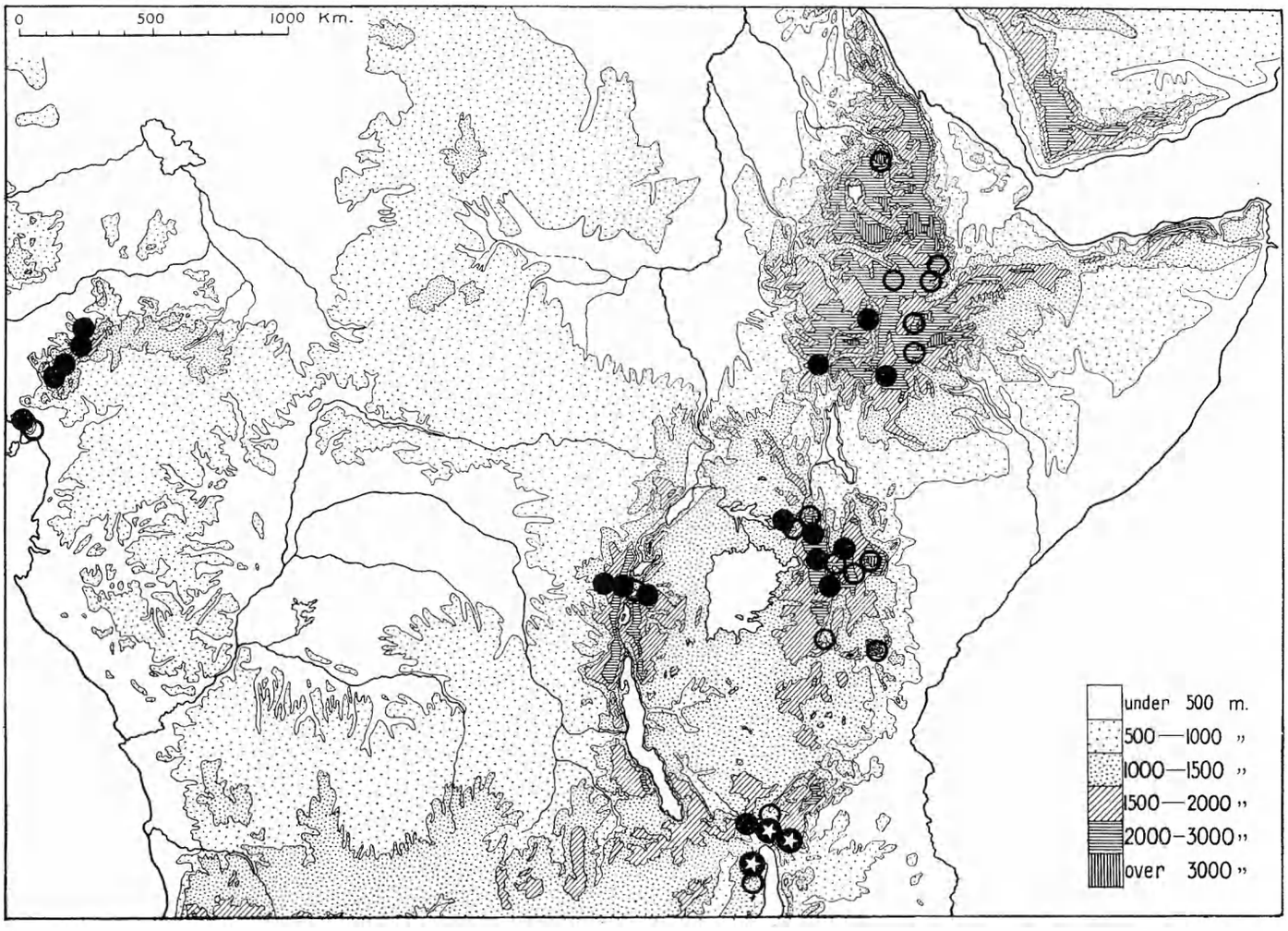


Fig. 6. Known geographical distribution of *Bartsia abyssinica* var. *abyssinica* (black dots), var. *nyikensis* (star dots), and of intermediate specimens not referable to any of the 3 varieties (open rings).

Key to the varieties

1. Inflorescence usually distinctly branched 2
– Inflorescence usually unbranched or with 1–2 branches ..... 3. var. *petitiana*
2. Style pubescent; seeds as a rule with less than length/width ratio mostly at least 1.8 ..... 1. var. *abyssinica*
– Style glabrous; seeds usually with more than 10 ridges; fruit length/width ratio usually less than 1.8 ..... 2. var. *nyikensis*

1. **B. abyssinica** var. **abyssinica**

Orig. coll.: see above.

B. mannii Hemsley 1906 p. 459; R. E. Fries 1924 p. 67; Hutchinson & Dalziel 1931 p. 224; Hepper 1963 p. 367. — Orig. coll.: Cameroons, Cameroons Mt. 2150–2750 m, Mann 1264 (K isotype) and 1986 (K lectotype, selected here).

B. elgonensis R. E. Fries 1924 p. 67. — Orig. coll.: Mt. Elgon, short grass and bush, 21.X.1916, J. D. Snowden 450 (BM isotype, K holotype — not refound!).

Inflorescence usually branched in its upper part. Fruit elongate (length/width ratio greater than 1.8 in 27 specimens of 29). Style pubescent. Maximum leaf width usually at least 5 mm (in 28 specimens of 33). Seeds with a maximum of 10 longitudinal ridges. Corolla usually pink, when young sometimes creamy white or yellow.

Distribution and habitat. Cameroons, Nigeria, Ethiopia, Zaire, Uganda, Kenya, Tanzania (Fig. 6). Grassland or scrub, forest edges etc. 1250–3000 m above sea level.

Additional collections. Nigeria: Okoja, Sonkwala, Ikwette, Savory & Keay 25258 (K). *Cameroons:* Cameroons Mt, Dunlap 198 (K); Hepper 2843 (K); Maitland 1025 (K); Mann 1862 (K); Menvillon 1168 (K); Morton K 609 and K 853 (both K); Tamajong 22213 (K). Adamawa, Mambila, Hepper 1661 (BR, K). Dschang, Mt Bamboutos, Sanford 5607 (K). Manenguba Mts, Mann 1927 (P). *Zaire:* Between Lakes Kivu and Edward, Humbert 7918 (P). Masisi-Kivu Lake, Lebrun

5085 (BR, K). *Ethiopia:* Tigre, Mt Scholoda, Schimper 1531 (BM, BR, K, UPS). Tossa Mt, Sutherland 223 (UPS). Kaffa, Maigudo Mt, Friis 480 (BR). Magi, Gilbert 363 (K). Sidamo, Amaro Mt, Gillett 14943 (EA, K). *Uganda:* Virunga Mts, Purseglove 2096 (EA, K); Taylor 1784 (BR); Thomas 1716 (BM, K). Elgon, Tothill 2257 (K). *Kenya:* Elgon, Lack 369 (EA, K); Lugard 53, 140 and 693 (all K); Symes 222 (EA); Tweedie 1378 (K, S). Cherangani, Mainwaring K 49 (K); Tweedie 3207 and 4179 (both K). Tindiret, Mainwaring 3079 (EA, K). Narok, Greenway 14917 (EA). Thomson Falls, Blake B 7666 (EA, K). *Tanzania:* Kyimbila, Stolz 2353 (BM, BR, EA, K, S).

2. **B. abyssinica** var. **nyikensis** (R. E. Fr.) O. Hedb. et al. comb. nov.

Bartsia nyikensis R. E. Fries 1924 p. 66. — Orig. coll.: Malawi, Nyika Plateau, c. 2250 m, Sept. 1902, M. Mc Clounie 60 (K holotype).

Inflorescence usually branched with long branches (in 14 collections of 15). Fruit subglobose (length/width ratio below 1.8 in 14 specimens of 15). Style glabrous. Maximum leaf width usually less than 5 mm (in 13 specimens of 15). Seeds with more than 10 longitudinal ridges. Corolla usually white, often with a pink or purple tinge, occasionally completely pink or purple.

Distribution and habitat. Zambia, Malawi, S. Tanzania (Fig. 6). Upland grassland, evergreen forest margins, et., 1750–3000 m above sea level.

Additional collections. Tanzania: Kinga, Goetze 1127 (BR). Kyimbila, Stolz 1391 (K, S) and 2136 (BM, BR, EA, K, P, S). Mbeya, Napper 1179 (EA); Pocs 6751 D (EA); Richards 9685 (BR) and 13984 (BR, K). Njombe, Gillett 17776 (EA); Prins 162 (EA); Procter 1857 (EA); Richards 6596 (K). Rungwe, Greenway 8403 (BR, EA, K); Procter 1443 (EA). *Zambia:* Nyika Plateau, Fanshawe 2753 (K). Lundazi, White 2748 (K). *Malawi:* Nyika Plateau, Brass 17169 (BM, BR, EA, K); Brummitt 10759, 11911 and 11959 (all K); Jackson 879 (K); Pawek 9997 (EA, K); Richards 10501 (BR). Ufipa, Brummit & Synge WC 68 (BR, EA, K, UPS).

3. **B. abyssinica** var. **petitiana** (A. Rich.) O. Hedb. et al. comb. nov.

Alectra petitiana A. Richard 1851 p. 118. — *Bartsia petitiana* (A. Rich.) Hemsley 1906 p. 460; R. E. Fries 1924 p. 65; Hedberg 1957 p. 171, 325; Hepper 1963 p. 367; Agnew 1974 p. 567. — Orig. coll.: Ethiopia, Ouodgerate, A. Petit s.n. (K, P holotype).

Inflorescence usually unbranched or occasionally with 1–2 branches. Fruit elongate (length/width ratio at least 1.8). Style glabrous (in 13 specimens of 17) or sparsely pubescent (in 4 specimens). Maximum leaf width at least 5 mm (in 15 specimens of 16). Seeds with a maximum of 10 longitudinal ridges. Corolla usually pink or pinkish-purple, rarely white.

Distribution and habitat. Cameroons, Ethiopia, Uganda, Kenya, Tanzania (Fig. 7). Open grassland, rocky ground, ericaceous scrub, and afroalpine moorland, 1750–4250 m above sea level.

Additional collections. Cameroons: Cameroons Mt, Boughey 12657 (K); Keay 28607 (K); Migeod 183 (BM). *Ethiopia:* Begemdir, Hedberg & Aweke 5373, 5410 and 5503 (all UPS); Nievergelt 1154 (EA). Gojjam, Evans & Flenley 333 (EA, K). Shewa, Amshoff 9793 (BR); Ash 1021 (K) and 2054 (EA); Gilbert 452 (EA, K); Gilbert & Tewolde 3244 (K); Mooney 6424 (K); Robertson 1268 (K) and 1449 (EA, K); West 5708 (EA). Harerge, Burger 1261 (K); Gillett 5322 (K). Arussi, Amshoff 9098 (BR); Hedberg 4158 (UPS). Gemu Gofa, Scott 133 (K). Bale, Ash 2181 (K); Hedberg 5672 (UPS). Sidamo, Gillett 14943 (BR). Debra Eski, Schimper 127 (S). Wouramboulchi, Omer-Cooper 151 (K). Vociacia, Amshoff 8478 (BR). *Uganda:* Elgon, Dummer 3362 (K); Lind 2101 (EA); Morrison 276 (EA); Rose 10140 (K); Rwaburindore 428 (K); Snowden 474 (BM); Synge S 855 and S 1899 (both BM); Thomas 595 and 2684 (both K); Tothill 2436 (K); Wood 157 (K). *Kenya:* Elgon, Bickford 56 (EA); Gardner 2246 (EA, K); Gillett 18454 (EA, K); Granvik s.n. (S); Taylor 3466 and 3513 (both BM); Tweedie 3227 (EA). Cherangani, Mabberley & McCall 246 (EA, K); Thulin & Tidigs 80 (EA, UPS); Tweedie 2811, 3510, 3869, 3895 and 4199 (all K). Aberdares, Fries 2353 (BR, UPS), 2598 (UPS) and 2895 (UPS); Hedberg 1646 (S, UPS); Meinertzhagen s.n. (BM); Pierce 1244 (EA) and 1477 (EA, K); Taylor 1287 and 1371 (both BM); Verdcourt 4000 A (EA). Mt Kenya, Allt 100 (K); J. Bally B. 3221 (K); Copley 169 (EA); Fries 1172 (S, UPS); Gillett 16231 (EA); Hedberg 2003 (S, UPS) and 4283 (UPS); Hepper & Field 4857 (K); Lugard 412 a (K); Mariën 639 (EA); Meinertzhagen 9460 (EA); Moreau 116 and 171 (both EA); Schelpe 2649 and 2790 (both BM); Slade 3438 (EA); Strid 4384 A (UPS); Synge 1728 (BM); Verdourt 2061 and 3493 (both EA); Williams B. 6404 (EA, K). Turkana, Sekerr Mt, Thorold 3217 (EA). Narok, Greenway & Kanuri 15065 (EA). Ol-joro Orok, Pierce 1667 (EA). Leikipia, Battiscombe 866 (EA). Timboroa, Mainwaring 2208 (EA); Napier 2208 (BR). Tindiret, Maas Gesteranus 5502 (BR, S). *Tanzania:* Kilimanjaro, Cooper 5 (BM); Cotton 37 (K); Gilbert K 25 (EA) and 571 (BR, K); Greenway 3732 (BR, EA); Harris & Jenik 848 (EA); Hedberg 1215 (S, UPS) and 1311 (UPS); King 37 (EA); Napper 610 (EA, K); Schlieben 4802 (BM, BR, P, S); Verdcourt 1214 (EA, K); Wood 927 (K). Mt Meru, Cooper 45 (BM); Gilbert 2143 and 2185 (both EA); Greenway 13509 (EA); Renvoize & Abdallah 2405 (K); Richards 26735 (K); Vesey FitzGerald 5315 (EA, K); White 1284 (BM). Arusha, Ol Doinyo Loldadwenye, Newbold 5945 (EA, K). Iringa, Image Mts, Carmichael 378 (EA). Oldeani, Moreau 54 (EA). Kyimbila, Stolz 1016 (P, UPS). Mbeya, Richards

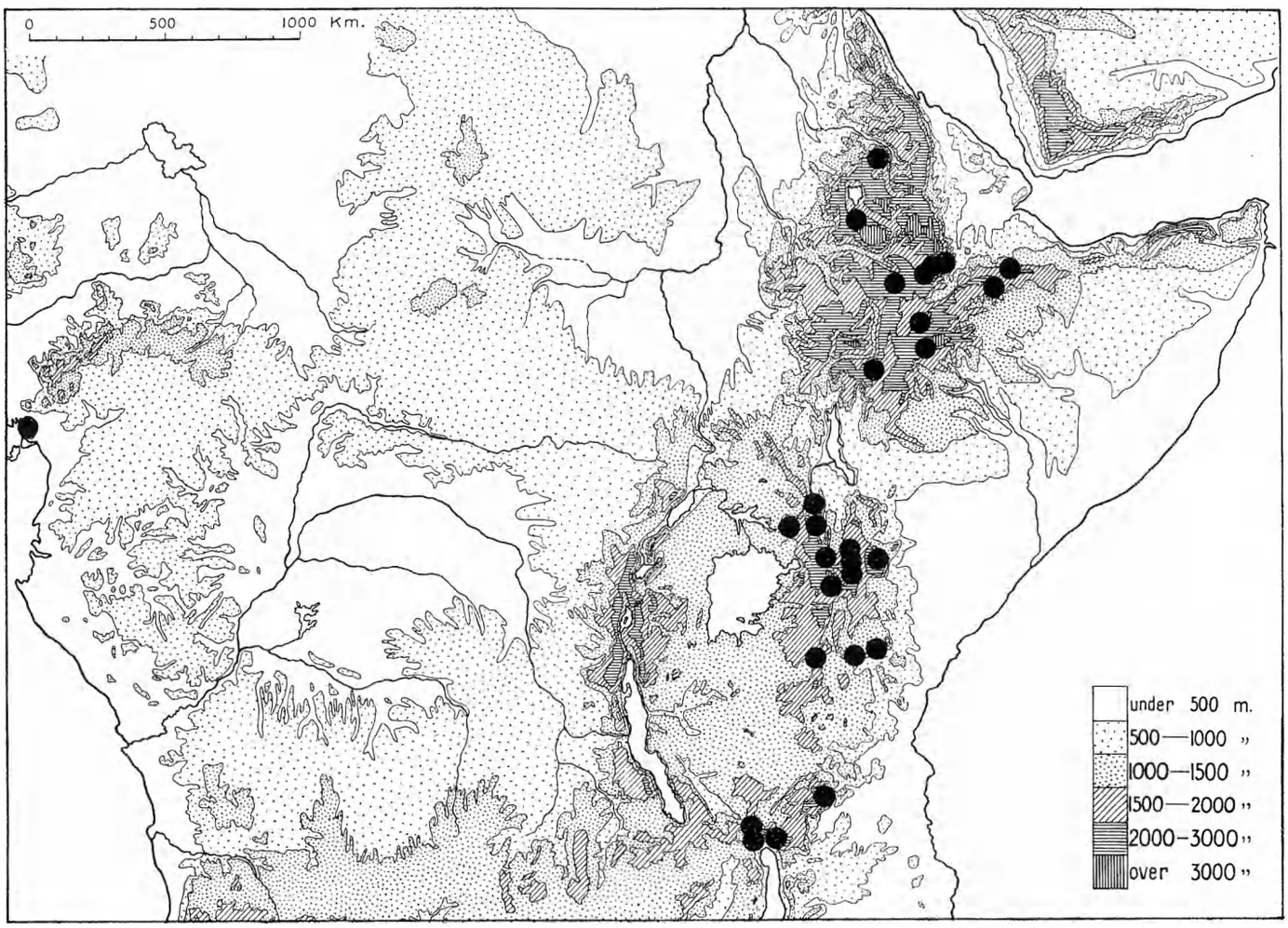


Fig. 7. Known geographical distribution of *Bartsia abyssinica* var. *petitiana*.

13980 (EA). Njombe, Gillett 17743 (EA); Procter 1584 (EA); Richards 7472b and 7753 (both K). Nyika Plateau, Henderson s.n. (BM). Rungwe, Thompson 884 (EA).

Intervarietal specimens

As emphasized above the distinctions between the three varieties are not clear—intermediate specimens are fairly frequent. Some deviate from var. *abyssinica* by having glabrous styles, as Dale 2426, K; Mooney 5170, K; Thulin & Tidigs 157, EA. Others depart from var. *nyikensis* by having more elongated fruits and fewer ridges on the seeds, as for instance Kerfoot 4254 (EA), Lees 72 (BR, K), Pawek 541 (K), Richards 22 416 (K), and Robson 340 (BM, K). Finally some collections are intermediate between the varieties *abyssinica* and *petitiana* as Hedberg 5672 (UPS), Lind 2885 (K), and Richards 13980 (K). These intergrade to such an extent between the varieties as to disqualify them from a higher taxonomic rank (cp. Fig. 5). The geographical distribution of these intermediate specimens is shown in Fig. 6.

Intermediate collections examined. Cameroons: Cameroons Mt, Morton 12657 (K). Buca Mts, Maitland 668 (K). Mt Oku, Letouzey 13470 (P). *Ethiopia:* Hedscha, Schimper 328 (BM). Arussi, Mooney 5170 (K). *Uganda:* Virunga Mts, Purseglove 2096 (BR). Elgon, Thomas 556 (K). *Kenya:* Elgon, Irwin 48 (K); Lugard 53 (EA). Cherangani, Dale 3426 (K); Irwin 368 (EA); Thulin & Tidigs 157 (EA). Aberdares, Hemsley 785 (EA); Lind 2885a (K); Nattrass 1405 (EA); Williams 6 (BR, EA). *Tanzania:* Kilimanjaro, Volkens 780 (BM). Usafua, Goetze 2982 (BR). Kyimbila, Stolz 1390 (BM). Ngori Crater, Geilinger 2735 (K). Kiwira River, Mac Innes 374 (BM). Mbeya, Davies M 18 (K); Kerfoot 1781 and 4254 (both EA); Richards 13980 (K). Njombe, Gillett 17743 and 17776 (both K); Prins 106 (EA); Procter 1857 (BR). Nyika Plateau, Robson 340 (K). *Malawi:* Nyika Plateau, Richards 22416 (BR). Nganda Peak, Pawek 541 (K). *Zambia:* Nyika Plateau, Lees 72 (BR, K); Robson 340 (BM).

Evolutionary aspects

From an evolutionary point of view *Bartsia abyssinica* provides an interesting example of parallel diversification under the influence of local geographical isolation (var. *nyikensis*) and of altitudinal differentiation (var. *petitiana*). The latter variety beautifully illustrates the autochtonous origin of an afroalpine taxon. It may appear surprising that a local variety has developed in the Nyika area rather than in West Africa for instance, the mountains of which are geographically more isolated, but also in other groups the amount of endemism seems to be unusually high in the Nyika Plateau, e.g. in *Ardisiandra* (Taylor 1958 p. 146) and *Leonotis* (M. Iwarsson, unpublished). A number of afromontane tree species reach their northern or southern limit, resp., in Malawi (White 1970 p. 75), and the area round the northern end of Lake Malawi shows a high concentration of species, e.g., of *Wahlenbergia* (Thulin 1975).

An intraspecific variation range of the sort found in *Bartsia abyssinica* is by no means uncommon—similar cases occur in many other afroalpine and afromontane taxa, as *Alchemilla johnstonii* Oliv., *Swertia crassiuscula* Gilg and *Cineraria grandiflora* Vatke (cp. Hedberg 1957) as well as *Bartsia decurva* Hochst. ex Bth. (Hedberg et al. 1979). An example of an even greater morphological variation is displayed by *Stachys aculeolata* Hook. f., which has the same general distribution (Bjørnstad, Friis & Thulin 1971). A still more extreme adaptation to afroalpine conditions is found in *Dipsacus pinnatifidus* (Hedberg & Hedberg 1977).

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Autonomous development of embryo in Paspalum conjugatum Berg

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Chao, C. Y. 1980 06 16: Autonomous development of embryo in Paspalum conjugatum Berg. *Bot. Notiser 133:* 215–222. Stockholm. ISSN 0006-8195.

The *Paspalum conjugatum* biotype studied has 40 chromosomes which are not paired during diakinesis and the first metaphase. At the end of meiosis, two megaspores are formed in many ovules. The embryo sac is diplosporic and invariably develops from the chalazal megaspore. Irregularities during megasporogenesis and later stages can occur and as a result the percentage of seed set is only 45.5 on the average. Development of the egg is autonomous and starts about two days prior to anthesis. However, pollination is necessary for the development of the endosperm. The pollen tube grows into the embryo sac through a PAS substance present in the intercellular spaces at the micropylar end of the ovule. The tube penetrates into the degenerated synergid and discharges its sperms and vegetative nucleus into it. After releasing the two sperms, the degenerated synergid contains two large and two small, darkly-stained bodies, which may be interpreted as X-bodies. Triple fusion results in the development of an endosperm with 120 chromosomes in each cell.

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Five out of nine species of *Paspalum* found in Taiwan are of particular interest to cytologists because of their peculiar way of meiosis, mode of reproduction and the prevalence of polyploids. Thus, the hexaploid (2n=60) of *P. orbiculare* was found to be asynaptic and diplosporic (Swanson 1957, Chao 1964). The chromosome numbers n=20 and 27 and 2n=54 have also been reported for this species (Cave 1958, 1965, Moore 1972, 1973) and in our cultures plants with 120 chromosomes were found in the progenies of the asynaptic hexaploid. In the case of the species *P. longifolium,* one tetraploid (2n=40) is desynaptic (Pi & Chao 1974) and diplosporic (Chao 1974) while the octoploid (2n=80) induced from the desynaptic tetraploid by colchicine treatment shows normal microsporogenesis (Pi & Chao 1974) with the embryo sac developing from the reduced megaspore (Chao 1974). Other chromosome counts reported for this species are n=25 and 30 (Moore 1973, 1974) and 2n=60 (Ornduff 1968).

In *P. commersonii,* the hexaploid (2n=60) and the dodecaploid (2n=120) induced from the hexaploid are both asynaptic (Pi & Chao 1974) and diplosporic (Chao 1974) but meiosis and embryo sac development in the dodecaploid collected from the same region as the asynaptic hexaploid are normal (Pi & Chao 1974, Chao 1974). Chromosome numbers 2n=20 (Ornduff 1967) and 2n=40 (Darlington & Wylie 1955, Cave 1958, 1964, Ornduff 1968, Moore 1972, 1973) have also been recorded for this species.

Meoisis and embryo sac development in the tetraploid (2n=40) of *P. thunbergii* are reported to be desynaptic and diplosporic, respectively (Chung 1974). Other chromosome numbers reported for this species are 2n=20 (Darlington & Wylie 1955) and 2n=60 (Ornduff 1968).

It could be seen that in each of the above-mentioned four species, different polyploids do exist and that all the asynaptic or desynaptic biotypes are diplosporic but the autonomous development of the unreduced egg prior to anthesis was not observed in all these biotypes (Chao 1964, 1974, Chung 1974). In the case of the remaining species, *P. conjugatum,* microsporogenesis in a biotype (2n=40) collected in northern Taiwan was reported to be asynaptic (Fang & Li 1966). Chromosome counts for this species

have consistantly been n=20 or 2n=40 (Darlington & Wylie 1955, Chen and Hsu 1961, Ornduff 1967, Moore 1972, 1973). This paper reports the mode of reproduction in a biotype of *P. conjugatum*.

Material and methods

The plants used for this study were raised from seeds collected from the campus of the National Taiwan University, Taipei, Taiwan. They were grown in the greenhouse of The Chinese University of Hong Kong. Voucher specimens have been deposited in the Herbarium of the Department of Biology, the Chinese University of Hong Kong. Spikes at stages ranging from megasporogenesis to late endosperm development were fixed in formalin acetic-alcohol (FAA) for 24 h and then washed with 70 % ethanol. Individual ovaries were dissected out for dehydration and paraffin infiltration. Paraffin sections were cut 15 μm thick and stained with iron hematoxylin. Chromosomes were examined in nine cells during diakinesis or pro-metaphase I.

Furthermore, to study the early development of the embryo and endosperm, individual ovaries were dissected out from the florets about 48, 24 and 0 h before pollination and 5, 8 and 12 after pollination and then fixed in 4 % glutaraldehyde (GA) and embedded in Epon 812 (Chao 1977). Some ovaries were freeze-substituted and Epon-embedded (Chao 1971, 1977). Sections were cut on a Sorvall ultramicrotome with a diamond knife at 2 μm thick. They were stained with periodic acid-Schiff's reagent (PAS) (Chao 1971), PAS and aniline blue black (ABB) (Chao 1971), toluidine blue (TB) (Chayen, Bitensky & Butcher 1973), or PAS and TB.

In order to study the meiosis in pollen mother cells (PMCs) and to determine the endosperm chromosome number, florets at appropriate stages were fixed in ethanol-acetic acid (3:1) solution for 24 h. Microsporocytes and endosperm were then squeezed out and stained with acetocarmine.

Results

Megasporogenesis

Megasporogenesis in the biotype of *P. conjugatum* studied is similar to that of the asynaptic or desynaptic taxa of the four species of *Paspalum* (Chao 1964, 1974) mentioned above. A single megasporocyte grows rapidly after it is differentiated (Fig. 1 A). The chromosomes are 40 in number and invariably not paired (Fig. 1 B). Pairing conditions at earlier stages could not be analyzed. During metaphase I, the univalents move to the equatorial plane where a restitution nucleus is later formed. Second division proceeds normally in many cases and leads to the formation of two unreduced megaspores (Fig. 1 C). In a number of ovules, however, irregularities during meiosis do occur and as a result, all meiotic products may degenerate (Fig. I D).

Microsporogenesis

Meiosis in the PMCs was also examined. Similar meiotic pattern was revealed in both male and female tissues. Forty chromosomes are also not paired during diakinesis and metaphase I and a restitution nucleus is formed later (Fig. 1 E). At the end of microsporogenesis, many PMCs form dyads.

Megagametogenesis

In the ovules in which two megaspores are formed after meiosis, the micropylar one invariably degenerates and the chalazal one develops into the embryo sac (Fig. 1 F, G). The developing megaspore enlarges rapidly and, after 2-, 4- and 8-nucleate stages (Fig. 1 H, I), forms an embryo sac with the egg and two synergids at the micropylar end, three antipodals at the chalazal end, and two polar nuclei just above the egg apparatus (Fig. 1 J). The three antipodals divide again to form 12–24 binucleate cells. Aposporic development of the embryo sac was not observed in this study. Therefore, *P. longifolium* is also diplosporic.

When the embryo sac matures, which takes place about two days prior to pollination, the egg is highly vacuolated (Fig. 2 A) and contains a number of large starch grains. Its nucleus is centrally located. Each of the two synergids has a filiform apparatus at the microcylar end (Fig. 2 B). The synergid nucleus is usually located at the micropylar side and close to the lateral wall. At this stage, the ovule of *P. conjugatum* also contains a periodic acid-Schiff's (PAS) substance around the micropylar outer integument, in the micropyle and in other intercellular spaces below the embryo sac (Fig. 2 C) as in that of *P. orbiculare* and other species (Chao 1971).

Autonomous development of the embryo prior to pollination

In more than half of the ovaries proembryos of up to seven cells were observed. The unfertilized, highly vacuolated egg divides transversely

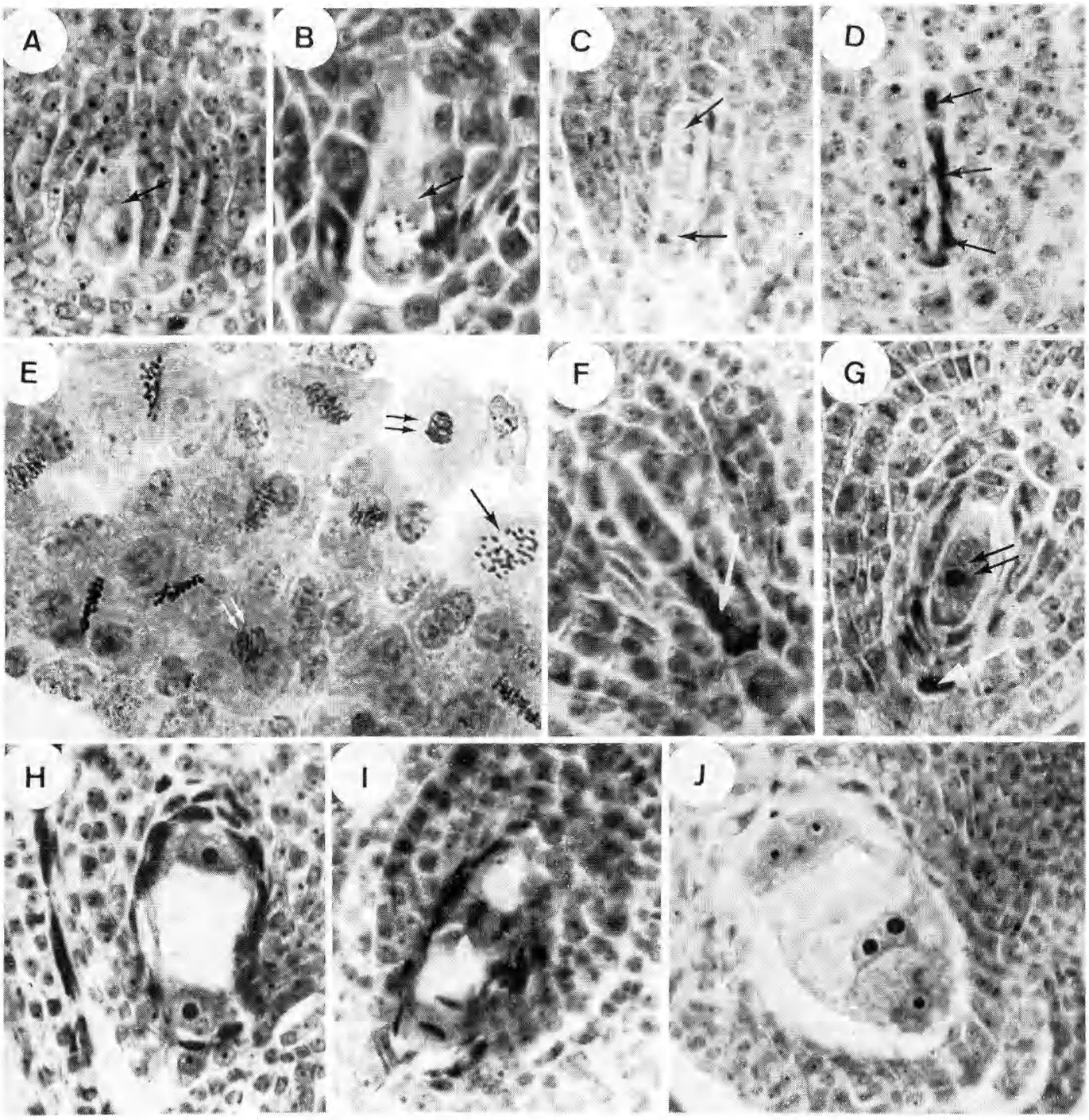

Fig. 1. A–J: *Paspalum conjugatum*. Portions of longitudinal paraffin sections of young ovules. — A: A megasporocyte (arrow) before onset of meiosis. — B: A megasporocyte (arrow) during diakinesis showing some of its 40 univalents (other univalents being present in the adjacent sections). — C: Two megaspores (arrows) produced after meiosis. — D: All sporogenous cells (arrows) degenerated as the result of irregular megasporogenesis. — E: A group of PMCs at different stages of the first meiotic division. Single arrow indicates a prometaphase cell in which 40 univalents can be counted under the microscope. Double arrows indicate cells in which the restitution nucleus is being formed. — F: The micropylar megaspore (arrow) degenerating. — G: The developing chalazal megaspore (double arrows) and degenerated micropylar megaspore (single arrow). — H: A 2-nucleate embryo sac. — I: An embryo sac during the second telophase. — J: An embryo sac containing the egg, 2 polar nuclei and 3 antipodals (2 synergids not seen in this section).

first into a basal cell and an apical cell one to two days before pollination (Fig. 2 D, E). At this time the two synergids beside the 2-celled embryo become highly vacuolated (Fig. 2 E). The basal cell of the proembryo divides transversely again while the apical cell usually divides vertically. Further divisions are usually longitudinal for the two apical cells to form a quadrant. The cell just

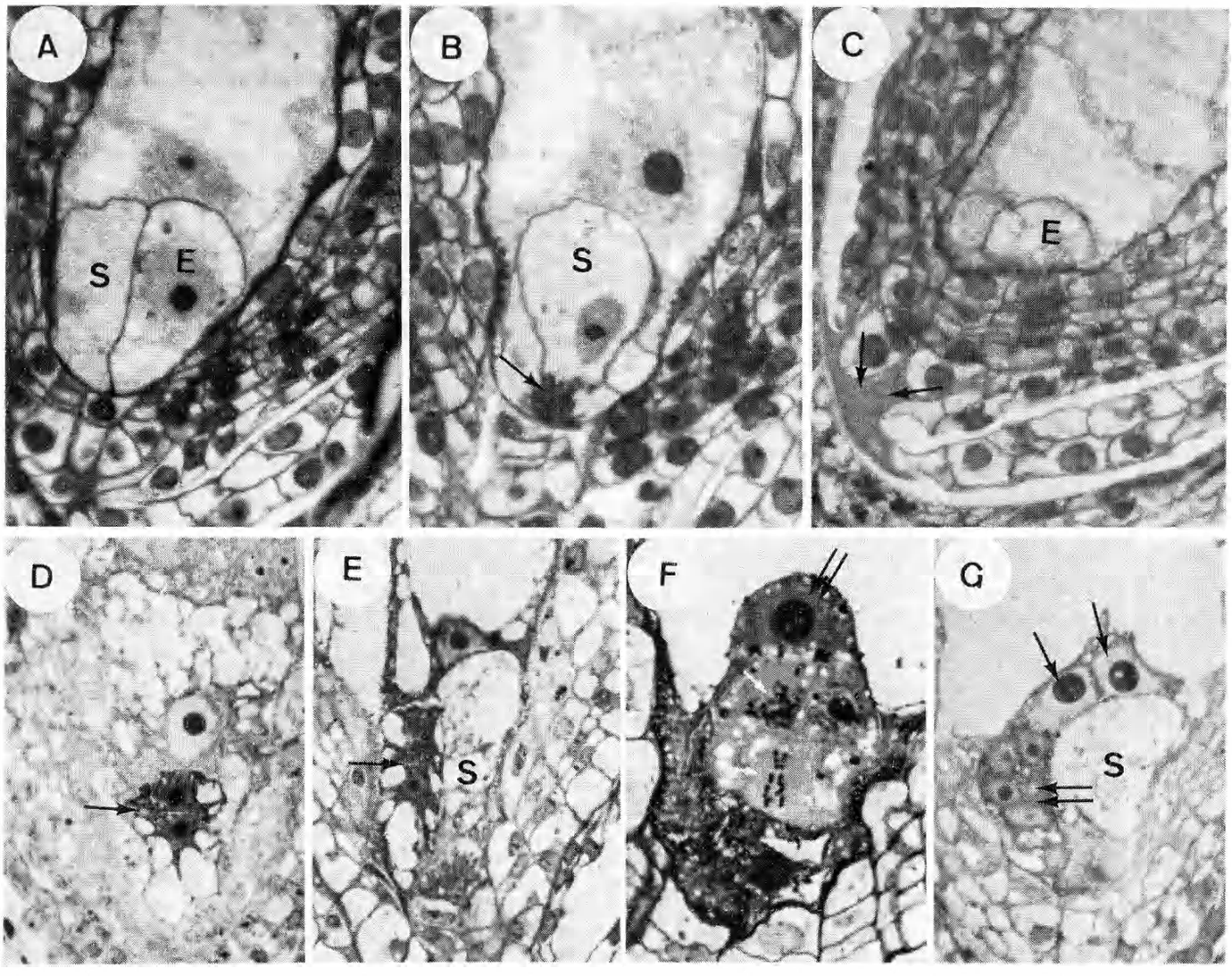

Fig. 2. A–G: *Paspalum conjugatum*. Portions of longitudinal Epon sections of ovules fixed before anthesis by freeze-substitution (A–C) or with GA (D–G). A–C, stained with PAS and ABB; D, E and G, TB; F, PAS and TB. — A: Mature embryo sac showing the vaucolated egg (E) containing some starch grains and one synergid (S). — B: Mature embryo sac showing one synergid (S) with a filiform apparatus (arrow) and a nucleus, and one polar nucleus. — C: PAS substance (arrows) present at the micropylar end of the ovule (E-egg). — D, E: Embryo sac containing 2-celled embryo (arrows) and one polar nucleus. Note the highly vacuolated synergid (S) in E. — F: Embryo sac showing one polar nucleus (double arrows) just above the proembryo. Two of the embryonic cells (single arrows) are dividing. — G: An ovule just before anthesis showing the 7-celled embryo (double arrows), one highly vacuolated synergid (S) and 2 polar nuclei (single arrows) in the process of fusion.

below this quadrant divides either transversely or vertically (Fig. 2 F). Thus, a 7-celled embryo may be formed before pollination (Fig. 2 G). At this time, one of the two highly vacuolated synergids degenerates. The fusion of the two polar nuclei begins at the time when the egg starts to divide. At first, their adjacent membranes make contact at several points and fuse together to form bridges between the nuclei. But this process of fusion progresses very slowly and just prior to pollination the two polar nuclei are still separated (Fig. 2 G).

Pollen tube growth and endosperm development

The mature pollen grain of *P. conjugatum* contains two sperms and one vegetative nucleus, all being spindle-shaped (Fig. 3 A).

After pollination, the pollen tube grows down from the style into the intercellular space between the ovary wall and the outer integument. When the tube reaches the micropylar end of the ovule, it touches the PAS substance (Fig. 3 B), by which it goes into the micropyle and intercellular space between rows of nucellar cells below the embryo sac. Finally it penetrates the embryo

sac wall, passes between the two synergid walls at the micropylar end and enters the degenerated synergid through the upper part of the filiform apparatus (Figs. 3 B, C). In some ovules, the pollen tube enters the degenerated synergid directly through its filiform apparatus. The tube then discharges its contents into the synergid, including the two sperms and the vegetative nucleus. This takes place about five hours after pollination. After the pollen tube discharges, the degenerated synergid becomes very dark in colour, especially when stained with PAS reagent (Fig. 3 B). It is rather light in colour when stained with TB. The two sperms then move to the tip of the synergid and become spherical. Their intensely-coloured nucleus is surrounded by a clear zone, probably the cytoplasmic sheath. The sperms leave the synergid through a small opening in the tip of the synergid wall and go into the central cell, leaving behind two small, darkly-stained bodies (Fig. 3 C, D). These two small bodies always lie close together at the tip of the synergid and there is an empty space above them which might have been formerly occupied by the two sperms (Fig. 3 C). In the middle of the degenerated synergid, there is a large, elliptical or irregular, darkly-stained structure, which may be the vegetative nucleus of the pollen tube (arrowhead in Fig. 3 D). Further down the micropylar end at the lateral side of this cell, there is another large, irregular, darkly-stained body which is believed to be its degenerated nucleus (single arrows in Fig. 3 D).

In one ovule, the upper portion of the degenerated synergid burst after the pollen tube penetrated it. The spindle-shaped sperms and the vegetative nucleus were then discharged from the degenerated synergid as shown in Fig. 3 E. In this figure, there is one small and one large spindle-shaped, darkly-stained body (single and double arrows) similar to those in the mature pollen grain (Fig. 3 A). The small one, being surrounded by a clear zone, may be the sperm and the large one the vegetative nucleus of the pollen tube. In another ovule fixed about eight hours after pollination, one sperm is already to be found in one of the polar nuclei, while the other one is located at the tip of the persistent synergid (Fig. 3 F). The latter is a darkly-stained, spherical structure, being surrounded by a clear zone. Sperms present in the persistent synergid have also been observed in barley (Cass & Jensen 1970).

As mentioned before, the two polar nuclei start to fuse as early as when the egg begins to divide. However, this process seems to proceed very slowly. At the time when one sperm penetrates one of the two polar nuclei, they are still only partially fused (Fig. 3 G, H). Penetration of the sperm into the polar nucleus takes place about eight hours after pollination. The contents of the sperm nucleus then gradually disperse into the polar nucleus (Fig. 3 H). The very triple fusion has not been observed so it must proceed very rapidly. As each endosperm nucleus was found to contain 120 chromosomes (Fig. 3 I), fusion of the sperm nucleus with the two polar nuclei, each with 40 chromosomes, must take place before the endosperm initial starts to divide. The second sperm was usually found lying at the periphery of the upper portion of the embryo (Fig. 3 J) and presumably degenerates later. The endosperm initial divides into two nuclei which are usually located at the lateral side of the central cell. About 12 hours after pollination, the endosperm may be composed of 4–8 nuclei and the embryo of about 20 cells. The endosperm nuclei divide actively and at about 30 hours after pollination, both the endosperm and embryo consist of about 50 cells. Since the endosperm cells are much larger than the embryonic ones, the endosperm is several times larger than the embryo at this stage.

Discussion

Fang & Li (1966), in their study on microsporogenesis in a biotype of *P. conjugatum,* found that about 98 % of the microsporocytes from a restitution nucleus and presumably unreduced microspores are formed in PMCs at the end of meiosis. Irregularities were observed during microsporogenesis and as a result only 42 % good pollen grains were scored in their material. In our biotype, it was found that chromosomes are not paired during diakinesis (Fig. 1 B, E) and usually only dyads are formed at the end of meiosis. Irregularities in megasporogenesis result in the failure of the development of the embryo sac in a number of ovules. The percentage of seed set from 19 samples consisting of 1389 counts is 45.5 which is close to the 42 % good pollen reported by Fang & Li (1966).

Our study reveals that this biotype is diplo-

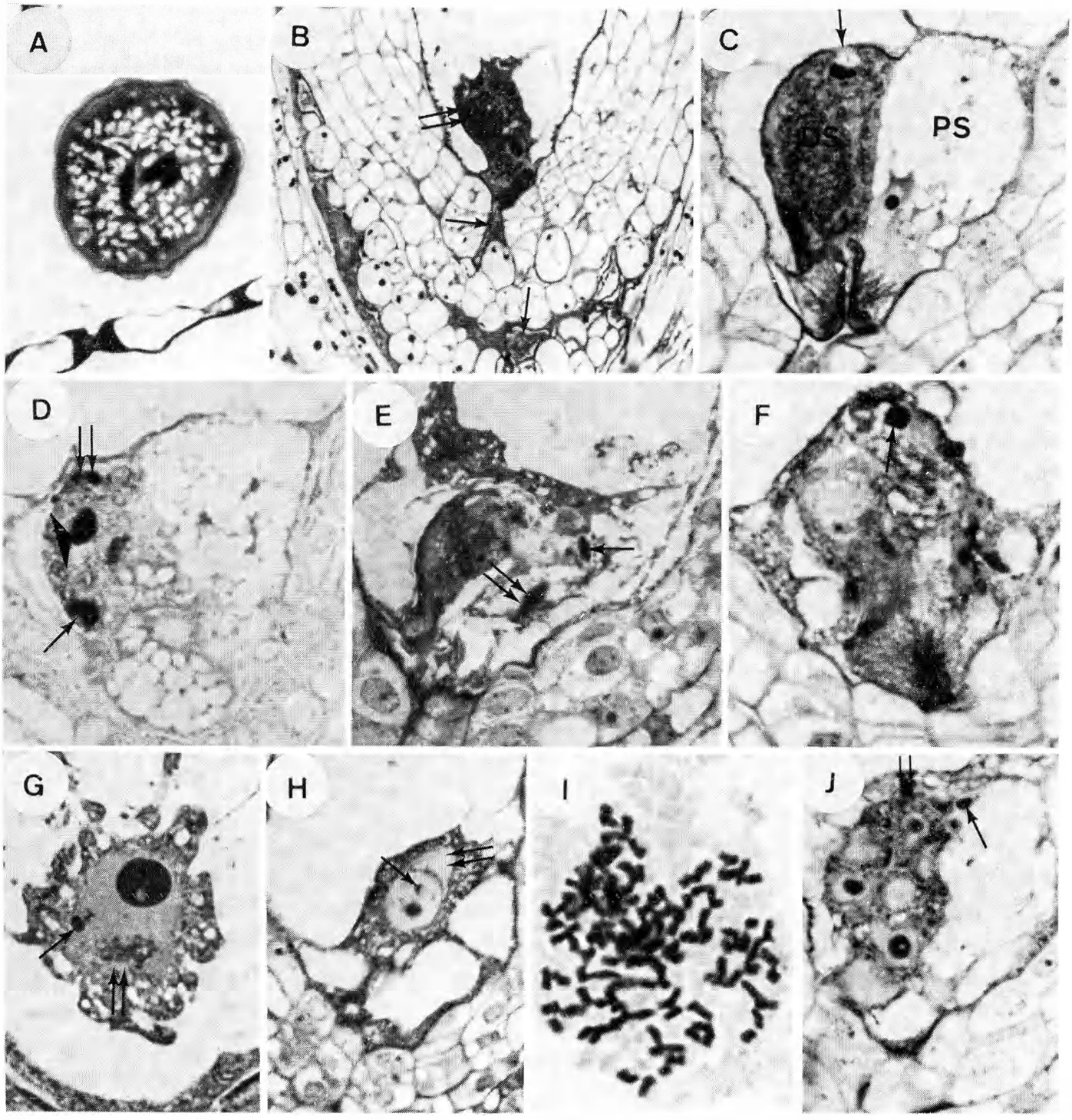

Fig. 3. A–J. *Paspalum conjugatum*. Portions of longitudinal Epon sections of ovules (A, mature pollen grain; I, endosperm nucleus) fixed after anthesis (A, mature pollen grain) with GA (B, freeze-substituted; I, acetic ethanol) and stained with TB (B, PAS; I, acetocarmine). — A: Mature pollen grain containing 2 sperms and one vegetative nucleus. — B: Ovule section showing the pollen tube (arrows) in the PAS substance around the integuments and between rows of nucellar cells, and the darkly-stained degenerated synergid (double arrows) after pollen tube discharge. — C: Degenerated and persisted synergids (DS, PS) about 8 hours after pollination. Note a small opening (arrow) at the tip of DS connected with an empty space, below which are two small darkly-stained bodies. Note also the entry of the pollen tube into the DS between two micropylar synergid walls. — D: The degenerated synergid containing several darkly-stained bodies. The lowest large one (single arrow) may be the degenerated synergid nucleus, middle large one (arrowhead) vegetative nucleus, and two top small ones (double arrows) remains of 2 sperms. — E: Upper portion of the degenerated synergid burst and some contents of the pollen tube discharged into the central cell. One small, spindle-shaped body surrounded by a clear zone may be the sperm (single arrow) and the large one the vegetative nucleus (double arrows). — F: One spherical, darkly-stained body surrounded by a clear zone at the tip of the persisted synergid may be the sperm (arrow) (another sperm already penetrated into the polar nucleus). — G: One sperm (single arrow) in one polar nucleus.

sporic and the development of the embryo is autonomous, starting about two days before anthesis, but the pollination and triple fusion are necessary for the development of the endosperm. Such a mode of seed development had been reported in some apomictic plants (Maheshwari 1950, Battaglia 1963, Steffen 1963)

The chromosome number in *P. conjugatum* is invariable (2n=40 or n=20). This is contrary to the other four species of *Paspalum* found in Taiwan, viz. *P. orbiculare, P. longifolium, P. commersonii,* and *P. thunbergii.* Different chromosome numbers exist in each of these four species. In all the diplosporic biotypes of these four species, pollination is a prerequisite for the development of the egg into an embryo although fertilization of the egg does not usually take place. Occasionally, however, the fusion of an egg with one sperm may occur in these taxa. Consequently, offspring with doubled chromosome number can sometimes be expected in the progenies. This has been observed in our cultures as well as reported in other plants and may also account for the prevalence of polyploids in nature. In *P. conjugatum,* however, the development of the egg starts prior to anthesis and is autonomous. Consequently, plants with doubled chromosome number can hardly be produced.

In angiosperms, the degenerated synergid, after the pollen tube discharge, usually contains two, sometimes more, darkly-stained bodies termed X-bodies (Maheshwari 1950, Fisher & Jensen 1969, Kapil & Bhatnagar 1975). These X-bodies have been variably interpreted but most research workers believe that they are the degenerated synergid nucleus and vegetative nucleus. This interpretation is based on their position as well as the presence of DNA (Fisher & Jensen 1969). However, other research workers believe that X-bodies are the cytoplasmic remains of the sperms. In the degenerated synergid of *P. conjugatum,* at least four darkly-stained bodies, two large and two small, are usually found after the pollen tube discharge (Fig. 3 D). The two large ones may represent the degenerated synergid nucleus and the vegetative nucleus of the pollen tube, respectively. The two small ones may be best interpreted as the remains of the two sperms left in the synergid, possibly the discharged cytoplasmic sheaths of the sperms. Thus, there may be four so-called X-bodies in the degenerated synergid of *P. conjugatum.*

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Double arrows indicate portion of another polar nucleus. — H: Contents of the sperm nucleus are being intermingled with those of polar nucleus. Double arrows indicate portion of another polar nucleus. — I: Endosperm nucleus during the metaphase with 120 chromosomes. — J: Young embryo. The darkly-stained body at its upper right side may be one of the two sperms (arrow). Double arrows indicate the two small, darkly-stained bodies at the tip of the degenerated synergid..

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Conostylis neocymosa sp. nov. (Haemodoraceae) from south-western Australia

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Hopper, S. D. 1980 06 16: Conostylis neocymosa sp. nov. (Haemodoraceae) from south-western Australia. *Bot. Notiser 133:* 223–226. Stockholm. ISSN 0006-8195.

C. neocymosa S. D. Hopper sp. nov. is described. It has no close relatives, and occurs at isolated localities throughout the northern and central wheatbelt of the South West Botanical Province of Western Australia. *C. cymosa* is synonymized under *C. aculeata*.

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This paper deals with a taxonomic problem arising out of a wider study of the systematics of the *Conostylis aculeata* R. Br. species group of southwestern Australia (Hopper 1977, 1978).

In his original description of *C. cymosa,* Bentham (1873) cited several collections including Blackwood River Oldfield, Champion Bay Oldfield, sand plain near Burnell's Spring, Greenough Flats C. Gray, and Busselton Pries. Green (1960), in a revision of *Conostylis,* reduced *C. cymosa* to synonomy under *C. aculeata* ssp. *aculeata* without comment, but from his list of specimens examined it would appear that only the Oldfield, Blackwood River syntype of *C. cymosa* was seen. However, a determinavit slip signed by Green and dated 17 December 1959 on the Oldfield Champion Bay type specimen of *C. cymosa* at MEL reads "Affin. *C. aculeata* R. Br.; not sufficiently distinct from *C. aculeata* to be regarded as a separate species".

I have examined this same specimen at Melbourne, and Mr B. R. Maslin has examined and photographed the Oldfield and Grey type collections at Kew. Our observations suggest that there are clear morphological differences between the northern (Champion Bay, Greenough Flats) and southern (Blackwood River) specimens in the type collections of *C. cymosa* (Table 1, Fig. 1).

Since the type material of *C. cymosa* is heterogeneous, and Bentham did not nominate a holotype, a lectotype must be chosen to clarify the identity of the species. The name must remain attached to that part of the type collection which corresponds most nearly with the original description (Stafleu 1972). It would appear that Bentham based his description of *C. cymosa* on the southern specimens, since the following details are given: "placentas stipitate, covered all over with numerous ovules" and "leaves often above lft (30.5 cm) long, . . . , bordered by a few distant rigid cilia". Hence it is necessary to choose one of the southern specimens as the lectotype. I propose to nominate the Oldfield, Blackwood River specimen as the lectotype, since I have not seen the Busselton specimen collected by Pries. Furthermore, I consider that these southern specimens are conspecific with *C. aculeata,* and therefore propose to synonymize *C. cymosa* under *C. aculeata.* This leaves the northern specimens, which are clearly distinct from *C. aculeata,* without a formal name. It is the taxon represented by these specimens which is described below as *C. neocymosa.*

Conostylis aculeata R. Br. subsp. **aculeata**

Brown, Prod. Fl. Nov. Holl. 1: 300 (1810).

C. cymosa Benth., Fl. Austral. 6: 439 (1873). Lectotype: Blackwood River Oldfield (K, photo seen) selected here. — Syntypes: Busselton, Pries?

Table 1. Morphological features of the two taxa included in the type collection of *Conostylis cymosa*.

Feature	Southern specimens (Blackwood River, Oldfield = *C. aculeata* R. Br. subsp. *aculeata*	Northern specimens (Champion Bay, Oldfield and Greenough Flats, C. Gray) = *C. neocymosa* S. D. Hopper sp. nov.
ovules	numerous, covering the entire placental surface	few, reflexed from the ventral surface of placenta
perianth lobe/tube length ratio	2–3:1	3–4:1
anther length	2–4 mm	4–6 mm
fruit shape	tapering toward base	globose near base
inflorescence height	much shorter than leaves	shorter than leaves
leaf dimensions	3–4 mm broad, greater than 25 cm long when mature	1.5–2 mm broad, up to 27 cm long when mature (usually less than 25 cm)
colour of leaf bases	dark brown	yellowish green
marginal spines	indurate, widely spaced	ciliolate, close together
leaf surface	nerves numerous, close together, separated by shallow sulcae	nerves few, well separated by deep sulcae

Conostylis neocymosa S. D. Hopper sp. nov. — Figs. 1 B, 2, 3

Orig. coll.: 3.9 km S of Eneabba Store along Brand Highway, in heath dominated by *Nuytsia, Banksia* and *Xylomelum,* yellow sand, 6 August 1975, S. D. Hopper 445 (PERTH holotype, CANB isotype).

C. cymosa Benth., Fl. Austral. 6: 439 (1873) pro parte (as to specimens Champion Bay, Oldfield; Greenough Flats, C. Gray; not as to lectotype).

A C. aculeata R. Br. differt: ovulis paucis a pagina ventrali placentae reflexis; lobis perianthii quam tubum 3–4-plo longioribus; antheris 4–6 mm longis, fructibus ad basin globosis, basibus foliorum flavovirentibus, marginibus spinis ciliolatis multis.

Perennial herb, caespitose, sometimes with short stems 1–4 cm long, producing slender stilt roots from leaf bases. *Leaves* yellow at the base, green elsewhere, equitant, conduplicate at the base, otherwise flat, 10–25 cm long and 1–4 mm broad, with numerous closely-spaced ciliolate marginal spines 0.5–2.0 mm long and rarely more than 3 mm apart. *Inflorescence* a loose cyme, usually of less than 10 flowers, on a once or twice divided scape 5–15 cm high, shorter than the leaves. *Flowers* yellow, 8–15 mm long with pedicels 3–6 mm long; perianth shortly tomentose outside, glabrous within, the lobes 6–8 mm long and 3–4 times longer than the tube. *Stamens* uniseriate, filaments 0.3–1.0 mm long, anthers 4–6 mm long. *Style* 5–8 mm long, the stigma ± level with the top of the anthers. *Ovules* few, reflexed from the ventral surface of the placenta. *Fruits* ± globose. *Chromosome number* n=8.

Distribution and habitat. The South West Botanical Province of Western Australia, at isolated localities near Geraldton, Eneabba, Watheroo, Jibberding and Merredin (Fig. 3). Near Eneabba

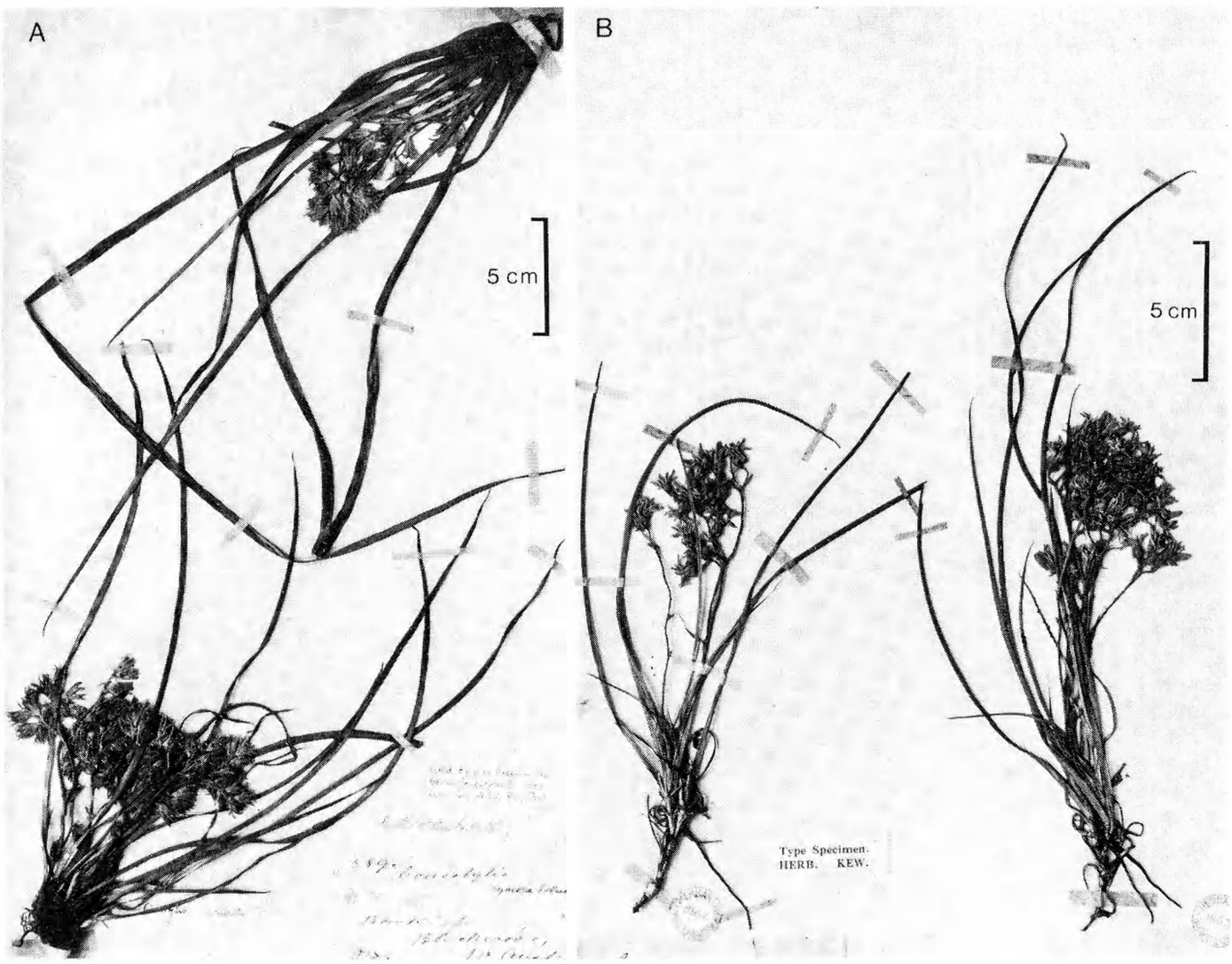

Fig 1 A–B. Type specimens of *C. cymosa* at Kew. — A: Banks of Blackwood River, Oldfield — B: Mixed collection of Champion Bay, Oldfield, and sandplain near Burnell's Spring Greenough Flats, C. Gray. Both specimens in B are now included in *C. neocymosa* sp. nov. — Photo: B. R. Maslin.

the species occurs in heath with scattered emergents of *Eucalyptus todtiana* and *Banksia* spp. on flat or undulating sandplain.

Specimens examined. W of Gunyidi, 5 September 1971, A. C. Burns 11 (PERTH); Moresby Range, 6 August 1970, A. C. Burns 5 (PERTH); sandplain near Burnell's Spring, Greenough Flats, C. Gray n.s. (K, photo seen); 14.7 km N of Eneabba Store along Brand Highway, 24 June 1976, S. D. Hopper 444 (PERTH); Eneabba township, 16 September 1976, S. D. Hopper 446 (PERTH); 13.9 km S of Eneabba Store along Brand Highway, 6 August 1975, S. D. Hopper 447 (PERTH); 12.2 km N of Eneabba Store along Brand Highway, 18 August 1975, S. D. Hopper 448 (PERTH); Jibberding, October 1905, M. Koch 1321 (MEL, NSW); rabbit proof fence near Watheroo, M. Koch 1321 (PERTH); Gunyidi, 11 November 1963, F. Lullfitz 2859 (PERTH); Champion Bay, Oldfield (MEL, K photo seen); Booraan, 7 August 1949, E. Salisbury (PERTH).

Despite the fact that it has ciliolate marginal spines on its leaves, *Conostylis neocymosa* appears to show little affinity with the *C. aculeata* group, differing noticeably in having few ovules reflexed from the ventral surface of the placenta and in having much longer perianth lobes and anthers (Table 1, Fig. 3). *C. neocymosa* has no obvious close relatives, but may be distantly related to *C. crassinervia* J. W. Green and a number of its undescribed allies which occur in the Eneabba heathlands. Further research is needed to clarify the situation.

Conostylis neocymosa occurs in large numbers along road verges and in burnt heath in the Eneabba area. Seedlings are quite common in such habitats, suggesting that the species may be relatively easy to germinate and grow in cultiva-

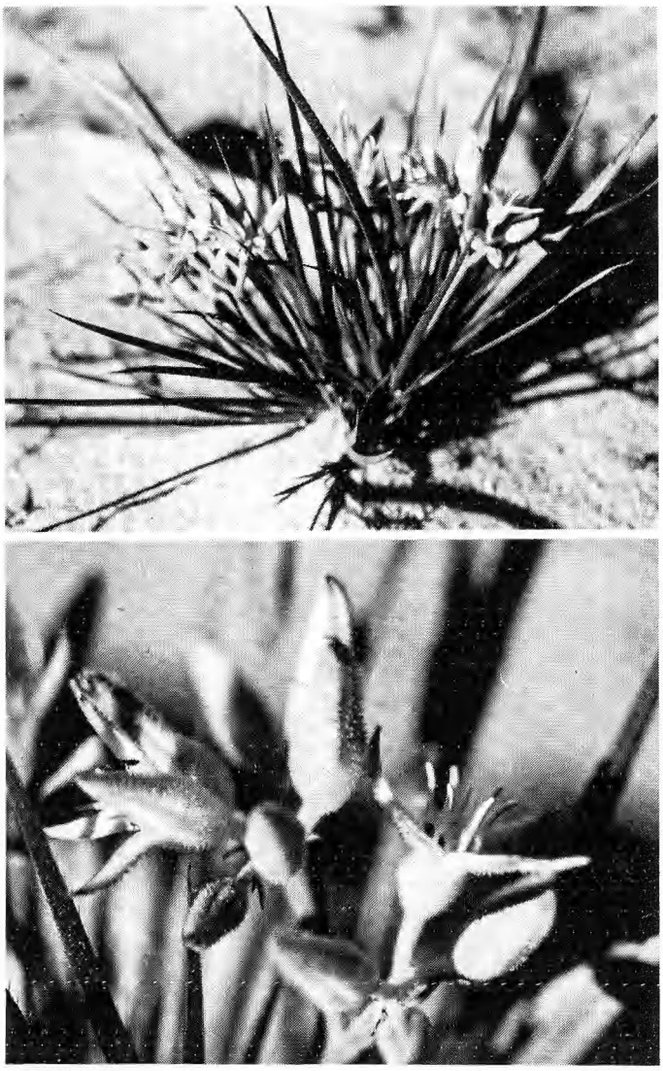

Fig. 2. Photographs of *C. neocymosa* on a road verge north of Eneabba (S. D. Hopper 448, PERTH).

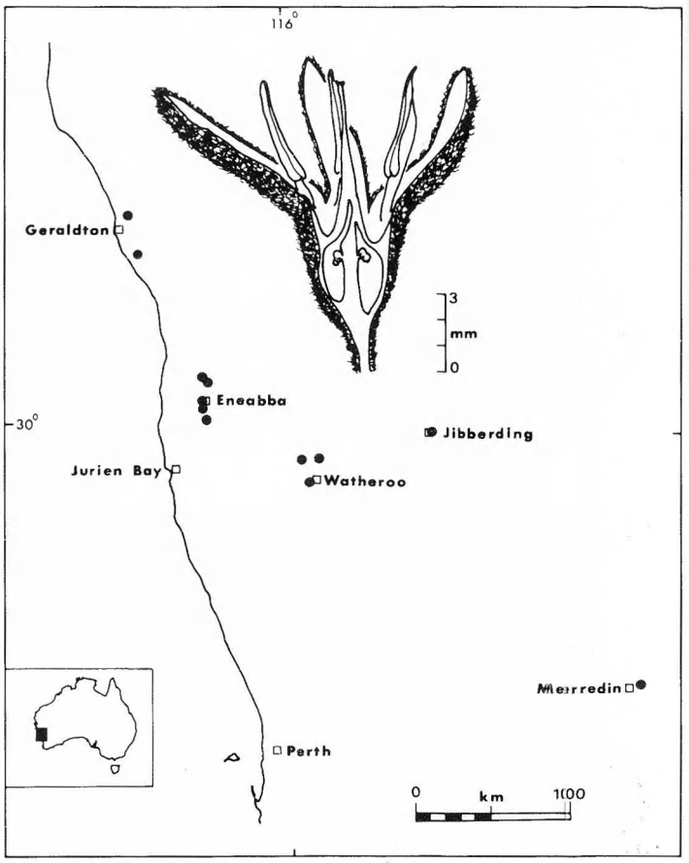

Fig. 3. Known distribution and camera lucida drawing of a half-flower of *C. neocymosa*.

tion. With its loose cymose inflorescences, relatively large flowers and yellow-green leaves it would make an attractive horticultural subject.

Acknowledgements. I wish to thank Mr B. R. Maslin (Australian Botanical Liaison Officer, Royal Botanic Gardens, Kew) for checking type specimens and commenting on the manuscript. Dr J. W. Green, Mr P. G. Wilson and Mr A. S. George, of the Western Australian Herbarium, also suggested improvements to the manuscript. Mr A. S. George provided the Latin diagnosis. I am grateful to the directors and staff at the Western Australian Herbarium, the National Herbarium, Melbourne and the National Herbarium, Sydney for providing facilities to examine their collections.

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Rubus arcticus L. subsp. × stellarcticus subsp. nov.

E. GUNNY K. LARSSON

Larsson, E. G. K. 1980 06 16: Rubus arcticus L. subsp. × stellarcticus subsp. nov. *Bot. Notiser 133:* 227–228. Stockholm. ISSN 0006-8195.

An artificial hybrid from two subspecies of *Rubus arcticus* L. is described here under the name *Rubus arcticus* L. subsp. × *stellarcticus*. Measurements are given for both parents and hybrid.

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Horticulturally interesting, artificial hybrids were made from two subspecies of *Rubus arcticus* L. (subgen. *Cyclactis*), Rosaceae. Parents of the hybrids were *R. arcticus* subsp. *arcticus,* the arctic raspberry, also called arctic bramble or nectarberry (in Swedish "åkerbär"), and *R. arcticus* subsp. *stellatus* (Sm.) Boiv. emend. Hult., the Alaskan raspberry (in Swedish "alaskaåkerbär" or "alaskahallon").

Evidence of treating the two parent taxa as subspecies was given by Hultén (1968) from studies in nature, by Larsson (1969) through experimental taxonomy, by Kallio (1975) from biochemical studies of the aromatic compounds and by Kotimäki and Hiirsalmi (1979) from cytogenetic studies. Ossiannilsson (1964), having studied Swedish aphids, produced the following information by correspondence in 1970: "The aphid *Macrosiphum rubiarctici* was never found in any other *Rubus* but *arcticus* and *stellatus*. It supports your conclusion that these species must be subspecies of the same species".

Material and hybridization work

The normally wildgrowing *Rubus arcticus* subsp. *arcticus* was easily cultivated at the Öjebyn Horticultural Experimental Station (65°19'N), now belonging to the Swedish University of Agricultural Sciences.

Rubus arcticus subsp. *stellatus* plants were brought from Alaska by Hultén. In spring 1933 some plants were transplanted in the Botanical Gardens in Lund in South Sweden, where they never produced any fruit; neither did they in the Botanical Gardens in Uppsala according to Hylander in 1970. I received a clone from Lund in 1951. In 1952 it had only one flower which was pollinated with subsp. *arcticus*. The cross-pollination resulted in one large, red, beautiful berry. The seeds were sown but unfortunately the plants died in the greenhouse after a couple of years. In 1957 the same cross was repeated successfully and also in 1963, this time in both directions. Valuable clones were selected for their delicious berries.

Rubus arcticus L. subsp. × **stellarcticus** G. Larsson subsp. nov.

Holotype: Sweden, Öjebyns trädgårdsförsöksstation (cult.), 20.VII.1964, G. Larsson (LD). Illustr: Larsson (1969) Fig. 11, upper part.

Rubus arcticus ssp. × *stellarcticus* plerumque ad *Rubum arcticum* ssp. *arcticum* accedit, sed saepe erectior et magis luxurians. Ad *Rubum arcticum* ssp. *stellatum* accedit floribus suaveolentibus et fructibus semper rubris.

The recommendation for the epithet *stellarcticus* comes naturally as *stellatus* is the mother plant of the first cross-breeding; furthermore the origin of the hybrid will be known by this epithet, which is also already known to those working with the plant. The Swedish name "allåkerbär" is suggested for the same reasons.

The hybrid *Rubus arcticus* subsp. × *stellarcticus* mostly resembles *R. arcticus* subsp. *arcticus,* but it is often more luxuriant and high yielding. Like *R. arcticus* subsp. *stellatus* the flowers have a pleasant fragrance and the berries are always red. Consequently, a new type of "åkerbär" has been produced which can be cultivated and produce berries also south of the natural area of distribution of *R. arcticus* subsp. *arcticus*

Table 1. Characters in *Rubus arcticus* subsp. × *stellarcticus* and its parents. Mean values ± standard errors; N in brackets; HCC, see Wanscher (1955).

	R. arcticus subsp. *arcticus*	*R. arcticus* subsp. × *stellarcticus*	*R. arcticus* subsp. *stellatus*
Vigour	Weak	intermediate or often luxuriant	strong
Height mm	150–250	250–450	200–400
Leaves	trifoliate	almost always trifoliate	trilobed
stomata length μm	23.91±0.23(100)	23.25±0.23(600)	26.05±0.28(150)
Flowering	early, continuous	early, continuous	two distinct blossom-periods
Flowers			
number/stalk	1 or 2(3), above the leaves	(1)2(3), above the leaves	1, below the leaves
diameter mm	25.91±0.31(75)	28.86±0.43(50)	34.15±0.40(75)
fragrance	none	very pleasant	very pleasant
colour	violet-purple HCC 30–31	violet-purple HCC 30–31	purple-violet HCC 32–34
Sepals			
number	6.29±0.11(75)	7.16±0.09(50)	7.77±0.09(75)
length/width mm	6.72±0.13(75)/2.52±0.10(25)	7.66±0.15(50)/2.44±0.10(25)	8.96±0.16(75)/2.0±0(25)
glands	red–reddish	yellow (generally)	yellow
Petals			
Number	6.41±0.15(75)	7.48±0.14(50)	7.71±0.10(75)
length/width mm	11.85±0.13(75)/7.44±0.21(25)	13.24±0.20(50)/7.0±0.26(25)	15.64±0.23(75)/8.36±0.18(25)
Anthers			
number	64.80±2.85(25)	78.64±1.81(25)	66.72±2.16(25)
Carpels			
number	26.84±1.83(25)	40.92±1.14(25)	35.20±1.07(25)
Pollen			
diameter μm	20.78±0.10(200)	20.62±0.07(1000)	22.74±0.17(200)
% activity	79.3 (several clones, 6 samples, 5388 grains)	49.0 (several clones, 31 samples, 17 810 grains)	75.2 (one clone, 8 samples, 7169 grains)
Fruit			
ripeness	middle of July	middle of July	beginning of August
colour	brownish red–light green	dark–bright red	dark red
500 g samples	6–700 berries	3–400 berries	3–400 berries
aroma	strong, typical	in some clones *arcticus*-like	weak *arcticus*
keeping quality	none (juicy berries)	none (juicy berries)	very good (dry berries)
Drupelets			
length/width mm	4.20±0.05(100)/2.94±0.05(100)	5.12±0.05(100)/3.75±0.04(100)	5.84±0.05(100)/4.45±0.05(100)
1000-seed weight mg	2659 (2600)	3269 (490)	4228 (2500)

in Europe—field experiments indicate this.

Table 1 shows some characteristics of parents and hybrids. All data are taken from Larsson (1969).

Acknowledgement. Dr O. Almborn, Lund, kindly made the Latin diagnosis.

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Notes on Aeollanthus (Labiatae) in West Africa

OLOF RYDING

Ryding, O. 1980 06 16: Notes on Aeollanthus (Labiatae) in West Africa. *Bot. Notiser 133:* 229–233. Stockholm. ISSN 0006-8195.

Two new species, *Aeollanthus angustifolius* Ryding and *A. cucullatus* Ryding, are described from the highlands of Cameroun, Central African Republic and Nigeria. Illustration and distribution map are provided. *A. engleri* Briq. is reported from West Africa for the first time. A key to the West African species of the genus is also provided.

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The genus *Aeollanthus* Mart. ex Spreng. (later often spelled *Aeolanthus*) is confined to southern and tropical Africa. There are about 35 species in all, most of them in the highlands of East Africa and South Tropical Africa. During revisional work on the genus it was found that the West African material of the otherwise East African species *A. repens* Oliv. actually consists of two different quite distinct taxa, described here as two new species, *A. angustifolius* and *A. cucullatus*. *A. engleri* Briq. is reported from West Africa for the first time, and a key to the five species now known from this area is given.

A. angustifolius Ryding sp. nov.—Fig. 1 A–D

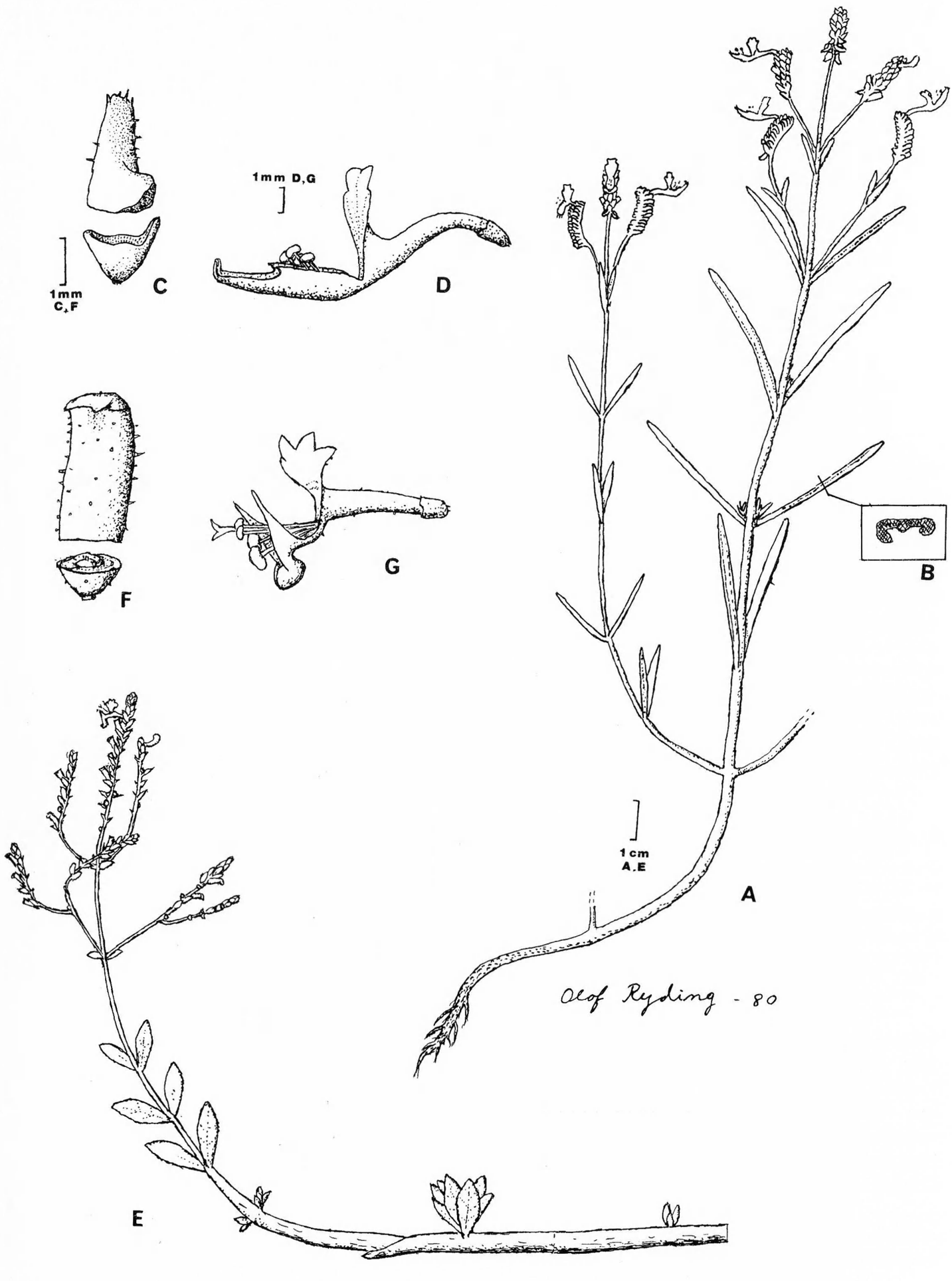
Orig. coll.: Letouzey 8067, Cameroun, Zabondo, 25 km NE of Linte, 30.IX.1966 (P holotype, UPS).

Species nova ab *A. repenti* foliis angustis integris, parte basali calycis fructiferi persistenti cupulata zygomorpha differt; ab *A. ambusto* spicis densis, bracteis foliis multo brevioribus, labio infero trilobato corollae apice (tri-) quinquedentato recedit.

Annual, decumbent or erect herb 10–50 cm high. Stem with few to many branches, rarely unbranched, often woody near the base, often reddish, ± pubescent. Leaves opposite, fleshy, narrowly linear to narrowly lanceolate, (6–)10 × 1.5–5 mm, usually more than 6 times as long as wide, obtuse at the apex, sometimes reddish, ± pubescent and with sessile glands; margins entire and revolute; midvein ± prominent beneath. Inflorescence composed of dense spikes, up to 2(–3.5) cm long, forming a lax panicle; spikes one-sided, naked on the back, with two flowers at each node on the main axis, otherwise alternately with one or two flowers at each node; bracts ovate, obovate or Hedera-shaped, with a large gland near the apex, 2–3.5 × 1–2 mm, sometimes red, pubescent or ciliate and sometimes with sessile glands. Calyx two-lipped, dehiscent, 3–4 mm long in fruit; upper lip obtuse or 3-dentate; lower lip obtuse; basal part cupular c. 1 mm high and 1.5–2.5 mm long with undulate margin and a long obtuse lobe pointing outwards. Corolla blue, pink or violet with markings inside, papillose or pubescent outside; tube narrow, 5.5–8 mm long; upper lip 4-lobed; lower lip boat-shaped, 3-lobed; lateral lobes short with a narrow tooth at the apex; central lobe long, truncate with (3)5 narrow teeth at the apex. Anthers all c. 0.5 mm long. Style bifid at the tip. Nutlets smooth black 1–1.3 × 0.8–1.1 mm.

Distribution and habitat. In the highlands of Cameroun, on the Mambilla Plateau in Nigeria and in the Bozoom Region in the Central African Republic (Fig. 2 A). Growing on rocks or in shallow soil, usually in humid places as depressions and seepage grounds; alt. 1200–1900 m.

Variation. Compared to most other species of the genus *A. angustifolius* is a fairly homogeneous species. Collections from Bamenda Region and S Cameroun, however, usually are more densely pubescent than the rest of the material.


1mm D,G
1mm C,F
C
D
F
G
B
1cm A,E
A
E
Olof Ryding - 80

Comments on taxonomy. A. angustifolius is a very distinct taxon. The three-lobed lower lip of the corolla with narrow teeth at the apex, is unique within the genus. Its taxonomic position is not quite certain, but its nearest relatives are most likely to be found among the species with a zygomorphic basal persistent part of the fruiting calyx (Stopp 1958 a, b). However, it deviates from them by its arrangement of the flowers in the spikes. *A. ambustus* Oliv. (= *A. virgatus* Gürke) perhaps is the one which is most similar to *A. angustifolius*. Like the latter species it has narrow leaves with entire revolute margins, and basal parts of the calyces with undulate margins, but in contrast to *A. angustifolius* the bracts of *A. ambustus* have the same shape as the leaves. The collections cited as *A. repens* by Morton (1962, 1963) actually all belong to *A. angustifolius*, with the exception of Hepper 1356 (see below). *A. repens* is confined to eastern Africa and originally described from Tanzania. It is not closely related to *A. angustifolius*. It is easily distinguished from *A. angustifolius* above all by the broader dentate leaves and the truncate actinomorphic basal part of the fruiting calyx. *A. edlingeri* Gürke was described from N'Gaoundere in Cameroun (Gürke 1905). The type material has been destroyed in Berlin and its identity is not quite certain. However, it cannot be conspecific with *A. angustifolius*. According to the description the leaves of *A. edlingeri* are 4–12 mm wide, while the leaves of *A. angustifolius* are not more than 5 mm wide. In the description of *A. edlingeri* Gürke also distinguishes between lanceolate-obovate blunt bracts 3–4 × 2 mm and lanceolate pointed "vorblätter" 2–3 × 1–2 mm. The German term "vorblätter" undoubtedly refers to the kind of sterile bracts present in most species of the genus, but not in *A. angustifolius*, where all bracts are of the same kind. Of the species in Cameroun only *A. heliotropioides* Oliv. agrees with the description of *A. edlingeri*. No other material of *A. heliotropioides* from N'Gaoundere has been seen, but one collection (Raynal 12101) is from Nangé only 60 km E of N'Gaoundere. *A. heliotropioides* has priority to *A. edlingeri*, but further investigations may, however, show that a still older name, *A. suaveolens* Mart. ex Spreng. has to be used for this taxon.

Collections besides the type. Cameroun, 16 km S Djouo, 24.II.1962, Letouzey 4390 (P, UPS); Mbolemba, 8 km N Ngola, 10.V.1963, Letouzey 4997 (P, UPS); near Ngat, 10 km SSE Mbalmayo, 16.VI.1972, Letouzey 11291 (P, UPS); Massif du Mbepit, 30 km SW Foumban, 21.X.1974, Letouzey 12950 (P, UPS); Bangoua, Meurillon 932 (P); Mokonessi, 20 km NNW Zoetele, 7.VII.1972, Letouzey 11446 (P); 3–5 km SW Choam, 40 km S Mesamena, 16.II.1962, Letouzey 4268 (P, UPS); Bamenda, R., Bum, IV. 1931, Maitland 1642 (K); Bamenda, Migeod 495 (K); Banja, 13.VIII.1951, Ujor 29962 (K); Nkambe, Binka Mt., 31.IX.1952, Savory 377 (K); Bombi, 17.IX.1951, Ujor 30222 (K); near Tello falls, W. de Wilde 4268 (BR); N'Gaoundere, Ngan Ha, Jacques-Felix 8674 (P); Sadolkoulay, 36 km E N'Gaoundere, 5.XII.1964, Raynal 12251 (P, UPS); Nangue, Jacques-Felix 8168 (P, UPS); Salal Haleo, 60 km NE Tibati, 24.IX.1963, Letouzey 5959 (P, UPS); Hosserengo 80 km NE Tibati, 10.IX.1963, Letouzey 5684 (P, UPS). *Central African Republic*, Region of Bozoom, Tisserant 2957 (P). *Nigeria*, near Gembu, 10.VIII.1973, Chapman 99 (K); 17.VIII.1973, Chapman 108 (K); Tugan, 10.XII.1968, Daramola 62441 (K).

A. cucullatus Ryding sp. nov. — Fig. 1 E–G

Orig. coll: Jacques-Felix 8461, Cameroun, Poli near Vokré, 3.X.1967 (P holotype).

Species nova ab *A. repenti* basi sagittata et apice cucullato labii inferi corollae, ab *A. tuberoso*, *A. rivulari* et *A. sedoide* calyce in statu fructifero longiore, parte basali truncata persistenti, dentibus labii superi deorsum curvatis, labium inferum p.p. tegentibus, ab *A. buchneriano*, *A. candelabro* et *A. neglecto* foliis sessilibus basi cuneatis differt.

Perennial decumbent herb. Stems 1 to many, often rooting at the nodes, glandular and often pubescent in the upper part. Leaves opposite, or on the short-shoots fasciculate, fleshy, sessile, elliptic, up to 12–35 × 4–11 mm, ± acute at the apex, cuneate at the base, ± glandular, sometimes papillose to pubescent; margin minutely crenate; veins obscure beneath. Inflorescence composed of spikes forming a panicle; the spike on the main axis usually with opposite flowers; other spikes one-sided with alternately 1 or 2 flowers at each node, with sterile bracts on the back; bracts elliptic 2–4 × 1–2.5 mm, ± glandular and papillose; sterile bracts smaller and narrower. Fruiting calyx

Fig. 1. A–D: *A. angustifolius*. — A: Habit. — B: Section through a leaf × 3. — C: Fruiting calyx. — D: Flower. — E–G: *A. cucullatus*. — E: Habit. — F: Fruiting calyx. — G: Flower.

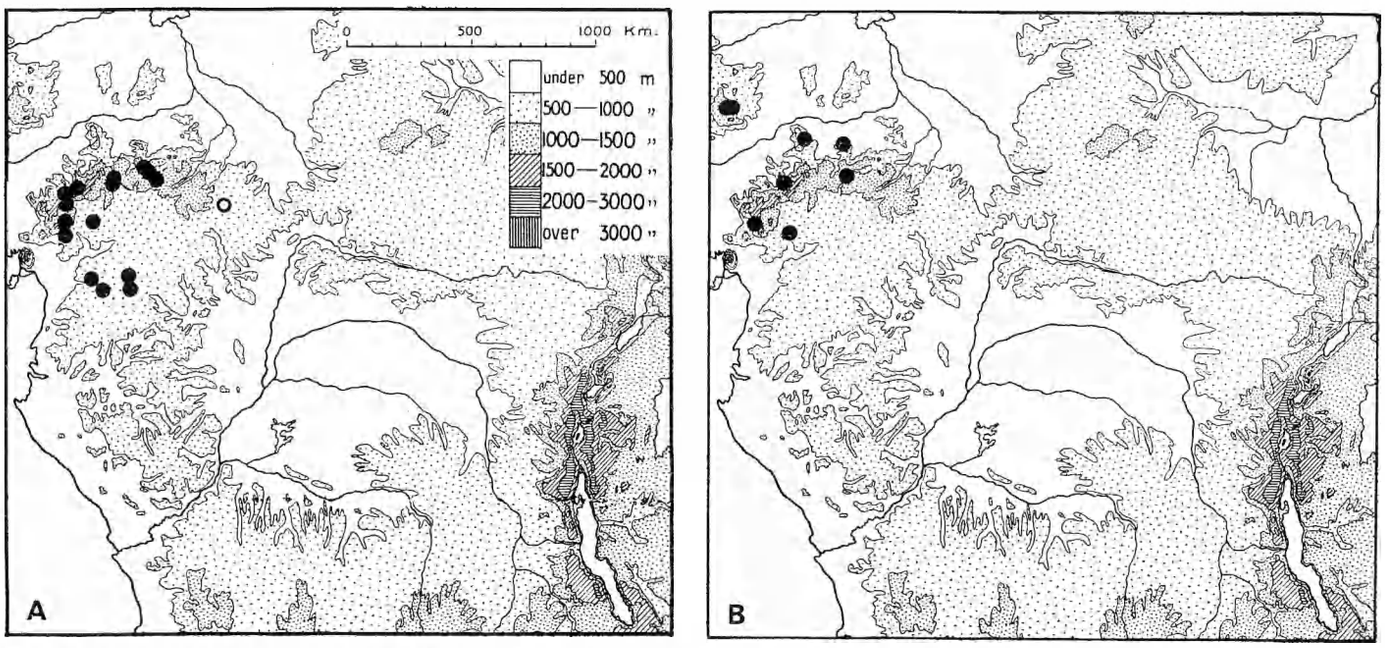


Fig. 2. A: Known distribution of *A. angustifolius*. ◯ = inexact locality. — B: Known distribution of *A. cucullatus*.

2-lipped, dehiscent at the base, 3–5 mm long, ± glandular and papillose; upper lip somewhat 3-lobed, whith the lobes folded over the lower lip; lower lip truncate or 2-lobed; basal part circular, truncate or almost so, often with a deep depression at the insertion of the pedicel 1.2–1.5 mm in diam., c. 0.5 mm high. Corolla 2-lipped, pale violet, glandular and papillose on the outside; tube 4.5–6 mm long; upper lip subequally 4-lobed with violet markings near the throat; lower lip boat-shaped, with a hood at the apex and 2 acuminate lobes near the base. Stamens 4; the 2 upper longer with c. 0.5 mm long anthers; the 2 lower with c. 0.9 mm long anthers. Style bifid at the apex. Nutlets smooth black, 0.8–1.0 × 0.7–0.9 mm.

Distribution and habitat. In the highlands of Cameroun and Nigeria (Fig. 2 B). Growing on rocks or shallow soil; alt. 1200–1900 m.

Variation and affinities. In most of the material of *A. cucullatus* the leaves are sparsely pubescent or papillose and with sessile glands, and the internodes of the spikes are not elongated in the fruiting stage. Some of the material deviates, however, by having pubescent leaves, with long both glandular and eglandular hairs, or by each second internode of the spikes in the fruiting stage being elongated up to 5 mm. Herbier C.N.A.D. 1747 is the most extreme collection in both these respects.

Hepper 1356, that was cited as *A. repens* by Morton (1962, 1963) belongs to *A. cucullatus*. *A. cucullatus* is, however, not closely related to *A. repens*, and is easily distinguished from this species by the hooded tip and the two acuminate lobes near the base of the lower lip of the corolla (Fig. 1 G).

The nearest relatives to *A. cucullatus* are undoubtedly to be found among a group of species, mainly occuring in Angola, which all agree with it in the shape of the lower lip of the corolla. Of these species *A. candelabrum* Briq. perhaps is the one which is closest to *A. cucullatus*. Both these species have about the same shape of the fruiting calyx, which is more than 3 mm long, with the upper lip folded over the lower one and with a ± truncate basal part (Fig. 1 F), but *A. candelabrum* is easily distinguished from *A. cucullatus* by the petiolate leaves and the usually more erect stem. At least superficially *A. tuberosus* Hiern and *A. sedoides* Hiern are even more similar to *A. cucullatus*. They have the same decumbent habit and sessile elliptical leaves as *A. cucullatus*, but differ from this species in the fruiting calyx being less than 3 mm long, with an unfolded upper lip and a deeply cupular or less than 0.35 mm high basal part, and also by the basal narrow part of lower lip of the corolla in the late stage of the anthesis being more than 1.5 mm long.

Collections besides the type. Cameroun, Nyafianga, 42 km NNE Bafia, 9.IX.1966, Letouzey 7822 (P, UPS); Mt. Golep, 36 km N Bafia, 22.XI.1969, Letouzey 9580 (P); Mt. Bamboutos, VII.1939, Lepesme Paulain Vil-

liers 562 (P); W Dschang Region, Bafou, 9.XII.1969, Herbier C.N.A.D. 1747 (P); N'Gaoundere, Ngan Ha, 14.X.1967, Jacques-Felix 8637 (P). *Nigeria*. Nguronje, 15.VIII.1966, de Leeuw 1763 (K); Bauchi P. Jarawa hills, E of Federe, 25.VIII.1962, Lawlor & Hall 354 (K); Adamawa Division, Vogel Peak Area, 14.XI.1957, Hepper 1356 (BR, K, P. S); Bauchi P. Sheve Mts., 21.VII.1968, Hall 551 (K).

A. engleri Briq.

The West African material of this species is all from the highlands near N'Gaoundere in Cameroun. The type collection (Welwitsch 5615) comes from Angola. The species also occurs in Malawi, Mozambique, Tanzania, Zambia and Zaire. The form in Cameroun has large and broad bracts, and particularly resembles the form in western Angola.

Collections from West Africa. Cameroun, Near Tello Falls, 47 km E N'Gaoundere, 27.XI.1964, W. de Wilde 4261 (K, P); 15 km N N'Gaoundere, 20.IX.1967, Jacques-Felix 8234 (P); N'Gaoundere, 11.X.1967, Jacques-Felix 8605 (P); 45 km E N'Gaoundere, 24.X.1967, Jacques-Felix 8828 (P); Natzaré, 10.III.1933, Lhote 122 (P); Gouloumou, 11 km N Belel, Raynal 12340 (P).

Key to Aeollanthus in West Africa

This key is constructed for the area dealt with in Hepper (1963) and for Cameroun. One of the species, *A. engleri* only occurs in the part of Cameroun which is not included in the area of this Flora.

1. Bracts more than 5 mm long ..... *A. engleri*
– Bracts less than 5 mm long 2
2. Spikes with 2 flowers at each or at each second node; lower lip of the corolla with narrow teeth or a hood at the apex 3
– Spikes with 1 flower at each node; lower lip of the corolla with neither teeth nor a hood at the apex 4
3. Basal part of fruiting calyx zygomorphic; lower lip of the corolla cuneate at the base and with narrow teeth at the apex; spikes dense ..... *A. angustifolius*
– Basal part of fruiting calyx actinomorphic or almost so; lower lip of the corolla with two acuminate lobes near the base and with a hood at the apex; spikes ± dense ..... *A. cucullatus*
4. Basal part of fruiting calyx zygomorphic and cupular; leaves attenuate at the base ..... *A. pubescens*
– Basal part of fruiting calyx actinomorphic and truncate; leaves rounded at the base ..... *A. heliotropioides*

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Botanical literature

Nannenga-Bremekamp, N. E. 1979: *De Nederlandse Myxomyceten. Ed. 2.* (In Dutch.) 460 pp. Published by Koninklijke Nederlandse Natuurhistorische Vereiniging (K.N.N.V.), Hoogwoud. Printed by Thieme & Cie B. V., Zutphen. ISBN 90-03-93130-5. Price DF1 54 (including surface mail postal rate).

The first edition of *De Nederlandse Myxomyceten* appeared in 1974. The second edition comprises an unaltered reprint bound together with a 20 pp. supplement. With references to pages and lines in the book the supplement provides corrections and supplementary remarks. It also brings the list of known species (in the world) up to date. The present review will consider the complete volume.

The book starts with a general and brief survey of the biology of the myxomycetes. Good advice is given on collecting, preparing of permanent slides, and keeping of specimens. However, the bulk of the book is a taxonomic treatment of the species found in the Netherlands. Forty-two genera and about 237 species are included. Keys are provided for families, genera and species. The descriptions are exhaustive and are accompanied by instructive illustrations. The specimens on which the illustrations are based are listed separately. Important synonyms are cited. The useful taxonomic comments and discussions are often extensive and include numerous taxa beyond the title of the book. From a scientific point of view the treatment fulfils high demands.

The gross systematics follows the system generally accepted today in so far as the endosporous species are divided into the orders Echinosteliales, Liceales, Trichiales, Stemonitales, and Physarales. The genera *Barbeyella* and *Clastoderma* are included in the Echinosteliales in accordance with the paper by Alexopoulos & Brooks in Mycologia, vol. 63, 1971. *Listerella* and *Diachaea* are maintained in the Trichiales and Stemonitales, respectively. *Dictydium* is merged with *Cribraria,* while *Lindbladia* is treated as a separate genus. No new taxa or combinations are formally established in the book; all taxonomic changes and novelties have been published previously in separate papers. As far as the order Stemonitales is concerned the taxonomy follows in the main Nannenga-Bremekamp's revision of the group (Proc. Kon. Ned. Akad. Wet., Ser. C, vol. 70, 1967). Persons used to Martin & Alexopoulos (1969, "The Myxomycetes", University of Iowa Press) may feel unfamiliar with such genera as *Collaria, Paradiacheopsis, Stemonitopsis* and *Symphytocarpus.* Nevertheless the reviewer is inclined to believe that Nannenga-Bremekamp's revision is a step toward a better understanding of the interrelationships of the taxa within the Stemonitales.

The circumscription of several species is narrower in Nannenga-Bremekamp's present book than in e.g. the world monograph by Martin & Alexopoulos mentioned above. Thus *Fuligo rufa* and *F. laevis*—both normally included in *F. septica*—are recognized as distinct species. So are also e.g. *Physarum lividum* and *P. reniforme.* In variable species intraspecific taxa are frequently distinguished. Three or four varieties are recognized in *Trichia contorta, T. decipiens, Fuligo septica* and *Craterium leucocephalum. Trichia favoginea* is treated in the broad sense but the characteristics of the forms sometimes regarded as species (*T. favoginea* s.str., *T. affinis, T. persimilis*) are described and illustrated.

The book is richly illustrated with line drawings of all taxa found in the Netherlands. Many of the illustrations are taken from the author's previous publications. The author has a well developed artistic talent. The general style of the

drawings is rather special, by close examination often giving the impression of roughness or even carelessness. However, the technique has turned out to be superb in this case and the illustrations are among the most instructive ever published on the myxomycetes. The whole range of variation in some species is beautifully covered by the drawings. A few species, e.g. *Enerthenema papillatum,* may perhaps be regarded as over-illustrated, in so far as some drawings could have been omitted without thereby losing any information or lessening the instructive or scientific value of the book.

A useful part of the book is formed by 13 plates with black-and-white spore drawings of species of the Stemonitales and the Physarales. The specimen on which each spore drawing is based is cited. The spores are figured as seen in the light microscope, and all are drawn to the same scale. The drawings are carefully prepared and the variation in ornamentation as well as spore size is instructively shown. According to the author (pers. comm.) the reason why only two orders have been illustrated in this respect is that a comparison of different species concerning the darkness of the spores is taxonomically most useful in these orders. Although the plates mainly comprise species found in the Netherlands, some others are also included. The spore drawing of *Amaurochaete comata* is based on a specimen from California. This is a noteworthy record since the species has only been reported from Europe.

Although hardly affecting the scientific value of the book the numerous typographical errors and inconsistencies are to be regretted. The reviewer is incapable of critisizing the Dutch text but the misprints affecting the scientific names in keys and descriptions are many and often conspicuous. It is a pity that the second edition of the book is an unaltered reprint in the sense that the typographical errors have been reprinted.

Elly Nannenga-Bremekamp has often referred to her research on myxomycetes as a hobby. That may be so, but it is a hobby that comprises a considerable part of her life. Today she is one of the world authorities on myxomycete taxonomy. Her private myxomycete collection in Doorwerth, Netherlands, comprises some 10 000 numbers and is rich in type material. It is to be hoped that it will be taken over and managed by an official scientific herbarium.

Nannenga-Bremekamp's book belongs to the important literature in myxomycete taxonomy. Although it is primarily a treatment of the species found in the Netherlands and as such includes less than half of the species known in the world, the breadth of the taxonomic discussions stretches far beyond that of a local flora. It is very useful also to those not familiar with the Dutch language, and it is not surprising that the first edition was sold out in a few years.

The book can be ordered from the Koninklijke Nederlandse Natuurhistorische Vereiniging. The price is low (DFl 54). Payment in advance is required, paid to the Dutch Postal Giro 130.28 of the "Bureau K.N.N.V., Hoogwoud". For those possessing the first edition the supplement can be ordered separately (price DFl 2).

Uno Eliasson

Shishkin, B. K. & Yuzepchuk, S. V. (eds.): *Labiatae.* In Flora of the USSR. Translation from Russian by Israel Program for Scientific Translations, Jerusalem. Vol. 20, 1976 (Bound c. 169 sFr.) and vol. 21, 1977 (c. 165 sFr.). Bound and paperback versions.

The two Labiatae volumes of the *Flora of the USSR* (1934–1964) have been translated into English under the editorship of Dr N. Landau. The translation project was commenced in 1963 by the Israel Program for Scientific Translations supported by the Smithsonian Institute, USA. The purpose is to make this enormous work (30 volumes and a general Index in Russian comprising c. 17,500 species) more available to a broader public. In 1973 the "Additamenta et corrigenda" was published by S. K. Czerepanov increasing the number of species to c. 21,000. Editors of vol. 20 were B. K. Shishkin & S. V. Yuzepchuk and of vol. 21 B. K. Shishkin, both volumes were originally published in 1954. Scientists contributing to these volumes were: A. G. Borisova, S. G. Gorshkova, M. V. Klokov, O. E. Knorring, L. A. Kuprinova, E. G. Levin, V. V. Pis'yaukova, E. G. Pobedimova, A. I. Poyarkova, B. K. Shishkin, S. V. Yuzepchuk, I. T. Vasil'chenko and E. V. Voltova.

The systematic index of the species, the diagnoses of the new taxa, all the figures and the general index to each volume have been photo-

copied from the original Russian version. The pagination from the original version is printed in the margin of the English translation. Unfortunately this information is lacking in the Addenda (vol. 21 pp. 463–489) containing the descriptions of new taxa. When using the flora, the lack of an alphabetic genus index to both Labiatae-volumes was a great obstacle. To facilitate matters for the readers, I have prepared such an index which can be copied and interfoliated in the volumes. The number of species in Flora Europaea compared to Flora of the USSR is indicated for each genus in the index. Each volume also contains two maps of USSR folded inside the cover. Probably due to photocopying of the originals with red borders, the printing quality of these maps is not good. The maps show the flora regions of USSR and extra-Russian flora regions. The floristic division of European USSR has in most cases been followed in Flora Europaea. In all, 913 species in 70 genera are keyed out. The "Additamenta et corrigenda" added 111 new species. Very few subspecific taxa are distinguished. Some cultivated and alien species such as *Salvia splendens* Ker-Gawl., *Lavendula spicata* L. etc. are included in this figure. The figures can be compared to Flora Europaea with 452 species in 41 genera (see Table). The number of subspecies and varieties maintained here is much higher while not many aliens are included. Five new genera were described in the Russian version of the flora, one of which (*Neustruevia* Juz.) however was withdrawn in the Corrigenda to vol. 20 (vol. 21 p. 462). About 75 new species were described in various precursory papers plus 62 new species described in the Flora itself. In all the new species comprise more than 15 % of the total number. Some new combinations and new names are presented in the text, unfortunately without references in the index. The seven largest genera with 62 % of the species are *Scutellaria* (148 species), *Thymus* (136), *Nepeta* (82), *Salvia* (75), *Eremostachys* (52), *Stachys* (50) and *Phlomis* (49). In Flora Europaea three genera have a comparable number of species: *Thymus* (66), *Stachys* (58) and *Teucrium* (49). Five, mainly Mediterranean-Azoric genera in the Flora Europaea are not represented in Flora of the USSR: *Cedronella, Cleonia, Horminium, Prasium* and *Thymbra*. The 34 genera not occurring in Flora Europaea are shown in the Table. The fourteen genera with more species in Flora Europaea than in Flora of the USSR are listed here: *Acinos, Ajuga* (+ = more than twice the number of species), *Ballota* (+), *Calamintha, Galeopsis, Lamium, Lavendula* (+), *Micromeria* (+), *Origanum* (+), *Prunella, Rosmarinus, Sideritis* (+), *Stachys* and *Teucrium* (+).

When comparing the Flora of the USSR with Flora Europaea it is soon evident that there is a difference in species concept and several of the new species described in Flora of the USSR are reduced to synonyms in Flora Europaea. To obtain a figure of the proportion, I have compared the names used in both floras in the genus *Thymus*. From 56 such names, nine were treated as synonyms in both floras. Of the rest, 23 were maintained in both floras while no less than 24 names were reduced to synonyms in Flora Europaea. Seven of these synonyms refer to names which were described as being new in the preparation of the flora. The lumping represents 17.65 % of the checked species and this would cut the total number of species (913–163) to 750. To illustrate the difference in species concept one example is chosen. Although *Salvia viridis* L. is generally accepted to be conspecific with *S. horminium* L. in European floras, both are maintained as species in Flora of the USSR and the hybrid between these colour forms is described as a new species *S. intercedens* Pobed. In the taxonomic note (vol. 21 p. 214) I quote: "A species intermediate between *S. horminium* and *S. viridis*, clearly of hybrid origin... As regards other hybrid forms produced by these species, displaying other combinations of characters, the occurence is rare and sporadic in areas of cohabitation of the parent species". As this discrepancy in species concept between Russian and European botanists will always form a source of confusion, there is a great need for dialogue regarding these questions.

The flora is amply illustrated and not less than 400 Labiatae species have been depicted. Unfortunately some of the original accuracy has been lost in the English version, e.g. Vol. 20 Fig. 4 and Vol. 21 Figs. 6, 11 and 23 are not acceptable, probably due to differences in black/white shade between figures on the same page. The translation seems to be acceptable and the species description and keys are detailed and accurate. Several spelling mistakes, omitted letters, words and references unfortunately lower the general impression of the volumes translated.

The great work of translating the Flora of the USSR is soon reaching its completion and we gratefully acknowledge the patient and careful work spent on the preparation of these two volumes.

Mattias Iwarsson

Comparison of the Labiatae genera in Flora Europaea and Flora of the USSR with an index to Vols. 20 and 21.

	Fl. USSR No. of species	Fl. Eur. No. of species	Vol.	Russ. page	Eng. page
Acinos	4	5	21	441	316
Agastache	1	0	20	273	181
Ajuga	4	10	20	17	13
Amaracus	1	0	21	447	320
Amethystea	1	0	20	69	47
Ballota	3	7	21	187	137
Betonica	7	0	21	237	172
Calamintha	4	5	21	429	307
Chaiturus	1	0	21	144	104
Chamaesphacos	1	0	21	243	177
Clinopodium	5	1	21	436	312
Dracocephalum	35	5	20	439	295
Drepanocaryum	1	0	20	228, 516	151, 350
Dysophylla	1	0	21	637	457
Elsholzia	3	1	21	634	455
Eremostachys	52	1	21	1	3
Erianthera	1	0	21	140	101
Galeobdolon (= *Lamiastrum*)	1	1	21	138	100
Galeopsis	5	9	21	111	79
Glechoma	3	2	20	437	293
Gontscharovia	1	0	21	628	450
Hymenocrater	2	0	20	488	328
Hypogomphia	2	0	20	491	330
Hyssopus	9	1	21	448	320
Kudrjaschevia	4	0	20	474	319
Lagochilus	27	0	21	160	116
Lagopsis	4	0	20	248	165
Lallemantia	5	0	20	482	324
Lamium	12	13	21	124	88
Lavendula	1	7	20	226	150
Leonurus	12	2	21	145	105
Lophanthus	8	0	20	275	183
Lycopus	7	2	21	591	423
Majorana	1	0	21	462	330
Marrubium	15	12	20	233	155
Meehania	1	0	20	529	363
Melissa	1	1	21	411	294
Melittis	1	1	20	498	336
Mentha	22	14	21	596	427
Metastachys	1	0	21	192, 652	140, 470
Micromeria	44	21	21	426	304
Moluccella	1	1	21	181	132
Nepeta	82	24	20	286	191
Neustruevia	0	0	20	501	338
			20	526	360
			21	642	462
Ocimum	1	0	21	641	460
Origanum	3	13	21	463	331
Orthodon	1	0	21	633	454
Otostegia	4	0	21	182	133
Panzeria	3	0	21	157	114
Perilla	2	1	21	630	452
Perovskia	6	0	21	374	267
Phlomidoschema	1	0	21	242	176
Phlomis	49	12	21	57	41
Plectranthus	3	0	21	638	458
Prunella	3	4	20	494	332
Pseuderemostachys	1	0	20	500	337
Pseudomarrubium	1	0	21	642	462
Rosmarinus	1	2	20	70	48
Salvia	75	36	21	244	178
Satureia	13	12	21	413	295
Schizonepeta	2	0	20	282	188
Schraderia	4	0	21	363	260
Scutellaria	148	13	20	72	50
Sideritis	10	28	20	253	168
Stachyopsis	3	0	21	108	77
Stachys	50	58	21	194	141
Teucrium	21	49	20	39	27
Thuspeinantha	1	0	20	232	154
Thymus	136	66	21	470	335
Wiedemannia	1	0	21	142	102
Ziziphora	22	6	21	381	272
Total	913	446			