Culture studies on the type species of Acrochaete, Bolbocoleon and Entocladia (Chaetophoraceae, Chlorophyceae)

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Acrochaete repens Pringsheim and *A. parasitica* Oltmanns were found by culture studies to be the same species. Quadriflagellate zoospores and biflagellate swarmers of two different sizes were observed. The swollen bases of the hairs are separated from the underlying cells by delicate walls. Hairs of the same type were observed in the type species of *Entocladia* Reinke, collected at the type locality. In consequence, Reinke's species is transferred to *Acrochaete* as *Acrochaete viridis* (Reinke) R. Nielsen, comb. nov. Isolation of a large number of similar algae from different regions showed *A. viridis* to be a very widespread and common species. Culture observations on *Bolbocoleon piliferum* Pringsheim showed this alga to be well separated from *A. repens,* distinct by its type of hairs and the morphology of its germlings. In this species only quadriflagellate swarmers were observed.

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The genus *Acrochaete* was established by Pringsheim (1862) with a single species, *A. repens,* growing as an endophyte in brown algae without a parenchymatous outer layer and forming hairs resembling those in *Coleochaete.* Huber (1892 a, b) studied plants from nature and found no sheath around the hair base but sometimes a collar. South (1968) as well as Kermarrec (1970) studied *A. repens* in culture. Neither observed any alternation of generations; Kermarrec saw biflagellate zoospores, but none of them found the sporangia considered to be antheridia by Pringsheim or the small swarmers Huber (1892 b) supposed to be gametes. A second species, *A. parasitica,* was described by Oltmanns (1894), growing as an endophyte in species of *Fucus.* South (1968) doubted the validity of the supposed parasitic nature of this endophyte as a basis for establishing a second species.

In the same paper where *Acrochaete* was first described, Pringsheim (1862) established the genus *Bolbocoleon* with a single species, *B. piliferum.* Since then these algae have been compared by Huber (1892 a, b), South (1968), and finally by Kermarrec (1970) who showed them to be different in respect to chromosome number.

The genus *Entocladia* was established by Reinke (1879) with a single species, *E. viridis,* growing as an endophyte in the cell wall of *Derbesia balbisiana* (Lamour.) Hamel from Naples. Reinke did not observe hairs on the filaments. Subsequent authors placed hair-bearing algae in the same genus, but these were later transferred to *Ectochaete* (Huber) Wille 1909 and by myself (Nielsen 1972) to *Phaeophila* Hauck 1876. Yarish (1975) studied *E. viridis* (from an unknown source) and found that it produced hairs, but maintained Reinke's generic name for it. On the basis of his observations, Burrows (in Parke & Dixon 1976) transferred the species into *Phaeophila.*

Material and methods

Unialgal cultures were started from material collected in nature as appears from the list at the end of this

paper. The standard culture medium was the same as previously described (Nielsen 1972); in addition, pasteurised sea water without enrichments was used for some purposes. To avoid diatom growth GeO_2 was added at the beginning. The plants were grown in test tubes and Petri dishes. A basement room with temperatures ranging between 12 and 18°C according to outdoor conditions was used as culture room with Philip fluorescent tubes TL/40W as light source, giving a light intensity of 800 lx at a 16/8 hours light/dark cycle. Plasmolysis as a means to observe delicate cell walls was achieved by addition of hypertonic sea water, saturated by evaporation.

Acrochaete repens Pringsheim

Pringsheim 1862.
A. parasitica Oltmanns 1894.

Cultures were obtained partly from the brown algal genera as indicated in the original descriptions, partly from various other sources. The algae collected among the paraphyses of *Chorda filum* (L.) Stackh. agreed with the original description of *A. repens* in morphology. They were fertile and both of the types of sporangia mentioned in literature were observed (Fig. 1 A, B). The hairs had no sheath or collar around their bases. The algae collected on *Fucus serratus* L. and *F. vesiculosus* L. agreed with the original description of *A. parasitica* as to the vegetative endophytic filaments. Both dead and living *Fucus* cells were seen around the filaments, but no indications of a parasitic relationship were observed. A large pyrenoid was seen in each cell, but only few hairs appeared on the plants from nature. The other isolates of *Acrochaete* were started from algae developed in crude cultures and were not determined until hairs were observed.

In culture the isolates were all alike. The branching could be very open (Fig. 1 I) or the filaments might be entangled to form compact plants, sometimes with free branches at the periphery. A pseudoparenchymatous basal layer or a cushion was usually formed by plants in contact with a firm substratum. In such plants very long-celled "runners" were sometimes observed with a small group of ordinary cells at the distal end (Fig. 1 J). The vegetative cells contained a parietal reticulate chloroplast with (1–)3–6 pyrenoids, one sometimes larger than the others. Their shape and size varied a lot, the diameter from 10 μm to 25 μm. Hairs appeared on plants transferred into sea water without enrichments or as the medium became depleted. They developed on terminal cells or on excrescences from intercalary cells. A few times two hairs were observed on the same cell (Fig. 1 G). Each hair had a broad base (Fig. 1 E–G). By plasmolysis a cell wall was shown to separate the swollen base from the ordinary cell below (Fig. 1 H). The hair bases and the hairs appeared absolutely hyaline. Every vegetative cell could develop into a sporangium during gradual elongation. At maturity the sporangia opened at the top. Two types of sporangia were observed. One was pale (Fig. 1 C), containing globular to pyriform biflagellate swarmers 2.5–3 × 3–3.5 μm large, each with a red eyespot but apparently without chloroplast. The other type was green, containing pyriform swarmers 3.5–5 × 5–7 μm large, each with a red eyespot and a posterior chloroplast, some biflagellate and some quadriflagellate. It was usually impossible to count the swarmers which escaped from a sporangium in a common mucilaginous envelope. In one case 32 quadriflagellate swarmers were counted, but there were often more. In two of the isolates all three kinds of swarmers were observed, while only one or two kinds were observed in the other isolates. The two differently sized types of biflagellate swarmers were once observed coming from the same mother plant. Copulation was never seen so a gametic behaviour of the biflagellate swarmers, though very probable, cannot be stated with certainty. The germlings (Fig. 1 D) grew into uniseriate branched filaments.

Acrochaete viridis (Reinke) R. Nielsen, comb. nov.

Basionym: *Entocladia viridis* Reinke 1879 p. 476.

This plant was collected at the type locality near Naples, growing as an endophyte in the cell wall of a plant that had the appearance of *Derbesia balbisiana* (Lamour.) Hamel. The host was sterile and may have been a young plant of the related *Bryopsis disticha* (J. Ag.) Kütz., often confused with *Derbesia balbisiana*; in any case, tubes with pinnately branched apices were found in the same collection. The endophytes agreed with Reinke's (1879) description, young plants consisting of uniseriate branched filaments (Fig. 2 A, B), older thalli forming a central pseudoparenchyma with mature and emptied

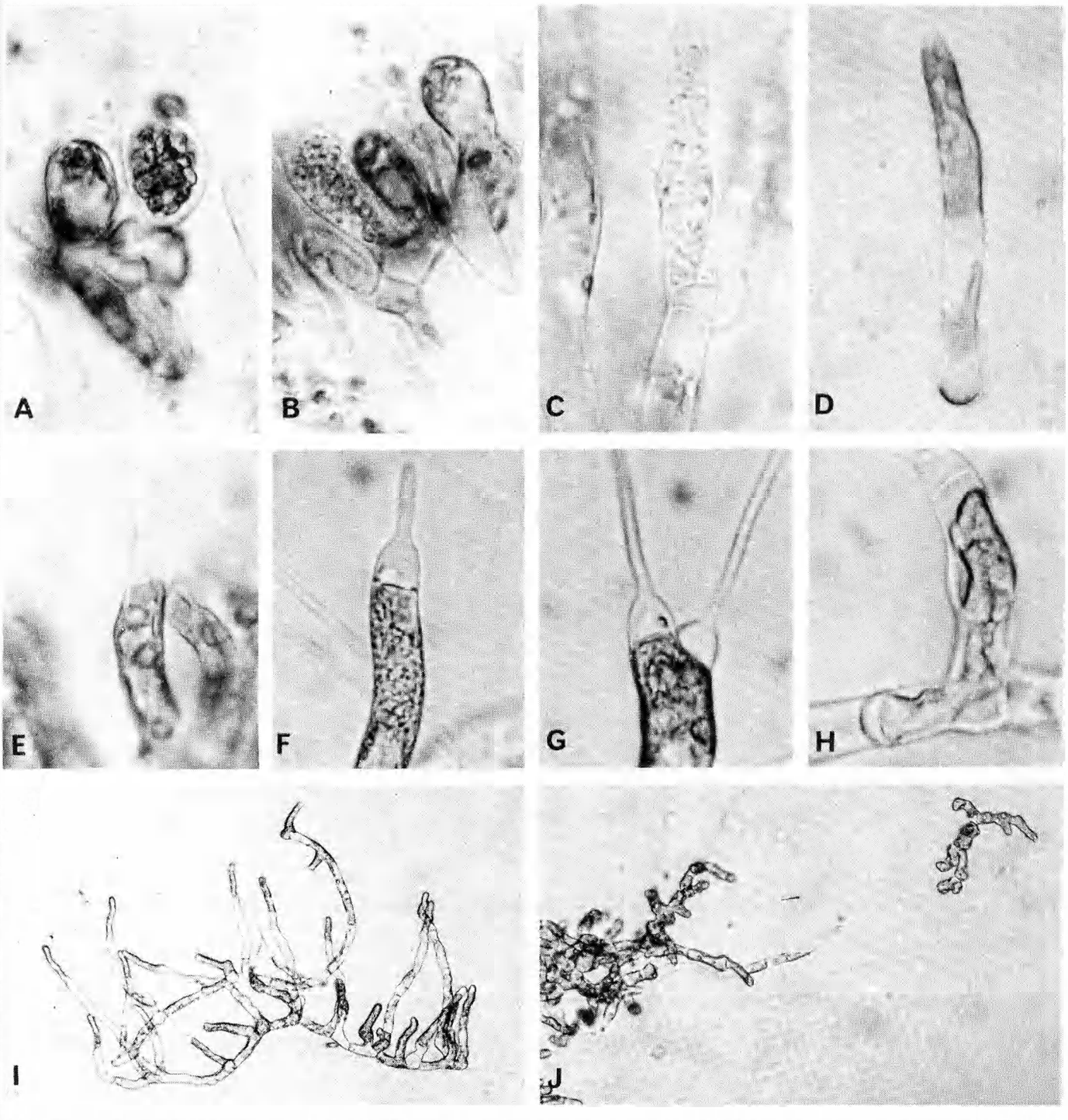

Fig. 1. *Acrochaete repens*. – A: Sporangium with green swarmers on a plant from nature. – B: Sporangium with small pale swarmers also from nature. – C: Same as B, on a plant in culture. – D: Germling. – E, F: Stages of hair formation. – G: Two hairs on the same cell. – H: Part of plasmolysed plant clearly showing the cell wall between the hair base and the cell below. – I: Unattached thallus with open branching and many hairs. – J: Part of attached thallus with a runner. – A–H: × 800. – I–J: × 150.

sporangia. Each sporangium had an exit tube. The vegetative cells of the filaments measured 5–10 μm in diameter; they had a parietal chloroplast with one pyrenoid. Hairs were observed on plants a week after collection (Fig. 2 C).

In culture the outer morphology of these plants varied a lot. When growing in contact with a firm substratum they first developed as more or less circular pseudoparenchymatous cushions (Fig. 2 G). Later branches grew freely into the medium from the cushion (cf. Fig. 2 I). Unattached thalli appeared as masses of uniseriate

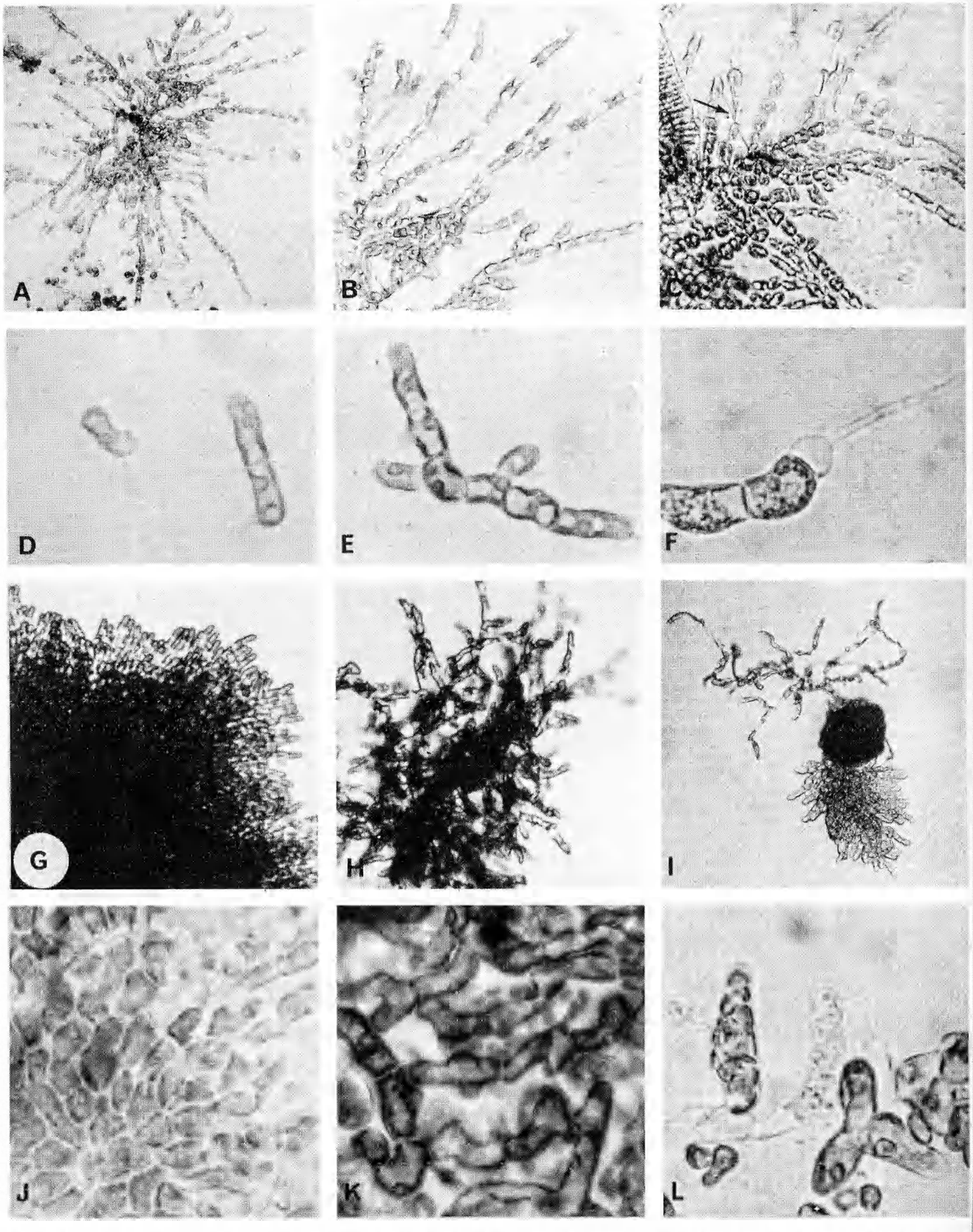

Fig. 2. *Acrochaete viridis*. –A–H: From the type locality. – A–C: Plants growing in the cell wall of *Derbesia balbisiana* or *Bryopsis disticha*, a hair at the arrow. – D: Germlings. – E: Young plant. – F: Hair. – G: Part of thallus attached to a firm substratum. – H: Unattached thallus. – I: Plant in culture isolated from *Cystoclonium purpureum*, at the bottom attached to a substratum, in the middle an unattached pseudoparenchymatous part, and the top composed of free filaments. – J: Part of pseudoparenchymatous epiphyte on *Desmarestia aculeata*. –

branched filaments entangled centrally and with free branches at the periphery (Fig. 2 H). The vegetative cells had one pyrenoid and measured 5–10 μm in diameter as in the material collected in nature. Sporangia developed from vegetative cells; in the basal layer they retained their shape, apart from developing an exit tube; in the free filaments they became cup- or bottle-shaped. At maturity a great number of pyriform swarmers escaped through the exit tube or through a hole at the top of the sporangium. Two different types of biflagellate swarmers could be distinguished, each with a red eyespot: one 1.5–2× 2–3 μm in size, pale and apparently without a chloroplast, the other 3.5–5× 5–7 μm with a posterior chloroplast. The two types were formed in different sporangia but sometimes on the same mother plant (cf. Fig. 2 L). Copulation was never observed. Germlings (Fig. 2 D) developed without formation of a germ tube and grew into uniseriate branched filaments (Fig. 2 E). On plants transferred into sea water without enrichments, hairs were observed after c. two weeks. They had a colourless swollen base separated from the ordinary cell (Fig. 2 F), just as in *Acrochaete repens*.

Collecting dates and localities for a number of similar algae isolated in culture are given at the end of this paper. In nature the algae were found as pseudoparenchymatous epiphytes (Fig. 2 J) or as epi- or endophytic branched filaments (Fig. 2 K). In culture they all agreed with the plants from Naples as to dimensions and contents of vegetative cells, morphology of the germlings, and type of hairs. The outer morphology varied from one plant to another in the same isolate and also between the isolates, but the range of variation did not go far beyond what was observed in the plants from Naples. In some of the isolates only quadriflagellate zoospores were formed; in others biflagellate swarmers of two different sizes were seen, but copulation was never observed.

Bolbocoleon piliferum Pringsheim

Since the identification of *B. piliferum* depends on the presence of hairs, unialgal cultures were established for the purpose of determination when plants of this type but without hairs were collected in nature. The cultures were maintained for comparison with other Chaetophoraceae. All the plants appeared as loosely tangled uniseriate branched filaments, but two different types could be distinguished. One type, represented by five of the isolates, had cylindrical cells 10–15 μm in diameter and 1–10 times as long (Fig. 3 A). In the other type, represented by two of the isolates, the cells were irregularly swollen, 25–45 μm in diamter (Fig. 3 B), sometimes with peripheral filaments of longer cylindrical cells 7–9 μm in diameter with a small group of swollen cells at the distal end like runners. Apart from these differences the two types were alike. The ordinary cells had a parietal reticulate chloroplast with 3–12 pyrenoids. Hairs were found on plants transferred to sea water without enrichments after two to four weeks (Fig. 3 A, D). In a single isolate hairs were only observed on plants grown in Petri dishes, not on plants in test tubes. In agreement with the original description (Pringsheim 1862), as modified by Huber (1892 a) the hair was part of a special hair-bearing cell (Fig. 3 D) which had a basal chloroplast with fimbriate edges and 2–3 pyrenoids.

The sporangia were modified vegetative cells. Their walls were transformed into a mucilaginous substance at the place where the 32–64 zoospores later escaped. The mucilage was pushed out and surrounded the zoospores like a common envelope at the moment of liberation. It remained attached to the tip of the sporangium for a short time (Fig. 3 F). The slender pyriform quadriflagellate zoospores measured 4.5–6.5× 9–12 μm; each had a prominent eyespot and a large pyrenoid in the posterior chloroplast. They showed positive phototaxis. Their development was similar to that observed by South (1968) and Kermarrec (1970), with an empty germ tube and a zoospore wall attached to the young germling (Fig. 3 C). Few-celled plants with sporangia and hairs similar to those called the reduced type by South (1968) were found in cultures where the medium had not recently been renewed. This supports the assumption by

K: Part of filamentous epiphyte on *Phycodrys rubens*. – L: Same as K, in culture. Filament of mature and emptied sporangia. The two mature sporangia contain different kinds of swarmers. – A: × 80. – B–C: × 200. – D–F, J, L: × 800. – G–I: × 150. – K: × 600.

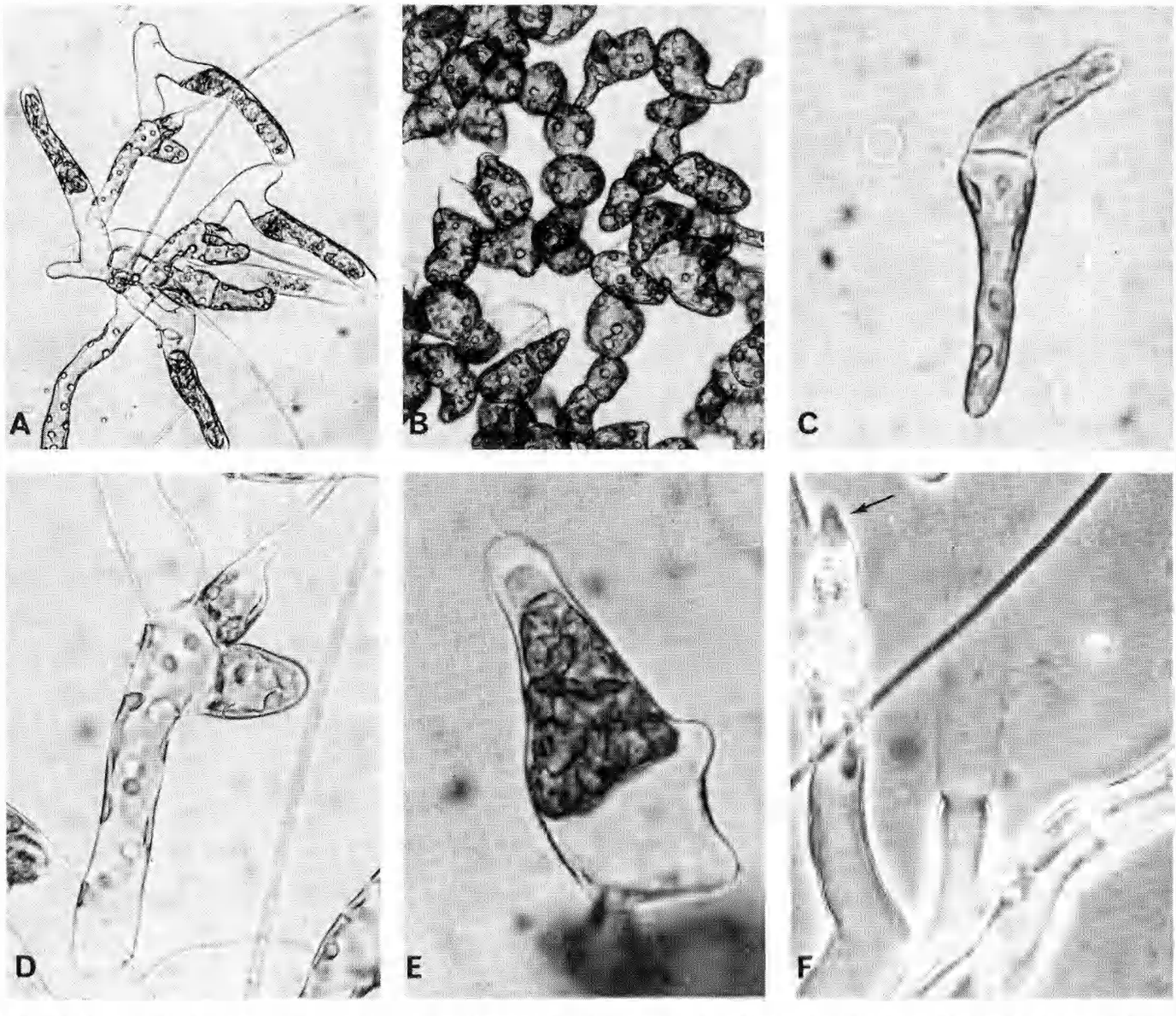

Fig. 3. *Bolbocoleon piliferum* in culture. – A: Plant composed of cylindrical cells with some hairs and sporangia. – B: Part of a plant composed of irregular cells with some emptied sporangia. – C: Germling. – D: Ordinary vegetative cells and a hair cell. – E: Mature sporangium. The cell wall is partly gelatinized at the future opening. – F: Emptied sporangium with the mucilage envelope attached to the opening. A very young hair at the arrow. Phase-contrast. – A, B: × 200. – C, D, F: × 600. – E: × 800.

Moestrup (1969) that they develop in connection with some changes in the composition of the medium. Biflagellate swarmers as reported for this species by Huber (1892 b), Hygen (1937) and Yarish (1975) were not observed.

Discussion

Some of the algae isolated in culture and mentioned in the present paper under the heading of *Acrochaete repens* were in agreement with this species as originally described, while others agreed with *A. parasitica* when collected in nature. According to the original description (Oltmanns 1894) *A. parasitica* differs mainly from *A. repens* in gradually killing the surrounding part of the host tissue and in having only one pyrenoid per cell, while several pyrenoids appear on the drawings of *A. repens* by Pringsheim (1862). The cell dimensions have later been used as an additional distinctive character (Hamel 1930–31). A parasitic effect was never observed on the host plants studied here, and the isolated endophytes grew well in culture without material from a host plant. A single large pyrenoid was observed in each cell in the plants from nature, while the plants in culture often had several smaller pyrenoids. Thus the characters originally

used to separate these species do not hold, and the cell dimensions vary too much. Therefore, *A. parasitica* must be regarded as conspecific with *A. repens*.

Since Pringsheim (1862) described the hairs of *Acrochaete* as *Coleochaete*-like, subsequent authors have discussed their formation. Huber (1892 a) found no sheath around the hair base, nor did South (1968); but both of them sometimes observed a collar around the base. In the present study none of these structures were seen. The development of the hairs agreed with the observations by South (1968). The *Acrochaete*-type of hair consists of a narrow terminal part and a swollen base which is separated from the underlying cell by a wall and is hyaline throughout, slightly reminiscent of the hairs of *Aphanochaete* as studied in EM by Tupa (1974, Fig. 244). The occurrence of two types of biflagellate swarmers confirmed the observations made by Pringsheim (1862) and by Huber (1892 b). As to the reproduction of the plant studied by Oltmanns (1894), he himself doubts that his Fig. 8 shows the same species as the rest. His Figs. 7, 8 and 9 resemble one another a good deal, but I am inclined to think they represent a different alga, so that Oltmanns saw only vegetative stages of *Acrochaete*.

The observation that *Entocladia viridis* forms hairs of the *Acrochaete-type* makes a merging of Reinke's species into *Acrochaete* more natural than a merging into *Phaeophila* as proposed by Burrows in Parke & Dixon (1976). Therefore, the new combination *Acrochaete viridis* is introduced here. As *Entocladia viridis* is the type species of that genus, the name *Entocladia* hereby goes into synonymy. A number of species later referred to *Entocladia* have never been found to produce hairs. Some of them may be able to do so under certain conditions, but others never do. For *Entocladia* a different generic name must be found. *Periplegmatium* Kützing (1843) was said by Hansgirg (1889) to be identical with *Entocladia viridis*, but a recent study of Kützing's material (Nielsen 1979) has shown that it is a brown alga, as also stated by Wille (1890). *Entonema pycnocomae* ("*pycnomonae*") Reinsch (1875) was mentioned by Lagerheim (1883) as probably belonging in *Entocladia*. However, Reinsch (1875) listed *Entonema* as a brown algal genus. A type species has hardly been selected, but since many of the species described in the same paper as *E. pycnocomae* do belong in the brown algae, it seems reasonable to choose one of these for typification of the genus. *Endoderma* Lagerheim (1883) is an illegitimate name (cf. Nielsen 1972). The same applies to the orthographic variant *Entoderma* which was first used by Hansgirg (1888). *Reinkia* Borzi appears as a generic name in De-Toni (1888), but De-Toni (1889) refers to a manuscript by Borzi in his comments on it so it seems that *Reinkia* was not validly published before 1889. This same year Reinke (1889) described *Epicladia* with the single species *E. flustrae* growing epizootically in the bryozoan *Flustra foliacea* (L.) Hincks. He remarked that it was close to the genus *Entocladia*. Some later authors, like Taylor (1937), have combined these two genera of supposedly hairless species under the name of *Entocladia*. Kylin (1938) pointed out that *Epicladia* is endozootic, and stated that it was parenchymatous in its older parts and thereby distinct from *Entocladia*. Unpublished observations on *Epicladia flustrae* in culture support the opinion that *Epicladia* is unable to form hairs. Yarish (1975, 1976) reported that plants referred by him to *Entocladia flustrae* (Reinke) Taylor, formed hairs under some conditions. However his plants did not agree with the original description by Reinke (1889) as to the number of pyrenoids, they were collected very far from the type locality, and they did not grow on bryozoans. Most probably, therefore, these plants were not identical with that studied by Reinke. Older thalli of *Epicladia*, as conceived by myself, are usually pseudoparenchymatous, but the occurrence of a true parenchyma seems very doubtful. Therefore this alga is very close to the hairless algae hitherto placed in *Entocladia*. In consequence, the genus *Epicladia* may be widened to include such allied hairless species after the necessary checking as to whether production of hairs can be induced by special treatment in culture.

The cultures of *A. viridis* from the type locality revealed great morphological variation, depending on substrate contact and medium. Relatively constant, however, were the dimensions of the vegetative cells, the presence of one pyrenoid in each, and the hair morphology. Comparison of this material with the large number of similar algae collected elsewhere leads to the conclusion that they are all identical. Thus *A. viridis* is a

very common and widespread alga growing epi- or endophytically on various algae and also on other substrata. There is nothing in the material to support Kylin's (1938) view that this is an aggregate species.

Comparison of the culture observations on *A. repens* with those on *B. piliferum* leads to the conclusion, also reached by Kermarrec (1970), that the two are very distinct. In *B. piliferum* the hair is part of a cell with a well-developed chloroplast, not of an optically empty cell as in *Acrochaete,* and the germlings are different, in *B. piliferum* with a germ tube which is not found in *A. repens*. The observations on isolates from various places agree with those made by Jaasund (1965) in material from nature, and suggest that *B. piliferum* comprises two different types.

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Isolates studied

Acrochaete repens

Denmark, Skagerrak, Kærsgård Strand 10.10.1976. Four isolates from *Chorda filum* (drift).

Denmark, N Kattegat, Deget 27.7.1972. *Laurencia pinnatifida.*

Denmark, N Kattegat, Deget 18.6.1977. Periostracum of *Littorina obtusata.*

Denmark, N Kattegat, Hirsholm 26.2.1975. *Fucus vesiculosus.*

Denmark, N Kattegat, Nordre Rønner 6.9.1972. *Fucus serratus.*

Denmark, N Kattegat, Læsø, Syrodde 31.10.1976. *Chorda filum* (drift).

Denmark, C Kattegat, Lyngså Strand 7.10. 1976. Four isolates from *Chorda filum* (drift).

Denmark, S Kattegat, Roskilde Fjord, Frederikssund 14.11.1978. *Fucus vesiculosus.*

Denmark, the Sound, West coast of Saltholm 8.6.1976. On limestone rock, collecting by Aase Kristiansen.
Denmark, the Baltic round Møen, Stevns Klint 15.11.1978. *Fucus serratus* (drift).
Channel Islands, Guernsey, Bordeaux Harbour 1.8.1978. *Fucus serratus*.

Acrochaete viridis

Great Britain, Orkney Islands, Mainland, Brough Head 29.7.1973. *Laminaria saccharina*.
Great Britain, Isle of Man 27.8.1974. On stone at a depth of 6–7 m, diving by M. Lauret.
Channel Islands, Guernsey, Côbo, Long Rock 31.7.1978. Two isolates, from *Callophyllis laciniata* and *Griffithsia flosculosa*, respectively.
Channel Islands, Guernsey, Bordeaux Harbour 1.8.1978. *Ceramium rubrum*.
Channel Islands, Guernsey, Lihou Island 5.8.1978. Two isolates, from *Griffithsia flosculosa* and *Laminaria saccharina*, respectively.
Channel Islands, Sark, near Venus Pool 4.8.1978. *Cryptopleura ramosa*.
France, Roscoff, near la Station Biologique 24.3.1974. *Chondrus crispus*.
France, Roscoff, Ile Verte 25.3.1974. Two isolates, from *Cystoclonium purpureum* and *Gastroclonium ovatum*, respectively.
France, dredging near Roscoff 28.3.1974. Two isolates, from *Caliblepharis ciliata* and *Phyllophora* sp., respectively.
France, St. Michel de Plougerneau 26.3.1974. Two isolates, from *Plocamium cartilagineum*, and two isolates, from *Gastroclonium ovatum* and *Cryptopleura ramosa*, respectively.
France, Santec 27.3.1974. *Dictyota dichotoma*.
Denmark, Skagerrak, Hirtshals 23.1.1973. *Desmarestia aculeata* (drift).
Denmark, N Kattegat, Hirsholm 10.11.1976. *Phycodrys rubens* (drift).
Denmark, N Kattegat, Hirsholm 7.7.1978. *Chaetomorpha linum* (unattached).
Denmark, Limfjorden, Helligsø 27.10.1973. *Chondrus crispus* (drift).
Denmark, Limfjorden, Helligsø 21.9.1977. Five isolates, from *Ceramium rubrum, Laurencia pinnatifida* (drift), *Laminaria saccharina, Zostera marina,* and stone in the littoral zone, respectively.
Denmark, Limfjorden, Engholm near Nr. Sundby 18.10.1978. Plastic imitation of *Zostera* leaves placed on the sea bottom. (Experiment by Birgit Bak).
Denmark, Limfjorden, Dam at Bygholm Vejle 28.10.1973. Stone in the littoral zone.
Denmark, the Samsø area, Røsnæs 26.9.1977. Two isolates, from *Polysiphonia violacea* and *Laminaria digitata*, respectively.
Sweden, near the Zoological Station of Kristineberg 22.6.1971. Two isolates, from empty shells of *Mya arenaria*.
Italy, Naples, Porto Sannazara 27.4.1978. Eight isolates, from *Scinaia forcellata, Phyllophora nervosa, Griffithsia* sp., *Nitophyllum punctatum, Dasya hutchinsiae, Polysiphonia violacea, Dictyota dichotoma,* and *Derbesia balbisiana* (or *Bryopsis disticha*), respectively.
Italy, Naples, Posillipo at Villa Volpicelli 28.4.1978. Three isolates, from *Derbesia balbisiana* (or *Bryopsis disticha*).
Italy, Sorrento 1.5.1978. Three isolates, from *Champia parvula, Polysiphonia violacea,* and *Porphyra leucosticta*, respectively.

Bolbocoleon piliferum

Denmark, N Kattegat, Deget 22.7.1972. *Cystoclonium purpureum*.
Denmark, N Kattegat, Hirsholm 10.11.1976. *Laminaria hyperborea* (drift).
Denmark, N Kattegat, Nordre Rønner 26.7.1977. *Polysiphonia violacea*.
Denmark, N Kattegat, Læsø, Horneks Odde 23.5.1976. *Dumontia incrassata*.
Denmark, N Kattegat, Læsø, Syrodde 31.10.1976. *Chorda filum* (drift).
Denmark, Limfjorden, Helligsø 21.9.1977. Two isolates, from *Chylocladia verticillata* and *Laurencia pinnatifida*, respectively.

Periplegmatium ceramii Kützing is a brown alga

Ruth Nielsen

Nielsen, R. 1979 11 15: Periplegmatium ceramii Kützing is a brown alga. *Bot. Notiser 132:* 450. Stockholm. ISSN 0006-8195.

A study of the type specimen of *Periplegmatium ceramii* Kützing, sometimes referred to the green algae, has shown that it is in all probability a brown alga. However, the genus cannot be determined.

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The genus *Periplegmatium* was established by Kützing (1843) with a single species, *P. ceramii,* which is consequently the type species. His illustrations show sterile, partly coalescing, creeping filaments growing on a *Ceramium*. Kützing listed it under his family Conferveae next to *Spongomorpha*. This suggests that it is a green alga. On the other hand he stated the colour to be "lutescens", and his illustration seems to show several small chloroplasts in each cell. This speaks in favour of regarding *Periplegmatium* as a brown algal epiphyte. Hansgirg (1889) briefly stated that inspection of the type material has confirmed that *Periplegmatium* is the same as *Entocladia* Reinke (1879). Wille (1890) supposed *Periplegmatium* to be a germling of a brown alga but listed (Wille 1909) *Periplegmatium* "proparte" under the green algae.

Thanks to the curator at L I have had the opportunity to study Kützing's type material. It consists of a few fragments of the host cell wall with various small epiphytes. Some of them are very similar to those illustrated by Kützing. Fig. 1 shows one of these. Each cell contains 5–7 chloroplasts. Addition of IKI gives no starch reaction. No sporangia or hairs have been observed. These observations definitely rule out the identity of *Periplegmatium* with any member of the Chaetophoraceae. In all probability *Periplegmatium* is a brown alga. Assignation to genus is impossible as the material is sterile.

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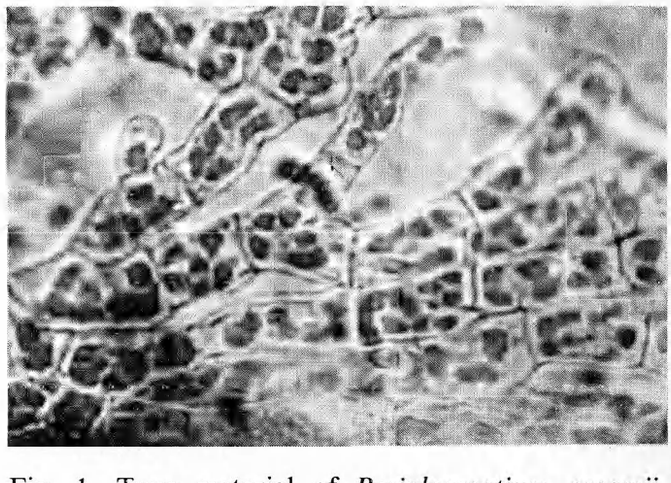

Fig. 1. Type material of *Periplegmatium ceramii*. × 600.

A revised species concept for endophytic and endozoic members of the Acrochaetiaceae (Rhodophyta)

David Garbary

Garbary, D. 1979 11 15: A revised species concept for endophytic end endozoic members of the Acrochaetiaceae (Rhodophyta). *Bot. Notiser 132:* 451–455. Stockholm. ISSN 0006-8195.

Six endophytic and endozoic isolates of four species of *Audouinella* were grown in the presence of *Ceramium rubrum* and *Antithamnion spirographidis,* in which they are not normally growing. All isolates of *Audouinella* established some relationship with *C. rubrum* varying from simple entanglement to development of epiphytic plants, or to true endophytic growth. *A. endophytica* was the only species to become endophytic in *Antithamnion spirographidis*. Cell size and shape were different in plants growing endophytically and in the free-living state, and differences were also noted in plants penetrating the two experimental hosts. These results suggest that evidence from culture studies is required before host identity can be used to establish species concepts and that these should be modified to reflect the limitations of plant morphology found in field material.

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The family Acrochaetiaceae is virtually unique among the Florideophyceae in possessing species that live endophytically and endozoically. The relationship between the acrochaetioid filaments and the hosts is, however, poorly understood. Although some species of *Audouinella* (sensu Dixon & Irvine 1977, Garbary 1979) have been reported to penetrate host protoplasts (Drew 1928, Aziz 1965), this is of rare occurrence and is more likely the result of growth of particular cells rather than a parasitic strategy on the part of the infecting species. The absence of photosynthetic nutritional dependence is suggested in that the endophytic and endozoic species of *Audouinella* are provided with abundant phycoerythrin. In addition, these plants are easily isolated and cultured in the same media (e.g. the supplemented seawater medium of von Stosch 1964, consisting of inorganic nutrients and vitamin B_{12}) as other red algae. Thus, endophytic and endozoic *Audouinella* spp. may only be using the hosts as substrata in which to grow.

Since the first of these forms was described (as *Callithamnion membranaceum* Magnus 1875) approximately fifty additional species have been recorded in the literature. Most of these species are uniseriate, irregularly branched plants that reproduce by monosporangia. Other diagnostic features include cell size and shape, presence of tetrasporangia and pyrenoids, chloroplast morphology and identity of the host. The last of these has been considered among the most important (see Drew 1928); new taxa have been described on the basis of minor morphological variations as long as plants were found in different hosts. To give some examples there are two species of *Audouinella* from two species of *Bonnemaisonia* and specific endophytes have been reported from species in the genera *Gastroclonium, Polyides, Heterosiphonia, Polysiphonia, Desmarestia* and *Liagora*. With regard to endozoic forms, host specificity is regarded to be less important, and most of the species are known from hydroids, sponges as well as bryozoa. On the basis of comparative morphology, host specificity was questioned by Woelkerling (1971) and Dixon & Irvine (1977),

Table 1. Sources of isolates used in the investigation.

Species	Isolate	Host	Collection site and date
Audouinella asparagopsis	AA	endozoic in hydroids	Rhosneigr, Anglesey, U.K.; 9.5.1976
Do.	N2	on and in *Membranoptera alata*	Port Erin, Isle of Man; 11.8.1976
Do.	S2	on and in *Nemalion helminthoides*	Port St. Mary, Isle of Man; 12.8.1976
A. bonnemaisoniae	Z	in *Bonnemaisonia hamifera*	Trearddur Bay, Anglesey, U.K.; 8.5.1976
A. endophytica	G2	in *Heterosiphonia plumosa*	Port St. Mary, Isle of Man; 14.7.1976
A. tetraspora	FF	in *Bonnemaisonia asparagoides*	Osund, Hordaland, Norway; 5.9.1975
Antithamnion spirographidis			Dorset, England; 8.1977
Ceramium rubrum			Trearddur Bay, Anglesey, U.K.; 1.1976

and possible synonymy was suggested for a number of taxa. However, White & Boney (1969) suggested that before two taxa can be considered conspecific, not only must they have the same morphology when grown in unialgal culture, but the hosts must also be cultured and cross-infection accomplished.

In the absence of any photosynthetic nutritional dependence, host specificity can only rest on characteristics that enable the infecting alga to penetrate one or at least only a limited number of host species. If these characteristics can be shown not to be critical taxonomic features (at least regarding the *Audouinella* spp.) then the systematics of the group could be revised with many specific epithets relegated to synonomy. With these considerations in mind, experiments were carried out to ascertain (a) the degree to which endophytic and endozoic isolates could penetrate two 'non-host' species, and (b) the influence of host identity on the morphology of the plants growing within it.

Material and methods

Six endophytic and endozoic isolates, representing four species of *Audouinella* were isolated from the places and hosts indicated in Table 1. Unialgal cultures were established using a similar technique to that described by White & Boney (1969, 1970). Cultures of *Ceramium rubrum* and *Antithamnion spirographidis* (see Table 1 for sources of isolates) were obtained by the excision and transfer of unepiphytized apical fragments to fresh medium. All algae were initially grown in the medium of von Stosch (1964) for periods of up to eighteen months, although experiments were carried out in Provasoli's (1968) ES medium. For the first month isolates were incubated with GeO_2 (5 mg/l) to discourage the growth of diatoms.

For experiments, plants of *Audouinella* spp. were inoculated into 100 ml conical flasks or crystallizing dishes, in which fragments of the alternate host (either *Ceramium* or *Antithamnion*) were placed for regeneration. Cultures were maintained at 15°C under continuous light, with an illumination of 400–500 lx provided by Osram daylight fluorescent tubes. To increase contact between the pairs of species, culture vessels were agitated each day for ten seconds during the first week and then sporadically for the duration of incubation. Medium was replenished after an initial two week period and then at weekly intervals. Fragments of the host plants were given a preliminary examination after two weeks and all plants were harvested after five weeks.

The nomenclature of Parke & Dixon (1976) is followed, except that *Audouinella tetraspora* is a new species to be described elsewhere (Garbary & Rueness in prep.).

Results

After five weeks of incubation all isolates established some degree of relationship with one or both of the offered hosts ranging from merely becoming entangled to true endophytic growth. This was primarily in association with *Ceramium rubrum,* and only *Audouinella endophytica* colonized the thallus of *Antithamnion.*

Audouinella bonnemaisoniae developed solely as an epiphyte on *Ceramium rubrum* and only rarely branches were able to attach and grow along the surface of the host. The absence of further development is attributed to the lack of sporulation on the part of the isolate due to its poor growth in suboptimal conditions. *A. asparagopsis* (isolate S2) showed slight sporulation and spores were able to settle and germinate on thalli of *Ceramium.* Considerable growth did not occur and epiphytic prostrate plants were small and uncommon. With longer incubation times further development might be expected.

More conspicuous, epiphytic prostrate growths occurred on the *Ceramium* plants with the remaining isolates. First, spores attached to the thallus and, with subsequent germination, the primary axis grew along the surface of the host with lateral branches often occurring. These growths were diffuse and mats of cells only began to develop with *Audouinella endophytica*. *A. tetraspora* was unique among these isolates being the only species in which upright axes developed from the prostrate base. A different epiphytic growth form was present on rhizoids of *Ceramium* and *Antithamnion* with all species except *A. bonnemaisoniae*, in that after spore germination the axis developed in a spiral around the rhizoid, occasionally resulting in a ring four or more cells wide. A similar growth was observed by White & Boney (1969) on the rhizoids of *Heterosiphonia plumosa* by its endophyte *Audouinella endophytica*. This habit was also produced when branches of free-living plants came into contact with rhizoids and may result from the adhesive nature of the rhizoid surface.

True endophytic growth among the cortical cells of *Ceramium* occurred with three isolates. These plants initially developed as described above for prostrate filaments, and with penetration of the surface by apical cells subsequent growth resulted in a proliferation of the endophyte around cortical cells of the host. Endophytic growths were also produced by another mechanism whereby the host was colonized in uncorticated or poorly corticated regions and the proliferating cortical cells covered the originally epiphytic *Audouinella*. None of the penetrating filaments appeared to damage the host and growth was limited to among cortical cells. The penetration of *A. asparagopsis* (N2, AA) was limited; extensive growths occurred only with *A. endophytica*. This may be attributed to a time factor inasmuch as *A. endophytica* grew faster with greater sporulation compared with the other isolates. In isolates of *A. asparagopsis* growth was primarily epiphytic with penetrating branches. This contrasts with *A. endophytica* in which endophytic growth was greater and occurred among the cortical cells of many nodes of the *Ceramium* host.

Audouinella endophytica was the only species to become endophytic in the cell walls of *Antithamnion* which occurred primarily in older cells at the base of plants. Penetration was only successful on the large segment cells of main axes and, within these cells, more often near the nodes where the cell wall was thicker (4–5 μm vs 2–4 μm towards the middle of the cell). Even at the nodes penetration often caused distortion in the cell wall that could be observed as slight swellings around the endophytic cells.

The absence of penetration into *Antithamnion* by the other species is regarded as a physical problem rather than a problem of host specificity resulting from some kind of biochemical incompatibility. The maximum diameter of cells of *A. spirographidis* in culture was about 60 μm, including a 2–5 μm cell wall. The isolates of *Audouinella* used in this study have cell diameters in the range 3–13 μm and unless endophytic filaments were to grow into the host cell protoplast, penetration cannot be carried out. Thus *Audouinella endophytica* with its small cell diameters (3–5 μm) was the only species that was physically able to penetrate the cell wall (other *Audouinella* species had larger cell diameters).

Morphological changes

Considerable morphological changes relating to cell size and shape were present in endophytic filaments compared with free-living material in the same cultures. Cells of free-living plants generally formed regular cylinders that were only slightly narrower at the ends. Branches originated at or near the apex of cells and generally did not markedly distort the cell outline. Endophytic cells were more varied, ranging from cylindrical to cigar-shaped to curved to irregular, the latter occurring primarily where branches developed. Branching was also more abundant in endophytic plants than in free-living material.

Host structure also modified cell dimensions of the endophytes in various ways that were characteristic for each host and penetrating species. Thus free-living cells of *Audouinella asparagopsis* associated with *Ceramium* were larger and more variable than endophytic counterparts (Table 2).

In *A. endophytica* associated with *Ceramium* cells were slightly longer than in free-living filaments. This contrasts with the absence of differences in cell length in the *A. endophytica*/

Table 2. Comparison of cell dimensions in free-living and endophytic plants of *Audouinella asparagopsis* and *A. endophytica*. Values (in μm) indicate means $\pm$ standard deviations. ** $p < 0.05$, * $0.05 < p < 0.10$.

Endophyte	Cell dimension	Free-living	Host	Endophytic	df	Significance
A. asparagopsis	Length	16.8 $\pm$ 2.3	*Ceramium*	12.7 $\pm$ 2.0	43	**
	Diameter	4.8 $\pm$ 2.2		4.6 $\pm$ 0.8	43	ns
A. endophytica	Length	8.2 $\pm$ 0.7	*Ceramium*	8.9 $\pm$ 2.2	42	*
	Diameter	3.5 $\pm$ 0.2		3.6 $\pm$ 0.7	42	ns
	Length	8.2 $\pm$ 0.7	*Antithamnion*	8.2 $\pm$ 0.8	22	ns
	Diameter	3.5 $\pm$ 0.2		4.7 $\pm$ 0.5	22	**

Antithamnion association. However, in the same association there were definite differences in cell diameter between free-living and endophytic cells (Table 2). Thus not only was the general appearance of *Audouinella endophytica* changed when growing endophytically, but the structure of the two hosts caused different modifications of cell morphology to occur.

Discussion

In previous experiments (White & Boney 1969) in which a variety of plant and animal substrata were offered as hosts to three endophytic and endozoic species of *Audouinella,* the results were different from those obtained in this study. Other than the penetration of *Heterosiphonia plumosa* by its normal endophyte *A. endophytica,* none of the *Audouinella* spp. was successful in penetrating any of the six algae that were offered. *A. endophytica,* however, turned out to be quite non-selective in its choice of hosts since penetration of mollusc and egg shells also occurred.

In this study, the penetration of *Ceramium rubrum* and *Antithamnion spirographidis* by both endophytic and endozoic isolates extends the results found above. Thus not only can endophytic isolates penetrate animal substrata and vice versa, but *Audouinella* can also be induced to grow in *A. spirographidis,* from which it was not previously reported. This is not entirely surprising inasmuch as examination of British algae over a two-year period has revealed acrochaetioid algae in a number of genera, including *Gracilaria* (pers. comm. W. Farnham), *Chylocladia, Laurencia, Callithamnion* and *Griffithsia* for which there are no published records of endophytic *Audouinella* spp.

The cross infection of endophytic and endozoic species into non-original hosts and the changes in morphology of the infecting filaments raises considerable problems for the identification and characterization of these algae. In most keys, the characteristic 'in plants' versus 'in animals' occurs as a principal dichotomy. The doubts raised concerning the importance of host specificity make meaningful identification difficult, and make the presently accepted species concepts for these organisms untenable. This problem can only be resolved by means of culture studies in which a detailed morphological examination is made of isolates under standard conditions from a large number of hosts. Thus taxa must initially be defined in culture before proper identification can be carried out. That the nature of the substratum can influence the morphology of *Audouinella* spp. has also been found in an epizoic species. West (1970) demonstrated that in culture *A. concrescens* only formed the characteristic morphology of its basal system when growing on chitinous substrata, on which it is found in nature. However, the taxonomic implications of this observation have not been examined.

White & Boney (1969) suggested that cross-infection of corresponding hosts must be carried out before two morphologically 'identical' algae (in culture) can be synonymized. This is too rigorous a species definition for the Florideophyceae where even some sexually reproducing isolates that cannot interbreed can be accommodated within the same species (Rueness 1978). This is especially so in light of the lack of dependence for particular substrata by all *Audouinella* spp. that have been examined for growth and reproduction. Even if such 'behavioural' differences do occur, where morphologies are similar, I do

not consider that host specificity should be utilized for specific delimitation. On the other hand, such differences, especially if they can be related to geographical isolation or ecological specialization, might indicate active speciation. An alternative hypothesis, viz. that such plants are derived from different ancestors needs also be considered, as delimitation of species in the Acrochaetiaceae rests on relatively few characteristics and similar morphologies can be the result of convergent or parallel evolution (Garbary 1978 a). Elimination of these hypotheses cannot be made using arguments from morphology at the light microscope level, although additional evidence of a biochemical (e.g. Richardson & Mallery 1973) or ultrastructural nature might help resolve such problems. The application of scanning electron microscopy for species characterization in the Acrochaetiaceae is a step in this direction (Garbary 1978 b). In conclusion, if morphology is to be the prime or only source of data for species delimitation, it is important that the endophytic and endozoic members of the Acrochaetiaceae be compared on the basis of cultured material, and that species concepts be adapted to this approach.

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A new species of Godronia (Helotiales) from India

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Sharma, M. P. & Thind, K. S. 1979 11 15: A new species of Godronia from India. *Bot. Notiser 132:* 457–458. Stockholm. ISSN 0006-8195.

Godronia alpina Sharma & Thind, sp. nov. is described from high altitudes of the Himalayas. The genus is new to India.

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The genus *Godronia,* monographed by Groves (1965), is herewith reported for the first time from India. The material turned out to belong to a new species, which is described below. The description is made up from living material, supplemented with dried specimens and material preserved in alcohol-formalin. Measurements and observations were made in KOH-phloxine-glycerine and cotton blue.

Godronia alpina Sharma & Thind, sp. nov.

Orig. coll.: India, Jammu & Kashmir, Khillanmarg, on dead stem of an angiosperm, 3600 m, 18.8.1974 M. P. Sharma 11238 (PAN holotype, TAA isotype).

Ascocarpi erumpentes, pergregarii, usque 2.5 mm diam. et usque 2 mm alti, lenti, profunde cupulati vel urceolati, distincte stipitati, a textu stromatico atrato ad fundum emergentes, externe atro-brunnei vel paene nigri et ex pilis gelatinosis longe etiolatis asperati; pili usque 4 μm lati, luteoli, muris crassis atque extremitatibus obtusis praediti; hymenii superficies vive luteobrunnea, siccitate nigrescens; margo integer sed fimbriatus, siccitate fortiter involvens et humide expandens. Stipes usque 1.5×1 mm, cylindratus, asperatus, niger. *Asci* 108–140(–147)×5–7.5 μm, clavati-cylindrati, 8-spori, apicibus rotundatis, in basin longam stipitiformem (utsi pede expansi) gradatim contracti. *Sporae* 9–14×3–4.5 μm, uniseriales, ellipsoideae usque subclavatae, hyalinae, muris tenuibus, leves, regulariter 1-septatae, aguttulatae. *Paraphyses* usque 1.5 μm latae, filiformes, hyalinae, muris tenuibus, leves, simplices, cum apicibus asci aequae.

Ascocarps up to 2.5 mm diam, up to 2 mm high, densely gregarious, erumpent, tough, deeply cupulate to urceolate, stipitate, arising from a basal stromatic blackish tissue; external surface dark brown to almost black, roughened due to the presence of gelatinized, strongly elongated hairs; hairs up to 4 μm wide, light yellow, thick-walled, with obtuse ends; hymenial surface yellowish-brown when fresh, becoming blackish on drying; smooth, margin entire but fimbriate, strongly infolded when dry, expanded when moist. *Stipe* up to 1.5×1 mm, cylindrical, roughened, black. *Asci* 108–140(–147)×5–7.5 μm, clavate-cylindrical, 8-spored, apices round, tapering below into a long stem-like part which is broadened at the very base. *Ascospores* 9–14×3–4.5 μm, uniseriate, ellipsoid to subclavate, hyaline, thin-walled, smooth, uniformly 1-septate, eguttulate, germinating after discharge. *Paraphyses* up to 1.5 μm wide, filiform, hyaline, thin-walled, smooth, simple, as long as the asci.

Anatomy. Ectal excipulum up to 105 μm thick, light yellow, of textura oblita, gelatinized, hyphae thick-walled with narrow or obliterated lumen, up to 4.2 μm wide, extending considerably at the margin to form teeth-like projections; medullary excipulum up to 72 μm thick, dark-brown, of textura angularis, cells thick-walled, up to 12×8.5 μm, becoming elongated at the

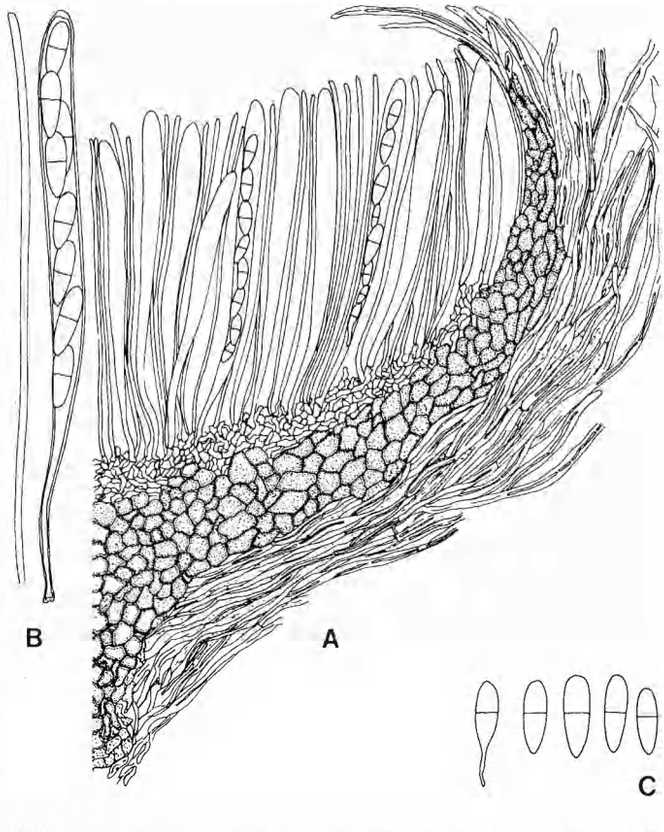

Fig. 1. *Godronia alpina*. – A: Vertical section through apothecium. ×240. – B: Ascus and paraphysis, ×600. – C: Ascospores (one is germinating), × 600.

margin; hypothecium up to 2 μm wide. Stipe differentiated into cortex and medulla; cortex of textura prismatica, cells thin-walled, hyaline; medulla of textura intricata, hyphae narrow, thin-walled, up to 2.2 μm wide.

This species is characterized by large, hairy, cupulate or urceolate apothecia, long asci with 1-septate, ellipsoid to subclavate spores arranged in one row, and filiform paraphyses. *Godronia symphoricarpi* Groves is similar but differs in having smaller asci and in growing on a different substrate. *G. lobata* (Cash) Seaver, also related, differs in having larger ascospores, smaller apothecia and in occurring on *Ribes menziesii* Pursh.

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Two new species of Pezizales from India

K. S. Thind and S. C. Kaushal

Thind, K. S. & Kaushal, S. C. 1979 11 15: Two new species of Pezizales from India. *Bot. Notiser 132:* 459–461. Stockholm. ISSN 0006-8195.

Two new species from W Himalaya are described, viz. *Melastiza flavida* and *Leucoscypha subimmersa*. A previous report of *Melastiza chateri* from India is incorrect.

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During research on the genera *Melastiza* Boud. and *Leucoscypha* Boud. we have come across two new species, which are described here. Moreover, on reinvestigation it was found that the report of *Melastiza chateri* (W. G. Smith) Boud. from India (Thind & Waraitch 1964) was based on specimens of *M. rubra* (Batra) Maas Geest., which is fairly common in NW Himalaya.

Melastiza flavida Thind & Kaushal, sp. nov. – Fig. 1 A–C

Holotype: India, Mussoorie, Dhanaulty, on soil, 7.9.1973, Kaushal 2581 (PAN).

Apothecia ad 3 mm diam. gregaria vel congesta, sessilia, discoidea, ordinata, mollia, carnosa; externa superficies subochracea, sensim pilosa; pili subfusci, appressi, ad 7.5 μm in diam.; hyphae affixae ad basim, subhyalinae, tenuitunicatae, ad 13 μm in diam.; margo integer; hymenium flavopallidum, glabrum. Asci 240–280 × 14–18 μm, octosporei, cylindracei, apex obtusus, jodo non caerulescentes. Ascosporae 22–27 × 12–16(–17) μm reticulis inclusis, hyalinae, uniseriatae, ellipsoideae vel late ellipsoideae. Paraphyses ad 4 μm latae infra et 7.5 μm in apicibus clavatis, rectae, septatae, simplices. – Excipulum ectale ad 55 μm crassum, textura angularis, subfuscum, cellae ad 30 × 15 μm; excipulum medullare textura dense intricata, hyphis ad 6.5 μm diam; hypothecium indistinctum.

Apothecia up to 3 mm in diam, gregarious to crowded, sessile, discoid, regular, soft, fleshy; external surface ochraceous, minutely pruinose, with inconspicuous pale brown, appressed hairs, hairs up to 7.5 μm wide; attaching hyphae present towards base, subhyaline, thin-walled, up to 13 μm wide; margin entire; hymenium light yellow, smooth. Asci 240–280 × 14–18 μm, 8-spored, cylindrical, apices obtuse, I–. Ascospores 16–18(–19) × 11–12 μm excluding ornamentation and 22–27 × 12–16(–17) μm including ornamentation, hyaline, uniseriate, ellipsoid to broadly ellipsoid; ornamentation consisting of rounded warts connected by thick or thin ridges to form a regular or irregular reticulum with meshes up to 5 μm across, warts usually larger at poles (up to 4 μm) than elsewhere (up to 2.5 μm). Paraphyses clavate, up to 4 μm wide below and 7.5 μm at the tip, slender, straight, septate, simple.

Anatomy. Ectal excipulum up to 55 μm thick, textura angularis of somewhat horizontally elongated cells, cell walls of outer few layers pale brown, clothed with a few inconspicuous pale brown appressed hairs (hairs as described above), cells up to 30 × 15 μm; medullary excipulum of dense textura intricata, hyphae up to 6.5 μm; hypothecium indistinct.

This species has a very characteristic spore ornamentation somewhat similar to that of *M. flavorubens* (Rehm) Pfister & Korf, which, however, differs in having much smaller ascospores (14–19 × 8–9.5 μm including ornamentation),

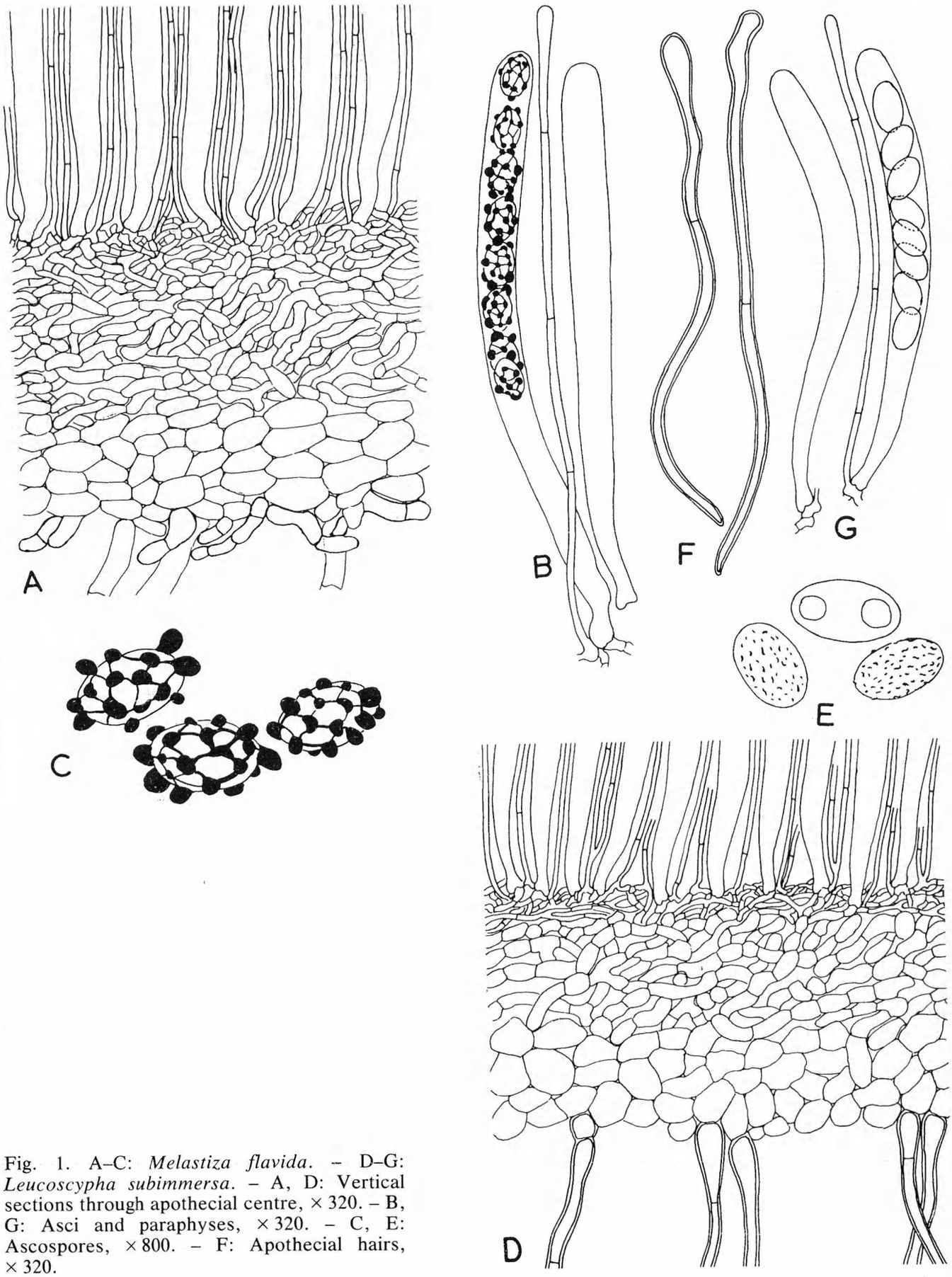

Fig. 1. A–C: *Melastiza flavida*. – D–G: *Leucoscypha subimmersa*. – A, D: Vertical sections through apothecial centre, × 320. – B, G: Asci and paraphyses, × 320. – C, E: Ascospores, × 800. – F: Apothecial hairs, × 320.

larger apothecia (3–6 mm) and a different colour of the hymenium (grey-red with a pinkish tinge).

Leucoscypha subimmersa Thind & Kaushal, sp. nov. – Fig. 1 D–G

Holotype: India, Dehra Dun, on soil in tropical forest, 10.9.1973, Kaushal 2583 (PAN).

Apothecia ad 2.5 mm diam, sparsa vel gregaria, sessilia, subimmersa, initio clausum, denique patellatum, discus discoideus; externa superficies subfusca, extra strigosa, pili ad 350(–500)× 6 μm, hyalini, recti vel subrecti, parce septati, crassitunicati, tunica ad 1.5 μm crassa, basis simplex vel parce bulbosa, apices obtusi; margo integer, fimbriatus capillis; hymenium flavopallidum. Asci 175–210× 10.5–16.5 μm, octosporei, cylindracei, jodo non caerulescentes. Ascosporae 15–20× 10–13(–15) μm, ample ellipsoideae, uniseriatae, hyalinae, verrucosae, biguttulatae. Paraphyses ad 2 μm amplae infra et ad 3.5(–5) μm in apicibus, parce septatae, simplices vel furcatae infra. – Excipulum ectale ad 60 μm crassum, textura angularis, cellulis 30× 17 μm; excipulum medullare ad 65 μm crassum; textura intricata, hyphis ad 9 μm amplae; hypothecium ad 12 μm crassum; textura dense intricata.

Apothecia up to 2.5 mm in diameter, scattered to gregarious, sessile, somewhat immersed in soil, closed at first, later opening, shallowly cupulate, soft, fleshy; external surface light brown, densely hairy; hairs up to 350(–500)× 6 μm, hyaline, flexuous or straight, denser and forming a fringe around the margin, sparsely septate, thick-walled, wall up to 1.5 μm thick, basal cell simple or slightly swollen, apex obtuse; margin entire, fringed with hairs; hymenium pale yellow, fading on drying. Asci 175–210× 10.5–16.5 μm, 8-spored, cylindrical, apex obtuse, base narrow, I–. Ascospores 15–20× 10–13(–15) μm, broadly ellipsoid, rarely subglobose, uniseriate, hyaline, warted, biguttulate. Paraphyses up to 2.0 μm wide below, up to 3.5(–5) μm apically, slender, straight, sparsely septate, simple or branched below.

Anatomy. Ectal excipulum up to 60 μm thick, textura angularis of irregular cells, cells 30× 17 μm, thin-walled; medullary excipulum to 65 μm thick, textura intricata of compactly arranged, short-celled hyphae, hyphae up to 9 μm wide; hypothecium very narrow, up to 12 μm thick, of dense textura intricata.

Leucoscypha subimmersa has small, pale yellow apothecia somewhat immersed on bare soil, and minutely warted, broadly ellipsoid ascospores. In spore ornamentation it is close to *L. alpestris* (Sommerf.) Eckbl. which, however, differs in having much smaller ascospores (13–16× 7.5–9 μm), bright orange apothecia, and finally 4-spored asci. It grows in the leaf axils of *Tetraplodon*.

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New species of Iridaceae from Galápagos and Colombia

Pierfelice Ravenna

Ravenna, P. 1979 11 15: New species of Iridaceae from Galápagos and Colombia. *Bot. Notiser 132:* 463–466. Stockholm. ISSN 0006-8195.

Sisyrinchium galapagense Ravenna is a new species endemic to the Galápagos Islands. It has previously been misidentified as *S. macrocephalum* R. Graham from eastern S America. Suggested relatives are *S. arizonicum* Rothrock and *S. convolutum* Nocca. The new species *Hesperoxiphion huilense* Ravenna from Colombia represents a considerable range extension for the genus, previously known from the Andes of Peru and Bolivia. A key to the species of *Hesperoxiphion* is provided.

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Sisyrinchium galapagense Ravenna, sp. nov. – Fig. 1

Orig. coll.: Adsersen 980 (C holotype and isotype).

Planta caespitosa perennis 15–36 cm alta. *Rhizoma* verticalis usque 30–75 mm longus 10–13 mm latus radicibus pluribus fibrosis emittens et fibris foliorum vetustorum valde obtectus. *Folia basalia* plura lineari-attenuata suberecta vel ascendentia 23–30 cm longa 4–11 mm lata sublaxe nervosa. *Caulis* ancipiti-alatus foliatus ramosus internodio inferiori c. 14.5 cm longus et 5–6.5 mm latus. *Folium caulinum* inferius usque 14–17 cm longum caetera apicem inflorescentiae versus gradate reducta. *Spathae* plures ad lateras compressae 3–12-florae 20–24 mm longae valvis subaequalibus vel leviter subaequilongis. Flores exserti pedicellati lutei. *Pedicelli* filiformes 15–20 mm longi. *Ovarium* obovatum glabrum ad 2.4 mm longum c. 1 mm latum. *Perigonium* late infundibulatum ad 16 mm latum. *Tepala* late oblanceolata castaneo-nervata usque 1 mm ad basin connata, exteriora 9–9.4 mm longa c. 3.5 mm lata, interiora subaequalia. *Filamenta* usque basin libera tenuissime filiformia apicem versus leviter clavata ad 5.4 mm longa. *Antherae* basifixae oblongae luteae inferne bilobatae 2–2.4 mm longae ad dehiscentiam provectam versatiles probabiliter minores. *Stylus* tenuis filiformis usque 6.5 mm longus apicem versus leviter ampliatus. Styli rami erecto-patentes 0.2–0.25 mm longi ad apicem stigmatosi. *Capsula* late elliptica 5–6 mm longa 3.5–4 mm lata. *Semina* subglobosa vel late ovata in regio hyli leviter acuta nigra minute foveolata c. 1 mm lata.

Sisyrinchium galapagense seems to be rather unrelated with the continental species. It has perhaps affinities with *S. arizonicum* Rothrock (Arizona, Mexico, C America, possibly Colombia) and *S. convolutum* Nocca (Mexico, Guatemala), which both have a similar inflorescence. However, they are vivaceous, rather small, have very short rhizomes and therefore do not form clumps. *S. convolutum* agrees with *S. galapagense* in having free filaments.

Porter (1971) includes this species in "Flora of the Galápagos Islands" under the name *S. macrocephalum* R. Graham, a very different species from S Brazil, Uruguay and C Argentina. The species is also, incorrectly, cited from Peru and Colombia. His description is rather conflicting and it contains features from both *S. galapagense* and *S. macrocephalum*. The figure, however, agrees completely with the Galápagos plant. The main characters separating *S. galapagense* and *S. macrocephalum* are given in Table 1.

Distribution and habitat. Only known from the Galápagos Islands. Montane; collected between 600 and 850 m. According to Porter (1971) the species occurs in swamps, meadows, on sand, and on rocky hillsides.

Collections. Santa Cruz, 1 km W of Puntudo, 700 m, montane "pampas", 4.10.1974, Adsersen 980 (C) – Los Huecos, Santa Rosa, 600 m, 7.2.1974, Adsersen

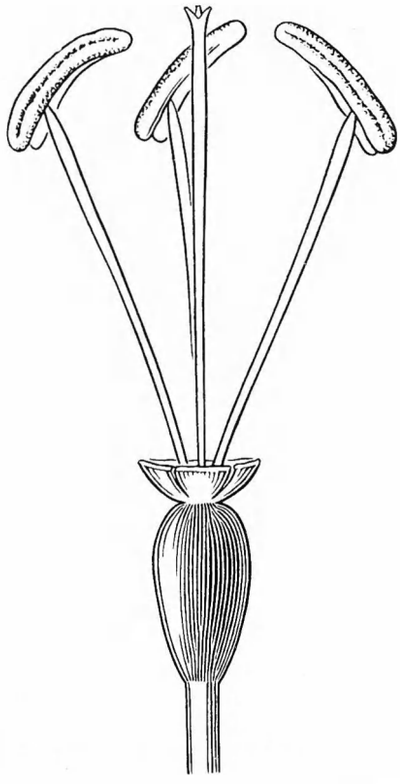

Fig. 1. *Sisyrinchium galapagense*. Androecium and gynoecium (× 7.5). Drawing by P. Ravenna.

1302 (C) – N slope of Mt Crocker, 750 m, in open areas between ferns, 2.3.1972 Hamann 538 (C) – s.loc., 27.2.1939, Taylor & Taylor G-55 (NY, K) – *Isabela,* Cerro Azul, S–SW slope, 800 m, occasional in open "pampas", 26.1.1972, Hamann 2366 (C).

Hesperoxiphion huilense Ravenna, sp. nov. – Fig. 2

Orig. coll.: Ravenna 2187 (herb. Ravenna holotype, COL isotype).

Planta sempervirens usque 26–48 cm alta (ad apicem inflorescentiae). *Bulbus* ovatus 25–28 mm longus 18–23 mm latus. *Folia basalia* ad anthesin 2–5 late oblanceolata plicata viridia glaucescentia erecta vel laxe recurva 30–82 cm longa 22–40 mm lata inferne in vagina 10–24 cm longa angustata. *Caulis* teres. *Folia caulina* dua inferius basalibus simile 20–69 cm longum superius bracteiforme 4–14 cm longum. *Spathae* usque duae pedunculatae 3–4-florae 16–25 mm longae valvis subaequalibus vel leviter inaequilongis. *Pedicelli* floriferi in spatha inclusi 14–26 mm longi. *Ovarium* ovato-clavatum pallide viride 4.8–5 mm longum 2.5–2.8 mm latum. *Perigonium* praecipue album 31.5–45 mm latum. *Tepala exteriora* late oblanceolata vel obovata 19–26 mm longa 9–17(–18) mm lata inferne macula obovato-triangularis fusco-ochraceo-purpurea c. 4.8 mm longa et 3.2 mm lata dense pubescens haud glandulosa et saepe punctis violaceis suffusa; lamina alba modice reflexa. *Tepala interiora* geniculato-recurvata 9.5–11 mm longa 4.6–5.8 mm lata; unguicula 7–8 mm longa pilosa prope basin maculis castaneis ad medium maculis transversis ad lateras punctis castaneis et luteo-ochraceis; lamina in fundo alba macula ovato-oblonga castanea ad basin area 1.8–2 mm longa glandulis oblongis densis (elaiophora) lutescentibus deinde dense pilosa ad lateras maculis et striis transversis luteo-castaneis et castaneis notata in summo minute penicillata. *Filamenta* tenuia albicantia ad basin purpurea incrassata. *Antherae* ovato-oblongae connectivo lato ad 2.3 mm longae c. 1.2 mm latae; pollen loculique olivacei. *Styli rami* dilute ochraceo-lutescentes ad 1.4 mm longi inferne c. 0.9 mm concrescentes; cristae tres vel subnullae albae, abaxial 0.5 mm longa abaxiales crenulatae c. 0.7 mm longae. Replicaturae stigmatosae laterales parvae. *Capsula* obovata 14–20 mm longa 8–11 mm lata cycatricis perigonii lata. *Semina* obovato-angulata ruguloso-foveolata ochracea 2–2.4 mm longa.

Reasons for reinstating the genus *Hesperoxiphion* Baker were recently given (Ravenna 1977). The main characters which distinguish it from *Cypella* Herb. are the inflorescence morphology, the several-flowered spathe having subequal valves, and the hirsute or densely pubescent blade of the inner tepals. Up to now,

Table 1. Main differences between *Sisyrinchium macrocephalum* and *S. galapagense*.

Character	*S. macrocephalum*	*S. galapagense*
Stem	scapiform	repeatedly branched
Cauline leaves	single, apical, reduced	several, lower one similar in length to basal ones, upper ones gradually shorter
Inflorescence	pseudolateral, congested, fasciculate, at the top of the stem	branches spread out along the stem
Spathes	sessile or subsessile	long-pedunculate
Filaments	connate below	free to the base
Style arms	longer than style	shorter than style

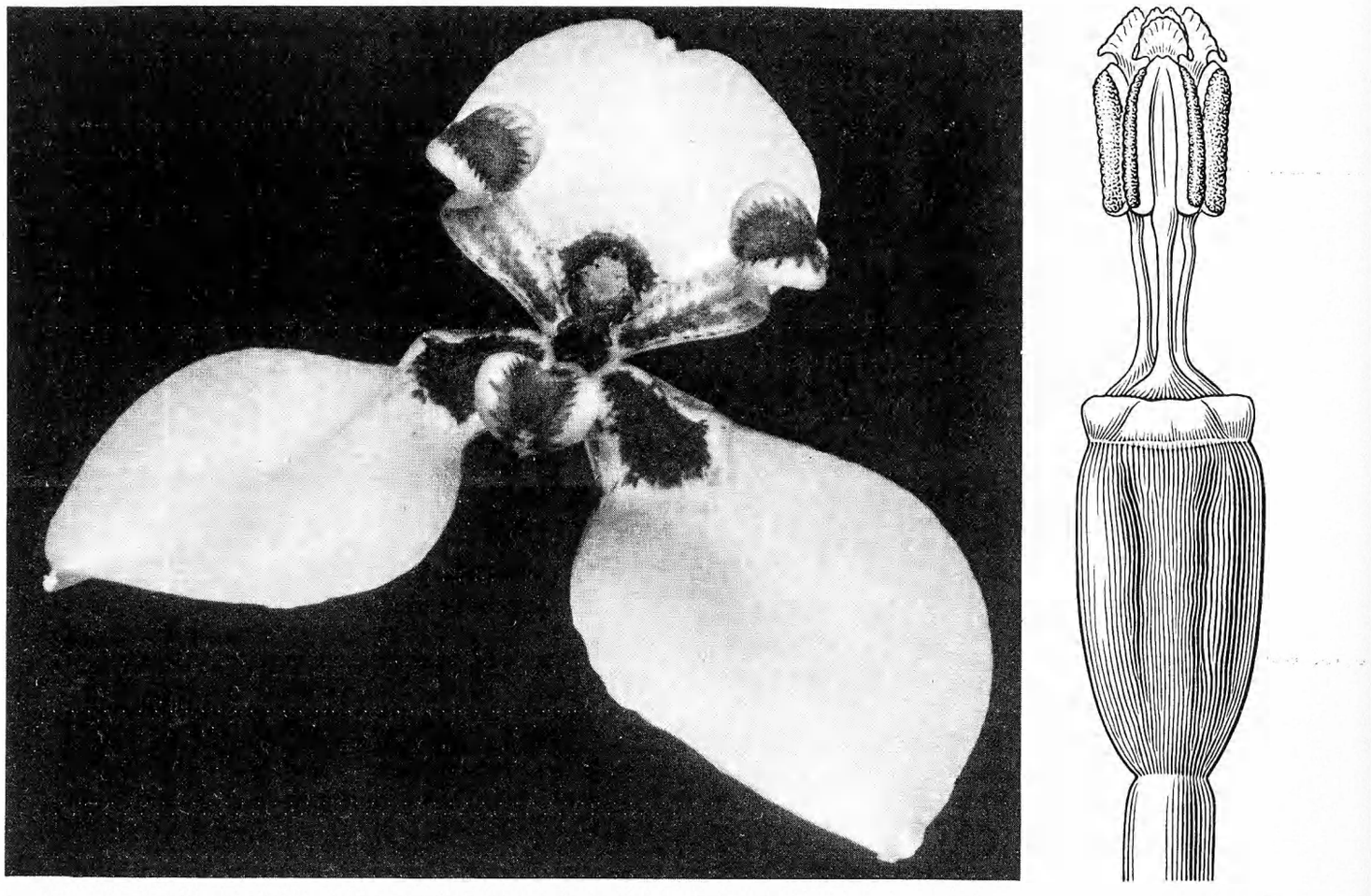

Fig. 2. *Hesperoxiphion huilense*. Flower (left); androecium and gynoecium (× 7; right). Drawing and photo by P. Ravenna.

four species have been known, all from the Andes of Peru and Bolivia. The species described here extends the range of the genus to the SE Andes of Colombia, where it grows in a very different habitat. A key to the species is given below.

Hesperoxiphion huilense is easily distinguished from the other species of *Hesperoxiphion* by the broad, almost ovate anthers, by the very short to nearly obsolete crests of the style arms, and by the evergreen leaves. Although the growth ceases for some time after fructification, there is no period of rest.

Only two species of Iridaceae-Tigridieae are previously known from Colombia, viz. *Cipura paludosa* Aubl. and *Larentia linearis* (H.B.K.) Klatt.

Habitat. Hesperoxiphion huilense grows in a secondary, fire-produced vegetation, which probably originated from a low open wood. Associated plants are *Dryopteris* sp., *Equisetum bogotense, Grammitis* aff. *bonariensis,* an undescribed species of *Hagenbachia, Hydrocotyle bonplandii, Selaginella* sp., *Solanum* sp., *Stellaria* sp.; *Cyperus eragrostis* (introduced), a grass allied to *Echinochloa*. There were also dense tufts of a species of *Setaria* 2–3 m high, and several woody species, which were, however, not identified.

The species is in urgent need of protection. It grows in a very restricted area which is strongly affected by the activities of the local inhabitants. Trees are felled or the vegetation is put on fire in order to make paths. As a result erosion has started. The region will probably be developed into coffee plantations. The writer has carefully transferred plants to less disturbed parts of the ravine. A few plants are grown in Santiago for seed production and for experimental purposes. The showy leaves and pretty, although small flowers make the species horticulturally valuable.

Collections. Colombia, dept. El Huila, c. 5 km W of Resina, S side of ravine, c. 1700 m (75°42′10″W,

1°54′22″N), 7.1976 Ravenna 2187 – Resina, 11.6.1956 Vogel 197 (B).

Key to the species of Hesperoxiphion

1. Anthers linear-oblong. Vivaceous 2
– Anthers ovate-oblong. Evergreen *H. huilense* Rav.
2. Blade of the inner tepals with a white, yellow, or white and yellow, hirsute central band 3
– Blade of the inner tepals with a brown, velvety pubescent area ..... *H. pardale* (Rav.) Rav.
3. Blade of the outer tepals yellow to orange, or white 4
– Blade of the outer tepals deep blue .... *H. herrerae* (Diels ex R. C. Fost.) Rav.
4. Blade of the outer tepals yellow to orange. Perigone 5–7(–8) cm across ..... *H. peruvianum* Bak.
– Blade of the outer tepals snow white. Perigone 3–3.5 cm across ..... *H. niveum* (Rav.) Rav.

Acknowledgements. My appreciation to Dr Ole Hamann, Copenhagen, who kindly sent good material of *Sisyrinchium galapagense* in flower and fruit, and also clarified some collecting data. Dr Stephan Vogel, Freie Universität Berlin, provided information that lead me to find *Hesperoxiphion huilense* in nature. Mr Thomas Karlsson helped with a photocopy of relevant pages in Wiggins & Porter's Flora.

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Ainea, a new genus of Iridaceae from Mexico

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Ravenna, P. 1979 11 15: Ainea, a new genus of Iridaceae from Mexico. *Bot. Notiser 132:* 467–469. Stockholm. ISSN 0006-8195.

A new genus, *Ainea,* is proposed to accommodate *Sphenostigma conzattii* R. C. Fost. The affinities are with the N American genera *Tigridia, Fosteria, Cardiostigma* and *Nemastylis* rather than with the S American *Gelasine* (including *Sphenostigma*). The species, which is only known from one population (near Oaxaca in S Mexico), has been studied in the field.

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Sphenostigma conzattii R. C. Foster (1950), from S Mexico, seemed an anomaly in the genus *Sphenostigma,* which is now considered a synonym of *Gelasine* Herb. (Ravenna 1977). For this reason, the type sheet ("camino Montelobos, de Nopalera a Huitzo", State of Oaxaca) was requested for study from F. The specimen was a very slender plant with a single flower at the top of a scapiform stem. The stamens and styles could be examined without dissection. The characters, particularly the morphology of the style-arms, indicated that the species had been improperly placed in *Sphenostigma;* a new genus was therefore suspected.

In June 1976 I visited Oaxaca to collect *Sphenostigma conzattii.* After several attempts in the area of Huitzo and northwards, a population was found in the region of Santiago-Tenango. Features displayed by living plants confirmed that the species represents a separate genus.

Ainea Ravenna, gen. nov.

Flos leviter zygomorphus cernuus. Ovarium obovatum glabrum. Tepala exteriora orbiculata vel obovata glabra obtusa vel acutiuscula. Tepala interiora exterioribus multo minora hastulata glabra lamina saepe in appendice longo arcte angustata. Filamenta libera tenuia. Antherae ante maturitatem lanceolatae ad lateras e fissura angusta dehiscentes connectivo lato post maturitatem circinatae. Stylus declinatus staminibus superans apicem versus gradate modiceque ampliatus. Styli rami usque medium bifidi. Stigmae sexapicales. Capsula obovata vel subclavata. Semina parva angulata.

Plantae bulbosae vivaceae exillimae. Bulbus tunicatus. Folia angustissime lineari-plicata. Caulis scapiformis ad apicem folio unico abbreviato spatha subtendenti instructus. Spatha unica sessilis bivalva pauciflora valvis convolutis. Pedicelli spathae breviores.

Monotypic: *Ainea conzattii* (R. C. Fost.) Ravenna.

Endemic in the hilly, wooded region c. 30 km NW of the town of Oaxaca in S Mexico. The generic epithet was taken from the Greek αινος meaning flattery, in the sense of being gratificant.

Generic relationships

The bulb, slenderness of the plant, scapiform stem, and spathe suggests *Cardiostigma,* particularly *C. longispatha* (Herb.) Bak.

Nodding flowers are otherwise found in the N American genera *Cardiostigma, Sessilanthera* and *Salpingostylis.* The perigone is slightly zygomorphic, as in *Cardiostigma* and *Salpingostylis.*

The outer tepals are orbicular and simple. The inner, much smaller ones are shortly unguiculate with yellow lateral areas and marked with black dots. They are either moderately or markedly

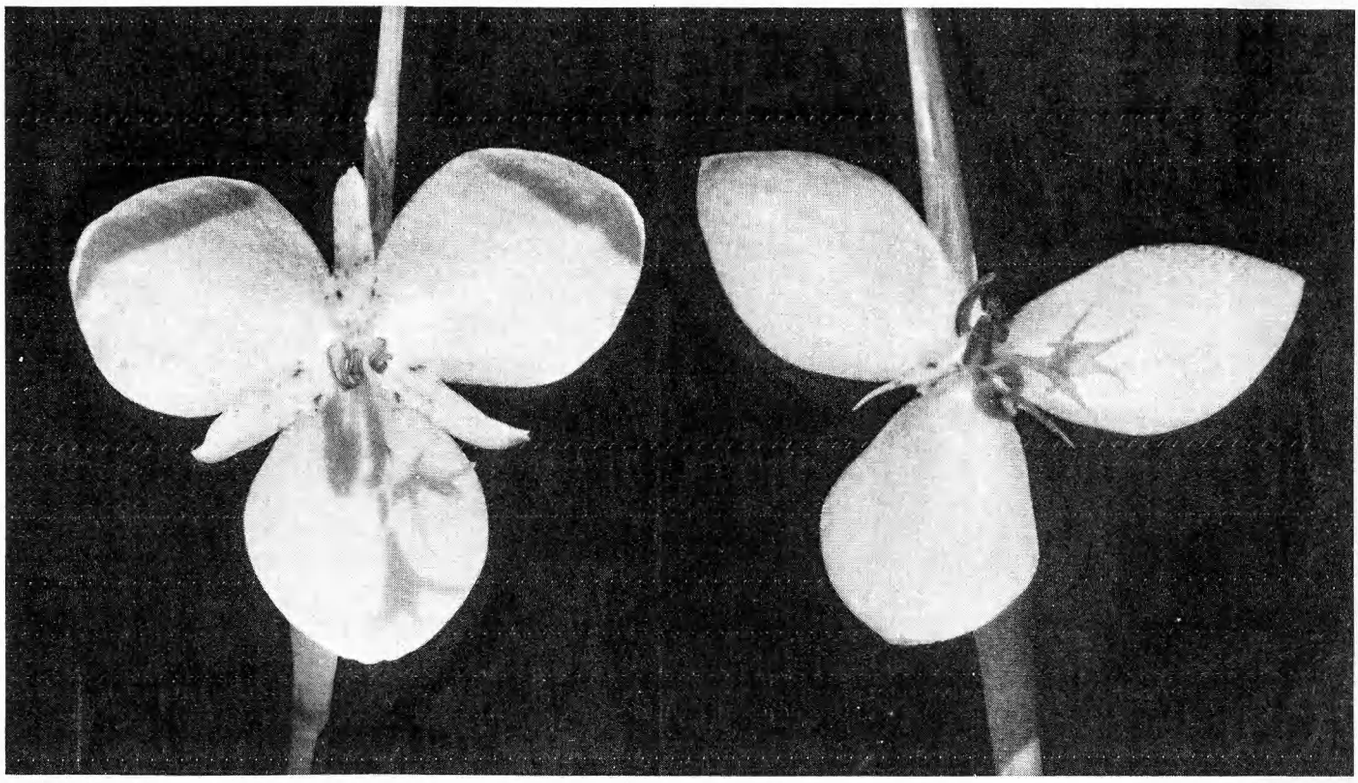

Fig. 1. *Ainea conzattii*. Two inflorescences, one of each flower type. Note difference in inner tepals. Photo by P. Ravenna.

narrowed for more than half of their length. Two rather different types are thus apparent. Although the shape and colouring of the tepals recall some species of *Tigridia,* the absence of glands (elaiophores) suggests a relationship with *Sessilanthera, Cardiostigma, Cobana* and *Nemastylis*. *Nemastylis convoluta* Rav. also shows a marked difference in size between inner and outer perigone segments.

The filaments are free, as in *Cardiostigma, Salpingostylis, Cobana,* and sometimes in *Nemastylis* and *Eustylis*. They are similar to those of *Cardiostigma*. Before dehiscence the anthers are lanceolate with a broad connective. As soon as the pollen is shed through the two very narrow, lateral slits, the anthers roll inwards, as in most *Nemastylis*.

The style is declined and longer than the stamens, as in *Cardiostigma*. The S American genus *Gelasine* (including *Sphenostigma*) which often has a long style, has very likely closer affinity to *Calydorea* than to *Cardiostigma* and the other exclusively N American genera mentioned.

In *Ainea* the style arms are deeply bifid with subulate stigmatic points, as in *Tigridia,* but in shape they resemble more closely those of certain *Nemastylis,* and differ substantially from the entire, cuneate style arms of *Cardiostigma* and *Gelasine*. Something of the aspect of the style and style arms of *Ainea* is to be seen in *Fosteria*.

From the features discussed, *Ainea* appears intermediate between *Tigridia* and *Fosteria* on one side and *Cardiostigma* and *Nemastylis* on the other.

Ainea conzattii (R. C. Fost.) Ravenna, comb. nov. – Fig. 1, 2

Basionym: *Sphenostigma conzattii* R. C. Foster, Contr. Gray Herb. Harv. Univ. 165: 106, 1950 – Orig. coll.: Conzatti 1904 (F holotype).

Plant 15–40 cm high. *Bulb* subglobose, sometimes producing a bulblet, up to 10 mm long and 9 mm wide, covered with many dark brown coats causing the bulb to seem larger (15–20 mm long, 12–18 mm wide); the coats prolonged upwards in a 5–7 cm long "neck." *Leaves* 3–5, narrowly linear, plicate, green, 10–20 cm long, 0.8–1 mm broad. *Stem* cylindrical, scapiform, 15–30 cm long, 1–1.2 mm broad, with a reduced stiff leaf subtending the spathe. *Spathe* terminal, sessile, 2–3-flowered, 20–25 mm long; valves

subequal, convolute, the outer embracing the inner. *Pedicel* shorter than the spathe. Flower cernuous. *Ovary* obovate-claviform, green, up to 2.3× 1.2 mm. *Perigone* 25–37 mm in diam. Outer tepals ovate or orbicular, white, glabrous, 14–21× 10–12.5 mm. Inner tepals hastulate, 6.5–9× 3–3.3 mm, narrowed below into a 0.6 mm long claw; the blade subcircular or rhomboid, marked by two lateral yellow areas and small blackish dots, moderately or markedly narrowed above for much of its length; the narrowed portion often appendicular, 5–5.9 mm long. *Filaments* free, filiform, weak, yellowish, slightly broadened at the base, 2.6–2.7 mm long. *Anthers* lanceolate, up to 6.7 mm long before dehiscence, 1 mm broad, dehiscing laterally by narrow slits and becoming circinate; connective broad, orange-yellow; pollen orange. *Style* narrowly obconic, yellow, up to 12.8 mm long, 16–17 mm wide at the apex. Style arms spreading, yellow, 2.6–3.3 mm long, moderately thickened, bifid for 2–2.2 mm; the secondary branches subulate, apically with stigmatic areas. *Capsule* obovate to almost club-shaped, 6–7 mm long, shortly trivalvate. *Seeds* very small, angulate, dark-brown.

Habitat. Rare in hilly pine and oak woodland near Cienaguillas, in the region of Santiago Tenango, 2000 m, State of Oaxaca, Mexico.

The first attempts to find this species in its native habitat were unsuccessful, due mainly to the obscure locality data "Camino Montelobos" and "Nopalera" accompanying the type specimen.

Although nothing resembling these names seemed familiar to the inhabitants of Huitzo, a few aged men did remember an old trail which in the past connected Huitzo with Nochitlán. However, it was unlikely that traces of this path had persisted to the present.

After finding the species, a section of the Montelobos trail was recognized between Cienaguillas and Santiago-Tenango. An inhabitant of the former hamlet recalled that Nopalera was a place at the northern border of the Santiago-Tenango district. Thus Conzatti probably collected this species in the same area where I found it. As further exploration of the surrounding region revealed no additional population, *Ainea conzattii* is evidently a local endemic.

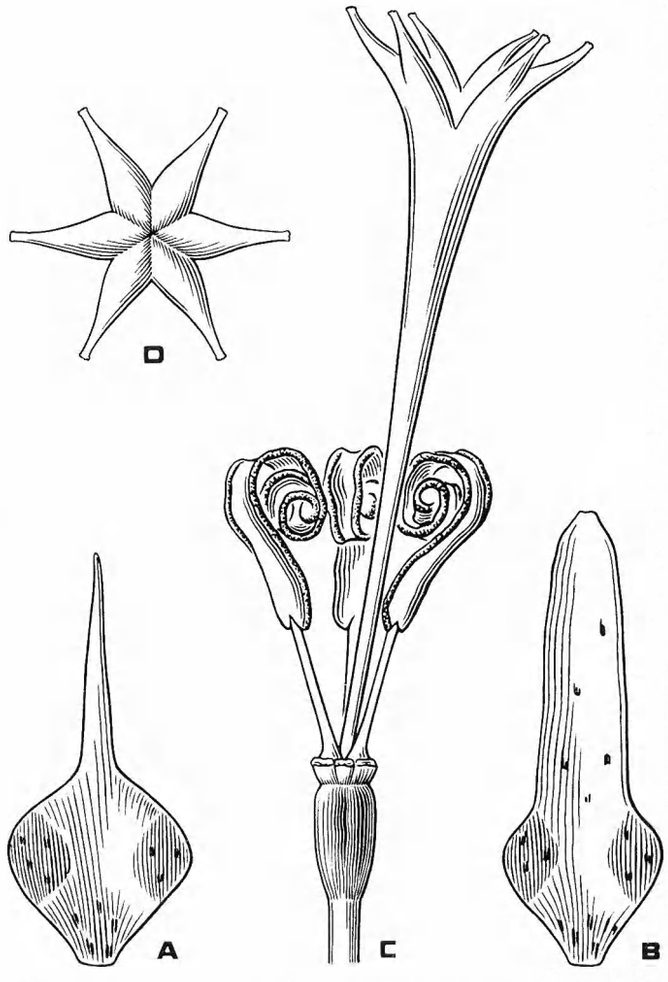

Fig. 2. *Ainea conzattii*. – A: Inner tepal, commonest type, × 6. – B: Inner tepal, less frequent shape, × 5. – C: Flower with tepals removed, × 5. – D: Style arms from above, × 5. – Drawings by P. Ravenna.

Collections. México, Oaxaca, Camino montelobos, de Nopalera a Huitzo, 23.6.1907, Conzatti 1904 (F) – Prope Cienaguillas ad viam Santiago-Tenango civit. Oaxaca Mexici, 6.1976, Ravenna 2171 (Herb. Rav., K, NY, MEXU).

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A new species of Centaurea from Mt Pangaion

Werner Greuter and Kostas Papanicolaou

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Centaurea pangaea sp. nova is described from Mt Pangaion in NE Greece. It is related to *C. parilica* Stoj. & Stef. from SW Bulgaria and N Greece, and also to *C. linifolia* L. and *C. hyssopifolia* Vahl from Spain. *C. pangaea* is a chasmophyte; the achenes lack a pappus. *C. parilica* var. *drenovskii* Stoj. does not deserve taxonomic recognition. The Macedonian calcareous mountains, to which both species of *Centaurea* are restricted, should be regarded as a distinct floristic province.

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Centaurea pangaea Greuter & Papanicolaou, sp. nova – Fig. 1

Typus: Greuter 16055 (B).

Differt a *Centaurea parilica* Stoj. & Stef., cui proxima, caulibus elatioribus dissitius foliatis saepe ramosis, surculis sterilibus foliosis florendi tempore obviis, capitulis subminoribus, imprimis autem appendicibus phyllorum involucri brevioribus, fimbriis paucioribus, et ovariis dense sericeo-pubescentibus epapposis.

Suffrutescent, densely tufted perennial with a woody taproot. *Innovations* basal, short, carrying an apical tuft of leaves and one to several herbaceous stems arising laterally from the axils of the previous year's leaves presumably in autumn (the lower cauline leaves being withered at flowering time). *Leaves* linear with a long (1–3 mm) subulate apex, 3-nerved, flat or with slightly revolute, entire margins, smooth, arachnoid-pubescent and with brilliant sessile glands especially below; those of the innovations 2–3.5 mm broad and up to 20 (–25) cm long; those of the stems 1–2 mm broad and up to 10 (–12) cm long. *Stems* 30–50 cm, arachnoid, flexuous, usually with up to 5 slender, partly sterile, partly fertile, simple side branches in their middle portion; internodes (8–) 10–20 mm long except near the base and apex where they are shorter. *Capitula* solitary at the end of the stems and main branches, subtended by the crowded uppermost leaves, 13–16 mm long, ovoid to broadly cylindrical with a rounded base. *Involucral bracts* with an ovate-lanceolate green base which is glabrous on the back and arachnoid-pubescent on the margins, and an apical, long-subulate, recurved appendage straw-coloured outside, light purplish-brown inside, shortly and stiffly barbellate all round and also on its pectinately arranged, slender fimbriae; the best developed appendages (of middle bracts) 5–6 mm long, with 11–14 pairs of fimbriae. *Corollas* purplish pink; those of the marginal, sterile flowers slightly radiate, 20–25 mm long, divided for c. 1/3 into lanceolate, spreading segments; those of the fertile flowers 16–18 mm long, the limb equalling the tube and divided halfway into linear, upright segments. *Anther tube* c. 7 mm long, purplish pink, exceeding the corolla by 1.5–2.5 mm. *Ovary* densely sericeous-pubescent with forwardly directed hairs crowning the apex, but devoid of pappus. *Fruit* 3.5–4 mm long, puberulent.

Table 1. Comparison between *Centaurea pangaea* and *C. parilica*. The following specimens of the latter have been considered: "in rupestribus aridis calcareis m. Ali-botusch supra vicum Golešovo", 11.7.1920, N. Stojanoff (B isotype); "in pratis alpinis montis Ali-Botuš, loc. class.", 22.7.1930, V. Skřivánek (B; var. *parilica*); "m. Orvilos (Ali-Botuš), in glareosis calcareis apricis lateris meridionalis et austro-occidentalis", 21.8.1978, Greuter 16673 (ATH, B, C, herb. Greuter, UPA, etc.).

Character	*C. pangaea*	*C. parilica*
Sterile monopodial innovations	present at flowering time	absent at flowering time
Stems	30–50 cm, branched	5–30 cm, simple
Middle internodes	(8–)10–20 mm	1–5(–7) mm
Indumentum	arachnoid only	arachnoid and often ± scabrid
Stem leaves	entire, 3-nerved	entire or toothed, 1–3-nerved
Capitula	13–16 mm long	16–21 mm long
Middle bract appendages	5–6 mm long, with 11–14 pairs of fimbriae, discolorous	7–8 mm long, with 15–17 pairs of fimbriae, concolorous
Pappus	absent	1–2 mm long

Specimens seen: Greece, E. Makedonia, Mt Pangaion (Pangeo, Purnar dagh), Kara-Giol tepe, c. 1320 m, calcareous cliffs of a rocky outcrop within beech forest, 18.7.1978, Greuter 16055 (ATH, B, C, herb. Greuter, UPA etc.); 23.8.1978, Papanicolaou 2051 (herb. Univ. Thessaloniki) – Mt Pangaion, Trikorfon, c. 1870 m, N-facing limestone rocks, 24.8.1978, Papanicolaou 2052 (C, herb. Univ. Thessaloniki).

Centaurea pangaea is closely related to *C. parilica* Stoj. & Stef. (of sect. *Lepteranthus* (DC.) Dumort., according to Dostál 1976), a relict species with a similarly restricted distribution (Table 1). *C. parilica* is confined to Mt Orvilos (or Ali-Botuš, or Slavjanka) on the Greek-Bulgarian border, and is more variable than *C. pangaea* (the apparent uniformity of the latter may be due, however, to the fact that most of the material comes from a single tuft. Of *C. parilica* three varieties are recognized by Stojanov et al. (1967), one of which (var. *drenovskii* Stoj.), said to differ by straw-coloured involucral appendages and white flowers, does certainly not deserve taxonomic recognition: the two characters vary independently and occur on plants growing side by side with normal ones. *C. parilica* var. *parilica* is a plant of lower elevations, relatively tall-growing (20–30 cm) and glabrescent (not glabrous as said in the original description (Stojanov & Stefanov 1923), but sparingly arachnoid-pubescent all over and often distinctly scabrid by stout multicellular hair bases). *C. parilica* var. *incanescens* Stoj. & Stef. is a high-mountain ecotype which is smaller (5–20 cm), more densely leafy and with a more conspicuous, often greyish, arachnoid indumentum.

C. pangaea and *C. parilica* have no close relatives in the E Mediterranean area. Their only obvious affinities are *C. linifolia* L. and, less similar, *C. hyssopifolia* Vahl, both endemic to Spain. Of the four species mentioned, *C. pangaea* is the only one lacking a pappus, and also the only that is a typical chasmophyte.

Mt Orvilos and Mt Pangaion, to which the two species here discussed are restricted, both belong to what should be considered a distinct, fairly characteristic floristic province: the S Macedonian calcareous mountains (Fig. 2). These range from Mt Pirin (Bulgaria) in the north, through Mts Orvilos, Menikion (Boz dagh Serron), Falakron (Boz dagh Dramas) and Pangaion, to Mt Athos and the Thessalian Olympus in the south. Examples of species characteristic of this floristic province include the following three (partly based on unpublished data):

Paronychia rechingeri Chaudhri (cf. Chaudhri 1968), collected on Mts Pirin, Orvilos, Menikion, Falakron, Pangaion, and Olympus; unknown elsewhere.

Viola delphinantha Boiss. (cf. Goulimis in Goulandris et al. 1968), occurring on Mts Orvilos, Falakron, Pangaion, Athos, and Olympus; also in a single locality in the Peloponnisos (Mt Chelmos).

Fig. 1. A–F: *Centaurea pangaea*. – A: Habit. – B: Involucral bracts (straightened), from right to left: outer, middle, inner (not innermost). – C: Marginal, sterile flower. – D: Central, fertile flower. – E: Young achene. – F: Ripe achene. – G–I: *Centaurea parilica*. – G: Involucral bracts. – H: Central flower. – I: Young achene. – Same scale, respectively, for C, D and H, and B and G.


A
10 cm
B
5 mm
C
D
E
F
3 mm
G
H
10 mm
I
2 mm

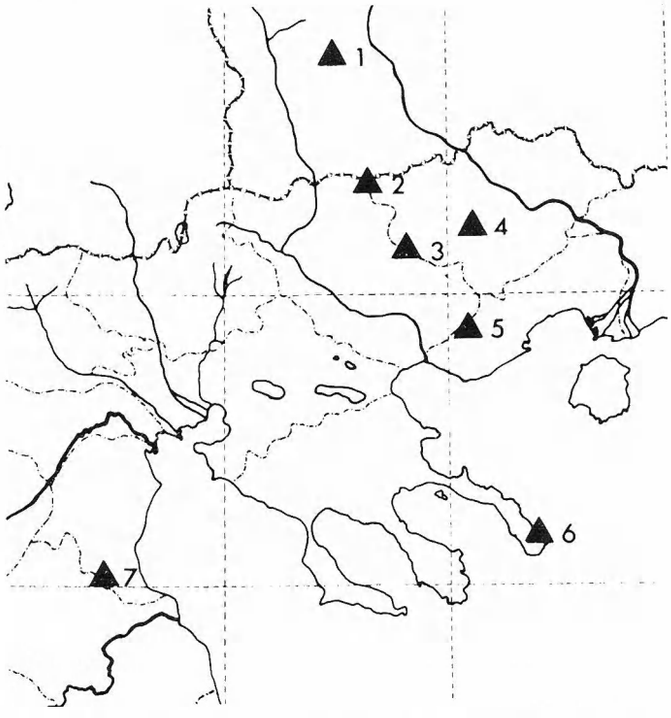

Fig. 2. Map showing the position of the S Macedonian calcareous mountains: 1 Pirin, 2 Orvilos, 3 Menikion, 4 Falakron, 5 Pangaion, 6 Athos, 7 Olympus.

Festucopsis sancta (Janka) Melderis (Melderis 1978), found on Mts Pirin, Orvilos, Menikion, Falakron, Pangaion, Athos and, outside our region, in a limited area in the C Pindus range.

The species pair *C. pangaea*/*C. parilica* adds to the endemic element of this floristic province, where single-mountain endemics play a prominent role especially on the southernmost, isolated massifs (Athos, Olympus). Most of these endemics, and certainly the ones dealt with here, must be considered as old, conservative relicts that have undergone little or no evolutionary change since the time of their establishment and isolation in their present area (cf. Greuter 1972).

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Cytology of Bignoniaceae

Peter Goldblatt and A. H. Gentry

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Bignoniaceae are remarkably consistent in chromosome number with n = 20 predominating. Most variation is found in the two putatively primitive tribes Tecomeae and Oroxyleae with n = 19, 18, 15, 13 and 11 (as well as n = 20) recorded in Tecomeae, and n = 15 and 14 in Oroxyleae. Available data suggest that x = 7 may be ancestral for the family, with palaeotetraploidy retained in Oroxyleae (*Oroxylum* n = 14, *Millingtonia* n = 15). The predominant n = 20 is, on this basis, interpreted as hexaploid on x = 7 with loss of one chromosome pair. Exceptions in Tecomeae such as *Tecoma, Tecomaria* and *Tecomanthe,* mainly n = 18, provide useful taxonomic information, but the significance of n = 18 is difficult to assess; the taxonomically isolated *Delostoma* with n = 21 may retain the original full palaeohexaploid complement. Original counts are given for 23 species, sixteen of which are first reports for species, and nine first reports for genera (*Arrabidaea, Lundia, Mansoa, Martinella, Memora, Pleonotoma* and *Stizophyllum* (all Bignonieae), *Delostoma* (Tecomeae), and *Schlegelia,* a genus of uncertain familial position, but placed here in Bignoniaceae – Schlegelieae).

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Bignoniaceae, a family which includes some 800 species in 113 genera and eight tribes (Gentry 1979), has been very poorly known cytologically like many other woody tropical angiosperm families. Nevertheless the family is of great cytological interest. Bignoniaceae are probably fairly close to the basal stock of the Tubiflorae, especially if woody habit is accepted as an important criterion of primitiveness. The fossil record of Bignoniaceae supports the family's claim to antiquity, going back (somewhat tenuously) to the upper Cretaceous (Darrah 1939) and with well-preserved flowers and fruits of *Catalpa,* one of the most advanced genera of the family on account of reduction of its androecium to two stamens, in the Eocene London Clay (Paclt 1952). In view of its key phylogenetic position and the fragmentary cytological record, Raven (1975) suggested Bignoniaceae as one of 16 families most in need of additional cytological investigation in his summary of current knowledge of angiosperm cytology.

We present here counts for 23 species of Bignoniaceae, sixteen of them previously uncounted and including the first reports of nine genera and one tribe. Our 13 specific counts and seven new generic counts for tribe Bignonieae almost double the cytologically known members of that tribe. The report of B chromosomes in *Cydista aequinoctialis* is the first for the family and one of the few records of accessory chromosomes in any group of woody tropical plants. We have also been able to pinpoint a number of probable errors in previously reported counts, especially in Tecomeae where the genera centered around *Tecoma* have very small chromosomes, making accurate counts difficult.

We have also tried to resolve here another kind of problem of Bignoniaceae cytology. Aside from a basic lack of counts, meaningful interpretation of even the known chromosome numbers of Bignoniaceae has been greatly hampered by the taxonomic instability of genera in this family. The problem of generic delimitation (Gentry

1973) is especially pronounced in the cytological literature where most counts have been uncritically reported using the largely erroneous names under which these plants are apparently cultivated in Indian botanical gardens. As a result, species of several genera whose chromosome numbers were supposedly unknown – e.g., *Clytostoma, Cydista, Distictis, Macfadyena, Pachyptera, Pandorea, Radermachera, Saritaea, Xylophragma* and *Amphitecna* – have actually been counted but reported under other generic names. Conversely, counts for several species are reported under two or three generic names in the cytological literature and the apparent cytological diversity of genera like *Bignonia* and *Tecoma* which frequently are used as virtual taxonomic wastebaskets by horticulturists, is mostly due to bad taxonomy. Because of these serious taxonomic problems we include here a summary of all known chromosome counts for the family rearranged according to modern generic concepts. Although we have not examined voucher specimens, the correct identity of most of the reported species is fairly obvious. Finally, we attempt a synthesis of the phylogenetic significance of the available cytological information on Bignoniaceae.

Material and methods

Plants studied were mostly grown from seed, collected in the wild, or occasionally from a horticultural source. Mitotic preparations only were made, root tips being obtained from germinating seedlings or young plants. Root tips were pretreated in 0.003 M hydroxyquinoline for eight hours at refrigerator temperatures, then fixed in Carnoy's 3:1 ethanol-acetic acid for 1–2 minutes and either stored in 70% ethanol, or immediately hydrolyzed in 10% HCl for 6 minutes. Root tips were squashed in lacto-propionic orcein.

Review of chromosome numbers

Tecomeae. One of the basal groups of the family, Tecomeae are cytologically heterogeneous. The majority of species and genera, both Old and New World have n = 20, including *Campsis, Catalpa, Chilopsis, Dolichandrone, Heterophragma, Markhamia, Pajanelia, Radermachera, Stereospermum* and *Tabebuia* (though there are two counts of n = 19 in the latter, which we regard as doubtful). *Newbouldia* probably also correctly has n = 20 although there is a report of n = 19 as well as one of n = 20 for the single species, *N. laevis* (Table 1).

The two probably unrelated but similarly herbaceous montane genera, *Argylia* (Chilean) and *Incarvillea* (Himalayan) have n = 15 and n = 11 respectively. *Jacaranda*, isolated in the tribe, clearly has an unusual number, probably n = 18, although 2n = 66 has also been recorded. The related genera *Tecoma* (mostly Andean), *Tecomaria* (S tropical Africa) and *Tecomanthe* and *Pandorea* (Australasia) are also exceptional, with n = 18 (as well as n = 20) recorded in *Tecoma*, n = 18 and 17 in *Tecomaria*, n = 19 and 18 in *Tecomanthe*, and n = 19 in *Pandorea*. We have tried to check the numbers in *Tecoma* and *Tecomaria* as carefully as possible, and feel that n = 18 is almost certainly correct for both genera. The chromosomes of *Tecoma* and *Tecomaria* are unusually small for Bignoniaceae and consequently difficult to work with, which may explain some anomalous counts.

Other exceptions from the predominant n = 20 are the taxonomically isolated Andean *Delostoma* in which we find n = 21 and in the monotypic African *Spathodea* where there are three separate counts of n = 13 and two others of n = 19 and 18. The situation in *Spathodea* is confusing and the range of numbers recorded seems most improbable. If, as appears likely, the n = 13 counts are correct, the n = 19 and 18 records may represent triploidy (2n = 39) with some associated loss of chromosomes.

Oroxyleae. This small Old World tribe of four genera, recently segregated from the now exclusively New World Bignonieae (Gentry 1979), stands out cytologically from all others, with n = 15 in *Millingtonia* and n = 14 in *Oroxylum*, the only two genera counted. Mehra & Bawa (1969) have recorded n = 15 in *Oroxylum*, but this may be a miscount. The numbers, being of significance, were recently checked with care (Goldblatt 1976; the count for *Oroxylum* was misprinted as 2n = 38). There seems little doubt that *Millingtonia* and *Oroxylum* have correctly n = 15 and n = 14, respectively.

Bignonieae. Of the 23 genera known cytologically, all but three have a base number of x = 20. The exceptions are *Amphilophium, Pachyptera* and *Mansoa*. The count of n = 22 in *Amphilophium paniculatum* by Venkatasubban (1944), however, seems incorrect, since we have

checked the number for this species and find quite clearly n = 20. *Pachyptera,* in which Simmonds (1954) reported n = 19, is aneuploid if this count is correct, and *Mansoa,* in which we without doubt found n = 18–19, is also aneuploid. *Pachyptera* and *Mansoa* are very closely related and a good case for their merger can be made so this number may represent a single aneuploid reduction.

All available data indicate a basic ancestral number of x = 20 for Bignonieae. Aneuploidy is apparent in only two genera, and the lower numbers in *Pachyptera* and *Mansoa* are presumably related though a single chromosome loss to the basic x = 20.

Coleeae. Only two genera of this Afro-Madagascar tribe, recently segregated from Crescentieae (Gentry 1976) have been counted. Both genera have n = 20, which we assume to be basic for the tribe.

Crescentieae. All three genera counted have n = 20, the number evidently basic for this exclusively New World tribe.

Tourrettieae. Tourrettia lappacea, the only species of the monotypic New World Tourrettieae has been reported to have 2n = ca 40 (Diers 1961). A basic number for Tourrettieae of x = 20 is probable, but confirmation of Diers' tentative count is needed.

Schlegelieae. Three Neotropical genera, variously placed in Scrophulariaceae or Bignoniaceae, constitute the tribe Schlegelieae (Gentry 1979). The single species of *Schlegelia* which has been counted has n = 20, suggesting a basic number of x = 20 for Schlegelieae.

Discussion

At least one chromosome count is now available for all tribes except the monotypic Eccremocarpeae. All information to date indicates that Bignoniaceae are in general remarkably constant cytologically (Table 1). By far the most frequent base number is x = 20 with 2n = 40 the only chromosome number known in the advanced tribes Crescentieae, Tourrettieae and Coleeae; x = 20 is also predominant and probably basic in Bignonieae. The less specialized tribes, Tecomeae and Oroxyleae, are more heterogeneous cytologically, though n = 20 is the most common number in Tecomeae.

The major discrepancy from n = 20 is found in the small exclusively Old World group of four genera which are often treated as belonging to Bignonieae but might better be separated as a distinct tribe Oroxyleae (Gentry 1979). On the basis of retention of five stamens in two of these genera, they may be among the most primitive living members of the family and thus of the Tubiflorae.

The n = 14 count in the 5-stamened *Oroxylum* (Goldblatt 1976), along with the high frequency of x = 20 in the family as a whole, is highly suggestive of x = 7 as basic for Bignoniaceae. This conclusion is compatible with accumulating evidence from other angiosperm families (Raven 1975), and in this light the very common number n = 20 is interpreted as hexaploid with the loss of one chromosome. *Millingtonia,* the other genus of Oroxyleae known cytologically, has n = 15, a number perhaps best regarded as tetraploid with the aneuploid addition of one chromosome.

In Tecomeae, numbers in the two specialized and derived herbaceous genera *Argylia* and *Incarvillea,* x = 15 and x = 11 respectively, might involve aneuploidy at the tetraploid level. The difference in number in these genera is consistent with the belief that though herbaceous, they are not related. Other exceptional Tecomeae are *Jacaranda* n = 18, *Pandorea* n = 19, and *Tecoma, Tecomaria* and *Tecomanthe,* probably with n = 18 (and possibly n = 19 also in *Tecomanthe*). Both number and unusually small chromosome size in *Tecoma* and *Tecomaria* support the contention that these two genera are very closely related. *Jacaranda* is taxonomically isolated.

The other remarkable exception is *Spathodea,* for which the record, if correct, suggests two cytological lines n = 13 and n = 19–18. We have not yet had the opportunity to explore this situation further, although the fact that the counts are nearly all from clonally reproduced horticultural material may be relevant. The remaining reports in Tecomeae other than n = 20 seem likely to be incorrect as do the counts of n = 20 in *Tecoma.* However, our count of n = 21 in the isolated Andean *Delostoma* may be significant in representing the relict of a hexaploid stock with x = 21.

In summary, it seems likely that most of the

evolutionary radiation in Bignoniaceae took place subsequent to an initial aneuploid loss of one chromosome from a palaeohexaploid stock. Only Oroxyleae (and perhaps the herbaceous Tecomeae) remain at an ancestrally tetraploid level. The predominance of the single number n = 20 in all tribes except Oroxyleae indicates a fairly close relationship of these tribes and a common ancestry in a single evolutionary line.

The uniformity of n = 20 in Bignoniaceae makes chromosome number a potentially useful taxonomic tool in evaluating the status of such problematical genera as *Schlegelia* and *Paulownia,* both of which are often placed in Scrophulariaceae. Thus the occurrence in both *Paulownia* and *Schlegelia* of n = 20 supports their placement in Bignoniaceae. All apparent trends in Bignoniaceae – high diploid chromosome numbers, constancy within a family, and rarity of polyploidy – are consistent with patterns expected for woody, predominantly tropical plants.

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Table 1. Chromosome numbers in Bignoniaceae. New records are indicated with an asterisk and collection data for these counts are listed. (A few older counts almost certainly incorrect are omitted.) All counts are tabulated as diploid, even if originally reported as haploid. Suspect counts are indicated by parentheses. Authorities for species listed can be found in Gentry (1979) and Gentry & Tomb (1979).

Species	2n	Reference/collection data
Tecomeae		
Argylia		
uspallatensis	30	Covas & Schnack 1946
Campsis		
grandiflora (also as *Tecoma*	(36)	Sugiura 1936
and as *C. chinensis*)	(38)	Venkatasubban 1944
	40	Sax 1933, Bowden 1940b
radicans (also as *Tecoma*)	40	Sax 1933, Raghavan & Venkatasubban 1940, Venkatasubban 1944
× *tagliabuena* (also as *Tecoma*)	(32)	Kondo 1972
	40	Vilmorin & Simonet 1927, Raghavan & Venkatasubban 1940
Catalpa		
bignonioides	40	Smith 1941, Delay 1948, Mehra & Bawa 1969
ovata	40	Smith 1941, Suzuka 1953
speciosa	40	Smith 1941
× *erubescens* (as *C. hybrida*)	40	Smith 1941
"*syringifolia*" (usually used for *C. bignonioides*)	40	Venkatasubban 1944
Chilopsis		
linearis	40	Bowden 1945
Delostoma		
lobbii	42*	Peru, Amazonas Dept., Gentry et al. 23133 (MO)
Dolichandrone		
spathacea (as *D. rheedii*)	40	Venkatasubban 1945
stipulata	40	Venkatasubban 1944
Heterophragma		
adenophylla (= *Fernandoa* fide van Steenis)	40	Venkatasubban 1944
Incarvillea		
compacta	22	Bowden 1940b
delavayi	22	Sugiura 1936, Bowden 1940b
mairei var. *grandiflora* (as *I. grandiflora*)	22	Sugiura 1936, Bowden 1940b

Species	2n	Reference/collection data
olgae	22	Bowden 1940b, Zakharyeva & Astanova in Fedorov 1969
semiretschenkia (as *Niedzwedzkia*)	22	Zakharyeva & Astanova in Fedorov 1969
sinensis	22	Matveeva & Tikhonova in Fedorov 1969
Jacaranda		
coerulea	36	Simmonds 1954
mimosifolia (also as *J. ovalifolia*)	36	Venkatasubban 1944, Mehra & Bawa 1969, Kendharnath 1950, Nanda 1962
	(66)	Pathak et al. 1949
hesperia	36*	Colombia, Chocó, Gentry & Renteria 24530 (MO)
Markhamia		
hildebrandtii	40	Venkatasubban 1945
platycalyx (and as *Dolichandrone*)	40	Venkatasubban 1944, 1945
Newbouldia		
laevis	38	Mangenot & Mangenot 1957, 1962
	40	Miège 1962
Pajanelia		
longifolia (as *P. rheedii*)	40	Venkatasubban 1944
Pandorea		
austalis (as *Tecoma*)	38	Venkatasubban 1944
jasminoides (as *Tecoma*)	38	Nakajima 1936
Radermachera		
xylocarpa (as *Stereospermum*)	40	Venkatasubban 1945
Spathodea		
campanulata (incl. *S. nilotica*)	26	Raghavan & Venkatasubban 1940, Venkatasubban 1945, Mehra & Bawa 1969
	36	Nanda 1962
	38	Mangenot & Mangenot 1962
Stereospermum		
chelonoides (and as *suaveolens*)	40	Venkatasubban 1944, 1945
kunthianum	40	Miège 1962
personatum	40	Mehra & Bawa 1969
Tabebuia		
chrysantha (as *Tecoma*)	(38)	Venkatasubban 1944
guayacan	40	Venkatasubban 1944
heptaphylla (as *T. ipe*)	40	Covas & Schnack 1947
heterophylla (as *T. pallida*)	40	Simmonds 1954
impetiginosa (as *T. palmeri*)	40	Bawa 1973
nodosa	40	Covas & Schnack 1947
"pentaphylla" (used for both *T. heterophylla* and *T. rosea*)	40	Venkatasubban 1944, Pathak et al. 1949
rosea	40	Venkatasubban 1944, Bawa 1973
serratifolia (also as *Tecoma*)	40	Simmonds 1954, Venkatasubban 1944
	(38)	Venkatasubban 1945
"spectabilis"	40	Venkatasubban 1945
Tecoma		
arequipensis	36*	Peru, Apurimac Dept., Gentry 23361 (MO)
garrocha	36*	Bolivia, exact loc. unknown, cult. MBG, Gentry 18054 (MO)
sambucifolia (as *Stenolobium*)	(40)	Diers 1961
× *smithii*	36	Venkatasubban 1944, Sugiura 1931, 1936
	36*	Peru, Junín Dept., Gentry 16446 (MO)
stans (also as *Stenolobium*)	(40)	Venkatasubban 1944, Bowden 1940b, 1945
	36*	ex hort. Iquitos, Peru, Gentry 16503 (MO)
stans var. *velutina*	36*	Peru, Piura Dept., Gentry 22662 (MO)
Tecomaria		
capensis (incl. *T. shirensis*)	34	Nakajima 1936, Venkatasubban 1944, Pai 1964
	36*	ex hort. Cape Town, S Africa, Goldblatt & Gentry 1580 (MO)

Species	2n	Reference/collection data
Tecomanthe		
dendrophila	36	Brighton in Van Steenis 1977
speciosa	38	Beuzenberg & Hair 1963
Oroxyleae		
Millingtonia		
hortensis	30	Narasinga Rao 1936, Venkatasubban 1944, Goldblatt 1976
Oroxylum		
indicum	28	Ghatak 1956, Mangenot & Mangenot 1962, Goldblatt 1976
	(30)	Venkatasubban 1944, Mehra & Bawa 1969
Bignonieae		
Amphilophium		
paniculatum (also as *A. mutisii*)	(44)	Venkatasubban 1944
	40*	Venezuela, Anzoátegui State, Gentry 10797 (MO)
Anemopaegma		
chamberlaynii	40	Venkatasubban 1944
orbiculatum	40*	Panama, Canal Zone, Croat 12742 (MO)
Arrabidaea		
corallina	40*	Venezuela, Guarico State, Gentry 10241 (MO)
Bignonia		
capreolata	40	Bowden 1940b
Callichlamys		
latifolia	40	Simmonds 1954
	40*	Panama, Canal Zone, Gentry 702 (MO)
Clytostoma		
binatum (as *Bignonia purpurea*)	40	Venkatasubban 1944
Cydista		
aequinoctialis	40, 40 + 1–2B*	Colombia, Cundinamarca Dept., Gentry 15149 (MO)
diversifolia (as *Bignonia*)	40	Venkatasubban 1944
Distictis		
buccinatoria (as *Bignonia cherere*)	40	Venkatasubban 1944
Lundia		
corymbifera	40*	Venezuela, Bolivar State, Gentry 10759 (MO)
Macfadyena		
unguis-cati (as *Bignonia* and *Doxantha*, and as *B. gracilis*)	40	Venkatasubban 1945, Simmonds 1954
	80	Venkatasubban 1944, 1945, Bowden 1940a, 1945
Mansoa		
difficilis	36(–38)*	Brazil, Para State, Gentry 13175 (MO)
Martinella		
obovata	40*	Panama, Canal Zone, Gentry 8736 (MO)
Memora		
patula	40*	Venezuela, Anzoátegui State, Gentry 10392 (MO)
Pachyptera		
hymenaea (as *Pseudocalymma macrocarpum*)	38	Simmonds 1954
Paragonia		
pyramidata	40	Simmonds 1954
Phryganocydia		
corymbosa	40	Simmonds 1954
Pithecoctenium		
crucigerum (as *P. echinatum*)	40	Fritsch 1970
	40*	Venezuela, Guarico State, Gentry 10811 (MO)
Pleonotoma		
jasminifolia	40*	Brazil, Amazonas State, Gentry 12861 (MO)
Pyrostegia		
cinerea	40*	Brazil, Amazonas State, Gentry 12773 (MO)
venusta (as *ignea*)	(60 = ?3n)	Joshi & Hardas 1956

Species	2n	Reference/collection data
Saritaea		
magnifica (as *Bignonia*)	40	Venkatasubban 1944
Stizophyllum		
riparium	40*	Brazil, Para State, Gentry 13127 (MO)
Tanaecium		
jaroba (as *T. albiflora*)	40	Venkatasubban 1944
Xylophragma		
seemannianum (as *Saldanhaea*)	40	(orig. 18, Lewis & Oliver 1969) corr. Lewis & Oliver 1970
Coleeae		
Kigelia		
africana (incl. *K. pinnata* and *K. tristis*)	40	Venkatasubban 1944, Bowden 1940b, Miège 1954, Mangenot & Mangenot 1962
Phyllarthron		
comorense	40	Venkatasubban 1944
Crescentieae		
Amphitecna		
latifolia (as *Crescentia*)	40	Simmonds 1954
montana	40*	Mexico, Chiapas, Breedlove 42783 (MO)
Crescentia		
cujete	40	Venkatasubban 1944, Simmonds 1954
Parmentiera		
aculeata (as *edulis*)	40	Venkatasubban 1944
cereifera	40	Venkatasubban 1944, Simmonds 1954
macrophylla	40*	Panama, Coclé, Gentry 754 (MO)
Tourrettieae		
Tourrettia		
lappacea	40	Diers 1961
Schlegelieae		
Schlegelia		
parviflora	40*	Venezuela, Aragua State, Gentry & Puig-Ross 14221 (MO)
Family position uncertain		
Paulownia	(34)	Delay 1948
tomentosa	40	Westfall 1949

Unaccounted for:

Bignonia megapotamica, 2n = 40 (Venkatasubban 1944) is a name applied to some unknown, presumably cultivated member of Bignoniaceae, although nomenclaturally the species is correctly *Vitex*.

Adenocalymma calycina, 2n = 40 (Venkatasubban 1944), apparently an invalid combination, is presumably based on *Bignonia calycina* which is a synonym of *Stizophyllum perforatum*.

Additional experimental studies in the Papaver radicatum group

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The genetics of some characters used to separate subspecies of *Papaver radicatum* Rottb. have been studied by means of crossing experiments. Flower colour seems to be a single factor character even in high polyploid material, whereas deciduous versus persistent petals, latex colour and quantitative characters are probably multifactorial. The number of stigmatic rays is modificative and decreases in depauperate plants. Morphological characters separating the neighbouring *P. radicatum* subsp. *groevudalense* Knaben and subsp. *ovatilobum* Tolm. are constant in cultivation. There is only a low degree of structural heterozygosity within colonies of *P. radicatum* subsp. *groevudalense,* subsp. *intermedium* (Nordh.) Knaben and subsp. *ovatilobum,* probably due to inbreeding in small colonies.

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My experimental studies of *Papaver radicatum* Rottb. and related species (Knaben 1958, 1959 a, b) were undertaken to elucidate the problems of differentiation in this group. The morphological variation is not easily analysed on herbarium material or with field studies only. In the high mountains and in the Arctic the climate is hard and individuals are modified to different degrees, and are therefore not comparable. Leaves and capsules are frequently badly developed and do not show the diagnostic characteristics. A large proportion of the collections comprise flowering specimens, but characters of the flowers are not taxonomically useful. A sound taxonomy must therefore be based on comparisons of cultivated specimens.

The *P. radicatum* group is a northern polyploid complex (2n = 28, 42, 56, 70 and 84). It belongs to *Papaver* sect. *Scapiflora* Reichenb., together with the diploid (2n = 14) *P. alpinum* L. group (C European mountains) and the *P. nudicaule* L. group (Siberia and C Asian mountains), in which both diploids and polyploids are known (2n = 14, 28, 56).

Tetraploids (2n = 28) are only known from Alaska and Yukon (e.g. *P. alboroseum* Hult.), hexaploids (2n = 42) from here and from the Rocky Mountains (e.g. *P. hultenii* Knaben). Octoploids (2n = 56) are known from America, Greenland and N Europe (*P. lapponicum* (Tolm.) Nordh. and *P. laestadianum* (Nordh.) Nordh., the latter endemic to a small area in N Scandinavia). Decaploids (2n = 70) are known from N Greenland, Iceland and N Europe (*P. radicatum* Rottb. and *P. dahlianum* Nordh.). 2n = 84 has only been counted in material from Brönlundsfjord (N Greenland), where also 2n = 56 and 70 have been found. Apart from this locality, the only area with sympatric occurrence of different polyploids is the Alaskan Arctic Slope, where species with 2n = 28 and 42 occur, even in the same localities.

Papaver radicatum is extremely variable and a number of subspecies have been described. Three subspecies are endemic to Iceland, one to the Faeroes, four to N Scandinavia, and six to S Norway. All are allopatric and restricted to rather small mountain areas (see map in Knaben 1959 a). The subspecies are composed of a few semi-isolated populations, which may be – at

Table 1. Material of *Papaver radicatum* used in the studies reported here; cultivated in 1957–1964.

P. radicatum subsp. **groevudalense** (Møre og Romsdal, Grøvudalen Mts)

10 – Hafsås, the stony river bank of Grøvudalselva, c. 8 km S of Grøvudalssetra (12 samples)
11 – Nonsfjell, 2 km N of Grøvudalssetra in a stony scree (4 samples)
12 – River bank 1 km N of Grøvudalssetra (8 samples)
13 – River bank at Grøvudalssetra (26 samples) (= 814 in Knaben 1959 a p. 35)
14 – Steep mountain side W of the valley Nedre Grøvudalen, between Røymoen and Jenstad, in a sand groove (44 samples)
16 – Vangsdalen, S of the outfarm (8 samples)
195 – Hafsås, stony river bank
207 – Røymoen, gravel
283 – Grøvudalen, Nonsfjell, scree

P. radicatum subsp. **intermedium** (Oppland, Jotunheimen)

15 – Sjoa, Hindseter, river banks (14 samples) (= 1320 in Knaben 1959 a p. 34)

P. radicatum subsp. **ovatilobum** (Sør-Trøndelag and Oppland, Dovre Mts)

18 – Drivdalen, Nystugubekk (11 samples) (= 1852 a in Knaben 1959 a p. 35)
19 – Drivdalen, Nystugubekk, 1 km S of no. 18 (11 samples)
135, 136, 183 – Kaldvelldalen, N of Kaldvellsjøen, scree under Nystuguhø, 10 km S of no. 18 (3 samples)
141 – Kaldvelldalen, E of Kaldvellsjøen not far from no. 135 (1 sample)
160–163 – N. Knutshø, in and above the upper *Salix* belt on NW side (4 samples)
174, 177 – Råtåsjøhø, W-exposed mountain slope in fissures and loose scree, 1600 m (2 samples)
281 – Nystugudalen, on sand near the rivulet 2–3 km W of Drivdalen

least temporarily – very small as they frequently occur on unstable ground.

There is also a differentiation in chromosome structure, first revealed in *P. radicatum*. Due to segmental interchanges and inversions in different races of this species, the interracial hybrids display multivalents and univalents in rather high numbers at meiosis (Knaben 1959 b). However, within populations great homogeneity was seen, apparently due to a high degree of homozygosity. This is valid not only for cytological and morphological characters, but also for developmental ones, like rate of development, time of flowering and seed setting, size of tufts, number of side rosettes and number of flower buds. The apparent homozygosity must be due to inbreeding in isolated populations with few specimens. *P. radicatum* is rather allogamous and artificial self-fertilization causes loss of seed germinability within few generations. The germinability in seeds from nature is also low, which may be due to a suffering from inbreeding.

The other polyploid species investigated, viz. *P. hultenii, P. lapponicum* and *P. dahlianum,* appear to be autogamous and show no loss of germinability after selfing. In these species the homozygosity within the populations – which is evident in chromosome structure as well as in morphology – must be due to selfing in pure lines.

The studies revealed that there are two levels of differentiation within *P. radicatum*. The Norwegian subspecies differ inter se to the same degree as they differ from the races from Iceland and the Faeroes. The populations constituting the races show slight differences in morphological characters and chromosome structure.

In this paper some additional experimental studies are published. They widen the factual basis, while the main conclusions reviewed above remain unchanged.

The experimental material is partly the same as described previously, and for collection numbers reference is given to Knaben 1959 a Tables 3, 7 and 9, and Knaben 1959 b Table 7. Some additional material obtained after 1959 is listed in Table 1. The seed material was either collected on natural localities, or produced each summer after isolation (with paper bags) of flower buds on cultivated specimens once raised from population samples. The plants were kept in garden plots in Oslo. For cytological studies anthers were fixed in absolute alcohol:glacial acetic acid (3:1) and squashed in aceto-carmine, aceto-orcein or Feulgen.

Table 2. Latex colour in hybrids with *Papaver radicatum* and related species. – 2x, 4x etc.: diploid, tetraploid etc.

1311 *alpinum* × 970 *alboroseum* (2x white × 4x yellow), F1 pale yellow
1311 *alpinum* × 943 *lapponicum* (2x white × 8x yellow), F1 shade of yellow
945 *nudicaule* × 946 *radicatum* subsp. *ovatilobum* (2x white × 10x yellow), F1 whitish
945 *nudicaule* × 815 *radicatum* subsp. *relictum* (2x white × 10x white), F1 white
945 *nudicaule* × 1011 *radicatum* subsp. *oeksendalense* (2x white × 10x pale yellow), F1 whitish
970 *alboroseum* × 815 *radicatum* subsp. *relictum* (4x yellow × 10x white), F1 shade of yellow
942 *lapponicum* ×815 *radicatum* subsp. *relictum* (8x yellow × 10x white), F1 shade of yellow
815 *radicatum* subsp. *relictum* × 946 subsp. *ovatilobum* (10x white × 10x yellow), F1 shade of yellow
2056 *radicatum* subsp. *groevudalense* × 815 subsp. *relictum* (10x pale yellow × 10x white), F1 cream
1372 *radicatum* subsp. *subglobosum* × 815 subsp. *relictum* (10x yellow × 10x white), F1 whitish
1320 *radicatum* subsp. *intermedium* × 815 subsp. *relictum* (10x yellow × 10x white), F1 yellow; F2 11 various shades of yellow, 14 whitish, 2 almost white
1011 *radicatum* subsp. *oeksendalense* × 814 subsp. *groevudalense* (10x pale yellow × 10x whitish), F1 whitish; F2 all whitish
dahlianum × *radicatum* subsp. *subglobosum* (10x white × 10x yellow), F1 shade of yellow; F2 7 whitish, 3 whitish-yellow, 3 yellow

Table 3. Variation in number of stigma rays in three subspecies of *Papaver radicatum*. Spontaneous material (data from Gjærevoll & Sørensen 1954) and cultivated material from the same localities (from Knaben 1959b). Code to localities, see Knaben (1959a p. 35). The figures give number of capsules. Md = median.

Origin	Number of stigma rays					
	4	5	6	7	8–10	Md
gjaerevollii – 1069						
Spontaneous	56	336	158	10	.	5.16
Cultivated	1	32	57	10	.	5.76
groevudalense – 814 + 2056						
Spontaneous	2	45	117	39	2	5.97
Cultivated	.	10	69	87	24	6.56
ovatilobum – 946						
Spontaneous	1	6	62	31	3	6.29
Cultivated	.	5	47	46	2	6.47
ovatilobum – 1852a						
Spontaneous	.	3	46	21	6	6.40
Cultivated	.	10	38	30	2	6.30

Inheritance of morphological traits

A study of the genetics of the taxonomic characters was planned, but had to be abandoned due to pronounced sterility in the F1 and F2 generations of interracial crosses. Some knowledge of the dominance and segregation conditions has, however, been gained from the experiments.

Material. F2 families were raised from the various F1 combinations described previously (Knaben 1959 a, b). The number of F2 specimens in each family did never exceed 75; usually it was much lower. Herbarium material representing each F1 combination, and of each of the F2 specimens is preserved at O.

Flower colour

In *P. dahlianum* (2n = 70) the flowers are white or sulphureous (white flowers always have a slight tinge of yellow at the base of the petals). In *P. radicatum* (2n = 70) the flowers are sulphureous. Three crosses with white *P. dahlianum* as one parent have been made, viz. 1546 × 1545, 1546 × 1562 and 1372 × 1545, the first two with sulphureous *P. dahlianum* as the other parent, the latter with *P. radicatum* subsp. *subglobosum* Nordh. In all cases, all F1 plants were white-flowered. In the F2 of the first-mentioned cross there was a segregation white: sulphureous = 35:8. Thus flower colour may be a single factor character in the polyploids as well as in the diploid *P. alpinum* group (Fabergé 1942).

In all hybrid combinations between diploids (*P. nudicaule*; cultivated at Kongsvoll, S Norway, or *P. alpinum*; 1311) and polyploids (*P. radicatum*, 2n = 70; 946, or *P. lapponicum* 2n = 56; 943) the sulphureous colour of the polyploid dominated completely over the flower colour of the diploid, either white or yellow. This may be an effect of the genes of the polyploid being in excess (the hybrids resemble the polyploid parent species in general appearance, only being luxuriant). However, the yellow pigments

Fig. 1. *Papaver radicatum* subsp. *groevudalense*. Specimens from nature. Note long petioles and scapes. – S Norway, Sunndalen, Vangsdalen S of Hafsås, sand groove. Coll. G. Knaben 1954.

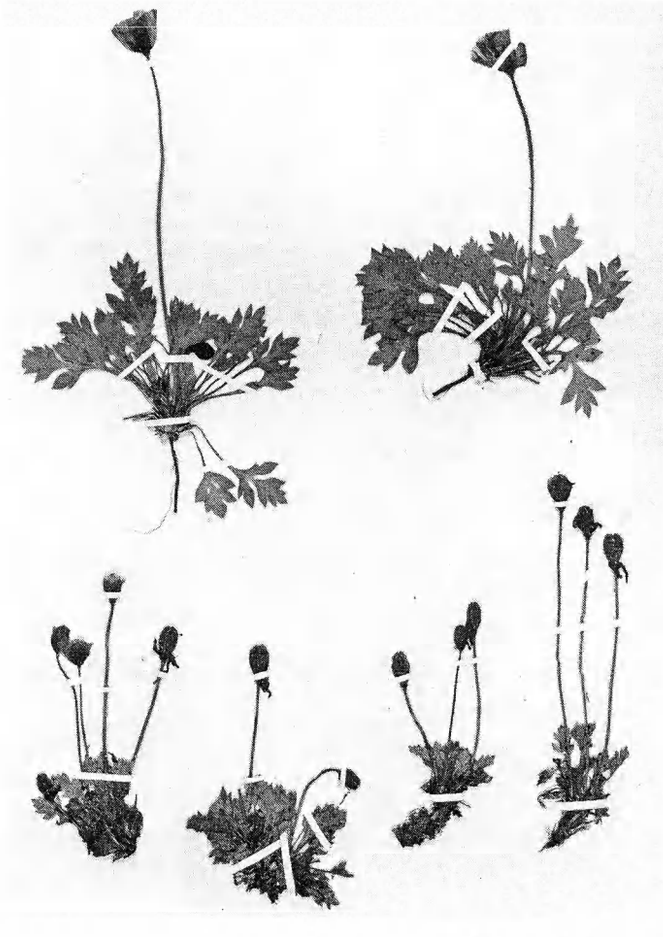

Fig. 2. *Papaver radicatum* subsp. *ovatilobum*. The two upper specimens cultivated in Oslo, the lower ones from nature. Note the different development of the leaves. – S Norway, Dovre Mts, Kongsvoll.

in diploids and polyploids differ (Fabergé 1942) and may thus have a different genetic background.

Similarly, when a polyploid species (2n = 56 or 70) is crossed with *P. alboroseum* (2n = 28; 970) the sulphureous colour dominates over the pale rose of *P. alboroseum*.

Deciduous versus persistent petals

The character deciduous versus persistent petals is potentially useful taxonomically in *P. radicatum*. The subspecies on Iceland and the Faeroes have deciduous petals; two endemic races of S Norway (subsp. *relictum* (Lundstr.) Tolm. and subsp. *intermedium* (Nordh.) Knaben) show a variable condition, even within populations, while the other subspecies have persistent petals.

In the cross subsp. *relictum* × subsp. *intermedium* (815 × 1320; deciduous × persistent) 25 specimens were raised. 23 had capsules with persistent petals as well as capsules with deciduous ones. In 2 plants the petals were shed, but the stamens remained at the capsule base, hanging down like a petticoat. The F2 family comprised 27 specimens: 15 had persistent petals, 8 had deciduous, 4 had both types.

In the cross subsp. *intermedium* × subsp. *intermedium* (1320 × 1325; persistent × deciduous) 8 F1 specimens had persistent petals, 2 had deciduous, while 4 had both types.

In the cross *P. radicatum* subsp. *subglobosum* × *P. dahlianum* (1372 × 1545; persistent × deciduous) the F1 individuals all developed both types of petals. In F2, 8 specimens had deciduous petals, 5 had persistent.

It appears that this character is not connected with complete dominance, and the genetic background is not a single gene difference.

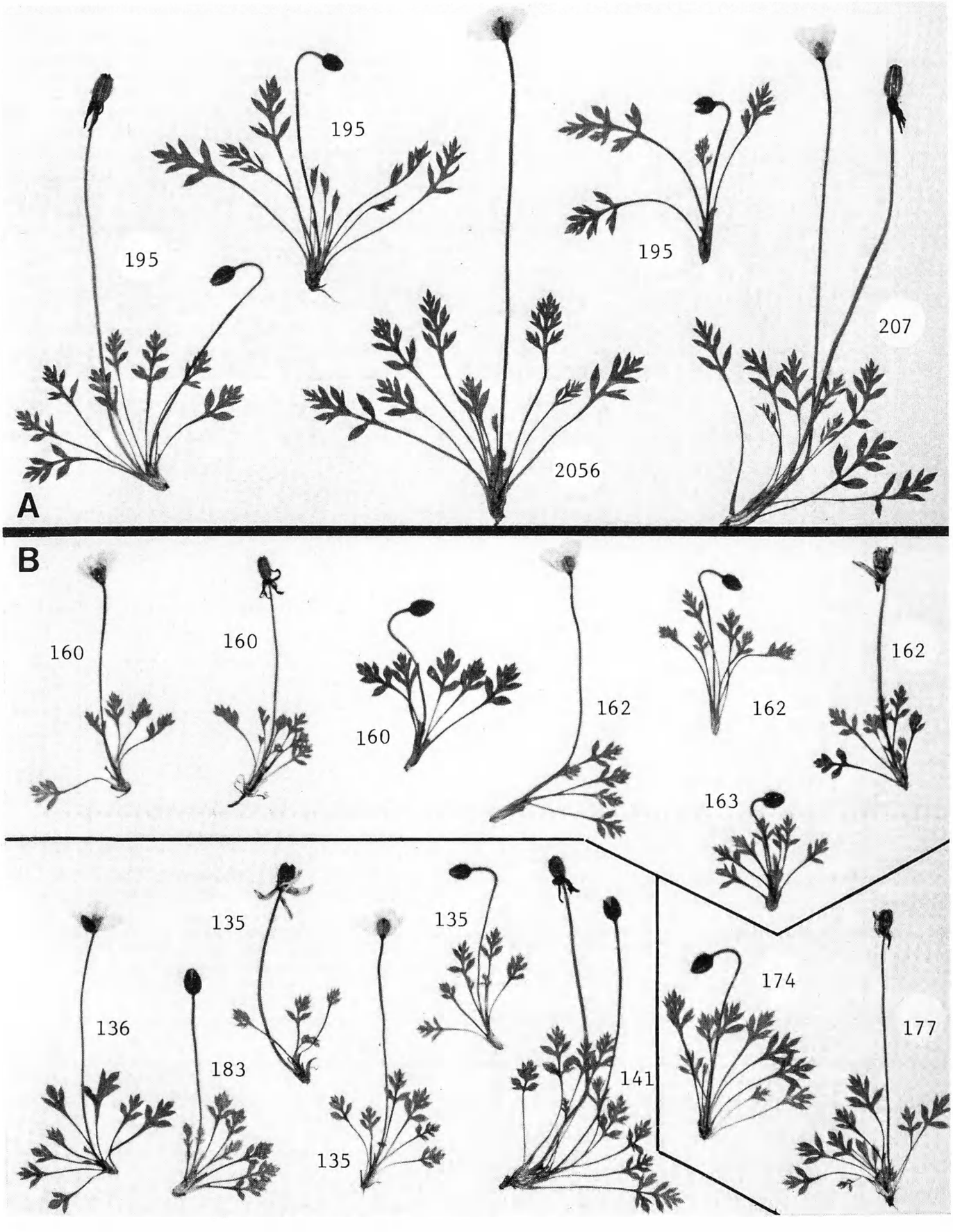

Fig. 3. Flowering specimens of *Papaver radicatum*, cultivated in Oslo in 1964. – A: Subsp. *groevudalense*, material from 3 populations (see numbers). – B: Subsp. *ovatilobum*, material from 3 populations (framed with narrow lines). – Collection numbers explained in Table 1 and Knaben 1959a p. 35.

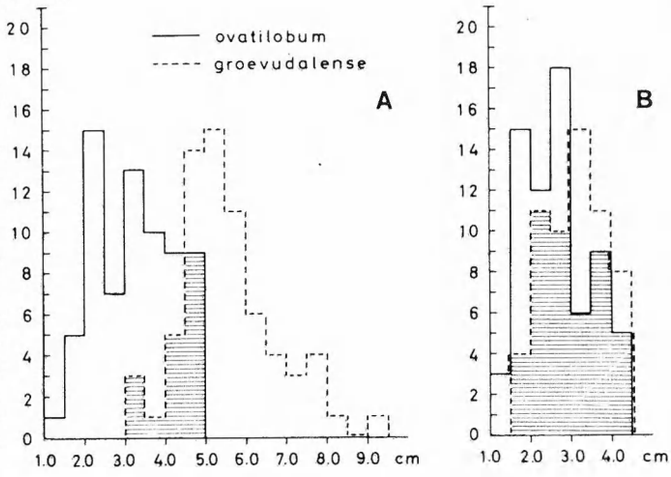

Fig. 4. *Papaver radicatum* subsp. *ovatilobum* and subsp. *groevudalense*. – A: Length of petioles (means ± standard errors for subsp. *ovatilobum* 3.54 ± 0.60, for subsp. *groevudalense* 5.28 ± 1.48). – B: Length of laminae.

Latex colour

Latex colour, white or yellow, has been regarded as taxonomically important. *Papaver radicatum* subsp. *relictum* was given the rank of species, i.a. with reference to its white latex (Nordhagen 1931, 1940). In other taxa of *P. radicatum* it is generally yellow (occasionally white in cultivated specimens of subsp. *groevudalense* Knaben and subsp. *oeksendalense* Knaben; Knaben 1959 a); in *P. dahlianum* it is normally white (variable in W Spitsbergen; Knaben 1958).

The latex colour was carefully determined in all plants (15–25) of some F1 progenies in garden plots (Table 2). The plants were vigorous, and when the stems or leaves were cut, the latex oozed out forming large droplets. In dry weather in the field, an almost colourless watery fluid may appear instead of latex; this fluid may easily be mistaken for a white latex.

All F1 families are more or less intermediate. The segregation in F2 seems complicated. Latex colour is probably a multifactorial character.

Quantitative characters

The diagnostic characters on which the races of *P. radicatum* are separated, viz. size and shape of leaves and capsules, are most probably multifactorial, like those of the *P. alpinum* group (Fabergé 1942). The F1 individuals obtained in interracial crosses are intermediate in leaf and capsule characteristics; likewise the F2 families are mainly intermediate.

Number of stigma rays – a modificative character

The number of stigma rays has received much attention as a taxonomic character (Nordhagen 1931, Gjærevoll & Sørensen 1954). The character evidently discriminates between some of the subspecies of *Papaver radicatum* (Knaben 1959 b Table 14). However, when Sørensen's data (Table 1 in Gjærevoll & Sørensen 1954) on spontaneous material are compared with mine (Knaben 1959 b Table 14) on cultivated material from the same populations (Table 3), it appears that this character may be somewhat modifiable. The average number of rays is higher in cultivated subsp. *gjaerevollii* Knaben and subsp. *groevudalense* than in spontaneous. The cultivated plants get somewhat larger capsules with broader stigma discs, leaving space for more stigma rays than a smaller capsule. In subsp. *ovatilobum* Tolm. no such tendency can be seen, but this may be due to the fact that the material analysed by Sørensen originated from sheltered sites in the valley Drivdalen. Spontaneous plants growing higher up in the mountains around Drivdalen have somewhat smaller capsules, probably due to modification.

Two subspecies of P. radicatum compared

Papaver radicatum subsp. *ovatilobum* and subsp. *groevudalense* differ in several quantitative characters (Knaben 1959 a Table 4). Each of them is endemic to small mountain areas in S Norway, and no intermediates have been seen in the large herbarium material examined, in spite of the small distance between them (10–15 km at the nearest).

The differences were tested by a cultivation experiment in 1964. Plants were grown in the open in Oslo, and the material was studied (and dried) in its first year in cultivation. The differences became even more conspicuous in cultivation; spontaneous material is often dwarfed due to extreme conditions, while material from more favourable places is comparable to cultivated material.

General appearance. The tufts of subsp. *groevudalense* are taller, less dense and less

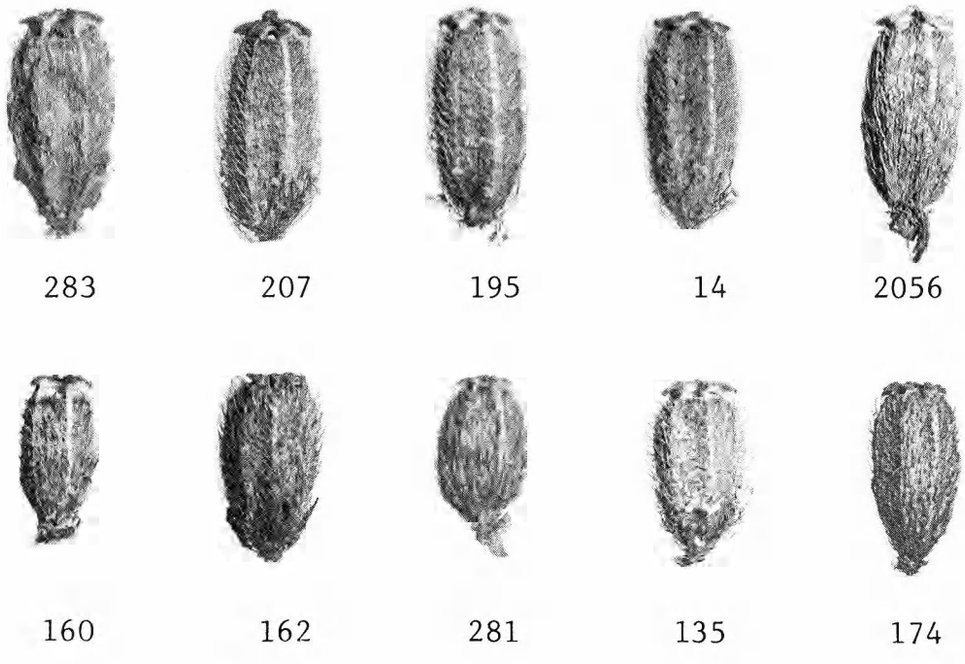

Fig. 5. Capsules of *Papaver radicatum* subsp. *groevudalense* (upper row) and subsp. *ovatilobum* (lower row). Material cultivated in Oslo in 1964. – Collection numbers explained in Table 1 and Knaben 1959a p. 35.

flattened than those of subsp. *ovatilobum* (Figs. 1, 2). This difference is conspicuous when the plants grow side by side. The more slender appearance of the lamina in subsp. *groevudalense* contributes to this impression. The scapes are also taller in subsp. *groevudalense,* a character maintained in cultivation (Fig. 3).

Petiole. The length of petioles and laminae were measured in three leaves from three different rosettes of each of 23 individuals from nine samples of subsp. *groevudalense,* and in the same number of leaves from eleven samples of subsp. *ovatilobum*. The petioles are significantly longer in subsp. *groevudalense* ($t = 10.0$; $P < 0.05$), but there is no pronounced difference in length of lamina (Fig. 4).

This difference is also obvious when plants from favourable natural localities are compared (Figs. 1, 2). In extremely dry localities the petioles become shorter (Fig. 2, lower versus upper row).

Lamina. In subsp. *groevudalense* the lamina is narrower in relation to its length (Fig. 3 A) and the pinnae are somewhat narrower and more distant than in subsp. *ovatilobum,* which has a more triangular lamina (Fig. 3 B).

Capsule. *P. radicatum* subsp. *groevudalense* has a longer and relatively narrower capsule than subsp. *ovatilobum* (Fig. 5, Knaben 1959 b Table 12). One collection of the former subspecies (2056; Fig. 5) has been kept in cultivation between 1953 and 1964, each year sown from seed of selfed parents, without changing its capsule characteristics.

Chromosome structure within races of P. radicatum

Plants from natural localities. Data on meiosis of 14 specimens of *Papaver radicatum* subsp. *groevudalense* were given in Knaben 1959 b. One of these appeared to be heterozygous for one segmental interchange, since it formed 33 bivalents and a chain of three or four chromosomes at MI. The others formed 35 bivalents (Knaben 1959 b Fig. 5).

In this paper a further 77 plants can be reported on, belonging to subsp. *groevudalense,* subsp. *intermedium* and subsp. *ovatilobum* (Table 4).

The occurrence of no or only single univalents indicates that the individuals are predominantly structural homozygotes. This is in contrast to conditions in intra- and interracial hybrids, which show much higher frequencies (Knaben 1959 b Table 3).

In ten individuals studied out of the group with no univalents, pairing was normal with 35 bival-

Table 4. *Papaver radicatum*. Analysis of meiosis in specimens raised from seed collected in nature. The figures give the number of individuals. Numerous PMCs have been studied in each plant. Code to localities in Table 1.

Locality	No. of univalents		
	0	1–2	1–6
groevudalense			
10	1	5	2
11	2	3	.
12	3	2	.
13	5	7	.
14	7	14	.
16	1	6	.
intermedium			
15	.	3	.
ovatilobum			
18	3	6	.
19	3	4	.
Total	25	50	2

Table 5. Intraracial crosses in *Papaver radicatum* subsp. *groevudalense*. The figures give the number of individuals. Numerous PMCs have been studied in each plant. Code to localities in Table 1.

Cross	No. of univalents		
	0	1–2	1–6
10 × 10	.	5	1
10 × 12	.	.	1
10 × 14	.	1	.
11 × 11	1	.	.
11 × 12	.	1	.
12 × 12	2	6	.
12 × 14	1	1	.
13 × 13	3	6	.
14 × 14	3	13	1
Total	10	33	3

ents. In two individuals of the group with 1–2 univalents there was a ring of four chromosomes, indicating heterozygosity for one segmental interchange. Thus, only three out of a total of 26 individuals investigated (12 here, 14 in Knaben 1949 b) were heterozygous with respect to a segmental interchange.

Intraracial hybrids. Seeds from a total of 78 intraracial crosses in *P. radicatum* subsp. *groevudalense* were obtained, and gave rise to 52 F1 families. Germination was late as compared with that of seed from interracial crosses.

Those intraracial hybrids which had been obtained from crosses between individuals from different colonies showed luxuriance resembling heterosis, though not to the very degree seen in the interracial crosses. The meiosis resembles that of individuals raised from seed samples from nature (Table 5).

Four individuals from the group with 1–2 and 1–6 univalents had the following multivalent configurations (one PMC per plant analysed); $1_I\ 33_{II}\ 1_{III}$; $3_I\ 32_{II}\ 1_{III}$; $32_{II}\ 2_{III}$; $2_I\ 32_{II}\ 1_{IV}$.

Conclusion. The above analyses have shown that there is a low degree of structural heterozygosity within the colonies of *P. radicatum*, especially subsp. *groevudalense*, at most concerning two or three pairs of chromosomes. This result agrees with the result of the analyses of the population samples studied up to 1959 (Knaben 1959 b). I think it is justified to maintain that inbreeding has lead to homozygosity within the colonies in nature, not only in the autogamous *P. dahlianum*, *P. hultenii* and *P. lapponicum*, but also in *P. radicatum* which seems to be more or less allogamous.

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Ovarian anatomy of Quararibea guianensis and Q. cordata

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The ovarian vascular organization and the pollen transmitting system of the flowers of *Quararibea guianensis* Aubl. and *Q. cordata* (Humb. & Bonpl.) Vischer (Bombacaceae) are described and analyzed. A system of amphicribral cortical bundles in the floral axis continues into the calyx tube. The subinferior ovary of these species results from intercalary formation of a cupshaped receptacle involving enlargement of the area of carpel insertion. Development of an essentially superior position of the fruit is interpreted as the result of differential enlargement of the free part of the ovary in relation to the invested part.

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Quararibea Aubl. (Bombacaceae) is a genus of mainly South American trees and shrubs. The two species dealt with here, *Quararibea guianensis* Aubl. and *Q. cordata* (Humb. & Bonpl.) Vischer are the nomenclatural types of the genera *Quararibea* Aubl. and *Matisia* Humb. & Bonpl. respectively. Today most authors apparently agree with Vischer (1920) that *Matisia* Humb. & Bonpl. is a synonym of *Quararibea* Aubl., the distinctive generic characters being quite variable (Robyns 1964, Nilsson & Robyns 1974).

Vischer (1920) showed that *Quararibea* and *Matisia* have in common a more or less inferior ovary and a prolonged central part of the "placenta", which as a rudimentary partition divides the bottom of each locule into two. However, no detailed account of the gynoecial anatomy in the genus *Quararibea* s.l. has been published.

Material and methods

Floral material of *Quararibea guianensis,* preserved in formalin-aceto-alcohol, was obtained from Instituto de Pesquisa Agropecuaria do Norte, Belém, Brazil. (The specimens will be cited as IPEAN 1975.) Of this material thirty flowers and flower buds, the latter being from 3× 5 mm to 6× 35 mm in size, were used for serial sectioning. Another portion of the material was used in preparing cleared, thick sections for supplementary information. Herbarium specimens of flowers (fl.) and flower buds (fl.b.) were obtained from the sheets listed below.

Q. guianensis: Irwin, Egler & Pires 47196 (S), Brazil, 1 fl.; Lanjouw 706 (S), Surinam, 1 fl.b.; Pennington 1268 (S), Brazil, 1 fl., 1 fl.b.; Sagot 49 (S), 1 fl.

Q. cordata; Schultes 6073 (F), Colomb. Amazonas, 3 fl.b.; Tessmann 3087 (S), Peru, 3 fl., 1 fl.b.

To reduce difficulties during microtoming, the tough outer tissues were, in some cases, trimmed off; in other cases only the hard trichomes were removed. The liquid-preserved specimens were dehydrated in a tertiary butyl alcohol series and embedded in Paraplast according to standard procedures. Both transverse and longitudinal sections were cut at 10 μm and stained with tannic acid–iron alum and safranin or with Heidenhain's iron hematoxylin. Dry floral specimens were boiled in water before trimming and further re-expanded and softened in 5% aqueous solution of sodium hydroxide at 70°. Then they were bleached in a 0.5%solution of hydrogen peroxide in ammonia water, thoroughly washed in water, and subsequently treated like liquid-preserved specimens. Some of this material was also softened and bleached by these agents. Softening and bleaching of each specimen was individually controlled.

While I have referred to the median and transmedian planes of the flower when describing the bicarpellate gynoecium of *Q. guianensis* to indicate the anteroposterior and transverse planes through the floral axis

these planes of symmetry must be considered to be provisional.

A *plicate* stele means a folded stele. An outward fold (ridge) will be called *plica* (Fig. 4 A). Inward folds are not referred to. According to the number of plicae the stele may be 2-plicate, 5-plicate, polyplicate, etc. Some further terms have also been used. When first met with and explained they are printed in italics.

Quararibea guianensis

The pedicel has three triangular, c. 2 mm long bracteoles at its lower part. The gynoecium has two carpels, positioned in the median plane of the flower; the ovary proper is bilocular, very small, the locules biovulate; the placentation is axile. The style is filiform, the stigma fleshy, bilobulate, protruding out of the c. 10 cm long staminal column. Glandular nectaries occur within the tubiform calyx. The fruit is drupaceous, ovoid, mamillate, coriaceous-fibrous with two 1-seeded locules, c. 4 cm long and partly enclosed in a stout calyx tube; the seeds are c. 2 cm long.

The coherent surfaces of the two carpels are completely fused. In the youngest stages studied (IPEAN 1975) the gynoecium has the shape of a pestle (Fig. 1 A) with its lower, somewhat broadened end forming the ovary. This is to some extent submerged into extracarpellary tissues, which constitute a hypanthium. The ovary may accordingly be described as being subinferior. Only the basal part of the hypanthium is adnate to the ovary. Its upper part forms a free collar from the rim of which the calyx tube, the corolla, and the staminal column arise (Fig. 1 A).

Floral axis

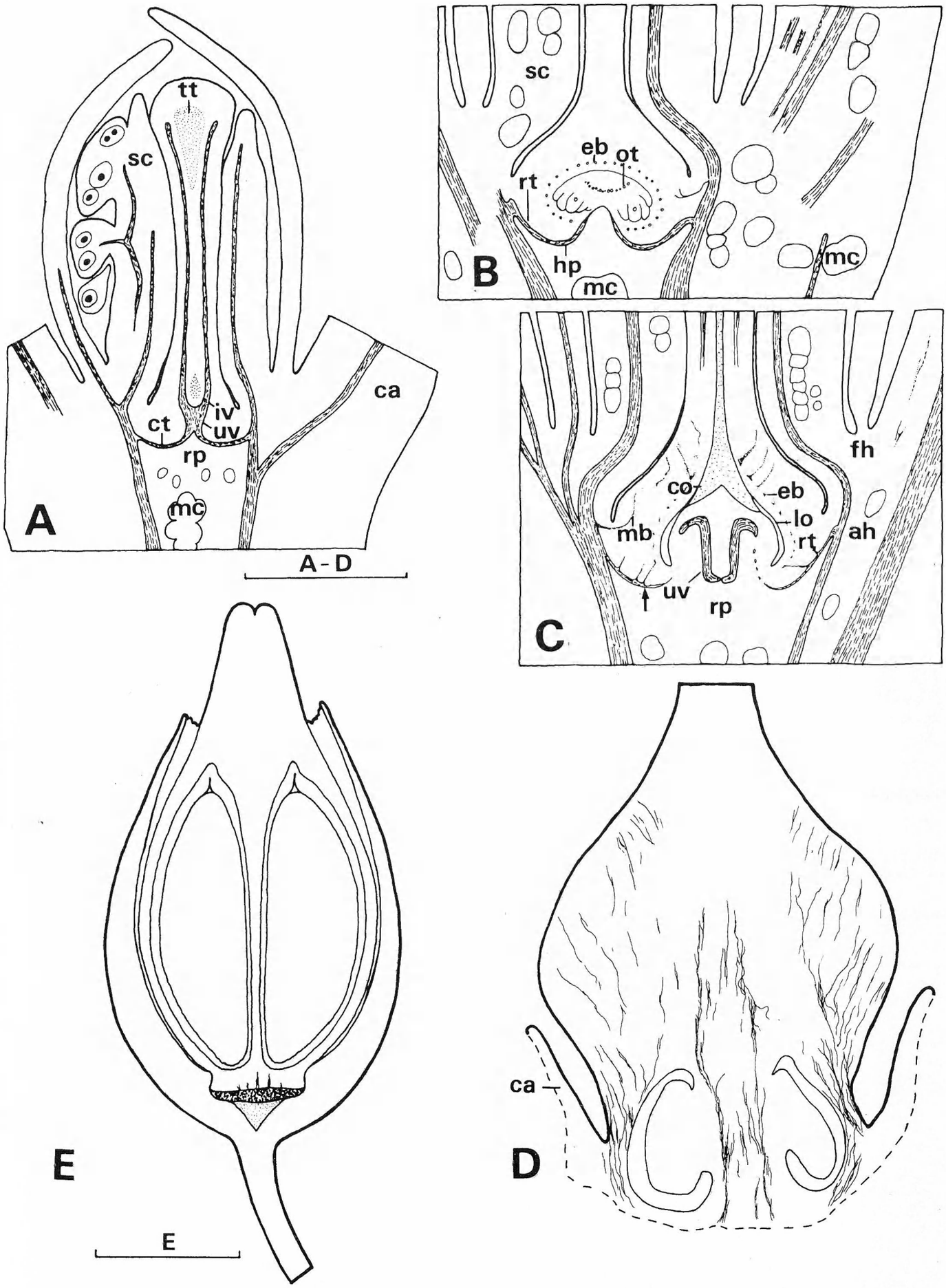
Pedicel. The vascular system of the pedicel consists of an eustele as well as of cortical, amphicribral bundles. In the undermost part of the pedicel the stele is circular or oval in transverse section and discontinuously bordered by phloem fibres, running either singly or a few together. In the cortex no amphicribral bundles are seen at this level. Upwards a 2-plicate and a 3-plicate stelar region may follow, related to the diverging bracteole traces (which remain collateral with phloem fibres along the outside). These regions are often obscured, however, by the transition to a polyplicate, mostly 6- to 8-plicate stelar condition (Fig. 2 A), preceding the departure of sepal traces. The phloem fibres are present above the insertion levels of the bracteoles although in decreasing numbers and then usually vanish.

At these levels the first few amphicribral bundles appear in different parts of the cortex. They start in the cortex parenchyma and have no vascular communication with stelar bundles. They apparently are formed de novo, through provascular differentiation in ground-tissue. Their thin, lower ends are composed of a few, minute cells that upwards are succeeded by phloem, then in addition by small tracheary xylem elements. The latter usually appear in the centre of the bundles and gradually increase centrifugally by additional xylem elements in either a regular or irregular manner. Upwards the cortical amphicribral bundles increase rapidly in size and branch repeatedly and the phloem undergoes centripetal sclerification. At anthesis the upper portion of the cortex is traversed by about a hundred such bundles. These vary greatly in size and are often extensively sclerified. The cortical bundles continue their upward course and enter the abaxial zones of the hypanthium and calyx.

In the upper part of the pedicel, which is widened to the double, some sepal traces are given off and depart as amphicribral traces into the cortex. These traces emanate singly or a few together from certain of the stelar plicae, eventually consuming them partly or wholly. The stelar plicae just mentioned will be referred to as *supernumerary plicae*.

Receptacle. In the receptacle the stele is 5-plicate (Fig. 2 B) or becomes so by the procedure described for the pedicel. Most sepal traces are

Fig. 1. *Quararibea guianensis*, IPEAN 1975. – A: Transmedian LS of young flower bud c. 3×5 mm. – B: Transmedian LS of flower bud c. 4 mm in diameter. – C: Median LS of flower bud c. 4.5 mm in diameter. – D: Median LS of fertilized ovary. – E: Median LS of immature fruit. – ah adnate hypanthium, ca calyx, co compitum, ct carpellary traces, eb endocarp zone bundles, fh free hypanthium, hp horizontal plate, iv individual ventral bundles, lo locule, mb mesocarp zone bundles, mc mucilage cavity, ot ovular traces, rp receptacular pith, rt recurrent carpellary traces, sc staminal column, tt transmitting tissue, uv united ventral bundles; arrow (in C) indicates upward deviation of endocarp zone traces from recurrent traces. – Scales A–D 1 mm, E 10 mm.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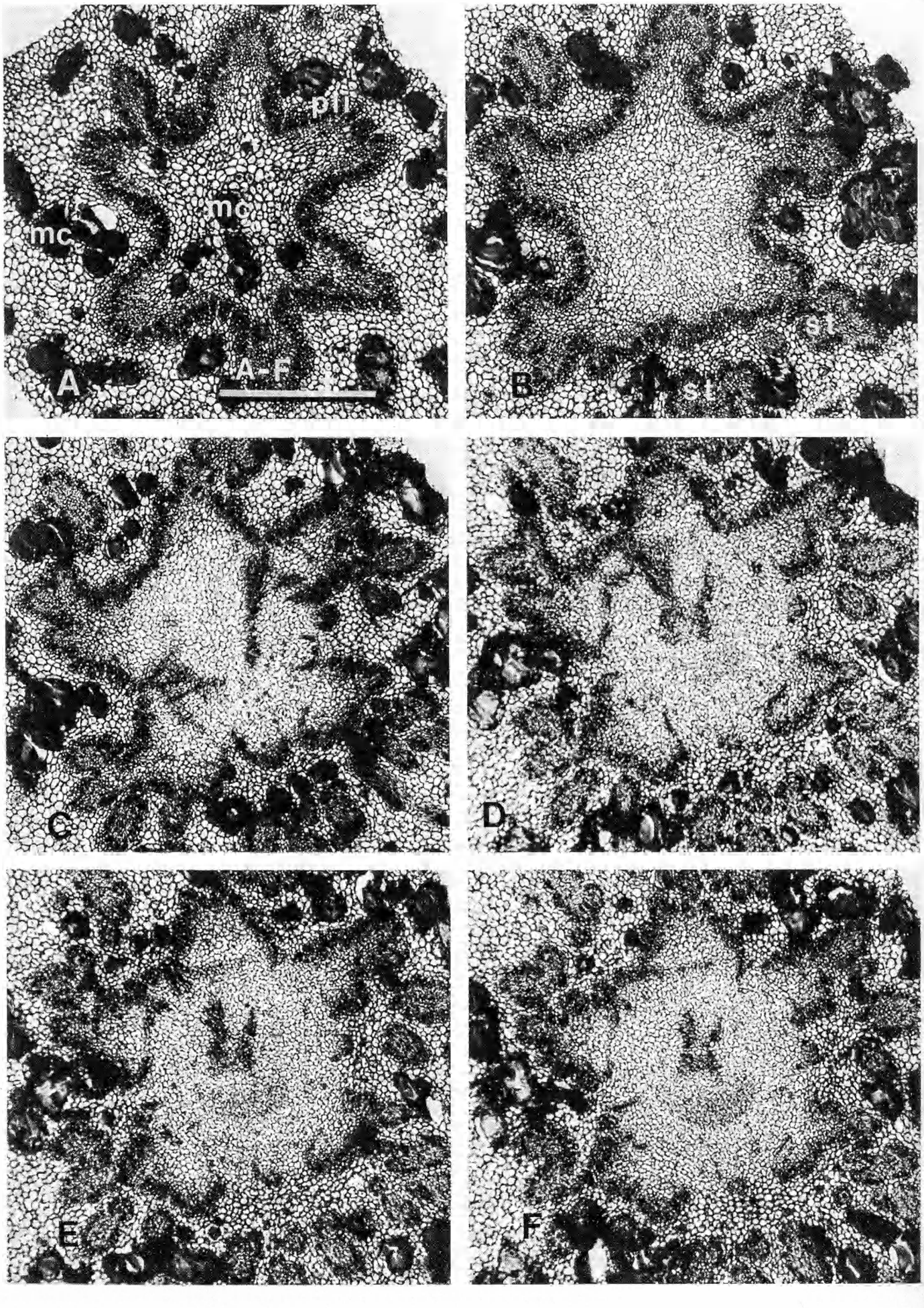
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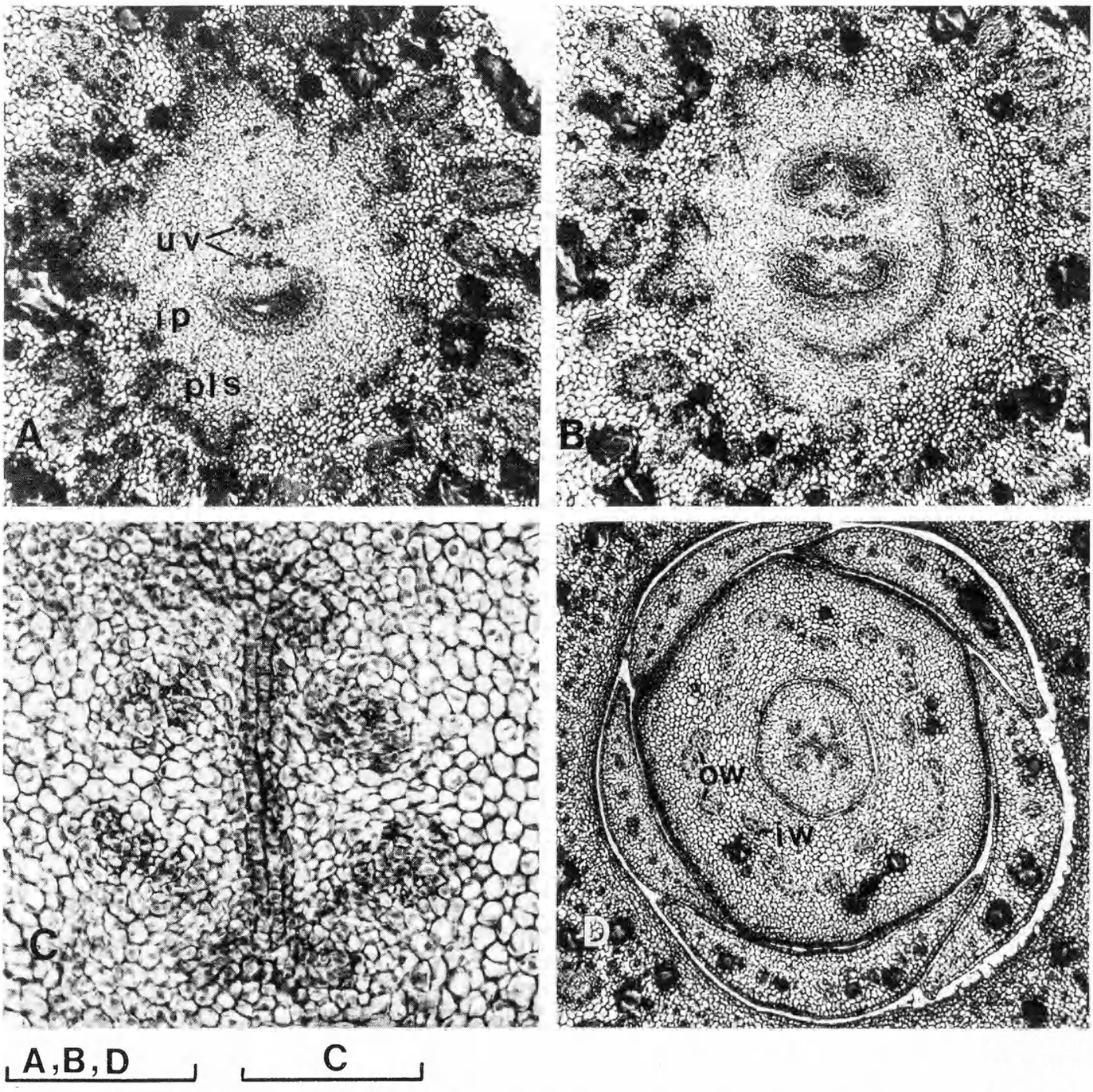

Fig. 3. *Quararibea guianensis*, IPEAN 1975. TS series of Fig. 2 continued. – A: Bottom of ovary proper; anterior locule appearing; united ventrals formed. – B: Zone of transition between adnate and free parts of ovary. In the partly appearing base of the free hypanthium (outside the interspace beginning to form round the ovary proper) the disintegration of stelar bundles is completed. – C: Central part of stylar base. Four individual ventrals; compitum joining the transmitting strands. – D: Style surrounded by staminal column, petals, and calyx tube (outer parts omitted). – ip interplical provascular strand, iw inner whorl staminal trace, ow outer whorl staminal traces, pls plical provascular strand, uv united vascular bundles. – Scales A, B, D 0.5 mm, C 0.1 mm.

Fig. 2. *Quararibea guianensis*, IPEAN 1975. Young flower bud, c. 3×7 mm. Series of slightly oblique TS. – A: 7-plicate stele of pedicel. – B: 5-plicate stele of the receptacle. – C: Carpellary traces coming from plical and interplical loci, forming migrating complexes in the receptacular pith. – D: Median-parallel sectors, the left one being in a final stage of completion. – E: Median-parallel sectors, the right one being transitional to border traces. – F: Uniting halves of divided border trace series. – mc mucilage cavities, pli stelar plica, st sepal traces. – Scale 0.5 mm.

given off from the ultimate five remaining stelar plicae, several portions from each of them, at successive levels of the receptacle inclusive of the adnate hypanthium. The traces departing from receptacular and hypanthial plicae are often collateral or hemiconcentric, especially those departing at top levels; but sooner or later all of them assume the amphicribral condition. The sepal traces (and bundles) branch variously in the adnate hypanthium, undergo extensive divisions in the free hypanthium and in the calyx tube, and finally become much smaller and more numerous than the cortical bundles. The sepal traces and bundles are less apt to become sclerified than the cortical bundles.

Organization of carpellary bundles

Four separate kinds of carpellary vascular bundles will be described, viz. ventral, intermediate, endocarp zone and mesocarp zone bundles. In young flower buds only the ventral bundles are present.

Young stages. The five ultimate stelar plicae of the receptacle, besides forming sepal traces, supply petal, staminal, and carpellary traces. Loci corresponding to the ultimate plicae will be termed *plical* while loci between *interplical* (Fig. 4 A).

In young flower buds provascular carpellary traces first arise in the receptacle from the innermost parts of the five ultimate stelar plicae, that is from 10 plical loci (Figs. 2 C, 4 A). Additional traces arise in pairs from 5 interplical loci. While branching and interconnecting these traces form complexes that grow inwards into the receptacular pith. The course is horizontal, though, in fact, slightly rising. During this course the trace complexes migrate laterally, showing rapidly changing patterns (Fig. 2 C, D). At the top the complexes finally become organized into two *median-parallel sectors,* which are separated by parenchyma (Figs. 2 D, E, 4 A, B). The two sectors form the horizontal plate; these structures, however, become more prominent in adult stages. In each of the sectors the carpellary traces run transmedianly inwards (adaxially). As they arrive at the inner borders of the sectors their slightly rising course shifts to upward. So two opposite, median-parallel series of vertical carpellary traces arise. The traces are collateral and normally oriented and will be referred to as the border carpellary traces, or *border traces*.

Little above their starting level each of the series of border traces divides transversally (Fig. 2 E, F, 4 C). The ensuing halves of the opposite series are interpreted as traces for the two submarginal bundles of one and the same carpel. The latter will be termed the *individual ventral bundles*. The halves unite by their new-formed ends and turn 90° (Figs. 2 F, 3 A, 4 D, E). In reality the first steps of divergence of halves and formation of converse connections appear already below the level of turning. The transformation results in two transmedianly extended opposite series of traces in which the positions of xylem and phloem are completely inverted, i.e. turned 180° from the normal. The two series are the *united ventral traces* (Fig. 4 D). They ascend in the central column of the ovary as *united ventral bundles* (Fig. 3 A, B, 4 E).

The loci of carpellary trace departure may be determined somewhat closer than in the above description. When provascular carpellary traces are given off inwards in pairs from five interplical loci they leave gaps on both sides of five single interplical provascular strands (Fig. 3 A) in the stele. It is concluded from this that the pairs of carpellary traces are derived from a stelar combination with the latter strands. By following them upwards through successive serial sections these strands were identified as being continuous with the traces for an inner whorl of rudimentary stamens (Fig. 3 D).

Above the departure of the last sepal traces there are seen, between the five interplical strands and adjacent to them, five plical provascular strands (Fig. 3 A). These release one trace to the outside and three aligned traces to the inside, which were identified as traces for the petals and for the outer staminal whorl, respectively. The carpellary traces departing from the ten plical loci, as previously described, obviously originate from the lateral parts of these five plical strands and are, on positional grounds, believed most likely to come from their stelar combination with traces from the outer staminal whorl.

To summarize, the floral stele, after departure of supernumerary plicae, is composed of five plical bundles in which are integrated sepal, petal, outer staminal traces, and carpellary traces, and, between the plical bundles, five

interplical bundles in which are integrated inner whorl staminal traces and carpellary traces.

Adult stages. In adult stages a modified and enlarged pattern of carpellary trace organization develops in the receptacle. As a result of differential intercalary growth the deviation points of the carpellary traces that emanate successively from the stele are elevated into the hypanthium. Consequently the connections between the deviation points and the points of trace entrance in the adaxial parts of the ovary will be maintained by lengthened, downwards running segments of the traces (Fig. 1 B, C). These segments, or *recurrent traces,* are inverted, i. e., turn the xylem to the outside.

In their inner course the recurrent traces form part of the horizontal plate, enlarging it. Accordingly the median-parallel sectors seem to arise directly as two lateral derivatives rather than in the way described above (Figs. 5 A, 6 A). In transverse sections of adult material, at the main level of the horizontal plate or slightly above, the ascendent border traces indicate the adaxial borders of the two sectors whereas ascendent peripheral segments of the recurrent traces indicate the abaxial borders (Figs. 5 A, 6 B).

From middle border traces further amounts of ventral traces arise and unite along the course already existing.

When the series of border traces arise approximately parallel to each other, which seems to be the ordinary condition, the opposite series of vertical border traces divide in the transmedian plane. The resulting ends of opposite series bend inwards and grow horizontally towards each other, traversing the separating parenchyma (Fig. 6 C). They meet and unite, forming two opposite, transmedianly extended series of strands. These subsequently turn the xylem abaxially. At successively higher levels the united series bend upwards, initially diverging from each other (Figs. 6 D, 1 C). They ascend in the central column, constituting the middle parts of the united ventral bundles. The outer parts of the medianly extended series of border traces become partly, by gradual adjustment of their position at appropriate levels, incorporated in the united ventrals and partly involved in the organization of a further kind of carpellary vascular traces (see below).

Another way of originating and uniting additional ventrals by rearranging middle parts of border trace series is seen when the latter do not arise parallel to each other but along two finally touching convex curves (Fig. 5 B). These break at the point of contact, and the detached parts underneath one and the same carpel unite. In this case horizontal growth of involved elements, though occurring, seems to be of little consequence, the crucial touching curves of the two border strand series having been brought about by adequate horizontal growth at the level of the median-parallel sectors (Fig. 5 A). The last mentioned course was observed only in one series of transverse sections (Sagot 49).

Those outer parts of border trace series that

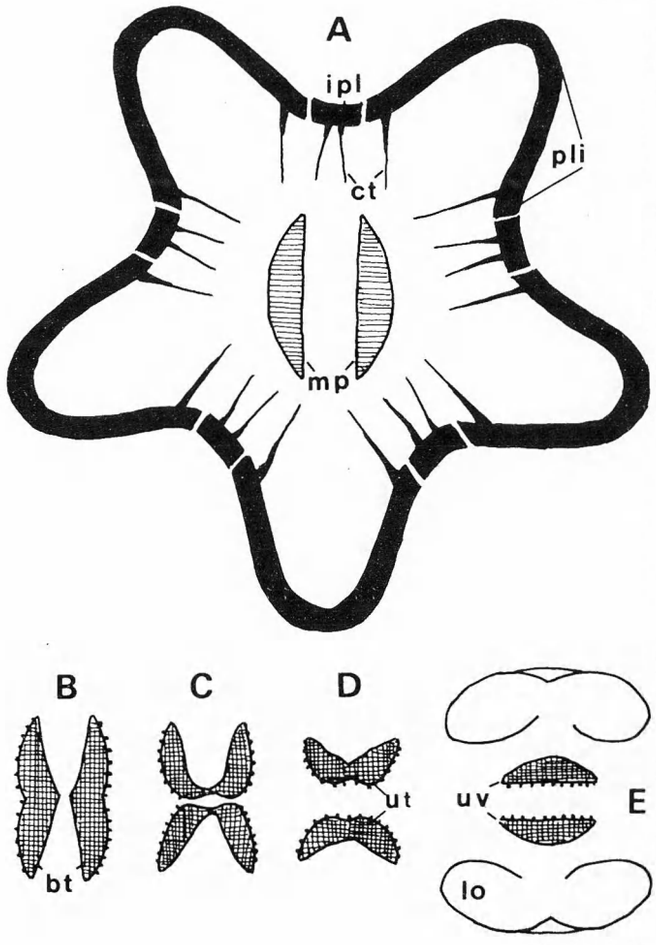

Fig. 4. *Quararibea guianensis.* TS diagrams of young flower bud. – A: Ultimate 5-plicate stele, inceptive carpel trace departure and median-parallel sectors projected into one plane. – B–E: Transformation of border traces into ventral bundles. – bt border traces, ct carpellary traces, ipl interplical stelar segment, lo locule, mp median-parallel sectors, pli ultimate stelar plica, ut united ventral traces, uv united ventral bundles. – Striation denotes horizontal, cross-hatching vertical strands; dots indicate phloem position.

were not consumed in forming united ventrals terminate somewhat converging. The open spaces left between their ends are filled in by traces from median points of the stele. In this way two slightly arcuate series of carpellary traces are formed (Fig. 6 D). These traces will be termed the *intermediate carpellary traces*. They run a short way upwards, entering the placenta as *intermediate carpellary bundles* (see "Placenta").

Outside each series of intermediate traces additional traces arise that will be termed the *endocarp zone carpellary traces* (Figs. 5 B, 6 E). These emanate from median and, later on, also from more lateral stelar bundles. Their peripheral parts will join the recurrent traces while inner parts will be seen to 'branch off' upwards (Fig. 1 C, arrow). In the receptacle bottom the endocarp zone traces form arcs that may be connected to the arcuate series of intermediate traces (Fig. 6 E). In their ascending course the arcs of *endocarp zone carpellary bundles* encircle the locules, reaching as far as to the ventrals (Figs. 5 D, 6 F). The endocarp zone bundles branch and anastomose and become numerous but remain thin and to a large extent incomplete (without tracheary elements) or provascular.

No definite dorsal carpellary bundles were identified.

The ovarian tissue that will form the mesocarp of the fruit is traversed by the *mesocarp zone carpellary bundles* (Figs. 5 E, F, 7 A). These are mainly supplied from the hypanthial stele by collateral or provascular traces. Traces coming from relatively basal parts of the hypanthium may partly join the recurrent traces while those coming from upper parts take a separate downward course to their points of entrance into the mesocarp zone (Fig. 1 B, C). They proceed upwards in the mesocarp zone as provascular or collateral vascular bundles, anastomosing and repeatedly branching. In the upper part of the free ovarian top some thin branches may have attained an amphicribral condition. – An additional vascular supply to the mesocarp zone comes from endocarp zone bundles that branch off strands outwards-upwards from the top of their zone (Figs. 1 C, 5 F; see also below).

Although there is great variation in different specimens, the united ventral bundles are strong veins, containing c. 8–14 xylem files. The united ventrals run medianly in the central column, each taking its place inside one locule (Figs. 5 C, 7 A, B). Thus, their union is homocarpellous sensu Eyde & Tseng (1971), as a consequence of the course of union accounted for. At a level not much below the upper limit of hypanthial adnation the united ventrals branch off traces supplying the ovules. Above this level the united ventrals disunite, forming each two individual ventral bundles (Fig. 5 E). The two ovule traces emanate from the middle part of the united ventrals and turn the xylem away from each other, toward each of the receiving ovules.

Terminus of carpellary bundles. The four individual ventrals resulting from the disunion are continuous upwards in the ovary and throughout the length of the style (Figs. 1 A, 3 D). At the top level of the locules some endocarp zone bundles migrate into the mesocarp zone and a few endocarp zone bundles join the four ventrals and partly fuse with them. The fusion results in four amphicribral bundles. Between them are usually some remaining small bundles, mostly provascular strands or bundles devoid of tracheary elements. In the lower parts of the style these 'extra' bundles may lengthen tangentially and partly fuse with the four 'main' stylar bundles and together with them form an incomplete ring. Further upwards in the style the vascular tissue may gradually be much reduced. It enters the two stigma lobes as two tangentially extended arches, one outside each of the separate strands

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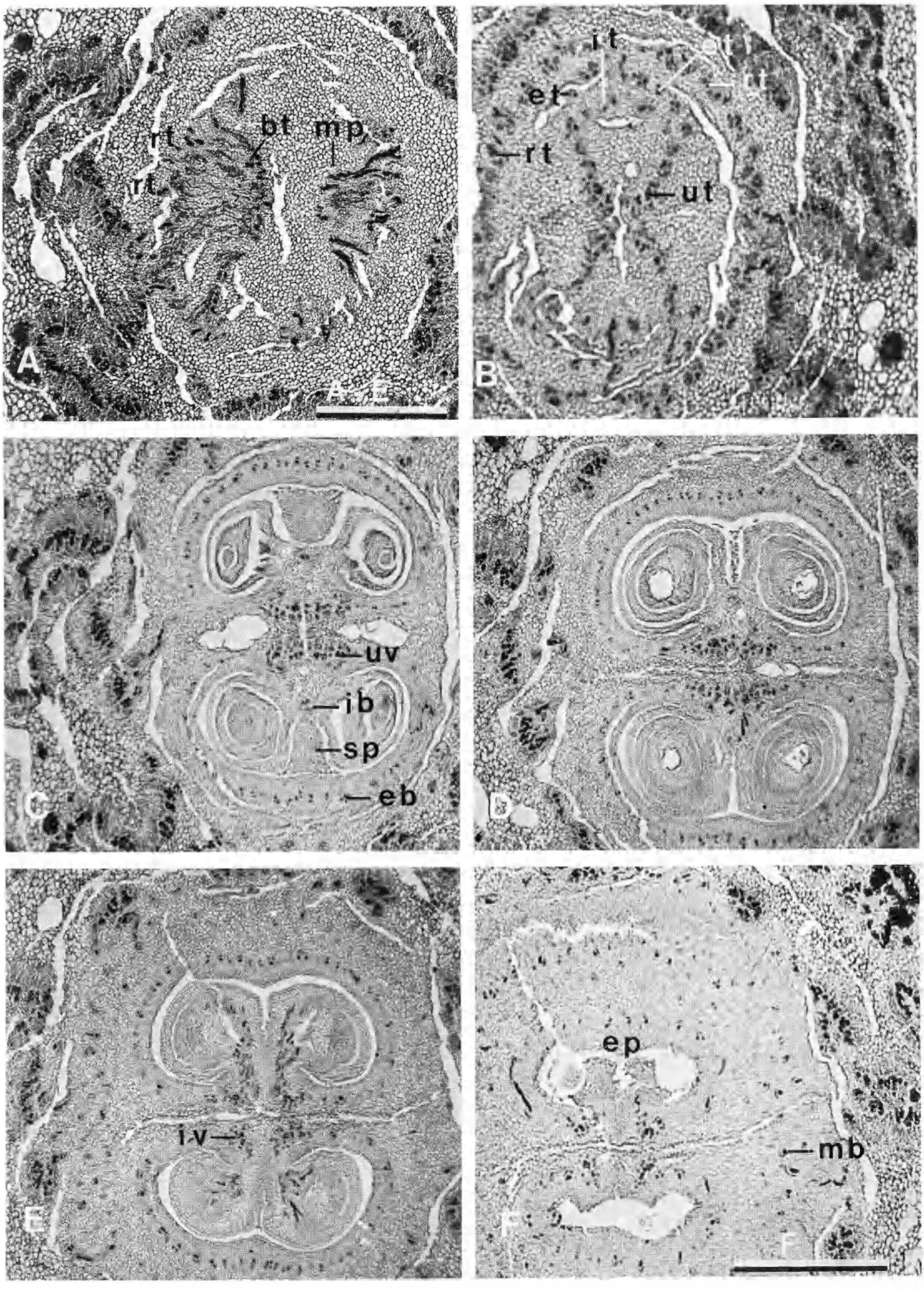
Fig. 5. *Quararibea guianensis*. Sagot 49. Flower. Series of slightly oblique TS showing central parts of receptacle and ovary. Fissures caused by specimen drying. – A: Horizontal plate of the receptacle, 'convex front type' of median-parallel sectors. Sector to the right not yet completed, that to the left already passing into recurrent traces and border traces. – B: Appearance of united ventral, intermediate, endocarp zone, and recurrent traces in the receptacle. – C: Lower part of ovary. Sterile projections broad, not adnate to the locule wall. – D: Ovular traces approach intermediate bundles. – E: United ventrals giving off ovular traces and splitting up into individual ventrals. Entry of mesocarp zone traces. – F: Endocarp zone bundles at the top level of locules migrate into the mesocarp zone. – bt border traces, eb endocarp zone bundles, ep emarginate sterile projection of fused carpel margins, et endocarp zone traces, ib intermediate bundles, it intermediate traces, iv individual ventral bundles, mb mesocarp zone bundles, mp median-parallel sector, rt recurrent traces, sp sterile projection of fused carpel margins, ut united ventral traces, uv united ventral bundles. – Scales 0.5 mm.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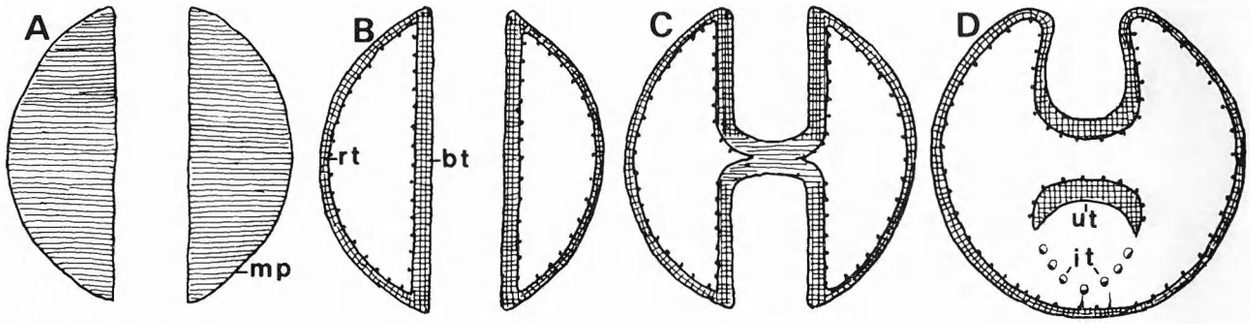


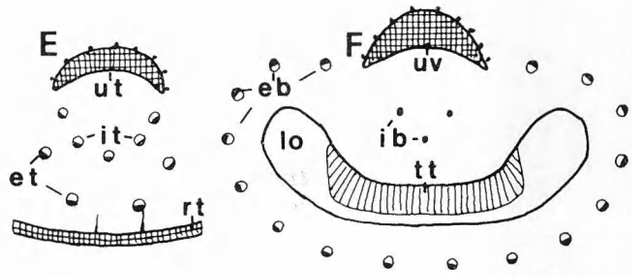


Fig. 6. *Quararibea guianensis*. TS diagrams of flower. – A: Median-parallel sectors at a low level. – B: Median-parallel sectors at a higher level transformed into border traces and recurrent traces. – C: Division of border trace series and horizontal connection of parts. – D: Formation of united ventral traces and intermediate traces. – E: Origin of first endocarp zone bundles. – F: Ovary bottom. Locule encircled by endocarp zone bundles; intermediate bundles reduced. – bt border traces, eb endocarp zone bundles, et endocarp zone traces, ib intermediate bundles, it intermediate traces, lo locule, mp median-parallel sectors, rt recurrent traces, tt transmitting tissue, ut united ventral traces, uv united ventral bundles. – Striation denotes horizontal, cross-hatching vertical strands; dots indicate phloem position.

of transmitting tissue (see below). Most of the mesocarp zone bundles end in the ovary parenchyma, a small number of them follow an upward course into the basal region of the style but do mostly not reach far and are absent from the main part of the style.

Placenta

The fused involute margins of each carpel abaxially form a *sterile projection,* protruding between the two ovules of the locule (Figs. 5 C, D, F); adaxially of this they form the placenta occupying the submarginal areas. The intermediate carpellary bundles of the placenta are just to the inner side of the sterile projection. When entering the placenta from below they may retain the somewhat arcuate arrangement of the traces and together with the united ventrals compose an abaxially thinned vascular ring. At successively higher placental levels the intermediate bundles mostly loose their tracheary elements and obtain a more irregular grouping. They fuse partly or completely, making one to three bundles in each of the placentas (Fig. 5 C). The ovular traces, given off from the united ventrals and descending into the placentas, join the intermediate bundles before entering the ovules (Figs. 5 D, 7 B).

Ovules

The ovules are small (c. 0.5 mm long) and broadly grown on to the placenta almost from their top all the way downwards. The micropyle faces the bottom of the locule. The position of the micropyle relative to the hilum suggests an origin of this ovule type from an anatropous (and apotropous) ovule through elimination of the funicle.

In regular transversal as well as longitudinal sections the ovules appear obliquely cut. This will, essentially at least, be due to the fact that the nucellar longitudinal axes of the ovules downwards deviate from the direction of the floral axis adaxially parallel to the median plane and abaxially parallel to the transmedian plane of the flower.

Locules

The locules are invested with about four anticlinally dividing, distinct cell layers outside succeeded by a similarly encircling tissue consisting

of cells that divide in various planes. These tissues, together constituting the future endocarp (or the essential part of it), are here referred to as the *endocarp zone* (Fig. 7 A). The outer part is traversed by the endocarp zone bundles. Adaxially the placenta takes the place of the endocarp zone. The fused carpel margins connect the bottoms with the tops of the locules but are essentially free from the abaxial parts of the locule walls. Their abaxial parts, or sterile projections, fill out the space of the locules not occupied by placenta and ovules and are accordingly modelled. They expand with their lateral edges, more or less, to both sides outside the ovules at middle levels and are emarginate or bilobed above (Fig. 5 C, F). Transmitting tissue covers most of the free surfaces of the placenta and sterile projections.

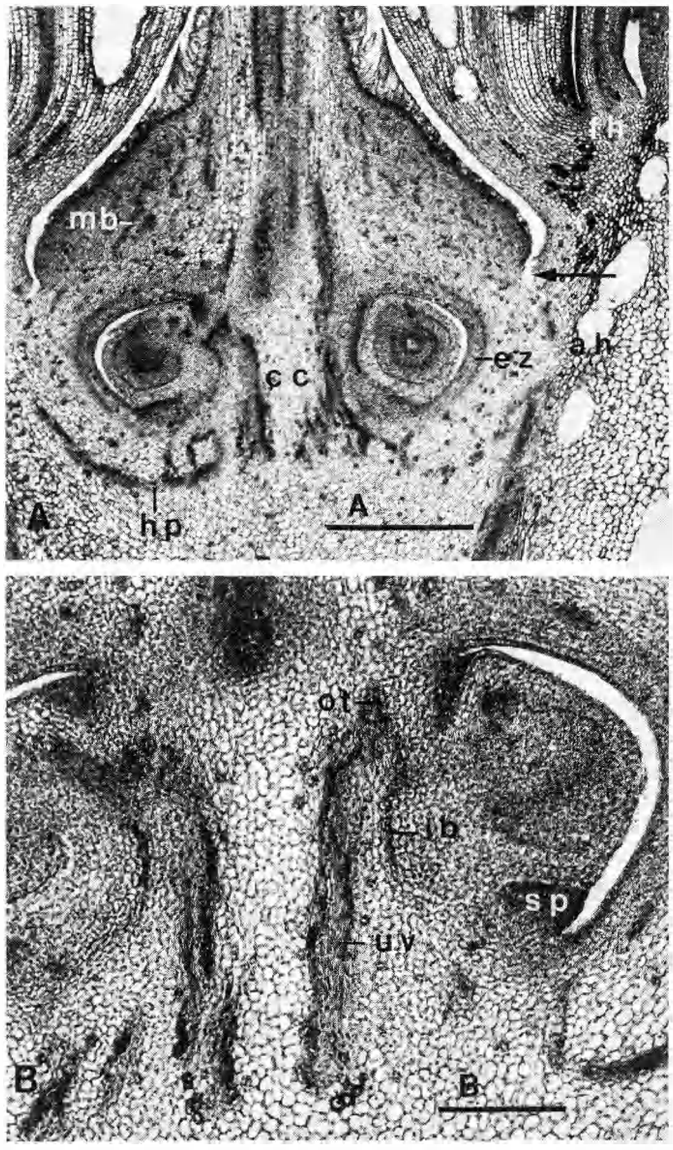


Fig. 7. *Quararibea guianensis*, IPEAN 1975. Large flower bud. – A: Median LS of ovary. Short vertical split in the uppermost region of ovary adnation to hypanthium (arrow). – B: Median LS of ovary, central part. Ovular traces joining intermediate bundles. – ah adnate hypanthium, cc central column, ez endocarp zone, fh free hypanthium, hp horizontal plate, ib intermediate bundles, mb mesocarp zone bundles, ot ovular trace, sp sterile projection of fused carpel margins, uv united ventrals. – Scales A 0.5 mm, B 0.2 mm.

Transmitting system

Two separate, solid transmitting strands, one from each of the papillose stigma lobes, join below, forming a double transmitting path that is uniform through most of the style. When descending into the widening stylar base the strands diverge. A short way downwards they become connected by a tissue composed of median cell-rows (a 'compitum', see below; Figs. 1 C, 3 C). Above the placentas the transmitting strands pass into the emarginate or bilobed sterile projections. The terminus of the transmitting system is supplied by the locule wall bottoms, which underneath the ovules form a cushion of transmitting tissue depicting the micropyle region.

The median cell-rows have distinctive compound middle lamellas. These are incrassate at the cell corners and stain heavily with tannic acid and iron alum, indicating abundance of pectic substances. Thus the median cell-rows are apparently suited for pollen tube growth and obviously form a path that allows the pollen tubes to choose their way to an optional locule. Carr & Carr (1961) draw the attention to the functional significance of a syncarpous gynoecium serving the purposes indicated above and suggest that this kind of connection should be called a compitum. The median cell-rows described above are located to the transition region of style and ovary and become disorganized below the top level of the locules. The disorganization begins at the center (Fig. 1 C).

Inferior part of ovary

At anthesis the ovary proper is a very small part of the flower. The vertical extension of the young receptacle is small relative to the width of the stele. The intercalary growth of the

hypanthium includes an upward prolongation of the disintegrating receptacular stele. The direction of the initial intercalary growth, as indicated by files of cells in the parenchyma underneath the basal carpel parts, is somewhat arcuate out- and upwards (Fig. 7 A). This direction of growth is concordant with the course of the recurrent carpellary trace segments. Because of this pattern of growth the receptacle becomes cup-shaped inside.

Since carpellary traces enter the carpels along the extension of the adnate hypanthium, this is interpreted as being the enlarged insertion region of the carpellary whorl. During the intercalary growth of the hypanthium the bases of the carpels, by this interpretation, spread upwards in the same measure as their receptacular insertion region extends. Consequently, the ovary becomes invested by the receptacle up to the level where the insertion of the carpellary whorl terminates. The expansion of the hypanthium and the carpel bases is obviously by means of an out- and upwards moving intercalary growth region. The formation of the carpellary traces branching off from the recurrent traces and of those deviating from stelar bundles above is apparently co-ordinated in time with the ascending hypanthial growth and with the spreading of the carpel bases. In the free part of the hypanthium, which is conceived to be cortical, the stelar bundles are succeeded by androperianthal traces (Fig. 3 B).

Free part of ovary

The free part of the ovary is thickened all around by periclinal divisions in a subepidermal file meristem. The resulting files of cells are nearly perpendicular to the ovary surface. The inner parts of the files are slightly curved downwards and abut to the primary mesocarp zone parenchyma or, at higher levels, to the parenchyma of the central column. This is composed of relatively large cells forming axial files continuous with the corresponding files of stylar parenchyma.

In the transition region of ovary and style the mesocarp zone files become shorter. The outline of the ovary in this region shows a slight constriction (Fig. 7 A) that is represented in the mature fruit by a mamillate appearance of its top. The derivatives of the lateral file meristem at anthesis constitute the main part of the mesocarp zone and a prominent part of the ovary as a sterile addition above the ovarian cavity. After fertilization the activity of the lateral file meristem is increased.

The tissues occupying the border region between the adnate and free parts of the ovary lack a strengthening of the cell walls and often show a vertical split (Fig. 7 A, arrow). This may be an artefact but will at least partly be caused by a tearing owing to the fact that the hypanthium in this region shows a slightly stronger upward growth than the ovary proper.

Superior fruit

An essentially superior fruit develops in *Q. guianensis* from a more or less inferior ovary, since the growth of the free part of the ovary is strongly furthered as compared with that of the invested part (Figs. 1 C–E). A degree of release of the ovary proper from the adnate hypanthium is probably also involved. This partial release may be accomplished through the above mentioned split.

A vigorous but mainly radial growth of the previously cup-like receptacle also takes place during the fruit development. The fruit is partly enclosed by the accrescent, stout calyx tube which is hypogynous in appearance (Fig. 1 E).

Special cell types

Tannin cells, inclusive of phlobaphene or 'pigment' cells, are fairly evenly distributed throughout the tissues. Early matured phlobaphene cells are abundant in the parenchyma of the receptacular horizontal plate. A consistent accumulation of tannins also occurs in the transition region between the free and adnate hypanthium parts.

Calcium oxalate druses occur mainly scattered in the parenchyma of endocarp and mesocarp zones and pith, and accompanying the carpellary strands.

Lysigenous mucilage cavities occur in most parts of the flower, even in the youngest material examined. They are similar to those in young shoots of *Tilia platyphyllos* Scop. (Walliczek 1893). In *Q. guianensis* they are rounded, 50 to 300 μm in diameter, and often rhexigenously

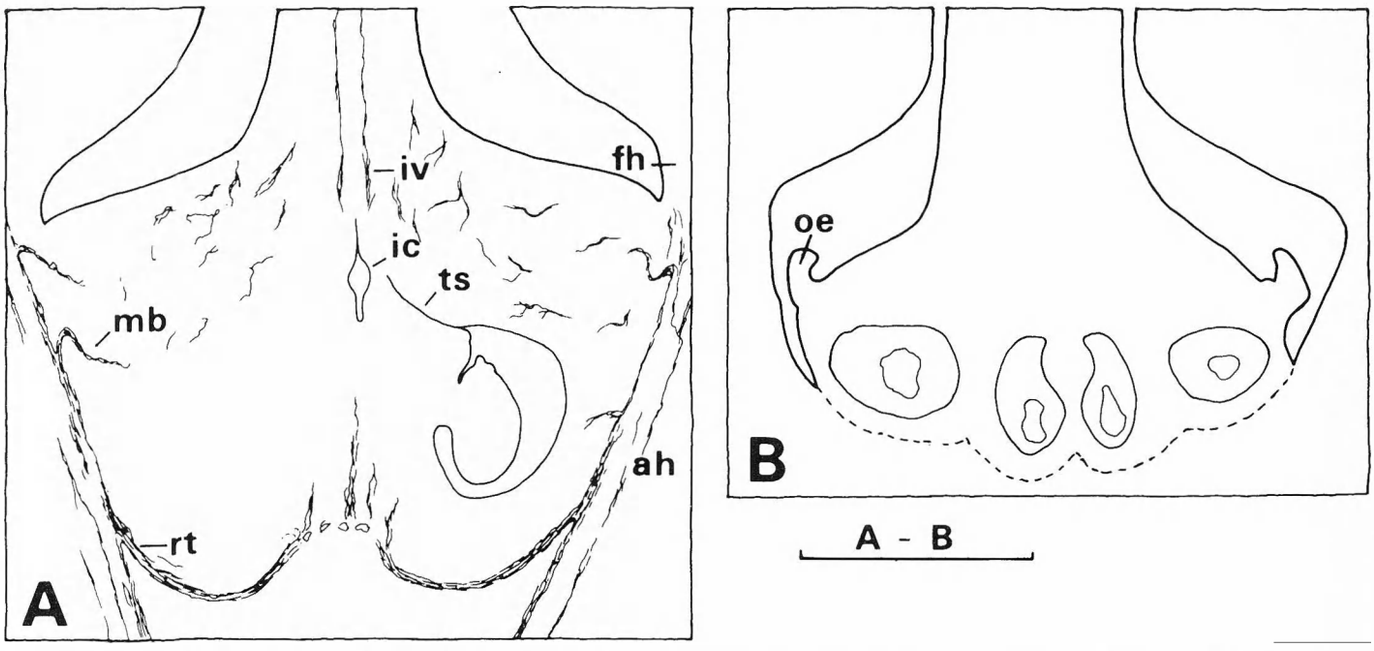


Fig. 8. *Quararibea cordata*. Large flower buds. LS of ovaries, outer parts omitted. – A: Tessmann 3087. – B: Schultes 6073. Margins of ovary proper separated from adnate hypanthium some distance down. – ah adnate hypanthium, fh free hypanthium, ic intercellular cavity, iv individual ventral bundles, mb mesocarp zone bundles, oe edge of raised ovarian margin, rt recurrent traces, ts transmitting strand. – Scale 1 mm.

enlarged, particularly lengthwise. They consist of up to 20 mucilage cells with eccentrically or sometimes concentrically lamellate walls. Two large mucilage cavities or groups of cavities are generally present in the septum of the ovary, one on each side of the axial centre. Mucilage cavities constitute a substantial part of the floral tissues but are absent from the pith of the receptacle.

Quararibea cordata

The pedicel has three minute bracteoles at its lower part. The gynoecium has five carpels; the ovary is 5-locular, subinferior, the free part 5-angled, the locules biovulate, and the placentation axile. A cup-like hypanthium is formed and has a long lower part adnate to the ovary and a short upper free part on the rim of which the androperianthal appendages are born. The style is filiform but sometimes swollen at the base, 5-angular or 5-sulcate, and the stigma is peltate. Glandular nectaries occur within the calyx. The fruit is a globose mamillate drupe that is c. 8 cm long, fleshy fibrous, and has five one-seeded stones; the seeds are up to 5 cm long and the fructiferous calyx is thick and shallowly cup-shaped.

Floral axis

The slightly 5-angular pedicel has a 5-angular or 5-plicate eustele and a cortical system of amphicribral vascular bundles with endarch xylem. The undermost part of the stele is structurally similar to that of *Q. guianensis* but differs in the occurrence of libriform fibres in the secondary wood and, at lower levels, a scattered distribution of fibres in the phloem. At higher levels, fibres located on the periphery of the phloem predominate. Above the divergence levels of the bracteole traces, xylem as well as phloem fibres terminate. Simultaneously the first small amphicribral bundles appear in the cortex. These bundles arise de novo in the ground tissue in the same way as in *Q. guianensis*. Upwards the cortex bundles enlarge and start branching a short distance above their level of origin. They do neither become as numerous as in *Q. guianensis* nor do they show any tendency towards sclerification. They are continuous through the floral axis and the abaxial tissues of hypanthium and calyx.

Subinferior ovary

The subinferior ovary of *Q. cordata* is interpreted on the same grounds as that of *Q.*

guianensis as having originated by cup-like growth of the insertion region of the carpellary whorl. The dorsal sides of the carpels are free as in *Q. guianensis*. The ovary proper is, however, invested by the receptacle to a considerably higher level than that of *Q. guianensis* (Figs. 8 A, 9 A).

Most of the true ovarian tissue is composed of very small, tightly connected cells with thin walls. This tissue encloses the five locules and the pithlike central column and also makes up the mesocarp zone of the ovary top (Figs. 9 A, B). The endocarp zones, surrounding the locules, exhibit their distinct character in this tissue. They are extremely fine-celled and composed of two concentric zones that are organized in conformity with those of *Q. guianensis*.

The ovules, being devoid of funicles, are broadly adnate to the placenta. The adnation involves mainly the upper portion of the ovules although that amounts to nearly half their length. The micropyle faces the bottom of the locule.

The placenta appears, in transverse sections through the locules, at the middle of their height as a large rounded projection that on its outside bears the ovules (Fig. 9 B). At that level the fused margins of each carpel are not prolonged to form a terminal structure of the kind seen in *Q. guianensis*. Just above the level where the adnation of the ovules to the placenta ceases, however, the fused margins are modified to a sterile emarginate end structure (Fig. 10 D). Downwards, where the undermost parts of the ovules are seen to be free from the placenta, the fused carpel margins reach the abaxial part of the locule wall and unite with it forming an incomplete septum, dividing the undermost part of the locule into two bottom compartments (Fig. 9 B). The free surfaces of the fused carpel margins are covered throughout with transmitting tissue. This is best developed on the emarginate end structure.

The mesocarp zone above the locules grows by a subepidermal file meristem. The files are prevailingly axially aligned but there is some variation in this respect.

In some specimens (Schultes 6073) the margin of the ovarian top is raised along the adnate hypanthium above the central ovarian top surface (Fig. 9 A, arrow). This condition is interpreted as an indication that only those carpel parts being contiguous to the hypanthium were participating actively in the final phase of insertion region prolongation. In a series of longitudinal sections (Schultes 6073) the edge of the raised ovarian margin was found to be slightly bent inwards (Fig. 8 B). Moreover, the edge and a further part of the ovary had become disconnected with the hypanthium, which was ruptured close to the ovary proper down to the middle level of the locules. This will be due to excessively continued upward growth in the outermost carpellary tissues.

Superior fruit

A weakness and a tendency to split was observed in the border region between the adnate and free parts of the ovary in *Q. guianensis*. It was suggested that this tendency constitutes a contributory factor in the development of an essentially superior fruit from the subinferior ovary. A similar suggestion may be warranted in the case of *Q. cordata*, since the calyx is inserted at the base of the fruit. The essential cause of such a development, however, will be the same as in *Q. guianensis*, viz. a strongly furthered growth of the free and released parts of the fertilized ovary.

Carpellary bundles

Four separate kinds of carpellary vascular bundles will be described, viz. ventral, dorsal, endocarp zone, and mesocarp zone vascular bundles.

In the receptacle, below the ovary proper, a somewhat irregularly developed counterpart to the horizontal plate of *Q. guianensis* is formed. This is supplied by amphicribral recurrent traces (Fig. 8 A) coming from lower parts of the hypanthial stele. The horizontal plate is a network of such traces, most of which are provascular.

Ten mature amphicribral traces, which arise in pairs from the horizontal plate, constitute the individual ventral traces. These ascend in the central column, uniting two and two along the locular radii. The united pairs by degrees become inversely collateral, constituting the five united ventral bundles. These, hence, are homocarpellous. They run inside the locules (Fig. 9 B) a short way upwards before giving off ovule traces and splitting into the individual ventrals (Fig. 10

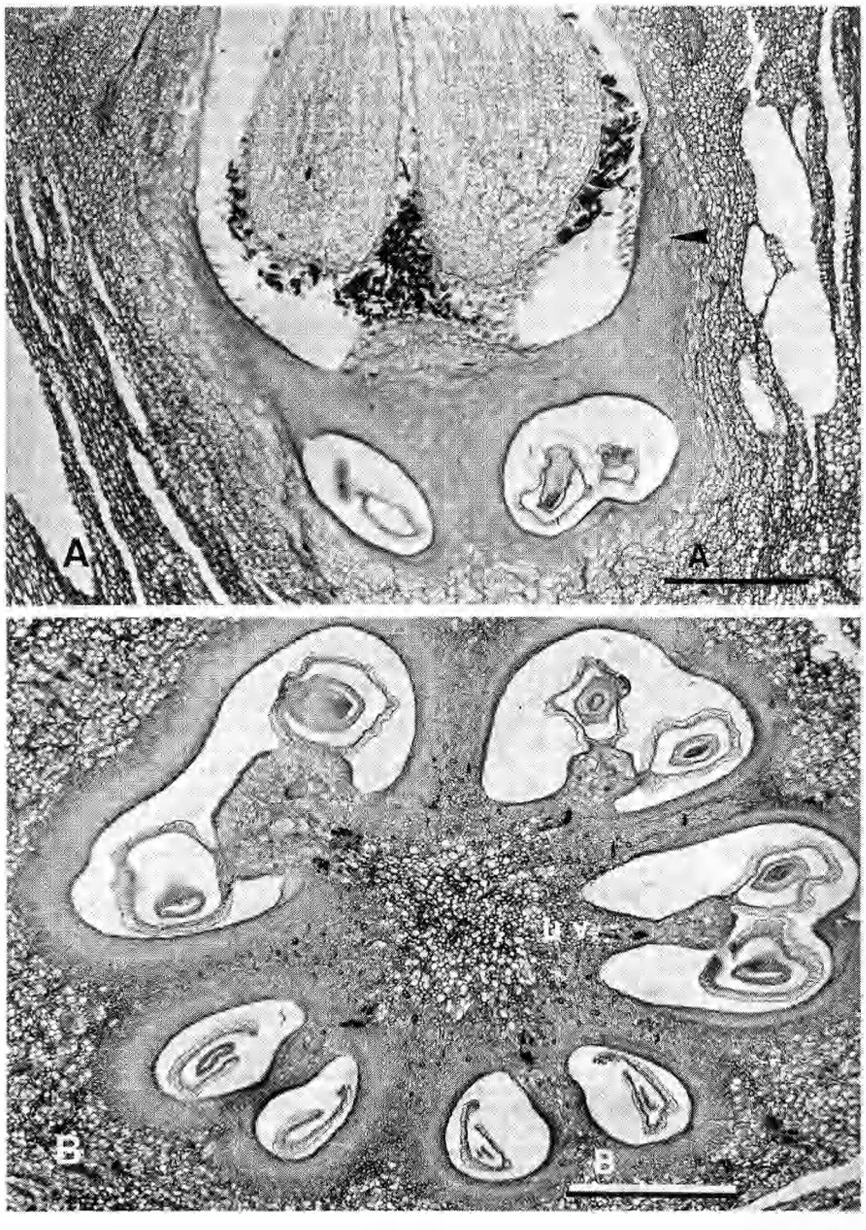


Fig. 9. *Quararibea cordata*. Schultes 6073. Large flower buds. – A: LS of ovary (outer parts omitted) and the swollen style base. Raised margin of ovarian top indicated by arrow. – B: Slightly oblique TS of central part of the ovary. Two locules (in the lower part of the figure) are each divided into two bottom compartments. Upper left locule supplied by a double set of ventrals, an anomalous condition. – uv united ventrals. Scales 0.5 mm.

D). The presence of intermediate carpellary bundles in the outer part of the placenta could not be ascertained. Above the departure of ovular traces a portion of phloem is attached to the ventral bundle xylem abaxially. Above the placental levels of the ovary and in the style the phloem surrounds all sides of the xylem except the side facing the other bundle in a pair of individual ventrals (Fig. 10 B).

Dorsal carpellary bundles may be present in some but absent in other flowers of the same collection. Dorsal traces given off from hypanthial stelar bundles enter the carpellary tissues as five slender collateral bundles at or above the summit level of the locules. They are continued in the style. The departure level of the dorsal traces is variable, even within a single flower. The departure thus may be just outside the entry into the ovary or, in other cases, just above the departure level of the recurrent traces.

The outer parts of the endocarp zones are supplied by provascular strands ascending from the horizontal plate. The endocarp zone bundles are mostly provascular, thin and sparse and often deviate into the mesocarp zone.

The mesocarp zone is supplied by provascular or amphicribral traces given off from hypanthial bundles (Fig. 8 A). The mesocarp zone bundles are provascular to amphicribral and branch mainly in the upper part of the zone.

Transmitting system

The following account is based on transverse and longitudinal sections of large flower buds coming from one and the same collection (Schultes 6073). The stylar transmitting tissue consists of five strands being the edgings of a longitudinal, solid, 5-angular core (Fig. 10 A). The core is obviously a compitum and similar to that of *Q. guianensis* as regards cell type. The transmitting strands are on the locular radii as are also the pairs of individual ventrals. These run some distance outside the strands. Between the ventrals and the strands are fine radial connections, one from each of the individual ventrals (Fig. 10 B). In the formation of these connections transmitting tissue as well as columnar parenchyma and ventral bundle phloem take part. Every two connections coming from a pair of ventrals converge and join the corresponding transmitting strand.

At successively lower levels the five angles of the core extend as thin radial wings. These lengthen to the extent that their edgings, i.e. the transmitting strands, move out- and downwards. Correspondingly the connections gradually shorten. In the upper region of the ovary each of the strands passes between the individual bundles of a pair of ventrals (Fig. 10 D). From there it goes nearly horizontally into an adaxially tapering bulge of its proper locule, just above the emarginate structure (Fig. 10 C, D).

The function of the connections between the transmitting strands and the ventrals is obscure. They may be supposed to indicate a dependence of the transmitting strands on the ventral vascular bundles for supply of solutes.

In the undermost part of the style the transmitting strands are disengaged from the wings of the core, and the core cells lose their features of specialization. Already before the disengagement of the transmitting strands the wings become somewhat branched; downwards they vanish. Meanwhile five new, subsequently somewhat branching wings are formed from the core. These are on the septal radii. Further downwards the resulting winged core forms a 5-armed intercellular chink. This is continued for a short distance, below showing a centrally widened cavity (Fig. 10 D) and finally closing at the placenta level of the ovary. The chink and the cavity are lined with a large-celled epidermis. They represent incomplete union of carpel surfaces.

Special cell types

Phlobaphene cells, most of which are probably artefacts originating from tannin cells during drying, occur scattered, often alternating with cells devoid of coloured contents. They are mainly found in the parenchyma of the horizontal plate and of the continuations of the stele. In the central column the phlobaphene cells occur mainly in the central part and around the ventrals.

The number of druses is considerably larger than in *Q. guianensis*. They are most abundant in the mesocarp zone and peripheral parts of the receptacular pith and central column. The endocarp zones, the central parts of the receptacular pith and central column, and the parenchyma sheathing the ventral vascular bundles are almost entirely free of druses.

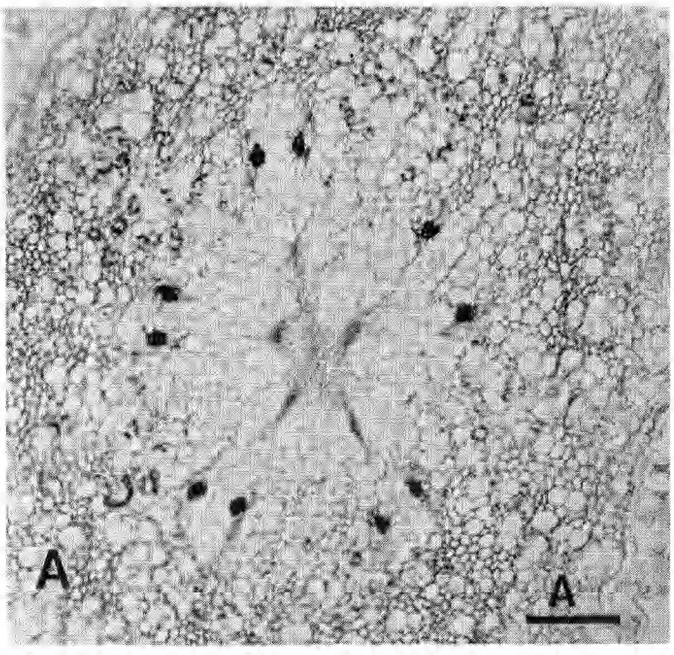
Lysigenous mucilage cavities occur in most parts of the flower. They are clearly the same as those described in *Q. guianensis* and show a similar distribution. They are absent in the receptacular pith, in the central column, and in the fine-celled ovarian tissue.

Discussion

Vascular supply

In the description of the vascular supply of the ovary five kinds of vascular bundles were distinguished, viz., ventral, dorsal, intermediate, endocarp zone, and mesocarp zone bundles. The ventral and dorsal bundles correspond to bundles usually so designated while the remaining types call for some discussion.

Fig. 10. *Quararibea cordata,* Schultes 6073. Large flower bud. – A: TS of style. Transmitting strands edging the 5-angular compitum core show fine connections with pairs of individual ventrals. – B: TS of style, undermost part. – C: LS of ovary, transmitting strand passing into a locule. – D: TS of ovary, upper part. Transmitting strands between individual bundles of ventral pairs (to the left) and passing out in a locule above its emarginate structure. Intercellular cavity in central column. – db dorsal carpellary bundle, ep emarginate sterile projection of fused carpel margins, iv individual ventral bundle, lo locule, ts transmitting strand. – Scales A–C 0.1 mm, D 0.2 mm.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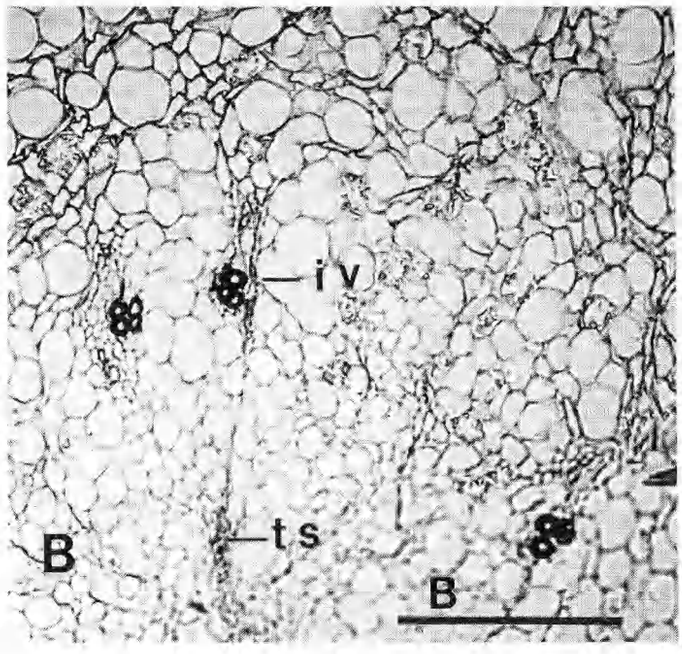
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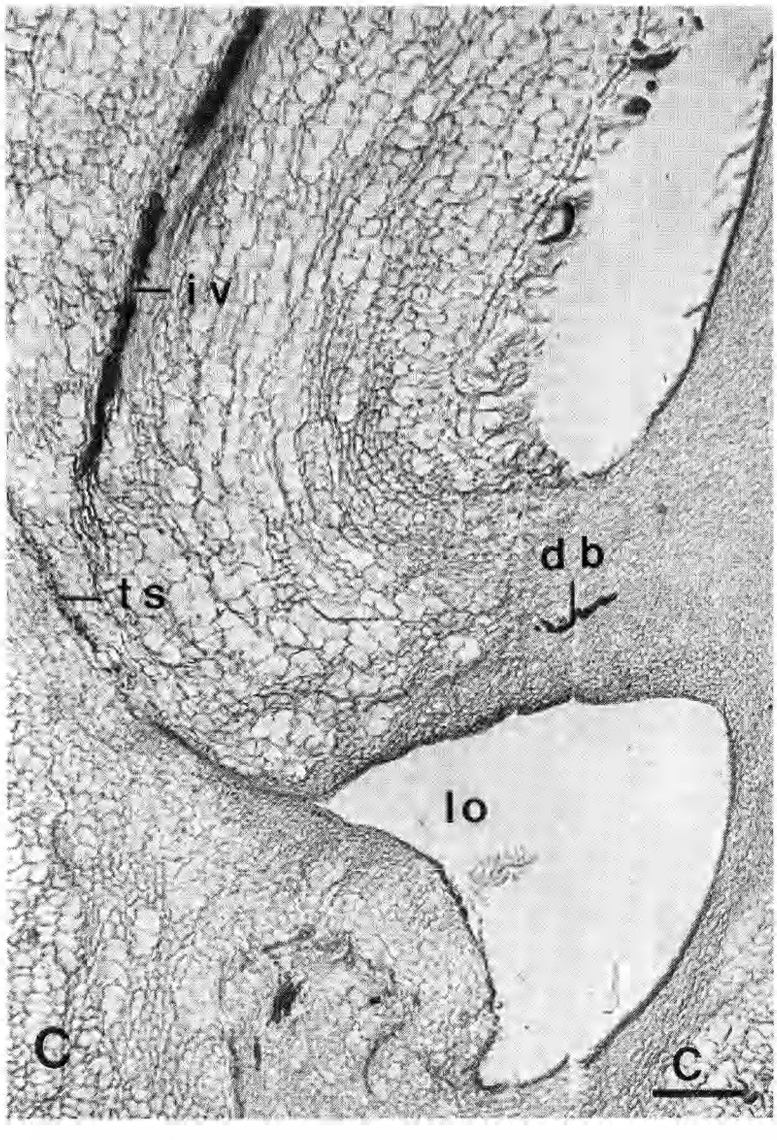
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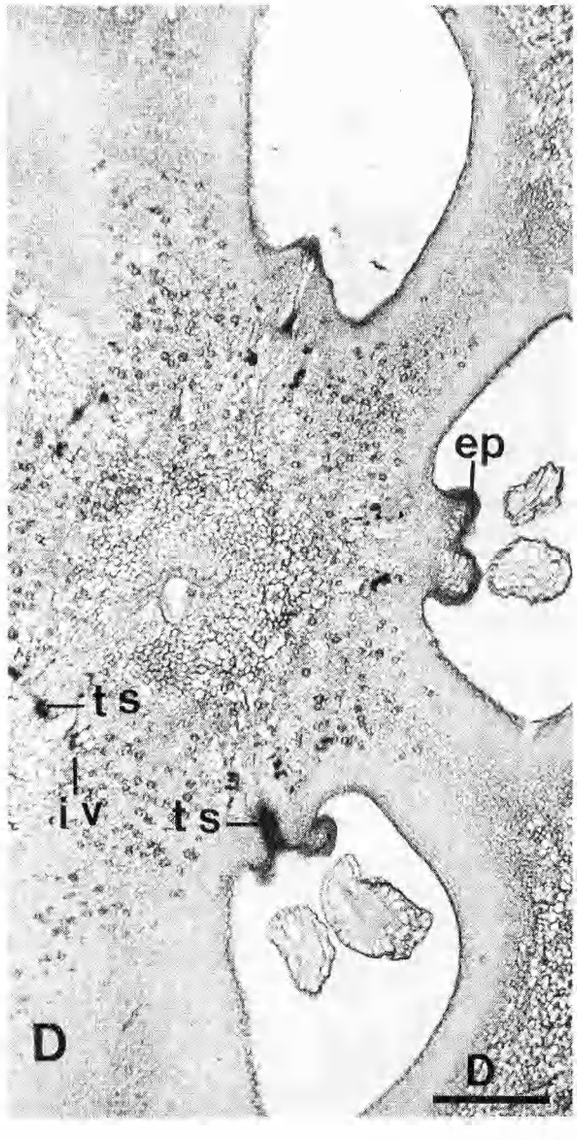
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Reduction in number and in formation of tracheary elements is involved in the development of the intermediate bundles in *Q. guianensis*. Nevertheless, the intermediates do not give the impression of being functionless vestiges and it would be difficult to explain them as such. They take their position in a placenta that is broadly adnate to the ovules, a condition which has probably developed through elimination of the funicle. Moreover they join the ovule traces which come from the ventrals. It seems plausible that their presence is associated with the elimination of the funicle and that they may be regarded as modified ventral branches. The common origin of the ventrals and the intermediates from the border traces of the receptacle bottom and the vascular ring formed by the two kinds of the bundles in the subplacental tissues support this interpretation.

The endocarp and mesocarp zone bundles constitute a main carpellary supply. They have much in common: both arise as thin bundles from a large number of traces, branch extensively and are to a large extent immature at anthesis, supplying tissues that form the pericarp of the fruit. The difference between them is mainly topographical.

The precocious departure of sepal traces from supernumerary stelar plicae asks for an interpretation. The supernumerary plicae of the pedicel most likely supply traces to supernumerary calyx segments. These may be bracteoles in origin, together with the five sepals proper forming the calyx tube.

Ovary position

The subinferior position of the ovary is interpreted as a result of the upward expansion of the insertion region common to the receptacle and the carpels. This position is not associated with an invagination of the floral axis, since no stelar parts are 'recurrent' or inverse. Nor is adnation of androperianthal parts to the ovary involved. An acceptance of the latter way of origin, i.e. accordant to the appendicular theory, would imply that the vascular strands that are here regarded as stelar bundles of the hypanthium should be interpreted as appendicular traces. In my opinion, however, the recurrence of the ventral and endocarp zone traces and the course of the mesocarp zone traces demonstrate that the hypanthial strands, from which these traces emanate, are stelar bundles.

An axial nature of the simple hypanthium has been suggested, for instance, by Bugnon (1926) and Bugnon & Bugnon (1953) for *Begonia* and by Leins (1972) for inferior ovaries in general. The proposition of Leins (1972) that "the base of the carpels elongates to the same extent as the intercalary 'cup' grows up" corresponds to my conception of the relation between the carpels and the intercalary receptacular cup, or hypanthium, in *Quararibea*. The conceptional agreement does not, however, include the structural evidence referred to. The type of a more or less inferior ovary reported here, characterized by the deviation and recurrence of carpellary traces from the vascular bundles of a simple hypanthium, seems not to have been described before.

Adaptive significance of ovary position

According to Grant (1950) *Quararibea, Matisia,* and many other genera of the Malvales show adaptation to bird pollination by means of the sheathing stamen column, which protects the ovary and ovules against the destructive habits of the birds. In *Quararibea* there are some further morphological features, which seem to be important in protecting the ovules. Thus a spatial separation of the nectaries and the ovary is brought about through the upward continuation of the hypanthium above the ovary. The nectaries are at the inside base of the calyx tube, viz., above the rim of the hypanthium. These species thus may be classed among those bird flowers in which, according to Grant, perigyny is a means of ovule protection.

The addition of mesocarp zone tissue by a file meristem also contributes to protect the ovules.

The small size of the ovules in relation to the ovary, though important in ovule protection, also will imply that the seeds must increase in size considerably during development. This, however, will be compensated for by the floral system of vascular supply, which is obviously more proportioned for the larger needs of the fruit. The adaptive value of the subinferior ovary of *Q. cordata* and *Q. guianensis* may mainly rest upon the requirements for a rapid after-fertilization development of ovary and seed, brought

about by the enlarged carpel and ovule insertion regions.

Acknowledgements. I thank Professors F. Fagerlind, T. Hemberg, and B. Walles for space and laboratory facilities. Thanks are also due to the Director of the Instituto de Pesquisa Agropecuaria do Norte, Belém, for the plant material generously collected and preserved for me; to the Directors and Curators of the cited herbaria for allowing me to sample material for anatomical research; to Dr A. Robyns, Jardin botanique national de Belgique, for giving me the opportunity of studying a representative collection of *Quararibea* on loan from various herbaria, and to Dr J. Rowley, Institute of Botany, University of Stockholm, for modification of the English text. Finally I would like to express my gratitude to Apotekarsocieteten, Stockholm, and Stipendienämnden för Apotekens Centrallaboratoriums Stipendiefond, Stockholm, for the financial support supplied.

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The African member of Taeniophyllum (Orchidaceae)

Lars Jonsson

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Illustrations and a diversified description of *Taeniophyllum coxii* (Summerh.) Summerh., the only African species of the genus, are given. A world distribution map of the genus is presented. *T. coxii* can be placed in the Guineo-Congolian phytogeographical region with an extension in Rhodesia. The differences between it and its closest relatives (in Asia) are minute but may prove constant. The seed morphology is taxonomically useful, as seen in some taxa in subgenus *Codonosepalum* (SEM). The root anatomy differs from that of the genus *Microcoelia* Lindl. The pollinium is enclosed by an irregular layer most probably containing fatty acids to a large extent. The mature individual pollen grains lack a normal exine layer. A fibrous layer, similar to "callose" is present instead. The presence of a well developed posterior lobe on the anther is regarded as a primitive character. In all the other aphyllous epiphytic orchids in Africa, and also in the superficially closely related Asian–Pacific genus *Microtatorchis* Schltr., the posterior lobe is to a very high degree reduced.

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The genus *Taeniophyllum* was established by Blume (1825) for the aphyllous Asian orchids characterized by four pollinia. Blume believed that the roots were narrow leaves, hence the generic name (*taenio* band-shaped, *phyllus* leaved). The leaves are in fact small and scale-like.

Schlechter (1913) distinguished two subgenera based on differences in flower morphology: *Codonosepalum* and *Taeniophyllum* ("*Eutaeniophyllum*"). Garay (1972) lectotypified the genus by *T. obtusum* Bl., a member of the subgenus *Taeniophyllum*. The greatest heterogeneity is found within this subgenus, which contains c. 130 species. *Codonosepalum* is more homogeneous and has c. 40 species.

Taeniophyllum is undoubtedly the most widespread aphyllous epiphytic orchid genus in the world (Fig. 1). It is centered in the Indo-Malaysian floral subkingdom (Good 1974). Oddly enough, the smaller subg. *Codonosepalum* has the most extensive distribution. Representatives reach all outpost localities, e.g. *T. aphyllum* (Mak.) Mak. in Japan, Korea and Szuchuan (Szechwan) in China, etc., *T. coxii* in Africa and *T. elegantissimum* Rchb. f. in Tahiti. The genus shows a markedly discontinuous distribution, particularly apparent in subg. *Codonosepalum*.

This account of *T. coxii* focuses partly on the relations to the Asian species, and partly on more general information of vegetative features, anatomy of the root, pollinia and seed morphology.

Material and methods

Material has been seen from BM, BR, K, L, P, PDA, S. SING, SRGH, TAI, UPS and W (abbreviations herbaria according to Holmgren & Keuken 1974). For the construction of the distribution map literature reports have also been used (see References).

For the SEM study the material was fixed in ethanol and formaldehyde, air dried and sputtered with gold.

The TEM study was based on material fixed as above. Flowers were transferred into 2.5% (v/v) glutaraldehyde in 0.1 M Na-cacodylate buffer at pH 7.2 and room temperature through an increasing concent-

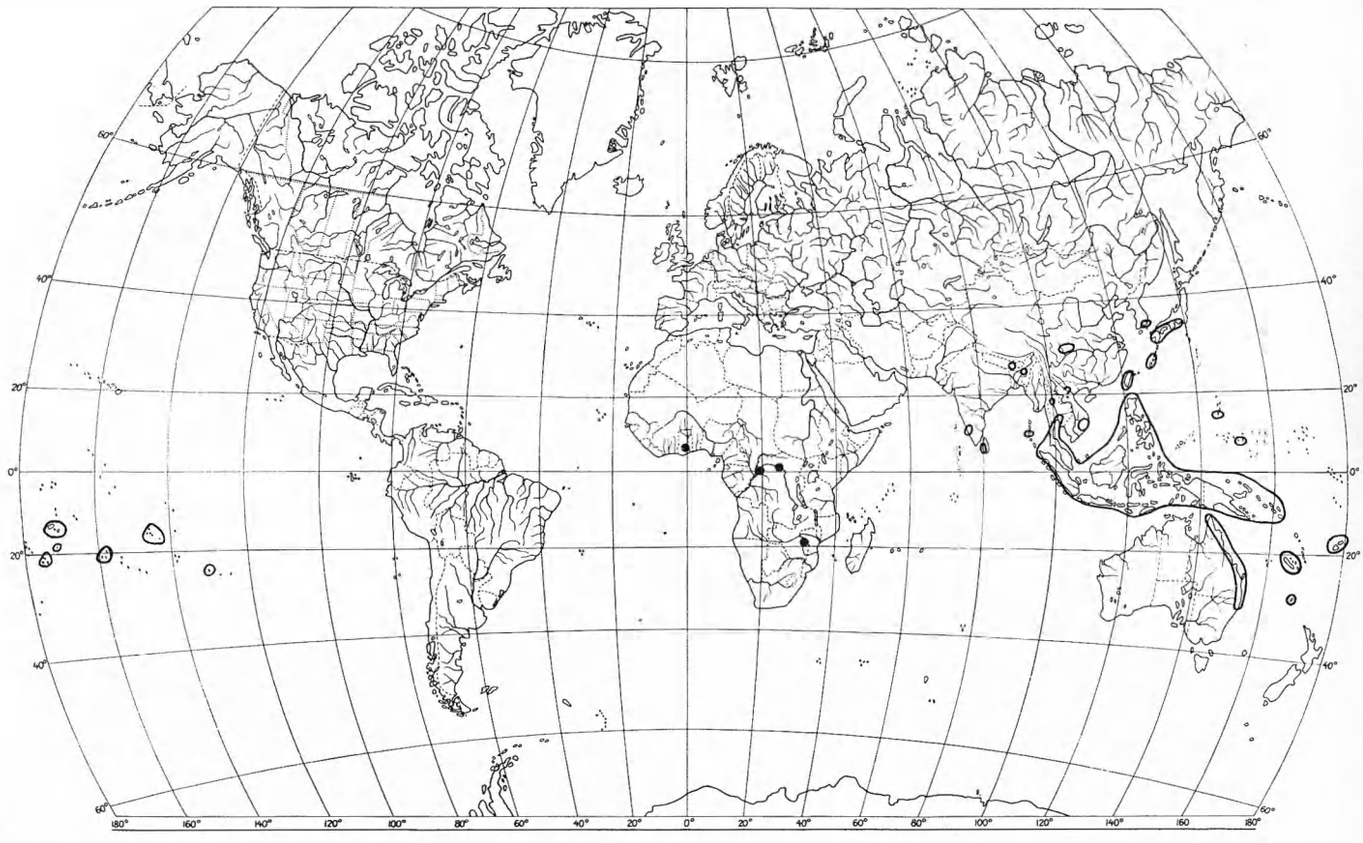

Fig. 1. Known distribution of the genus *Taeniophyllum*. The dots in Africa indicate known localities for *T. coxii*.

ration gradient, postfixed for 1 h in 2% (w/v) aqueous $KMnO_4$, dehydrated in a graded ethanol series, embedded in Epon and sectioned with a LKB Ultrotome 1 using a diamond knife for TEM and a glass knife for LM. Coarse serial sections of the apical part of the flower were taken until the smaller pair of pollinia was reached. These sections were stained according to Sato & Shamoto (1973) and studied in LM. The thin sections were then taken from a site located by LM, stained in 2% (w/v) aqueous uranyl acetate (20 min) and Reynold's lead citrate (5 min).

Taeniophyllum coxii (Summerh.) Summerh. – Figs. 2, 3

Summerhayes 1958: 278, 1968: 257 – *Ankylocheilos coxii* Summerhayes 1943: 168 – Orig. coll.: Ghana, NNE Accra, Aburi, IV.1938 Cox 92 (K holotype).

New material has made it possible to extend Summerhayes' description, particularly in vegetative and minute characters.

Whole plant up to 60 mm in diameter, aphyllous, forming small ± conical tufts on the phorophyte. *Stem* minute, 1–2 (–5) mm long, up to 1 mm in diameter. *Scale-leaves* protecting the stem apex, convex, subacute to obtuse, thin, c. 5-nerved, containing large amounts of raphides, up to 1 mm long. *Roots* short, well developed, fasciculate, ± firmly attached to the substrate, ± radially spreading from the stem, irregularly twisting, ± linear, ± circular to obtusely triangular in transverse section, up to 30(–40) × 1–2 mm. *Inflorescence* short, erect, up to 10(–15) mm long, with rows of wart-like excrescenes, few-flowered, in anthesis one by one; *peduncle* distinct, ± terete to slightly angular, up to 5.5 mm long; rachis ± flattened, obtuse-angled, subflexuose. *Glandular hairs* 2-celled, ± appressed, sparse, on the peduncle and rachis, base of bracts, ovary, and more rarely at the base of the tepals. *Flowers* small, erect, subsessile, 2.5(–2.8) mm long including ovary. *Labellum* with a variably inflexed, distinct or indistinct, ± subulate or flat process at the apex, apical part angular in outline. *Column* short, truncate; dorsal lobe slightly incumbent; side lobes ± oblong, projected or ± infolded, obtuse, basal part fleshy, apical part thin and transparent; *rostellum lobes* minute, ± triangular, at the central basal part of the androclinium, transparent. *Stipes* minute, deltoidal, saddle-shaped; *viscidium* minute, asymmetric, obtusely rounded-cylindric apically, irregularly truncate at the

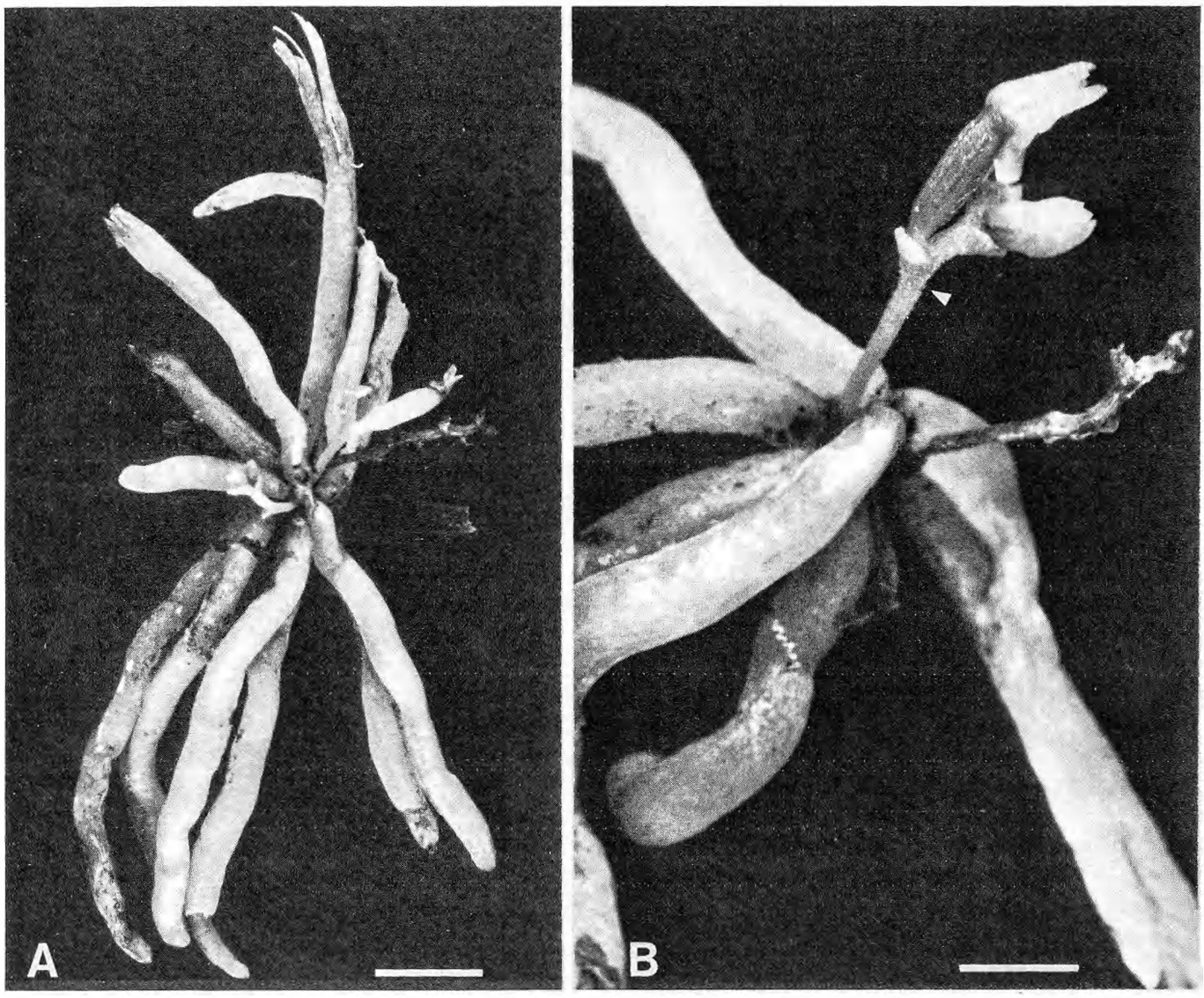

Fig. 2. *Taeniophyllum coxii*. – A: Habit. – B: Detail, note rows of excrescences on the rachis (arrow). – Ball 1185 (SRGH). Scales: A 5 mm, B 2 mm.

distal end. *Anther* bilobed, posterior lobe deeply hidden in the column, each lobe ± hemispherical; the larger frontal lobe is subdivided into two valve-shaped loculi as also the smaller posterior lobe; when mature the valves easily fall apart. *Pollinia* four, dissimilar; larger pair in side view ± kidney-shaped, 260–280 × 140–160 μm, in median section ± elliptic; smaller pair asymmetric, drop-shaped, 190–200 × 120 μm. *Capsule* straight, ± ellipsoidal, 4.5–5 mm long, 1.3–2 mm in diameter. *Seeds* (Fig. 4) truncately cylindric or ± bottle-shaped, testa cells narrowly elongated; anticlinal wall ± sulcate with finer striations; periclinal wall thin, ± destroyed in this material (cf. Rauh et al. 1975 pp. 353–358 for terminology), 180–250 μm long (sample mean 209 μm), 40–80 μm in diameter (sample mean 52 μm), measurements made on 25 dry seeds.

Remarks. The short roots (± obtusely triangular in TS), the diminutive stem and the floral axis with its rows of minute excrescences (Fig. 2 B) makes *T. coxii* distinct from the other aphyllous orchids in Africa. The overall shape and sculpturing of the testa cells seem to be useful characters. Seeds from e.g. the Fijian and Japanese species of subg. *Codonosepalum* resemble those of *T. coxii* very much, but the reticulum pattern and the fine structure of the anticlinal wall are distinctive features.

Distribution and habitat (Fig. 1). The species has previously been recorded from one locality in

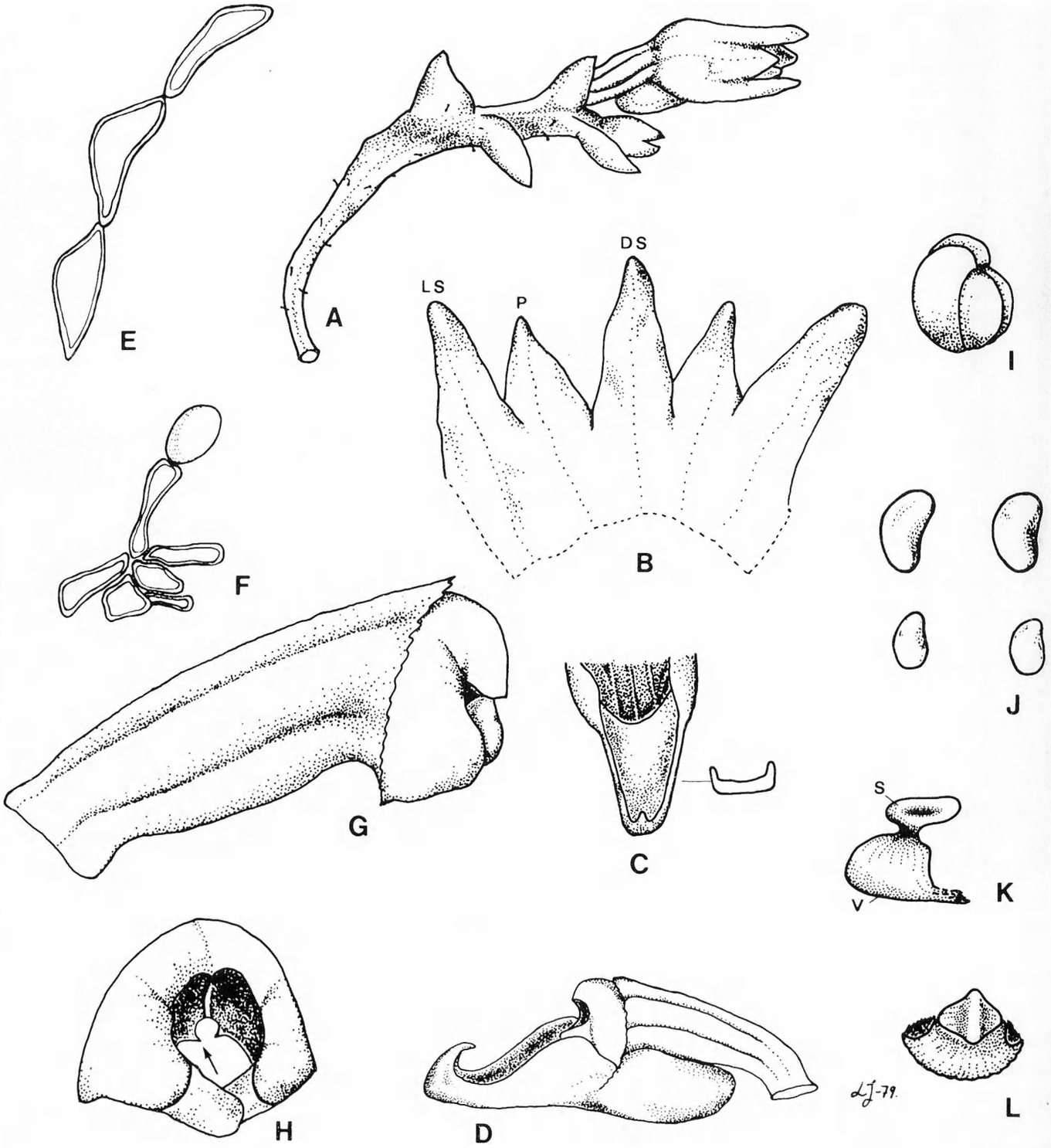

Fig. 3. *Taeniophyllum coxii*. – A: Inflorescence. – B: The connate tepals, lateral sepal (LS), petal (P), dorsal sepal (DS). – C: Labellum from above. – D: Flower with tepals removed, note the hook-shaped process of labellum. – E: Wart-like excrescences from the peduncle. – F: Glandular hair. – G–H: Column, side and front views, note the prolonged side lobes and rostellum lobes (arrow). – I: Anther, bilobed and subdivided into 4 loculi. – J: Pairs of pollinia. – K–L: Stipes (S) and viscidium (V), from the side and from above. – Ball 1185 (SRGH). Magnifications: A × 9.6, B–D × 20, E–F × 100, G–J × 40, K–L × 80.

Ghana and one in Zaïre, and is here reported from a second locality in Zaïre (Eala) and from Rhodesia. Most probably *T. coxii* is widely distributed in suitable habitats and less disjunct than it may appear, but its inconspicuousness in combination with the epiphytic mode of life makes it very difficult to discover. It is an epiphyte on the understorey vegetation in rain

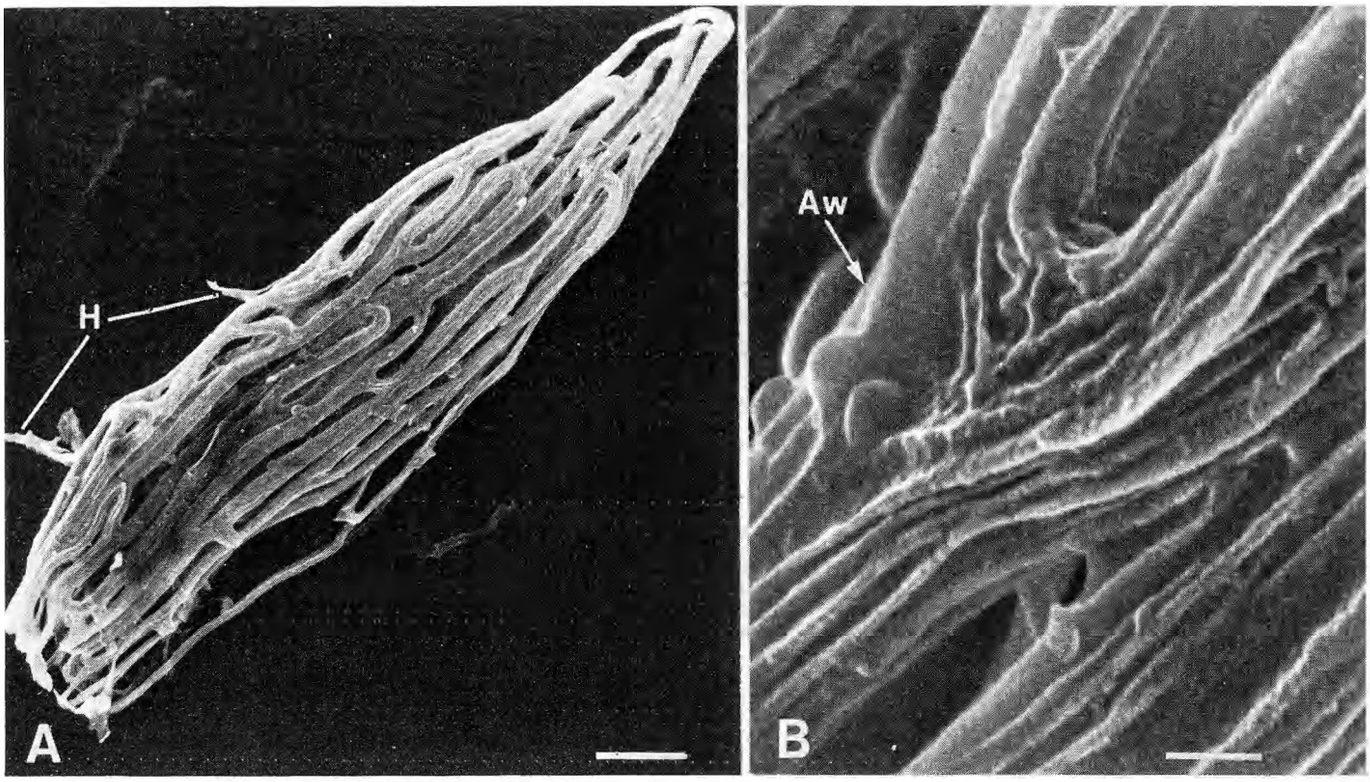

Fig. 4. SEM of seed from *Taeniophyllum coxii*. – A: Overall view, note that the thin periclinal wall is destroyed. Fungal hyphae (H). – B: Detail, sulcate anticlinal wall (Aw) with fine striations. – Ball 1185 (SRGH). Scales: A c. 20 μm, B c. 1 μm.

forest and riverine forest, occasionally in secondary vegetation and in plantations, at 200–1200 m altitude.

Phorophytes. *Adina microcephala* (Del.) Hiern and *Coffea* sp. (Rubiaceae), *Syzygium* sp. (Myrtaceae), *Araucaria cunninghamii* D. Don (Araucariaceae; introduced).

Collections. *Ghana*, NNE Accra, Aburi, 10.IV. 1938 (in fl.) Cox 92 (K) – *Zaïre*, Haut-Zaïre, NW Kisangani, S side of Zaïre R., Barumbu, 7.XI.1913 (in fl.) Bequaert 1116 (K) – Equateur, Eala, in the botanical garden, VII. 1936 (ster.) Ghesquière 3386 (BR) – *Rhodesia*, E Prov., S Melsetter, Lower Chambuka R., Tarka Forest, 4.IV.1968 (in fl.) Ball 1185 (SRGH).

Phytogeography and taxonomy

T. coxii could be placed in the Guineo-Congolian phytogeographical region (White 1970 p. 53), but the new record in Rhodesia points to a phytogeographical discontinuity within the African flora of today. This problem has been discussed by Lawton (1962) and Wild (1968) for the scattered rain forests and evergreen riverine forests in Zambia and Rhodesia. These forests contain elements (e.g. *Adina microcephala* and *Syzygium* sp., the phorophytes of *T. coxii*) indicating past connections to W Africa, and have therefore been considered as remnants of a Guineo-Congolian vegetation type.

Taeniophyllum coxii is geographically widely separated from the other species of the genus (Fig. 1). The nearest Asian species are found in Ceylon and SW India (Cottayam). In spite of intense search in herbaria no material has been found from the Mascarenes or Madagascar. On Madagascar I have also looked for it in the field without success.

In Asia there are several species closely related to *T. coxii* (see Table 1). At a superficial comparison *T. coxii* shows the strongest affinities to the Indian *T. scaberulum*, while *T. glandulosum* and *T. rubrum* are more different, but instead show strong affinities to each other. A closer inspection of the flower morphology supports this general impression. However, there are minute but striking differences between *T. coxii* and the other species, e.g. in the features of the column. If such a character may prove constant, the more easily discernible characters as the general features of the roots and rachis,

Table 1. Differences between *Taeniophyllum coxii* and some related Asian species.

Species	Published	Habit	Root, TS and general shape	Rachis	Labellum, apical part	Column, side lobes	Pollinia, larger pair
T. coxii	1943	minute tufts	terete to obtusely triangular, ± linear	short, erect	obtuse, angular	oblong, flattened, apex ± membranous	kidney-shaped
T. glandulosum Bl.	1825	± robust tufts	obtusely triangular to flattened, ± linear	long, ± lax	acute, conical	oblong, inner sides concave, apex fleshy	–
T. rubrum Ridl.	1894	minute tufts	obtusely triangular to ± flattened, ± linear	± long, ± lax	acute, conical	oblong, inner sides concave, apex fleshy	drop-shaped
T. scaberulum Hook. f.	1890	minute tufts	sharply triangular to ± elliptic, ± club-shaped	short, erect	acute, conical	oblong, flattened, apex fleshy	± kidney-shaped

the shape of the labellum, could also be of diagnostic value, if correctly interpreted. In *T. coxii* is, for example, the general shape of the labellum remarkably constant in the whole area of distribution, indicating that over-all characters might be of great significance.

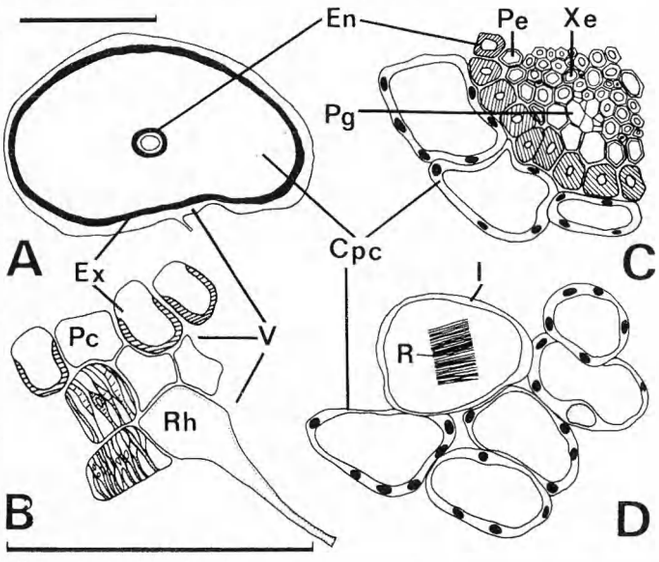

Fig. 5. *Taeniophyllum coxii,* TS of root. – A: Overall view. – B: Velamen (V) with lignified band-shaped thickenings, root hair (Rh), exodermis (Ex) with u-shaped thickening, passage cell (Pc). – C: Endodermis (En), pericycle (Pe), phloem group (Pg), xylem elements (Xe). – D: Cortical parenchyma cells (Cpc) with chloroplasts (black dots), idioblast (I) with raphides (R). – Ball 1185 (SRGH). Scales: A 0.5 mm, B–D 0.25 mm.

The scarcity of adequate material available makes it impossible to state if the differences given (Table 1) really are constant or only expressions of a wide variation. The taxa compared may eventually all turn out to be conspecific, or to belong to only two species. The earliest legitimate name of the respective species pairs would then be *T. scaberulum* Hook. f. (1890) and *T. glandulosum* Bl. (1825) respectively.

Judging only from the drawing on which the description of *T. alwisii* Lindl., the Ceylonese species, was founded (cf. Reichenbach 1874 p. 67, T. 116) it seemed impossible to keep *T. coxii* as a separate species. However, material of *T. alwisii* collected in the field and herbarium material seen in PDA shows that it is quite distinct both from *T. coxii* and the other species discussed here. Material and a drawing of *T. alwisii* is kept in UPS.

Within this leafless genus there are for obvious reasons a limited number of useful characters. This is especially notable within subg. *Codonosepalum* with its uniform and minute flowers. There is a great risk here that unique, even if minute, structures are neglected if a wide species concept is accepted uncritically. There is a great

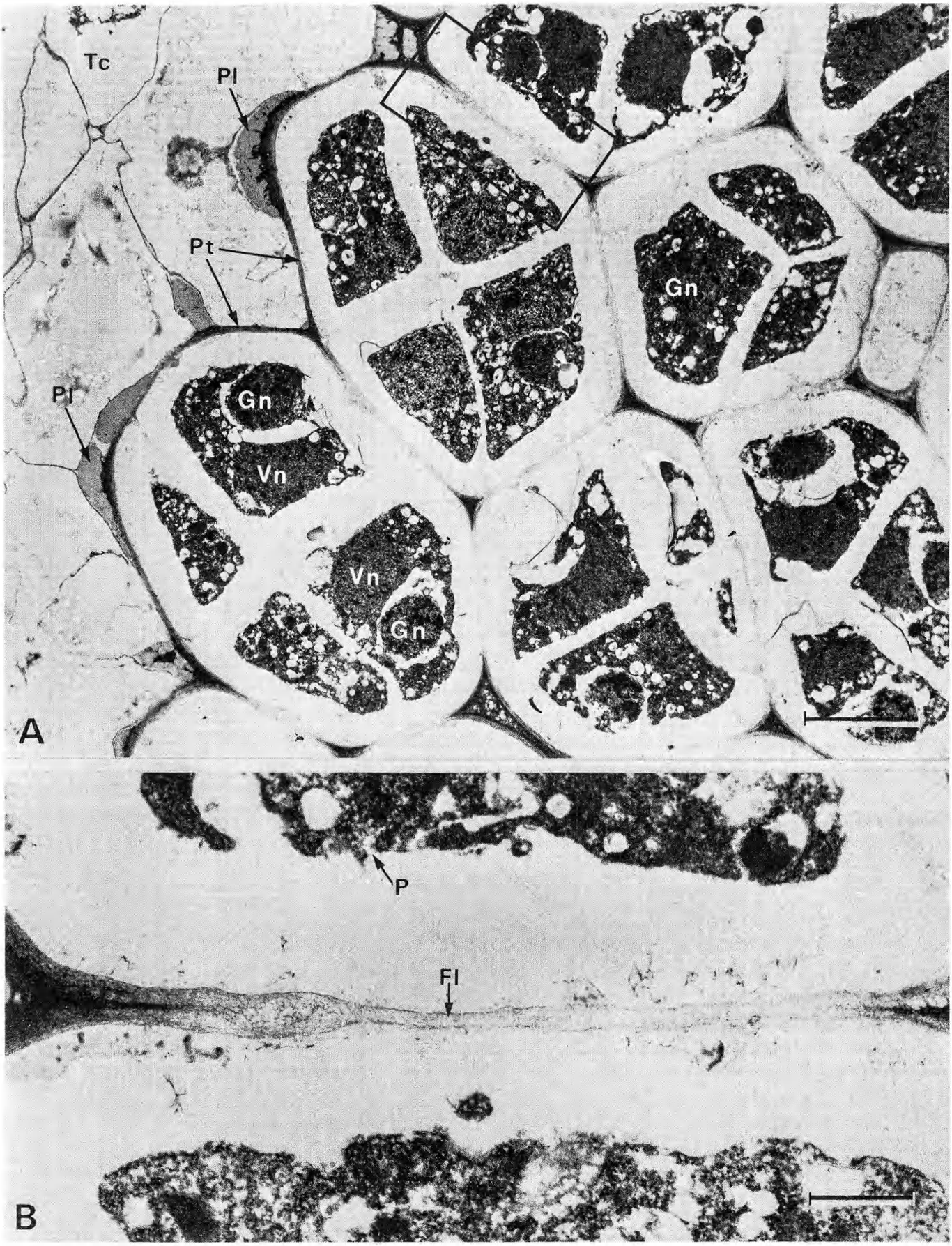

Fig. 6. TEM of the smaller pollinium in *Taeniophyllum coxii*. – A: Pollen tetrads (Pt), degenerating tapetum cell (Tc), protection layer (Pl), generative nucleus (Gn), vegetative nucleus (Vn). – B: Detail of pollen wall, from the framed-in area in (A), fibrous layer (Fl), plasmalemma (P). – Ball 1185 (SRGH). Scales: A c. 5 μm, B c. 1 μm.

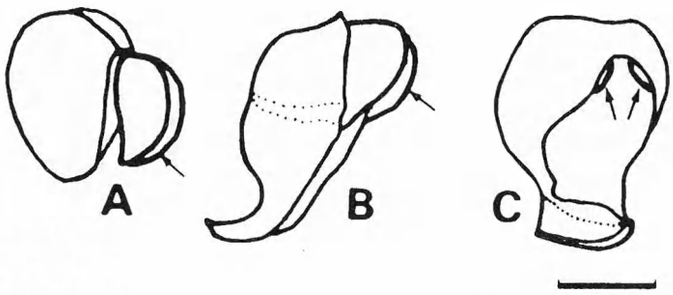

Fig. 7. Comparison of different stages in the reduction of the posterior lobe (arrows) in varying types of anthers. – A: Subg. *Codonosepalum* (*T. coxii;* Ball 1185, SRGH). – B: Subg. *Taeniophyllum* (*T. gracile* (Rolfe) Garay; Smith 636, K). – C: *Microtatorchis schlechteri* Garay (Schlechter 15300, S). – Scale: 0.2 mm.

need not only of more material, but also of more diversified studies, e.g. in anatomy, ecology, pollination biology, etc., to obtain a better knowledge of the variation.

Anatomy of T. coxii

Root – Fig. 5

Epidermis. Root hairs often present on the lower side where the root is attached to the substrate. *Velamen cells* (1–)2-layered, with branched, lignified, band-shaped striations similar to the type termed "category II" by Sanford & Adanlawo (1973).

Cortex. *Exodermis* 1-layered, cell walls with characteristic u-shaped thickenings; interrupted by thin-walled passage cells at irregular intervals. *Cortex proper* approximately 8 cell-layers thick, with enlarged thin-walled parenchyma cells, all provided with chloroplasts. Idioblasts containing raphides scattered, more densely in the peripheral regions. *Endodermis* 1-layered, derived from the periblem (cf. Shushan 1959 p. 62); cells thick-walled, irregularly interrupted by thin-walled passage cells.

Central cylinder. *Pericycle* 1-layered, forming the outermost layer of the central cylinder, consisting of alternating segments with thick- and thin-walled cells so that the thin-walled cells are mainly found opposite the phloem groups. Phloem forming 3–4 groups of thin-walled cells close to the pericycle. *Xylem* elements ± polygonal in outline and lignified, radiating between the phloem groups.

Remarks. The general structure of the velamen layers and the u-shaped thickenings in the exodermis cells appear rather homogeneous within *Taeniophyllum*. Only very few samples have been seen, but they represent both subgenera. The corresponding features in *Microcoelia* Lindl., the largest African aphyllous orchid genus, are different.

Anther and pollinia – Figs. 3 I, 6

The anther consists of two main lobes, each divided into two distinctly valvate loculi with one pollinium in each. The pollinia are composed of tetrahedral and isobilateral pollen tetrads; the isobilateral type seems to predominate. The pollinium is surrounded by an irregular layer (Fig. 6 A), most probably with a protective function. This layer has been corroded as the material had been fixed in a mixture of ethanol and formaldehyde for c. 10 years. In situ this layer is easy to crush by slightly pressing it with a needle; then the tetrads float around ± freely. Positive staining in Sudan black and Sudan III (Jensen 1962 p. 264) indicates that the main components of this structure are a mixture of saturated and unsaturated fatty acids. Structural investigation of the pollinia in species of *Microcoelia* (L. Jonsson unpublished) also support this conclusion.

The outer layer of each single pollen grain is fibrous (Fig. 6 B). This is remarkable since the pollinia were taken from a flower in early anthesis and at that stage the whole pollinarium is mature and one would have expected an "ordinary" exine layer. The fibrous layer reminds of the "callose" found in early stages of pollen grain and spore development in a wide range of plant groups. The filaments in this loosely formed layer are similar to structures found in e.g. the etched exine of spores of *Lycopodium clavatum* L. (Sengupta & Rowley 1974, Rowley 1975) and in the cavities of the exine, i.e. between the bacula, of pollen grains of *Artemisia vulgaris* L. (Rowley & Dahl 1977) and *Swertia crassiuscula* Gilg (Jonsson 1974). This is also in accordance with the preliminary results obtained from material of *Taeniophyllum alwisii* (L. Jonsson unpublished). The wide gap between the fibrous layer and the plasmalemma is most probably to some extent caused by plasmolysis; however, material of *T. alwisii,* fixed in the field

according to standard methods used in TEM, has also a similar tendency.

It seems as if the normal pollen development is interrupted before the mature stage is reached. The result is premature, but viable, pollen grains.

Remarks. Within the otherwise derived subg. *Codonosepalum* it is remarkable to find a "relic" structure in the anther consisting of a well developed posterior lobe, i.e. the lobe facing the androclinium, giving the impression of an ordinary anther. In all the other epiphytic aphyllous orchid species in Africa this lobe is reduced to ± minute flaps on the posterior side. Steps towards the same reduction have also been seen in members of subg. *Taeniophyllum*, and more so within the superficially closely related genus *Microtatorchis* Schltr. (see Fig. 7).

Acknowledgements. I am particularly indebted to the curators of the herbaria mentioned in Material and methods who above all put many important types at my disposal, to Professor O. Hedberg and Dr Ö. Nilsson for critically reading the manuscript, and to Dr I. Hedberg for linguistic revision. Professor F. Fagerlind kindly revealed the locality for *T. alwisii*. I also want to acknowledge Dr A. von Hofsten for laboratory facilities concerning the TEM work and Ms A. Axén, Ms U.-B. Sahlström and Ms G.-B. Örlander for technical assistance.

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New taxa of Cruciferae from East Tropical Africa and Madagascar

Bengt Jonsell

Jonsell, B. 1979 11 15: New taxa of Cruciferae from East Tropical Africa and Madagascar. *Bot. Notiser 132:* 521–535. Stockholm. ISSN 0006-8195.

Five new taxa are described: *Diceratella inermis* from N Kenya and S Ethiopia, *Erucastrum elgonense* from Mt Elgon, Uganda, *E. meruense* from Mt Meru, N Tanzania, and *Rorippa laurentii* subsp. *laurentii* and subsp. *tsaratananae* from Madagascar. The generic characters of *Diceratella, Matthiola* and *Morettia* are compared and *Diceratella* is redefined to include species previously attributed to *Matthiola* with septate siliquae but lacking valval horns. *Diceratella elliptica* (DC.) Jonsell, comb. nov. is accordingly transferred. The chromosome numbers of *E. meruense,* 2n = 64, and *R. laurentii* subsp. *laurentii,* 2n = 48, were established.

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In this paper some new descriptions and combinations of *Diceratella* (Hesperideae s.lat.) and *Erucastrum* (Brassiceae) needed for the Flora of Tropical East Africa (FTEA) are published. Moreover, a new Madagascan species of *Rorippa* (Arabideae) is described.

Methods

Seed-coat anatomy was studied in seeds pretreated in diluted ammonia, embedded in paraffine, sectioned at c. 10 μm and stained in safranine-tannine.

SEM studies of seeds, pollen and hairs were usually made in untreated organs covered by a gold/palladium layer. For studies of slime bodies in the seed-coat of *Diceratella* and allied genera seeds were immersed in water, dehydrated in graded ethanol and amyl-acetate, and dried in CO_2 in a critical point dryer (Stork & Wüest 1978). Some seeds, particularly from old herbarium specimens did not show slime bodies after this treatment.

The chromosome preparations were made from root tips. Those of *Erucastrum* were fixed in chrome-acetic formalin, stained in gentian violet, embedded in paraffine and sectioned, those of *Rorippa* fixed in Carnoy's fluid, stained in aceto-orcein and squashed. Voucher specimens are preserved in UPS.

Diceratella

In the Sahara region and NE Tropical Africa the three closely related genera *Diceratella, Matthiola* and *Morettia* are well represented. They have been defined almost exclusively by characters of the ripe fruit: *Diceratella* by the possession of two valval horns and transverse septa (cf. Jonsell 1978 Fig. 1), *Matthiola* by lack of valval processes and transverse septa but mostly with stylar processes, *Morettia* by short and short-styled siliquae without processes but with transverse septa. Owing to this emphasis on some few characters all three genera are circumscribed in unnatural ways and much in need of reclassification (cf. also Hedge & Miller 1977). Here only the case of *Diceratella elliptica* (up to now called *Matthiola elliptica* R. Br. ex DC.), and its close ally, *D. inermis,* described in this paper, will be dealt with.

Table 1 lists a number of features which contribute to characterizing the three genera. *Matthiola,* by far the largest and most variable one, may still include a number of misplaced taxa.

The states of characters cited for the genus refer to species of all sections recognized by Schulz (1936) except the Central Asiatic *Microstigma,* long regarded as a separate genus. Nor have the divergent species included by Hedge & Rechinger (1968) been considered. For *Diceratella* the statements are based upon the African species *D. incana* Balf. fil. and *D. smithii*

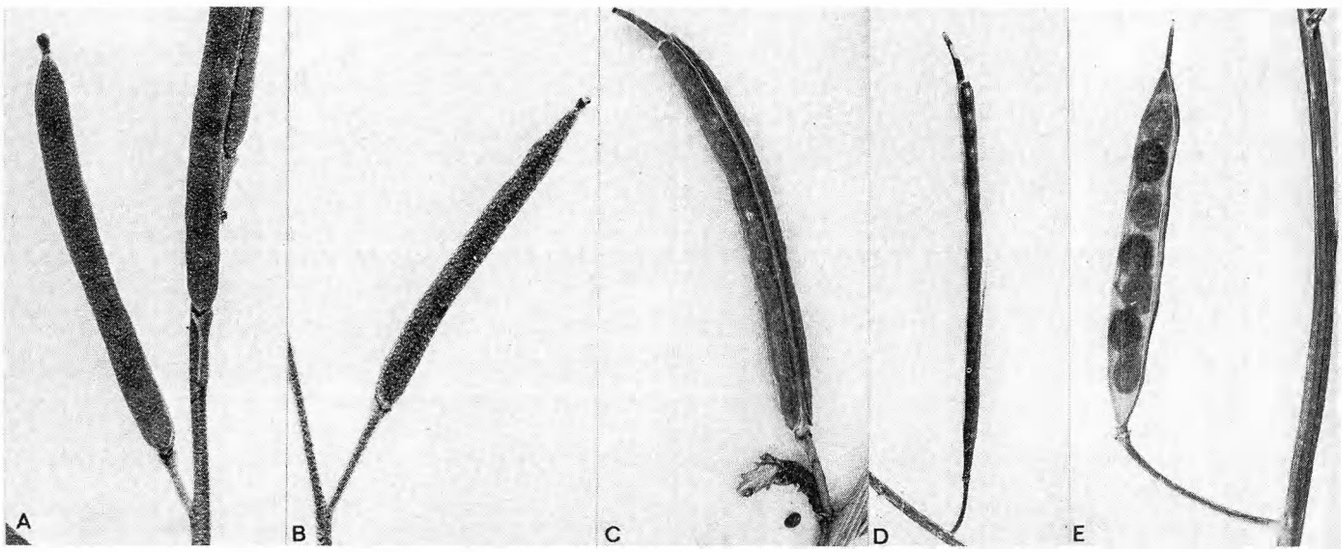

Fig. 1. Siliquae. – A: *Diceratella elliptica* (Gilbert & Thulin 1373, UPS), × 1.5. – B: *D. inermis* (Gilbert & Thulin 1408, UPS), × 1.5. – C: *Erucastrum elgonense* (Tothill 2346, K), × 1.4. – D: *E. meruense* (Hedberg 4744, UPS), × 0.9. – E: *Rorippa laurentii* (Jonsson 1090, UPS), × 1.5.

(E. G. Bak.) Jonsell and the Iranian *D. canescens* (Boiss.) Boiss., for *Morettia* on *M. parviflora* Boiss. and *M. philaeana* DC., the only undoubted species of that genus. *M. revoilii* Franch., from the Horn of Africa, shows signs of incorrect generic position and was not considered.

Diceratella elliptica shares the majority of referred characters with *Diceratella* s.str. The major discrepancy is the lack of valval horns. The transverse septa between the seeds are not always well developed in *D. elliptica,* but there are at least marked thickenings on the inner side of the valves. The inner valval surface of the *Matthiola* species is smooth. Trichomes, pollen, nectaries and seed-coat are characters of particular interest.

Glandular trichomes occur in most species of *Matthiola,* but not in the other genera. In all genera radiate trichomes cover stems, leaves and siliqua valves, often densely. Variation between species is often distinctive. The one-celled trichomes have a stipe, which is very short in e.g. *Matthiola erlangerana* (Fig. 2 B). In *Diceratella* it is also short but often attached to a coarser, basal stalk (Fig. 2 A). In *Morettia* the stipe is more slender and the stalk often taller than in *Diceratella.*

Erdtman (1952) reported nonaperturate or slightly colpate pollen grains for a few *Matthiola* species, a very unusual state in Cruciferae (cf. also Rollins & Banerjee 1979). This is confirmed for the 18 *Matthiola* species studied by me (Fig. 3 B, C), while *Diceratella elliptica* and *inermis* as well as *Diceratella* s.str. and *Morettia* have the distinctly colpate pollen normal for the family and mostly also a more finely reticulate sexine pattern (Fig. 3 A).

In *Matthiola* s.str. the lateral nectaries form a closed or nearly closed ring (open inwards) around the lateral stamen bases. In the other taxa there are two separate glands at each side of each lateral stamen, though with characteristic variations (Table 1).

As seen in available specimens (c. 90) from BM, K, S and UPS untreated seeds of these taxa have a reticulate surface pattern (Fig. 4 A, B), which may be useful as a character on the species level but not for genera. As a rule the epidermal cells of the seed-coat contain slime bodies, which break in water and grow out through the outer wall layer to a more or less definite shape (Fig. 4 C; cf. Stork & Wüest 1978). In *Diceratella,* including *D. elliptica,* there are slime columns, which in sections show interior, rather loose bands (Fig. 3 E). In SEM tney look like stumps, often with marked side ribs (Fig. 4 D–E). In *Matthiola erlangerana,* a NE African species, the slime bodies both in sections and surface view are small and low (Fig. 3 D, 4 G), while other *Matthiola* species lack slime bodies (Vaughan & Whitehouse 1971). In *Morettia* the slime bodies appear as very densely piled disks (Fig. 3 F, 4 F). The fine structure of slime bodies may be characteristic for a species but there

Table 1. Morphological characteristics of *Matthiola, Diceratella* and *Morettia*.

Matthiola	*Diceratella*		*Morettia*
	D. elliptica/ *D. inermis*	*Diceratella* s.str.	
Herbs or shrublets	Shrublets		Herbs
Glandular trichomes often present	Glandular trichomes absent		Glandular trichomes absent
Radiate trichomes with short, thin stipe	Radiate trichomes with very short, thin stipe, sometimes attached to a short, coarse stalk		Radiate trichomes with long, thin stipe, sometimes attached to a coarse stalk
Lateral sepals saccate to poached	Sepals non-saccate		Sepals non-saccate
Lateral sepals often with broad hyaline margins	Sepals with narrow hyaline margins		Lateral sepals with broad hyaline margins
Petals clawed to non-clawed	Petals ± clawed		Petals non-clawed
Petals > 2× sepal length	Petals 1.5–2× sepal length	Petals > 2× sepal length	Petals 1.2–1.5× sepal length
Lateral nectaries annular or horse-shoe shaped	Lateral nectaries lobate, subcylindrical or sub-conical, at each side of stamen base		Lateral nectaries trigonous to sub-conical, at each side of stamen base
Ovary with inconspicuous style	Ovary with inconspic-uous style		Ovary with distinct style
Pedicel non-cupulate at siliqua base	Pedicel cupulate at siliqua base		Pedicel cupulate at siliqua base
Siliqua lumen without trans-verse septa	Siliqua lumen transversely septate or inner valval wall indulged	Siliqua lumen transversely septate	Siliqua lumen transversely septate
Siliqua septum usually with rectangular areoles between the fibres	Siliqua septum with very dense ± undulate fibres, no areoles		Siliqua septum with very dense fibres, no areoles
Stigma of siliquae with or without processes	Stigma of siliquae without processes	Stigma of siliquae with short lateral processes	Stigma of siliquae without processes
Siliqua valves not keeled, nearly always without horns	Siliqua valves keeled or not, without horns	Siliqua valves keeled, with horns	Siliqua valves not keeled, without horns
Epidermal slime columns of seed-coat absent or as piled disks	Epidermal slime columns of seed-coat containing a diffuse network		Epidermal slime columns of seed-coat as densely piled disks
Palisade layer cells of seed-coat isodiametric	Palisade layer cells of seed-coat ± isodiametric		Palisade layer cells of seed-coat compressed
Pollen grains non-aperturate or indistinctly colpate, sexine ± coarsely reticulate	Pollen grains distinctly colpate, sexine finely reticulate		Pollen grains distinctly colpate, sexine finely reticulate

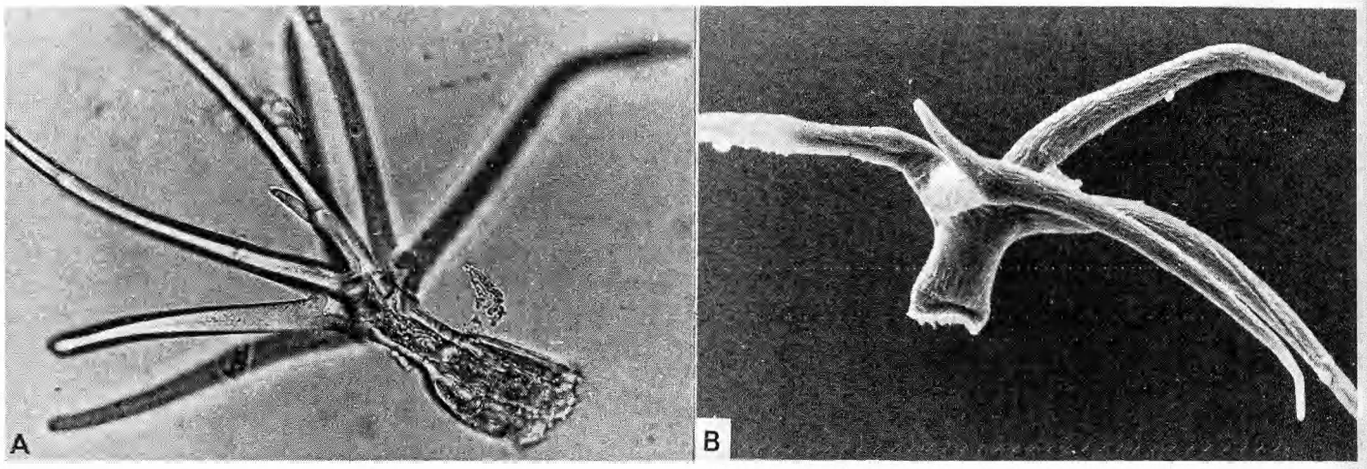

Fig. 2. Sepal hairs. – A: *Diceratella elliptica* (Bally & Melville 15919, K), LM, × 270. – B: *Matthiola erlangerana* (Burger 3000, K), SEM, × c. 450, one hair.

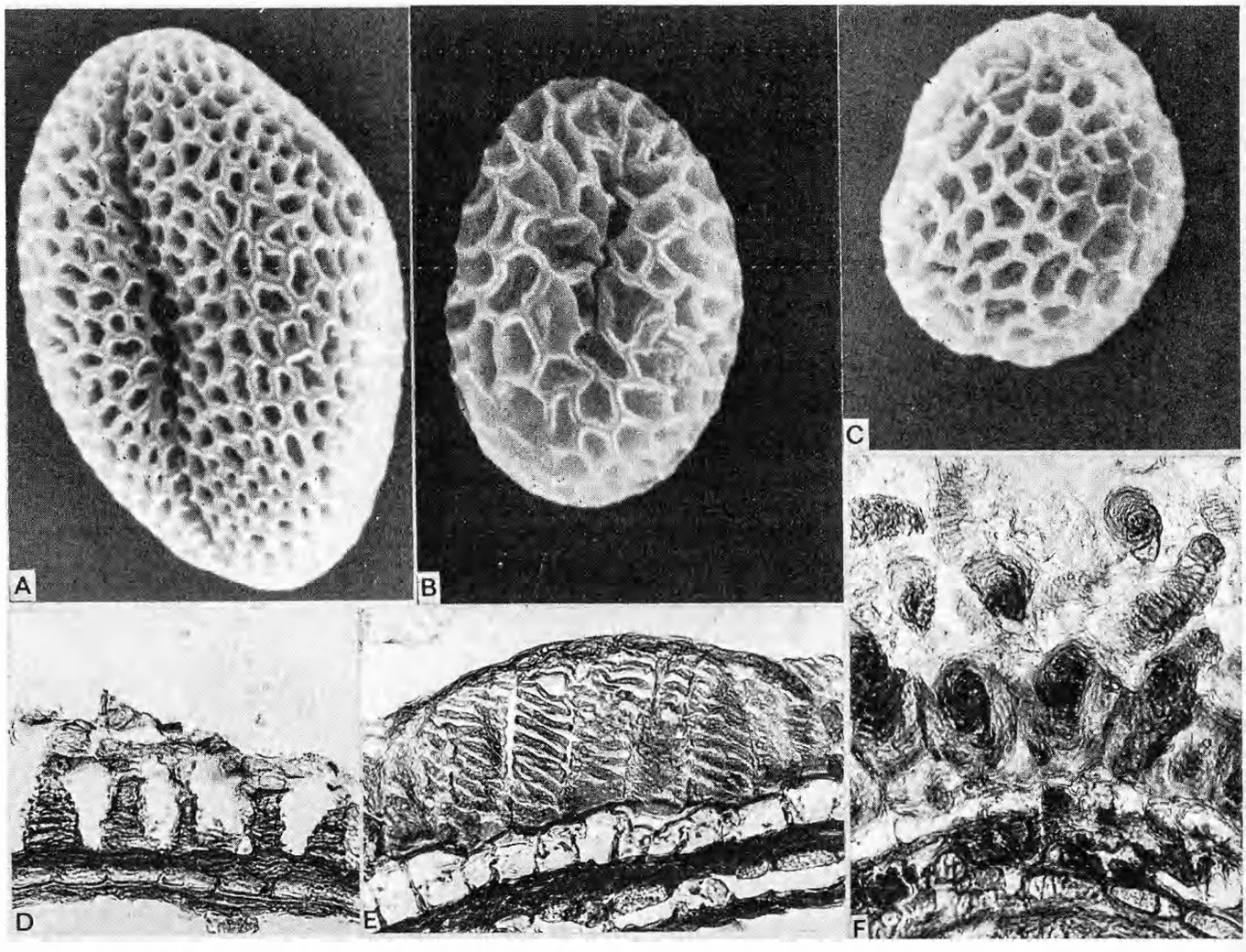

Fig. 3. A–C: Pollen grains, SEM, all × c. 2300. – A: *Diceratella incana* (Stewart 981, K), colpate pollen grain. – B: *Matthiola longipetala* (Dickson 592, K), indistinctly colpate pollen grain. – C: *Matthiola bicornis* (Dickson 137 A, K), nonaperturate pollen grain. – D–F: Sections of seed-coats with swollen slime bodies, all × c. 400. – D: *Matthiola erlangerana* (Gilbert & Thulin 1514, UPS). – E: *Diceratella elliptica* (Popov 1191, K). – F: *Morettia philaeana* (Newberry 1928–9, K).

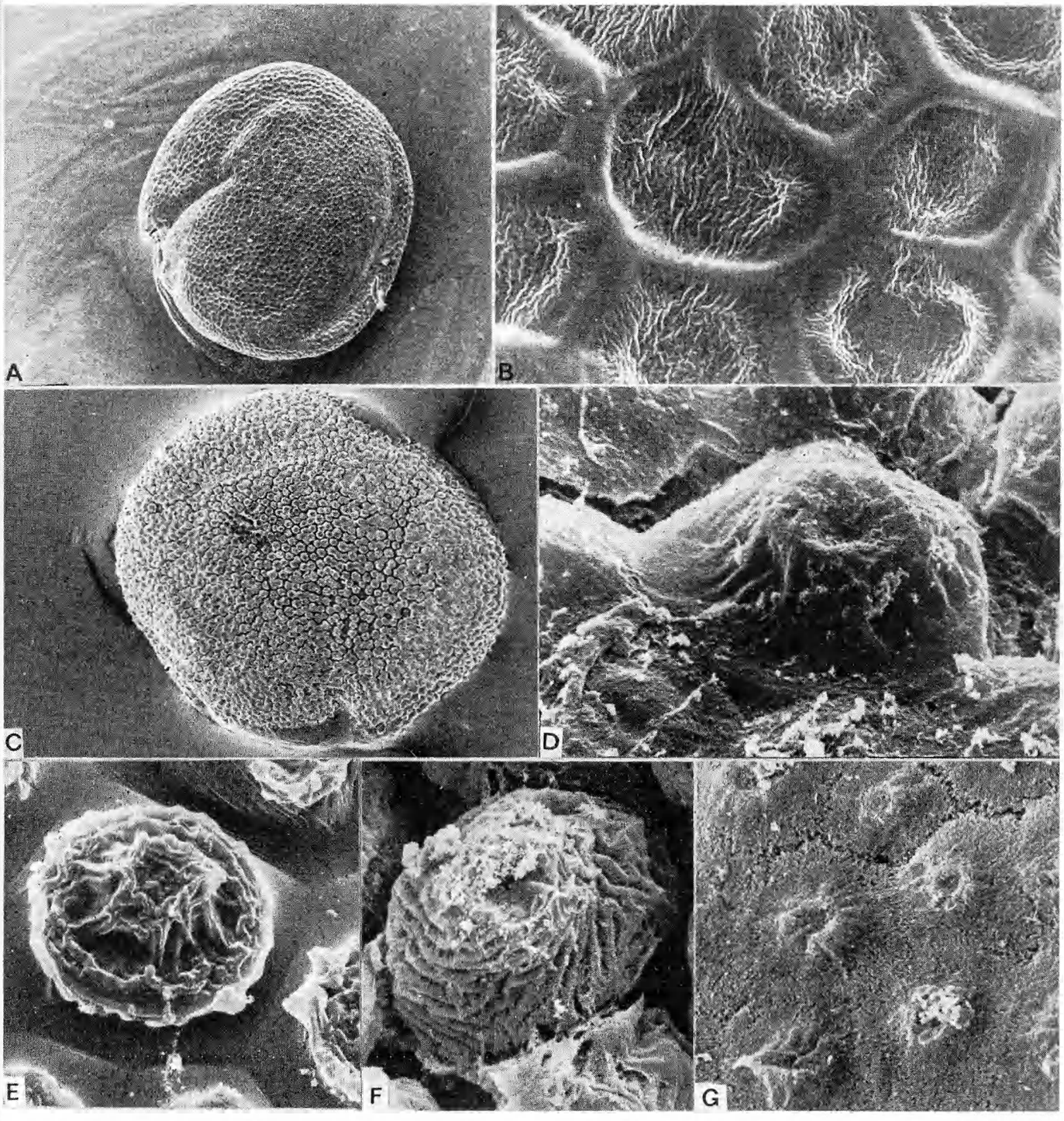

Fig. 4. Seeds, SEM. – A–D: *Diceratella smithii* (Hemming 2247, EA). – A: Untreated seed, × 25. – B: Surface of untreated seed, × 900. – C: Immersed and dehydrated seed covered with slime-bodies, × 30. – D: Slime body, × 1200. – E–G: Details of immersed and dehydrated seeds. – E: *D. elliptica* (Popov 1191, K), slime body, × 950. – F: *Morettia philaeana* (Kanas 126, K), slime body, × 1000. – G: *Matthiola erlangerana* (Burger 3000, K), seed surface with low slime bodies, × 900.

seems to be a main type for each of the genera *Diceratella* and *Morettia*.

The seed-coat was studied in sections and/or in SEM in c. 20 collections. *D. inermis* could not be studied since fully ripe seeds are not present. In unripe seeds of all species, the slime-forming epidermal cells contain only scattered granules.

Thus there are clear differences between *Matthiola* s.str. and the hornless *Diceratellas*. A case could be made for including them in *Morettia*, but there are important differences in e.g. seed-coat anatomy, trichome shape and shape of nectarial glands. The agreement in transverse valval septation seems rather to be a result of

parallellism. *Diceratella* and *Morettia* may be sister groups derived from a common ancestor.

Chiovenda (1919) observed that *Diceratella elliptica* was anomalous within *Matthiola* and erected the monotypic genus *Pirazzia*. However, the similarities with *Diceratella* s.str. are so far-reaching (Table 1) that the species must be included here. The valval horns seem to have evolved as an adaptation for dispersal within a part of *Diceratella,* just as in *Matthiola* prominent stigmatic processes and rarely even valval horns (e.g. *M. longipetala* (Vent.) DC.) are found only in some taxa.

D. elliptica is the most wide-spread species of *Diceratella*. The genus is represented in Egypt, the Sudan, Ethiopia, Somalia, N Kenya and Socotra as well as in S Iran (cf. Jonsell 1978). A Saharan species, *D. sahariana* Corti, known from one very incomplete collection, needs confirmation (cf. Maire 1977).

Diceratella elliptica (DC.) Jonsell, comb. nov.

Basionym: *Matthiola elliptica* De Candolle 1821: 167 *Pirazzia elliptica* (DC.) Chiovenda 1919: 147 – Orig. coll.: Ethiopia, Salt (BM holotype)

Illustrations: Andrews 1950 Fig. 42, Täckholm 1974 Fig. 53 B.

Subshrub up to 100 cm high with numerous stiff, spreading branches, the lower ones ± decumbent. *Stems* woody to considerable height, light brown, up to 0.5 cm thick. Young branches and leaves whitish to greyish green from a dense cover of radiate hairs. *Leaves* scattered or congested on young branches (older parts without leafy shoots); petioles 5–20 mm; lamina elliptic to ovate, 11–45 × 7–25 mm, obtuse, attenuate at base, subentire to sinuately dentate, rather thick with prominent mid-nerve beneath. *Racemes* 5–20-flowered, in ripe fruit lax, up to 25 cm. Pedicels ascending to erect, stiff, 7–15 mm, widened below the flower. *Sepals* oblong, obtuse, 12–17 mm × 2.5–4 mm, the inner markedly broader than the outer. *Petals* lilac to pale pink, whitish at base, 25–38 mm long, distinctly clawed; blade at least 15 mm long, 10–15 mm broad, apically rounded. *Stamens* distinctly tetradynamous with linear filaments; pollen grains distinctly tricolpate. *Nectaries* prismatic, subconical or lobate, one on each side of each lateral stamen. *Siliquae* linear, usually somewhat curved, 30–80 × 2.0 mm with transverse septa to low valval thickenings between the seeds; valves keeled, hornless. Style c. 0.5 mm long, stigma usually with short lateral projections. *Seeds* mucilaginous, minutely reticulate, red-brown, elliptic to subrectangular in outline, compressed, 1.3–1.6 × 1.0–1.2 mm, with a very narrow wing.

Distribution and habitat: Known from SE Egypt, Sudan, Ethiopia, Somalia, N Kenya. Preferably on dry base-rich cliffs; 300–1800 m.

Representative material. Egypt, Wadi Rabdit, Gebl Elba, 1.II.1933, Drar 108 (S) – Sudan, Red Sea Prov., 1913, Lynes s.n. (BM); Kasala Prov., Tokai Distr., Karora Hills, Robbie 44 (K) – Ethiopia, Agow, near Tageros, 15.IX.1866, Schimper ed. Hohenacker no. 2259 (BM, K, S); Eritrea, Assaorta, 10.V.1902, Pappi 5149 (K) – Djibouti, Le Day, 3.IV.1957, Curle 86 (K) – Somalia, Ahl-Mountains, III.1873, Hildebrandt 826 (BM); Wagga Mts, 1897, Lort Phillips K 6 (K); Goton, 23.XI.1932, Gillett 4638 (K); Erigavo, 10.I.1954, Popov 1191 (K); Mas Alled, 7.VIII.1957, Newbould 831 (K); Las Kiorei, 14.I.1973, Bally & Melville 15919 (K) – Kenya, N Frontier Prov., Mandera Distr., Mandera–Ramu road, 3.V.1978, Gilbert & Thulin 1373 (BR, C, EA, K, MO, UPS, WAG).

Diceratella inermis Jonsell, sp. nov. – Fig. 5

Orig. coll.: Kenya, N Frontier Prov., Mandera Distr., Ramu–Malka Mari road, limestone valley, c. 400 m, 8.V.1978, Gilbert & Thulin 1573 (UPS holotype, BR, C, EA, K, MO, WAG isotypes).

Herba perennis vel suffrutex pilis radiatis dense vestita. Caulis 20–50 cm altus, sat tenuis, ramificans. Folia dispersa, 2–6 mm longe petiolata; lamina elliptica vel obovata, obtusa, basin versus attenuata, sinuato-dentata, 22–50 × 7–25 mm. Racemi ebracteati, post fructificationem laxissimi. Pedicelli ascendentes, rigidi, ad apicem dilatati. Sepala oblonga, obtusa 7–11 × 1.2–1.5 mm. Petala albo-rosacea, postea flavescentia, 15–25 × 2.5–5 mm, vix unguiculata, ad apicem rotundata. Siliquae lineares, strictae, 14–25 × c. 2 mm, inter semina transverse septatae, valvis convexis, non cornutis. Stigma sine processibus. Semina matura non visa.

Perennial herb or subshrub, green with rather dense cover of somewhat golden, radiate hairs or, in woody parts, light grey brown. *Stems* 20–50 cm with numerous long ascending branches, rather thin. *Leaves* scattered; petioles 2–6 mm; lamina elliptic to obovate, 22–50 × 7–25 mm, obtuse, attenuate at base, sinuately dentate. *Racemes* ebracteate, 5–10-flowered, in ripe fruit very lax, up to 25 cm. Pedicels ascend-

Fig. 5. *Diceratella inermis* (holotype). Upper parts of plant, × 0.5.

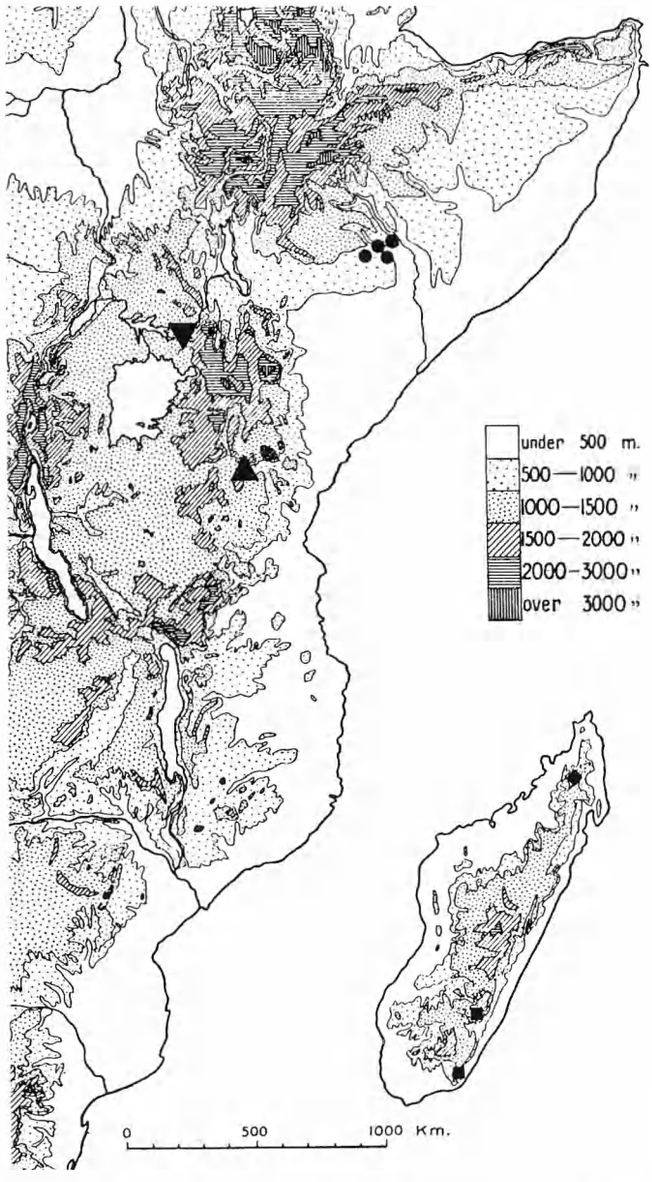

Fig. 6. Known total distribution of *Diceratella inermis* (●), *Erucastrum elgonense* (▼), *E. meruense* (▲), *Rorippa laurentii* subsp. *laurentii* (■) and *R. laurentii* subsp. *tsaratananae* (◆).

ing, stiff, widened at apex, 5–9 mm long. *Sepals* oblong, obtuse, 7–11× 1.2–1.5 mm. *Petals* white to pinkish, yellowish with age, 15–25× 2.5–5 mm, not markedly clawed, apically rounded. *Stamens* distinctly tetradynamous with linear filaments; pollen grains distinctly tricolpate. *Nectaries* ± prismatic, one at each side of each lateral stamen. *Siliquae* linear, straight, 14–25× c. 2.0 mm, transversely septate between the seeds; valves not keeled, hornless; style c. 1 mm long; stigma without projections. *Seeds* not seen ripe, probably very finely reticulate, perhaps with narrow wing, c. 1.5 mm long.

Distribution and habitat: *D. inermis* is only known from a restricted area in the NE corner of Kenya and the adjacent part of Ethiopia (Fig. 6). It grows on dry, ± stony limestone cliffs, at 400–800 m.

Additional material. Ethiopia, Sidamo Prov., Bogol Mayo, 13.XI.1972, Rippstein 883 (UPS) – Kenya, N Frontier Prov., Mandera Distr., E of Banissa, 22.V.1952, Gillett 13265 (EA, K, S); Ramu–Banissa road 4.V.1978, Gilbert & Thulin 1408 (C, EA, K, MO, UPS, WAG).

Erucastrum

Erucastrum includes nearly 20 species and has a disjunct distribution with the majority of taxa in Central Europe, the Mediterranean, NE Africa and Arabia while two species are regarded indigenous in Southern Africa (Marais 1970). The boundary against *Brassica* is not clearcut but *Erucastrum* seems to constitute a natural assemblage. Three closely related species form the *E. arabicum* group in Ethiopia (Jonsell 1976); *E. arabicum* Fisch. & Mey has spread, largely as a weed, to great parts of Tropical and Southern Africa.

Two new species were revealed during the revision for FTEA, viz. *E. elgonense* from Mt Elgon (Ugandan side) and *E. meruense* from Mt Meru in N Tanzania. They both grow in upper montane forest, *E. elgonense* in the ericaceous belt as well, and have been collected only three times each.

E. elgonense might be conspecific with or very close to a plant collected by Schimper in Ethiopia (Semien; Schimper No. II, 1367), misidentified as *Brassica tournefortii* Gouan (cf. Richard 1847, Oliver 1868). The Schimper specimens are unripe and no later similar collections have been traced. In some respects *E. elgonense* recalls the *E. arabicum* group, notably in habit and gross morphology (e.g. bracteate inflorescences, rather small flowers, stiff ± curved siliquae with keeled valves; Fig. 1 C). Other features agree more with *Brassica,* particularly the elongate median nectaries and the distinctly reticulate seed-coat (Fig. 7 A, B). The palisade layer of the seed-coat has a structure typical for *Brassica,* but the type occurs in *Erucastrum,* too. *E. elgonense* contributes to making the boundary between *Brassica* and *Erucastrum* more diffuse and its generic position is not self-evident. It is not attributable to any particu-

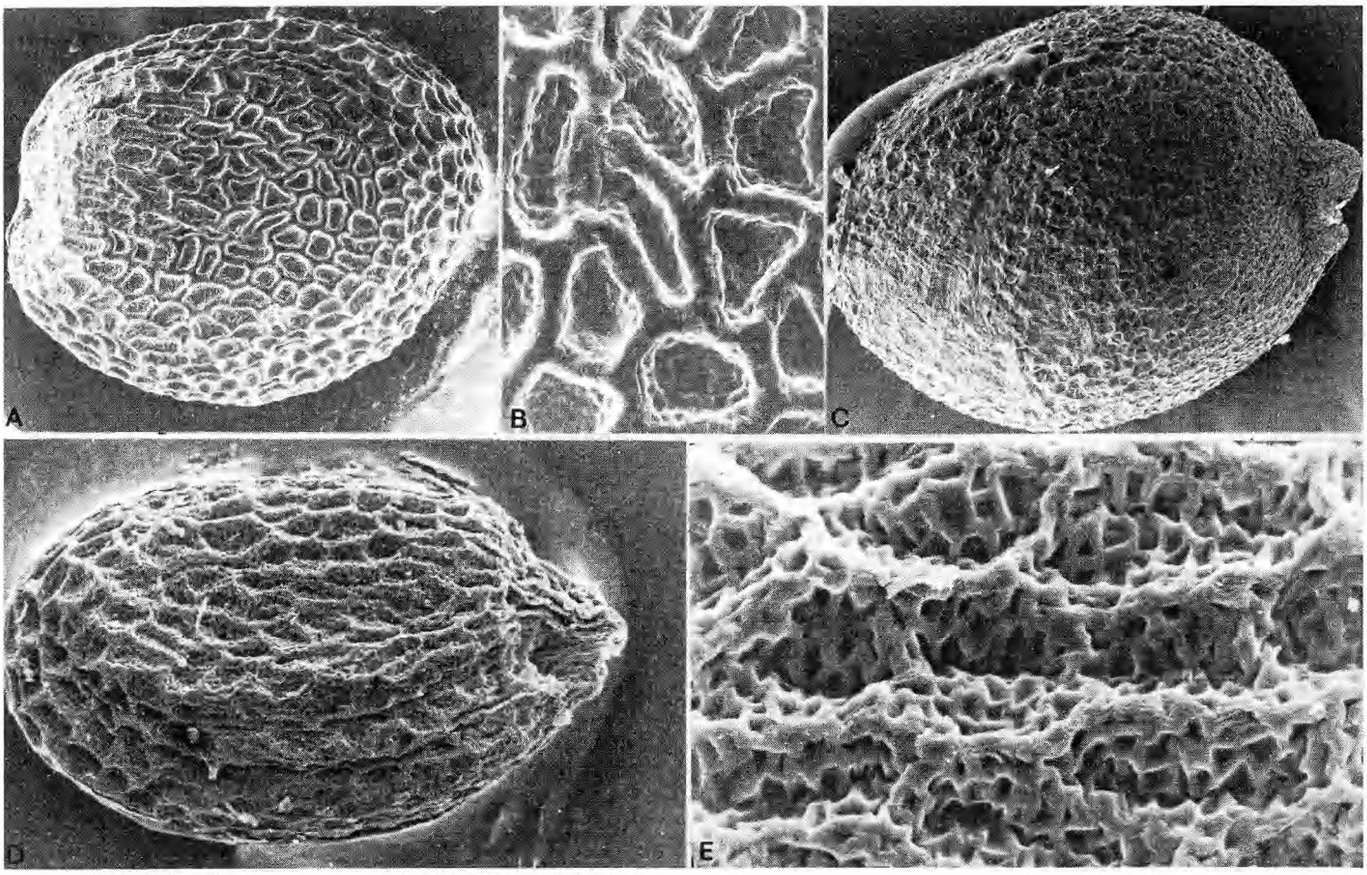

Fig. 7. *Erucastrum* seeds, untreated, SEM. – A: *E. elgonense* (Tothill 2346, K), × 30. – B: Do., × 120. – C: *E. strigosum* (Acocks 21628, K), × 40. – D: *E. meruense* (Jonsell 2176, UPS), × 40. – E: Do., × 200.

lar species group in *Brassica* but rather to the *E. arabicum* group and is therefore included in *Erucastrum*.

E. meruense agrees in several respects with the S African *E. strigosum* Thunb., which is, however, completely herbaceous, has appressed retrorse stem hairs, spheroidal, finely rugose (Fig. 7 C) seeds and truly horseshoe-shaped lateral nectaries (cf. description of *E. meruense* below and Fig. 7 D, E). *E. meruense* is a taller and much more robust plant. It is a more long-lived perennial with repeatedly branched, very woody, up to 5 mm thick lower stem portions. My cultivated specimens grew as leaf-rosettes for more than a year before raising flowering shoots. It grows scattered in rather bare, shaded places in the *Hagenia*-forest. The chromosome number was found to be 2n = 64, which is at the octoploid level. So far no number above the tetraploid one was known in the genus (Harberd 1972). *E. strigosum* has not been cytologically studied.

The two new species, though seemingly narrow endemics (Fig. 6), make the distribution of *Erucastrum* more coherent. *E. meruense* is another southern element of the montane flora. The affinity of *E. elgonense* is less clear but must be sought in the north. *Erucastrum* may well have more representatives in Tropical Africa, e.g. a non-fruiting specimen from Mt Gelai in N Tanzania (Carmichael 137, in EA).

Erucastrum elgonense Jonsell, sp. nov. – Fig. 8 A

Orig. coll.: Uganda, W slope of Mt Elgon, above Budadiri along the track via Mudangi to the caldera, ericaceous belt in burnt *Philippia* scrub, c. 3400 m, 5.XII.1967, Hedberg 4475 (UPS holotype, EA, K isotypes).

Herba erecta, ad 120 cm alta, sparse ramosa, in caule, foliis pedicellisque dense hispidula. Folia caulina vix petiolata vel sessilia, oblonga, dentata; inferiora lobo terminali majori et lobis lateralibus 1–5-jugis lyrato-pinnata; superiora indivisa, paulatim magis magisque bracteis similia. Racemi bracteati, densiflori; post fructificationem laxi cum pedicellis rigidis ascendentibus et bracteis persistentibus, plerumque pedicello parum longioribus. Sepala oblonga, c. 4 mm

longa. Petala flava, spathulata c. 8× 2,5 mm. Siliquae immaturae arcuatae, maturae praeter in apice rectae, 25–40× 2,5–3,2 mm; rostrum nervis manifestis munitum, 2,8–5,2 mm longum; valvae costa manifesta munitae. Semina rufa, subspheroidea, manifeste grosse reticulata, 1,2–1,5× c. 1,2 mm.

Erect herb (probably annual or short-lived perennial), 50–120 cm high, with a few long ascending branches, ± densely hispidulate on stem, leaves and pedicels. *Cauline leaves* indistinctly petiolate to sessile, up to 12× 5 cm, oblong in outline; the lower pinnatipartite to lyrate-pinnatifid, with up to 5 pairs of oblong doubly dentate lateral lobes and a larger terminal lobe, the upper undivided and coarsely dentate, successively bract-like. *Racemes* bracteate, dense, with numerous small flowers, in fruit with persistent bracts, very lax, up to 35 cm long, with 4–9.5 mm long, ascending, stiff pedicels. *Bracts* elliptic to narrowly elliptic, doubly serrate to dentate, up to 12 mm, usually somewhat longer than the pedicels. *Sepals* green-purplish, oblong, hispidulous, ± 4 mm long. *Petals* yellow, spathulate, c. 8× c. 2.5 mm. Longer *stamens* c. 6 mm long; pollen grains tricolpate. *Nectaries* as two small prismatic glands inside each lateral stamen and one elongate lobe between the median stamens. *Siliquae* when unripe curved, when ripe usually straight except apically, 25–40× 2.5–3.2 mm; beak 2.8–5.2 mm, with prominent nerves; valves with prominent midnerve; stigma rather flat. *Seeds* non-mucilaginous, red-brown, spherical to oblong in outline, 1.2–1.5× c. 1.2 mm, with distinct reticulum.

Distribution and habitat: Only known from the upper montane forest (*Hagenia*-zone) and ericaceous scrub on the W slope of Mt Elgon (Uganda), where it grows in clearings at c. 3050–3400 m.

Additional material. Uganda, Mt Elgon, Bulambuli, 4.IX.1932, Thomas 586 (K); do., hilltop towards top camp, 12.XI.1933, Tothill 2346 (K).

Erucastrum meruense Jonsell, sp. nov. – Fig. 8 B

Orig. coll.: Tanzania, Arusha Distr., Mt Meru, inner slope of N portion of the crater, c. 2700 m, 6.I.1971, Hedberg 4744 (UPS holotype, EA, K isotypes).

Suffrutex valde ramosus ad 100 cm altus. Caulis in basi crassus, lignosus saepe ramos novos creans, in altioribus partibus herbaceus, ut folia et pedicelli, hispidus vel strigosus. Folia inferiora saepe aggregata, petiolata; lamina lyrato-pinnata, ad 18× 4 cm magna, obtusa, truncata, lobo terminali magno et lobis lateralibus 1–4-jugis, triangularibus vel oblongis, margine sinuato-dentata vel repanda; folia superiora abrupte minora, breviter petiolata vel sessilia, unijugate lyrato-pinnatifida vel indivisa, paulatim magis magisque bracteis similia. Racemi ebracteati vel subtus solum bracteati, sat aperte corymbosi, post fructificationem laxi cum pedicellis patentibus. Sepala oblonga, c. 5,5 mm longa. Petala flava, sat unguiculata, 10–12 mm longa. Siliquae rectae vel subarcuatae, subtorulosae, 42–65× 1,3–1,8 mm; rostrum tenue, 5,5–7,0 mm longum; valvae costa manifesta munitae. Semina laete rufa, subspheroidea, humile et laxe reticulata, c. 1,7× 1,2 mm.

Perennial subshrub, extensively branched, up to 100 cm high; lower parts of stem and old branches strongly woody, up to 0.5 cm in diameter, often sprouting new branches. *Stem* (except woody parts), leaves and pedicels hispid to strigose by patent hairs. Lower *cauline leaves* rather crowded, with up to 5 cm long petioles; lamina truncate, oblong in outline, up to 18× 4 cm, lyrate-pinnate, with up to 4 pairs of triangular to oblong lateral lobes; terminal lobe 1/2–1/3 as long as the leaf, triangular to ovate, obtuse, truncate; margin sinuately dentate to repand; leaves upwards rapidly smaller and with short petioles, lyrate-pinnatifid, with usually one pair of lateral lobes and oblong terminal lobe, more than half as long as the leaf; uppermost leaves and bracts sessile, undivided, lanceolate, acute, truncate to cuneate, dentate. *Racemes* ebracteate or with bracts at lowest pedicels with many flowers in a rather open corymb, in fruit lax, up to 30 cm long, with 8–12 mm long spreading pedicels. *Sepals* oblong, moderately hispid, c. 5.5 mm long. *Petals* yellow, clawed, 10–12× c. 4 mm, apically truncate. Longer *stamens* c. 8 mm; anthers c. 1 mm long; pollen grains tricolpate. *Nectaries* low 2-topped glands inside each lateral stamen and a prominent spheriod gland outside each pair of median stamens. *Ovary* linear, glabrous; stigma bifid. *Siliquae* straight to slightly curved, somewhat torulose, 42–65 × 1.3–1.8 mm; beak narrowly conical, 5.5–7 mm long; valves glabrous with prominent midnerve. *Seeds* non-mucilaginous, light red-brown, elliptic in outline, c. 1.7× c. 1.2 mm, with a low, loose reticulum. Chromosome number 2n = 64 (Jonsell 2176).

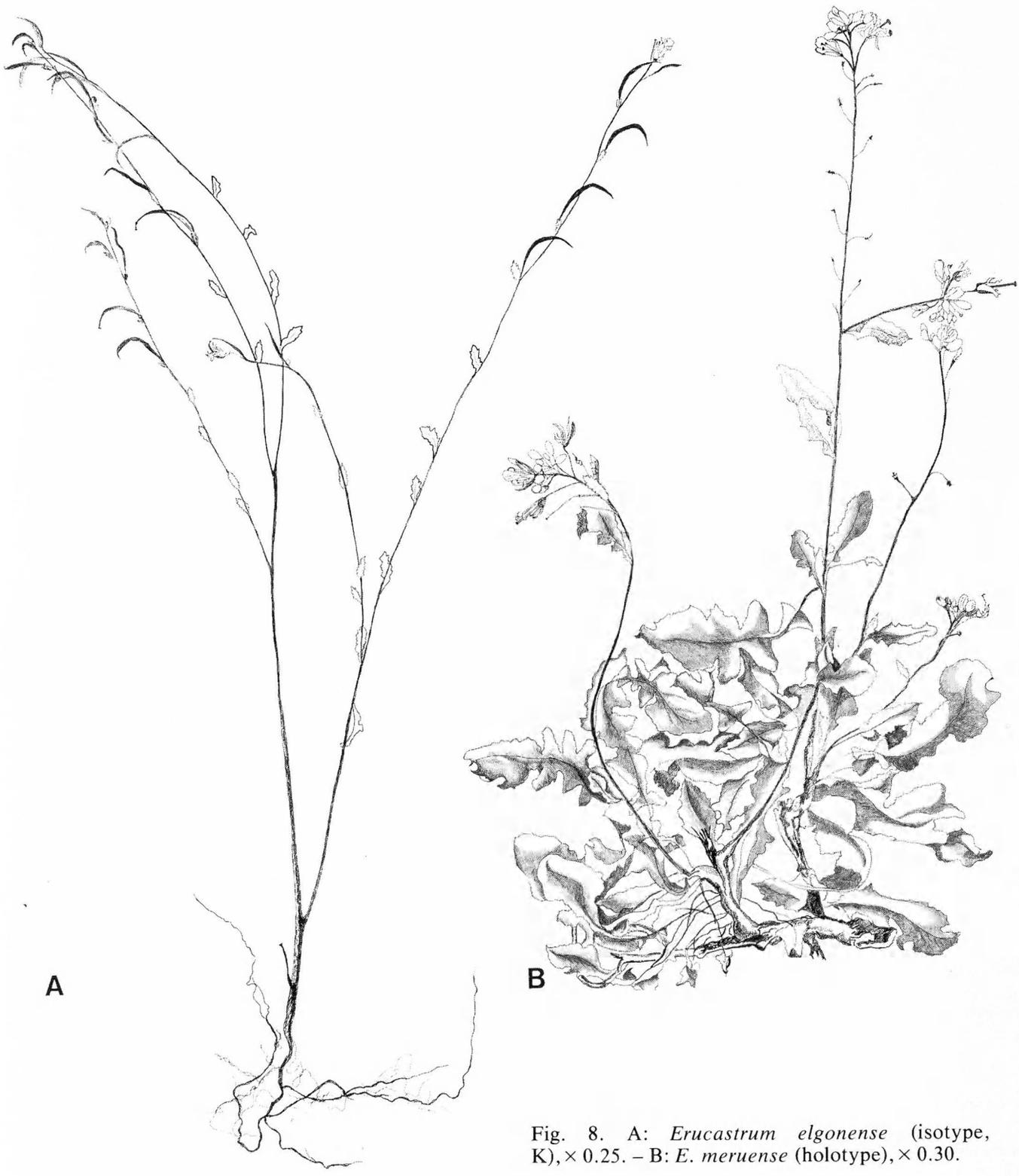

Fig. 8. A: *Erucastrum elgonense* (isotype, K), × 0.25. – B: *E. meruense* (holotype), × 0.30.

Distribution and habitat: Only known from Mt Meru in N Tanzania, where it grows in open *Hagenia*-forest at c. 2500–2700 m.

Additional material. Tanzania, Arusha District, Mt Meru, E slope, slope N of caldera wall, 12.XII.1967, Vesey-FitzGerald 5497 (EA); do., inner slope of N portion of the crater, 17.I.1970, Jonsell 2176 (UPS).

Rorippa

In a previous paper I treated the Tropical African taxa of *Rorippa* (Jonsell 1974). After that I discovered among undetermined *Cardamine* in the Paris herbarium several collections of an undescribed Madagascan species of *Rorippa*.

The new species *R. laurentii* is a mountain plant usually growing between 1800 and 2700 m, occasionally as low as at 900 m. It grows in cleared forest preferably on recently burnt ground and has probably expanded locally with increasing forest devastation. In virgin forest humid cliffs are reported as growth-places. It may form large colonies one year after burning, in association with *Philippia trichoclada* Bak. and *Stoebe* sp. (L. Jonsson, Uppsala, personal communication). It is now cultivated at the Botanical Institute, Stockholm University.

R. laurentii is known from three of the five larger high mountain areas of Madagascar, viz. the Tsaratanana massif in the north, Mt Andringitra in the south central and Mt Andohahelo in the southern part of the island (Fig. 6). As far as available material is representative there are morphological differences between the populations. Plants from the north have pinnatisect leaves, stout, somewhat inflated siliquae and very large seeds (Fig. 9 C, 10 C, D). Those from the two southern mountains are rather similar and have lyrato-pinnatifid leaves, linear, often torulose siliquae and smaller seeds (Fig. 9 A, B, 10 A, B). On this ground *R. laurentii* is divided into subsp. *tsaratananae* and subsp. *laurentii*. This is in accordance with the situation that endemism is very considerable on the old isolated Tsaratanana massif, but taxa vicarious between the southern mountains are also frequent (Humbert 1928, Koechlin et al. 1974 p. 388 ff.; cf. another case in Thulin 1975, pp. 66, 105–110).

With its pure white ground colour of the petals and large ridged seeds *R. laurentii* is outstanding among African *Rorippa* species, to none of which it seems particularly related. Nor is it close to the other Madagascan species, which are all non-montane (Jonsell 1974). *R. laurentii* agrees instead in several characters (petal shape and colour, siliqua and style shape, seed-coat structure and seed size) with some *Rorippa* species distributed in New Zealand (*R. gigantea* (Hook. f.) Garnock-Jones; cf. Garnock-Jones 1978), Australia (*R. gigantea, R. dictyosperma* (Hook. f.) L. A. S. Johnson, *R. laciniata* (F. Muell.) L. A. S. Johnson) and Java (*Rorippa backeri* (O. E. Schulz) Jonsell). These species were included in *Nasturtium* sect. *Ceriosperma* by Schulz (1933, 1936) together with a number of other, mostly Australian species. The section is heterogeneous and many species ought to be excluded. The species mentioned form, however, a group with a clearly southern distribution and *R. laurentii* is an addition to the Madagascan montane taxa with eastern instead of western connections, the latter of which are more numerous (cf. Humbert 1928, Koechlin et al. 1974 p. 390 ff.).

Most species of this southern group of *Rorippa* were originally described within *Cardamine,* but they do not have the siliqual opening mechanism nor the nectarial organization characterizing that genus. The group takes an isolated taxonomic position in the genus comparable to that of sect. *Cardaminum* in N Eurasia.

Rorippa laurentii Jonsell, sp. nov.

Orig. coll.: Madagascar, prov. Fianarantsoa, massif Andringitra, Antanifotsy, NE slope of Andranotily, c. 1900 m, 29.IV.1978, L. Jonsson 1090 (UPS holotype, K, P, TAN isotypes).

Herba glabra, ramosa, 15–120 cm alta. Caulis ad basin decumbens, sursum erectus. Folia caulina petiolata, pinnatisecta vel lyrato-pinnatifida cum lobis lateralibus 2–3-jugis breviter petiolulatis vel sessilibus; superiora sessilia, minores, 1-juga. Racemi ebracteati, sat laxi; post fructificationem ad 50 cm longi. Pedicelli patentes vel divaricati. Sepala navicularia, c. 3–4 mm longa. Petala alba, in basi viridia, late obovata, c. 5–6.5 mm longa. Siliquae lineares et sat torulosae vel ellipsoideae et leviter inflatae, 16–45 × 2.5–4.5 mm. Semina brunnea, cristis manifestis, densis, griseis munita, 2.8–4.5 × 2.0–3.8 mm.

Perennial (sometimes probably annual) glabrous herb with taproot, with age extensively branched from the base. Stems in basal parts arcuately decumbent, rooting at the nodes, for the rest erect, usually patently branched, 15–120 cm high. Basal *leaves* evanescent. Cauline leaves petiolate, pinnatisect to lyrate-pinnatifid, 4–18 × 2–10 cm; lateral lobes in 2–3 pairs, shortly petiolate to sessile and connate, elliptic in outline, acute, serrulate; terminal lobe larger than or nearly equalling the lateral ones, of similar

Fig. 9. *Rorippa laurentii*. Specimens from each of the three distribution areas, upper parts of plants, × 0.9. – A: Subsp. *laurentii* (Perrier de la Bâthie 4982, P). – B: Do. (Humbert 6170, P). – C: Subsp. *tsaratananae* (Humbert 18471, P). – Drawings preserved in P; artist not known.


A
B
C

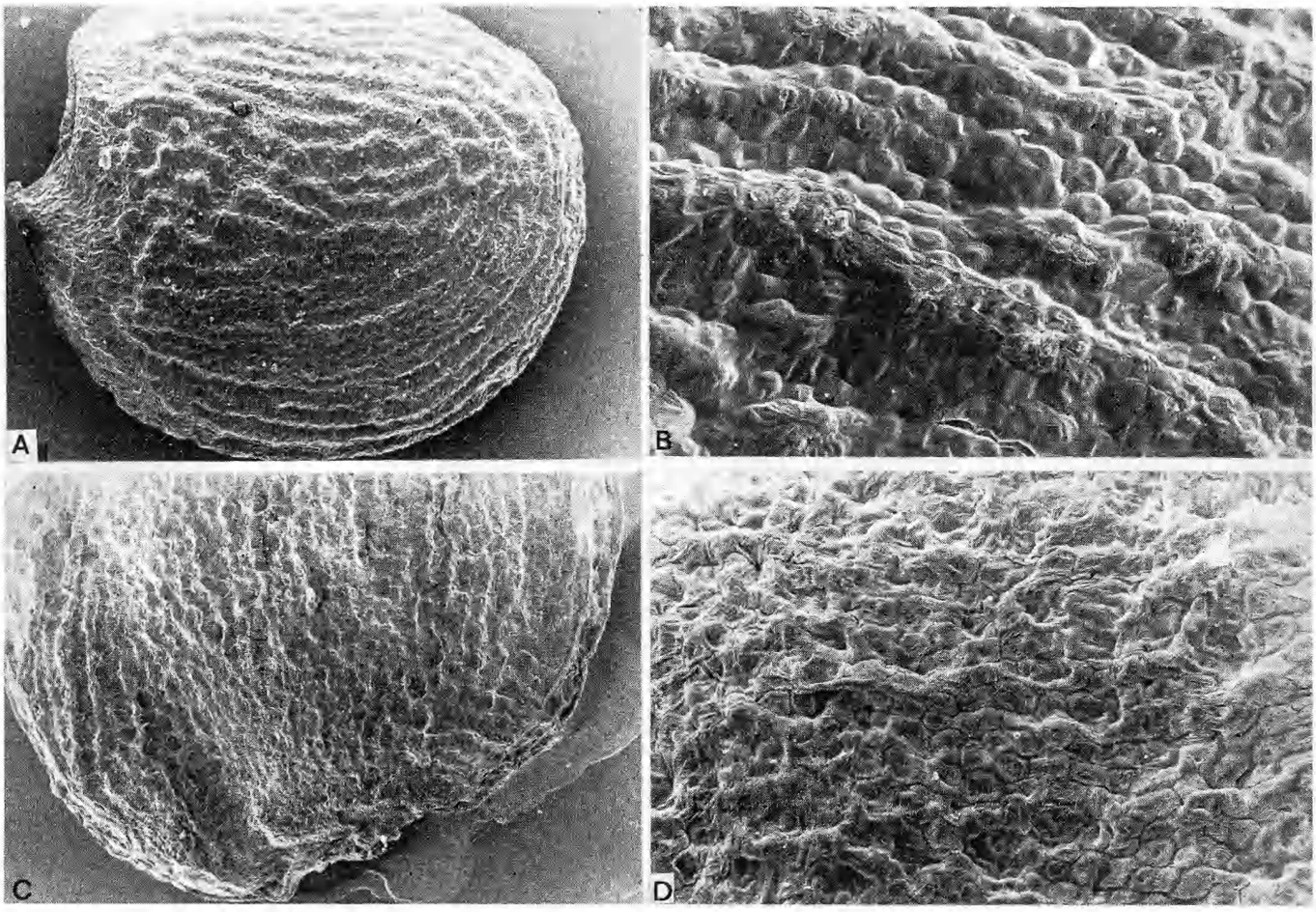

Fig. 10. Seeds of *Rorippa laurentii*, untreated, SEM. – A, B: Subsp. *laurentii* (Jonsson 1090, UPS). C, D: Subsp. *tsaratananae* (Humbert 18471, P). – A, C × 20, B, D × 80.

shape. Uppermost leaves sessile, smaller, with one pair of segments and proportionately larger terminal lobe. *Racemes* terminal, ebracteate, rather lax, in fruit up to 50 cm long. Pedicels patent to divaricate, usually with ± erect fruits, c. 1–2.5 cm long. *Sepals* boat-shaped, light green, c. 3–4 mm long. *Petals* with a white, broadly obovate blade and a very short greenish claw, c. 5–6.5 × 4.5 mm. *Stamens* indistinctly tetradynamous, c. 3–3.5 mm long with c. 0.7 mm long anthers. Filaments subulate with a bulbiform base. Pollen grains tricolpate, subprolate with finely reticulate sexine. *Nectaries* as a closed ring outside and below the stamens, and with projections between each of the stamens. *Ovary* cylindrical, 3–4 mm long, including c. 1 mm long conical style. *Siliquae* linear and ± torulose or ellipsoid and somewhat inflated, uniseriate with 2–10 seeds, 16–45 × 2.5–4.5 mm, including 2.6–4.5 mm long style. Stigma small, capitate. *Seeds* non-mucilaginous, brown, with distinct, dense greyish ridges, bean-shaped, 2.8–4.5 × 2.0–3.8 mm.

Distribution and habitat: See Fig. 6 and the text.

subsp. **laurentii** – Fig. 9 A, B

Leaves lyrato-pinnatifid. Siliquae linear, often torulose. Seeds 2.8–3.5 × 2.5–3.0 mm. Chromosome number 2n = 48 (Jonsson 1090).

Additional material. Madagascar, massif of Andringitra, eastern slope, 2200 m, IV.1911, Perrier de la Bâthie 2786 (P); at western foot of mountain, from 900 m, 7.V.1915, Perrier de la Bâthie 4983 (P); above 2000 m, IV.1921, Perrier de la Bâthie 13653 (P); Androhariana, 10.III.1950, Razafendrakoto 2384 (P); 8.VIII.1956, Razafendrakoto 8925 (P); path to Pic Boby, IV.1964, Bosser 19477 (P), Anjavidilava, 12.I.1971, Guillaumet 3719 (P) – Massif of Andohahelo, 1800–1900 m, 21/22.X.1928, Humbert 6170 (P).

subsp. **tsaratananae** Jonsell, subsp. nov. Fig. 9 C

Orig. coll.: Madagascar, massif of Tsaratanana, Amboabory–Antsianongalata, 2600–2700 m, XI/XII.1937, Humbert 18471 (P holotype).

Folia pinnatisecta. Siliquae ellipsoideae, sat inflatae. Semina 4.0–4.5 × 3.3–3.8 mm.

Leaves pinnatisect. Siliquae ellipsoid, somewhat inflated. Seeds 4.0–4.5 × 3.3–3.8 mm.

Additional material. Madagascar, massif of Tsaratanana, Mahahavy Valley, XI.1966, Morat 2296 (P).

Acknowledgements. *Rorippa laurentii* is named in honour of Mr Lars Jonsson (Lars = Swedish short form of Lat. Laurentius), who collected the decisive fresh material. My thanks are further due to Prof. O. Hedberg and Dr M. Thulin for providing fundamental collections from E Africa, to Mrs I. Eriksson for laboratory work, to Mrs P. Montrevel-Dufbäck for the drawings Fig. 5 and 8, to Dr E. Svenberg for checking the Latin diagnoses, and to the institutes, which have supplied material on loan. Financial support was given by the Swedish Natural Science Research Council.

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Rorippa backeri (Cruciferae), a new combination

Bengt Jonsell

Jonsell, B. 1979 11 15: Rorippa backeri (Cruciferae), a new combination. *Bot. Notiser 132:* 536. Stockholm. ISSN 0006-8195.

Rorippa backeri (O. E. Schulz) Jonsell, a Javanese species, is transferred from *Nasturtium* to *Rorippa*.

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Rorippa backeri (O. E. Schulz) Jonsell, comb. nov.

Basionym: *Nasturtium backeri* O. E. Schulz 1925: 291
Orig. coll.: Indonesia, Java, Prov. Bezuki, Mt Hjang, 2100–2300 m, 23.X.1913, Backer 9694 (isotype K!).

This distinctive species shows by its coarsely reticulate-foveolate seeds, firm, reticulate siliqua septa as well as in general habit clear affinity to the Australian *R. gigantea* (Hook. f.) Garnock-Jones and the Madagascan *R. laurentii* Jonsell (cf. Jonsell 1979). Just as the latter it is a mountain plant recorded also from the Javanese mountains Argopura, Wilis and Merbabu at 1300–3000 m.

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The pollination ecology of Herminium monorchis (Orchidaceae)

L. Anders Nilsson

Nilsson, L. A. 1979 11 15: The pollination ecology of Herminium monorchis (Orchidaceae). *Bot. Notiser 132:* 537–549. Stockholm. ISSN 0006-8195.

Observations, mainly from Öland, Sweden, on the pollination of *Herminium monorchis* (L.) R. Br. are presented. Hymenoptera Parasitica, Chloropidae and Scatopsidae (Diptera) together made up 94% of the flower-visitors. The genera *Tetrastichus* Hal. (Hym. Chalcidoidea, Eulophidae) and *Trachysiphonella* End. (Dipt. Chloropidae) represented 32 and 33% of the visitors, respectively. Pollination occurred mainly by *Tetrastichus* spp. which carried 65% of the pollinaria. Of this genus females were more than seven times as frequent as males. The occurrence of pollinaria on visitors indicates that the flowers are optimally adapted to pollen vectors about 1.30 mm long and 0.35 mm wide. Experiments with traps demonstrated that the floral fragrance is essential for the attraction of pollinators. The visitors feed on nectar which is secreted and concealed in a short spur. Various data indicate that the plant is completely and successfully entomogamous. The habit of pollen vectors to revisit flowers in the same inflorescence for hours suggests considerable geitonogamy. A theory is presented that the flower-type of *H. monorchis* has arisen by an evolutionary shift from more long-spurred ancestors adapted to larger pollen vectors.

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The genus *Herminium* R. Br. has its main centre in C Asia and extends to W Europe with only one species, viz. *H. monorchis* (L.) R. Br. This small plant occurs mainly on calcareous soils and often in damp places. The yellow-green subcampanulate flowers, borne in a dense spike, are c. 4 mm long (Fig. 1 A). The petals are longer and narrower than the sepals (Fig. 1 C). The petal forming the labellum is only slightly differentiated, 3-lobed and has a very short spur (Fig. 1 B, sp). The inner wall of the spur has two distinctly green, lateral, rounded protuberances, which are separated from each other by a narrow slit (Fig. 1 D, n). The rather conspicuous viscidia are placed at the upper corners of the entrance of the spur and are in the posterior part connected to the very short caudicles of the pollinia (Fig. 1 E). When a pollinarium is removed from its pocket the pollinium moves forward in relation to the viscidium (Darwin 1862). The bilobed narrow stigma is situated behind the viscidia in the "ceiling" of the cavity (Fig. 1 B, D, st). The flowers emit a powerful odour, usually described as honey-like (Godfery 1933). Hampton (1925) placed the scent in "the musk and honey group".

If nectar is present in the flowers is not clear from the literature. Darwin (1862) could not perceive any nectar and believed that it remained "enclosed in the intercellular spaces" in the nectary. Later (Darwin 1869) he noted that the insects "suck the nectar". Others have stated that nectar is not produced (Lubbock 1875, Rosvall & Pettersson 1951) or that free nectar has never been observed in the species (Ziegenspeck 1936) while others consider that nectar is exposed (Pijl & Dodson 1966, Proctor & Yeo 1973).

The pollination by insects has been masterly described by Darwin (1869). The visitors enter the flowers more or less upside down and insert their heads and fore legs into the short spur.

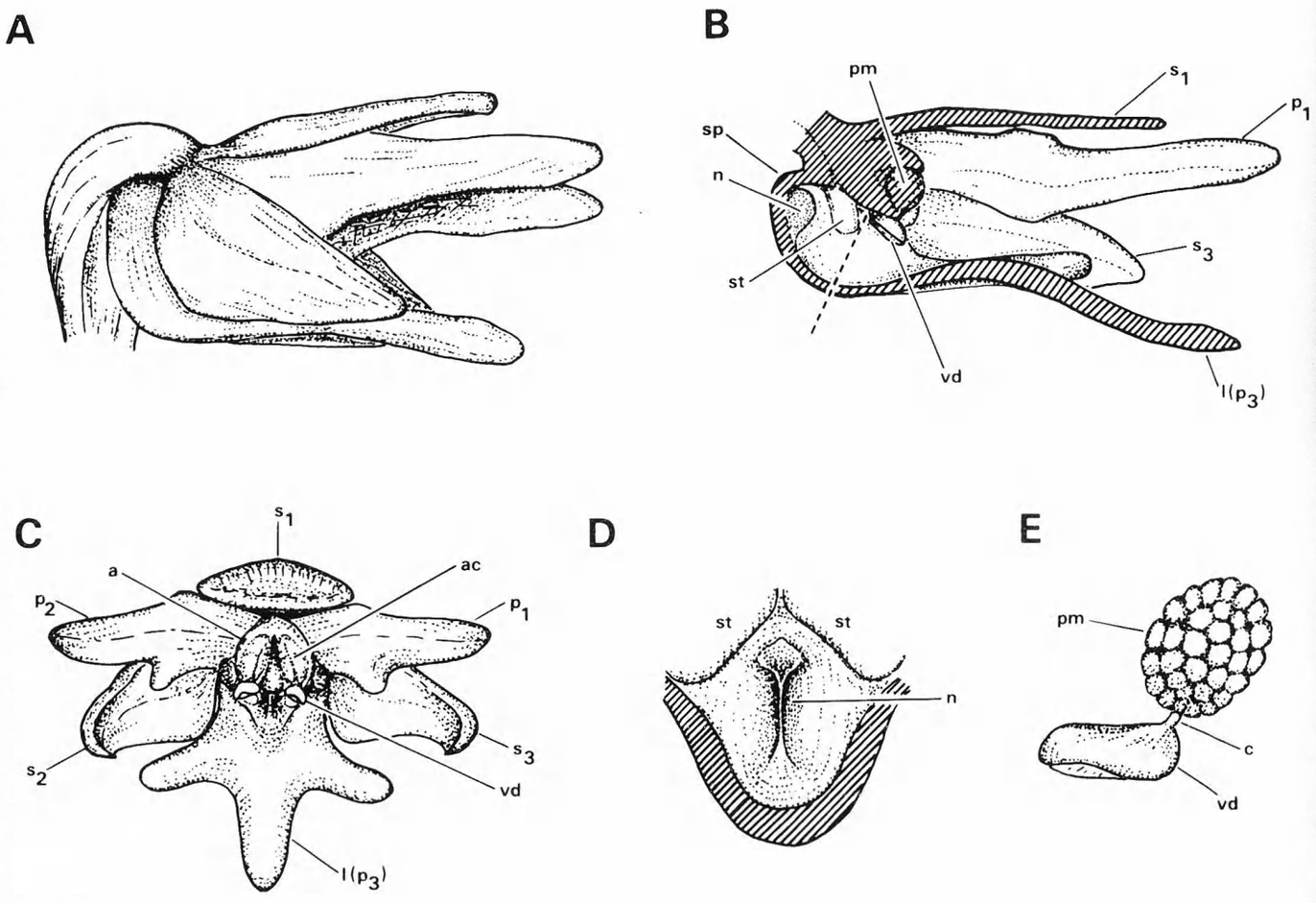

Fig. 1. The floral morphology of *Herminium monorchis*. – A: Flower, lateral view (15×). – B: Flower, longitudinal section (15×). – C: Flower, front view (15×). – D: Front view of the spur (40×). The position of the section is marked in B with a line of short dashes. – E: Pollinarium (50×). – Abbreviations: a anther, ac anther cell, c caudicle, l labellum, n lateral protuberance, p_1–p_3 petals, pm pollinium, s_1–s_3 sepals, sp spur, st stigma, vd viscidium.

Their front femora then slip into the viscidia which become attached to the outer surface of the femur and generally to the projection formed by the articulation of the femur with the coxa. At subsequent flower visits a few massulae from the projecting pollinium adhere to either of the two stigma lobes. If insect visits fail pollinaria or massulae are said to fall onto the stigma and cause self-pollination (Kirchner 1922, Hagerup 1952, Rosvall & Pettersson 1951, Summerhayes 1951, Proctor & Yeo 1973).

Till now, the identity of the flower-visitors has not been well known. Darwin (1869) found that the visitors and pollinators consisted of minute Hymenoptera (especially *Tetrastichus diaphantus* (Walk.) (Chalcidoidea, Eulophidae)), Diptera and Coleoptera (*Malthodes brevicollis* (Payk.) (Cantharidae)). In the Alps Müller (1881) noted that unidentified parasitic wasps 1–1.5 mm in length (Braconidae and Pteromalini) pollinated the plant. Ziegenspeck (1936) mentions that *Anopheles* (Dipt. Culicidae) have been observed with the pollinaria of *H. monorchis* attached to their proboscis. That species of *Leptura* and *Grammoptera* (Col. Cerambycidae) have been regularly encountered on the flowers (Pijl & Dodson 1966) must be a misinterpretation. Thus the only visitors hitherto identified to species are the two presented by Darwin (1869). The purpose of the present study was to provide information on the visitor and pollinator fauna and on details on the interactions between the plant and its pollen vectors.

Material and methods

Populations of *Herminium monorchis* were investigated in C Öland in June–July 1974–78 and at Stångby in Skåne in July 1976. The study localities are referred to as A–F (Öland, Fig. 2) and G (Skåne). With the exception of D, which is similar to A–C, they have all

been briefly described in an earlier paper although not under the same letters (Nilsson 1978 b).

The behaviour of flower-visitors was observed by the unaided eye, by a binocular tube and from 16 mm cinematographic films. Visitors were collected from inflorescences by the quick use of a killing bottle with one hand kept behind the flowers to prevent escape. The total collecting time and the number of occasions (within parenthesis) at A–G were 3.5 (4), 13.5 (11), 5.0 (3), 3.5 (3), 3.5 (3), 1.0 (2) and 1.0 (1) hours, respectively. The presence of pollinaria on visitors was investigated. Collected insects are deposited in the author's collection in UPS with the exception of some Chalcidoidea which have been kept by the specialists consulted.

Percentages of cross-pollination and removed pollinaria were recorded (under magnification) for spikes towards the end of anthesis. Some plants, transferred to a greenhouse, were used in experiments on autogamy. Plants were isolated by a very fine synthetic net which excluded also the smallest insects (e.g. Thysanoptera) from the flowers. Fibres of paper sensitive to glucose (Clinistix, Ames Co.) were carefully inserted into spurs (under magnification) and checked for colour changes to find out if nectar was secreted.

The floral fragrance was collected in pre-column tubes and analysed by gas chromatography – mass spectrometry (GC–MS; see Nilsson 1978 a). In addition, some pentane extracts of flowers were prepared and analysed. To characterize main peaks of extracts a Perkin-Elmer F-30 gas chromatograph equipped with a sniffing vent was used.

The influence of scent on the frequency of visiting insects was studied by enclosing single spikes within plastic cylinders (L 4, I D 3 cm). The upper end of each cylinder was covered with tape so that the sticky surface was turned inward. Thereafter the cylinders were attached to the ground by steel wire in such a way that the lowermost flowers were situated well above the lower edge. For comparison, spikes from which the flowers (except the ovaries) had been removed were enclosed in the same way. Small insects which entered from below were then trapped by the sticky surface in the "ceiling". The tape-traps were set out in the morning and examined in the afternoon. The experiments were carried out in the beginning of July 1978 at locality A.

Floral fragrance

Collection in pre-columns gave only a few compounds on the chromatograms, all in the monoterpene region. They have been tentatively identified as α-pinene, myrcene, limonene (highest peak) and possibly γ-terpinene (smallest peak). No sesquiterpene hydrocarbons were traced, although such compounds are common constituents in the fragrances of many other species within the subtribe Orchidinae (Nilsson, unpubl.). The odours of the four monoterpenes are not responsible for the powerful ingredient in the fragrance. Pentane extracts from flowers, studied with the F-30 gas chromatograph sniffing vent revealed that the compound which gives the characteristic scent is very similar to anisaldehyde (*p*-methoxybenzaldehyde). The mass spectrum is identical with that of Ar-methoxybenzaldehyde in Stenhagen et al. (1974). Extracts also gave a distinct peak of nonanal.

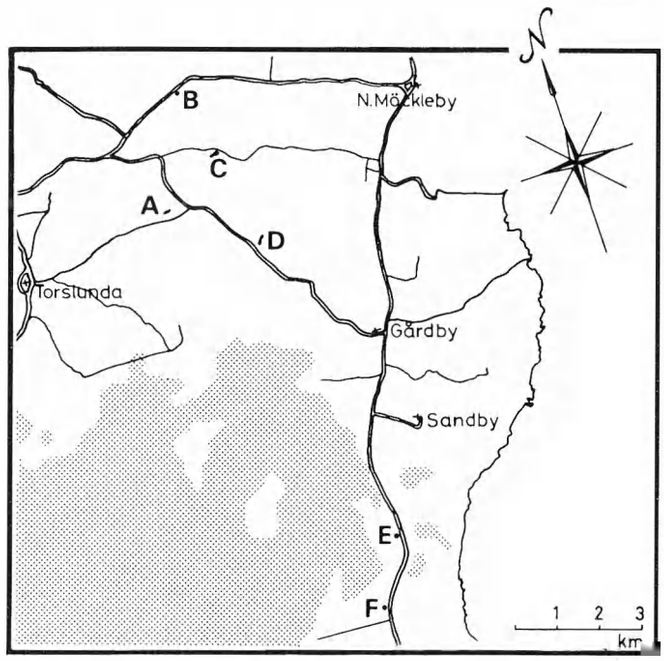

Fig. 2. Observation sites on C Öland (A–F). Dotted area represents alvar.

Nectar

Fibres of indicatory paper carefully inserted between the two lateral greenish swellings in the short spur gave a clear blue reaction i.e. glucose was present. The test was repeated many times and on various occasions. The small quantity of secreted fluid is normally visible in the slit between the swellings. In inflorescences taken indoors sometimes no nectar was found which perhaps indicates that the nectar can be resorbed or that the quantity is easily influenced by environmental factors.

Flower visitors

In all, 331 specimens of 69 species of insects were recorded (Table 1). Individuals of Hymenoptera Parasitica, Chloropidae and Scatopsidae (Diptera) made up 50, 38 and 6% of

Table 1. Insects recorded as flower-visitors and pollen vectors of *Herminium monorchis* (no. of specimens with pollinaria within parenthesis). – * Observed but not collected. – ** Stuck in the flower. – Two (or three) numericals appended to some of the species names denote: 1st: no. of certain identifications; 2nd: tentative identifications; 3rd: no. belonging to that group of species.

Visitors	Localities	No. of specimens	No. of pollinaria
Lepidoptera			
Adela croesella (Scop.)	B	1♀	.
Scythris laminella (Den. & Schiff.)	A	1	.
Coleoptera			
Meligethes aeneus (F.)	G	6	.
Diptera			
Trachysiphonella ruficeps (Macq.)	A B C D E F	34♂♂(2), 41♀♀(1)	3
T. pygmaea (Meig.)	A B C D E F G	10♂♂, 24♀♀	.
T. scutellata (v. Ros.)	A	1♂	.
Oscinimorpha sordissima (Stbl)	A B C D	4♂♂, 7♀♀	.
O. minutissima (Stbl)	B E	3♂♂, 1♀	.
Meromyza triangulina Fed.	F	1♂	.
Swammerdamella brevicornis (Meig.)	A B D E F G	6♂♂, 9♀♀(4)	6
Rhegmoclema verralli (Edw.)	G	1♀(1)	1
Coboldia fuscipes (Meig.)	E	1♂	.
Scatopsidae*	A B	3(1)	2
Herina frondescentiae (L.)	A C	2♂♂, 2♀♀	.
Bradysia vernalis Zett.	A C	4♀♀	.
Plastosciara Berg sp.	B	1♀	.
Lestriminae sp.	B	1♀	.
Hymenoptera			
Andrena haemorrhoa (F.)*	E	1♀	.
Microchelonus Szépl. sp.n.?	B	1♂	.
Synaldis ? distracta Nees.	F	1♂	.
Cothonaspis pentatoma Htg	E	2♀♀	.
C. longula Nordl.	C	1♂	.
Kleidotoma Westw. spp.	D E F G	1♂(1), 8♀♀(5)	7
Platygaster Latr. sp.	B	1♀	.
Anopedias lacustris Kieff.	G	1♂	.
Synopeas Först. sp.	G	1♂	.
Telenomus nitidulus (Th.)	A B G	2♂♂, 5♀♀(1**)	(2)
T. harpyiae Mayr	E	1♂	.
T. othus Hal.	B	1♀	.
Gryon misellus Hal.	E	1♀	.
Aphanogmus vicinus Först.	B	1♀	.
Litomastix truncatellus (Dalm.)	G	1♀	.
Bruchophagus platyptera Walk.	B	1♀	.
Eurytoma incrassata Th.[0,1]	B	1♀	.
Trichogramma Westw. sp.	E	1♀	.
Torymus ventralis (Fonsc.)[1,2]	C G	3♂♂(2)	4
T. galii Boh.[1,1]	B D	1♂(1), 1♀(1)	2
T. brachyurus Boh.	A	1♀(1)	1
Euderus viridis (Th.)	G	1♀(1)	2
E. albitaris Zett.	B	1♀	.
Necremnus tidius (Walk.)	G	1♀(1)	2
Achrysocharella formosa (Westw.)	A C	2♀♀(1)	1
Omphale clypealis (Th.)	B	1♀(1)	1
Pediobius fascialis (Giraud)	B	1♀	.
Tetrastichus pausiris (Walk.)	B	19♀♀(9)	9
T. conon (Walk.)[8,8]	B C E	4♂♂(2), 12♀♀(7)	12
T. leucone (Walk.)	B	14♀♀(7)	7
T. caudatus (Westw.)[1,5,8]	A B E	1♂(1), 13♀♀(7)	9

Table 1 (continued).

Visitors	Localities	No. of specimens	No. of pollinaria
T. cecidomyiarum (Bouché)[0,8]	A B G	8♀♀(6)	10
T. agrus (Walk.)[1,5]	B E F	1♂, 5♀♀(3)	5
T. diaphantus (Walk.)[0,5]	A B C	5♀♀(5)	6
T. apama (Walk.)	G	4♀♀(3)	6
T. terebrans (Erd.)	B G	3♀♀	.
T. charoba (Walk.)	G	2♀♀(2)	2
T. orithyia (Walk.)	G	1♀	.
T. actis (Walk.)	A	1♀	.
T. vacuna (Walk.)[0,1]	B	1♀(1)	2
T. lycidas (Walk.)[0,1]	C	1♀(1)	1
T. Hal. spp.	B C D	7♂♂(1), 5♀♀(3)	6
Ecrizotes longicornis (Walk.)	B	1♀	.
Pirene penetrans (Kirby)	G	1♂(1)	1
P. conjugens Grah.	G	1♀	.
Gastrancistrus acutus (Walk.)[0,2]	B C	2♂♂(1)	1
G. fulvicornis (Walk.)[0,1]	E	1♀(1)	1
Eupteromalus Kurd. sp.	D	1♀	.
Trichomalus helvipes (Walk.)	C	1♂(1)	2
T. campestris (Walk.)	E	1♂	.
Mesopolobus amaenus (Walk.)	B G	2♂♂(1)	1
M. aequus (Walk.)	G	1♂(1)	2
M. laticornis (Walk.)	B	1♀	.
Meraporus graminicola Walk.	G	1♀	.

the visitors respectively. The most important genera among parasitic wasps were *Tetrastichus* (Eulophidae) (32%), *Torymus* (Torymidae) (1.8%) and *Kleidotoma* (Eucoilidae) (2.7%). The genus *Tetrastichus* alone represented 65% of Hym. Parasitica. The visitors belonging to Chloropidae and Scatopsidae were mainly of two genèra, viz. *Trachysiphonella* and *Swammerdamella,* respectively. These genera represented 33 and 4.5% of all visitors and 87 and 88% within their families. The most common visitor species were *Trachysiphonella ruficeps* and *T. pygmaea, Oscinimorpha sordissima* (Chloropidae), *Tetrastichus pausiris, T. conon, T. leucone* and *T. caudatus, Swammerdamella brevicornis* and *Telenomus nitidulus* (Scelionidae). The numeric relations of visitor groups can be compared in Fig. 3 (left bars). In addition, Thysanoptera were present in the spikes but it could not be established that they fed on the nectar. They never carried pollinaria.

Females of visiting chalcids were more than four times as frequent as males (ratio 113:25) and within *Tetrastichus* females were even more than seven times as frequent (94:13). For Chloropidae the sex-ratio was more equal (73:53).

Several visitor species were recorded at more

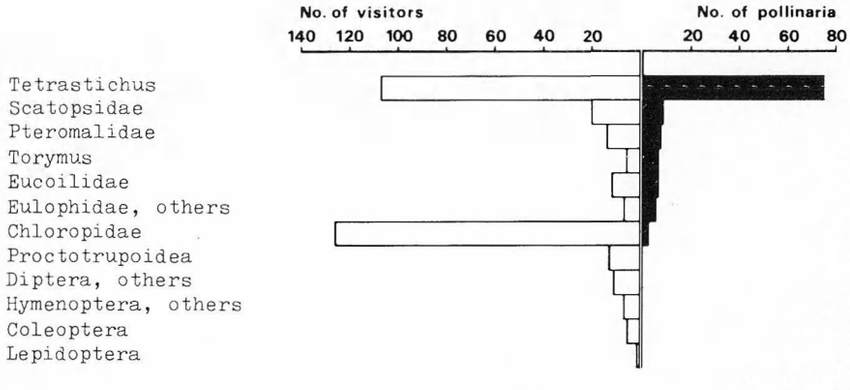

Fig. 3. Number of visitors of different groups to flowers of *Herminium monorchis* and the occurrence of pollinaria.

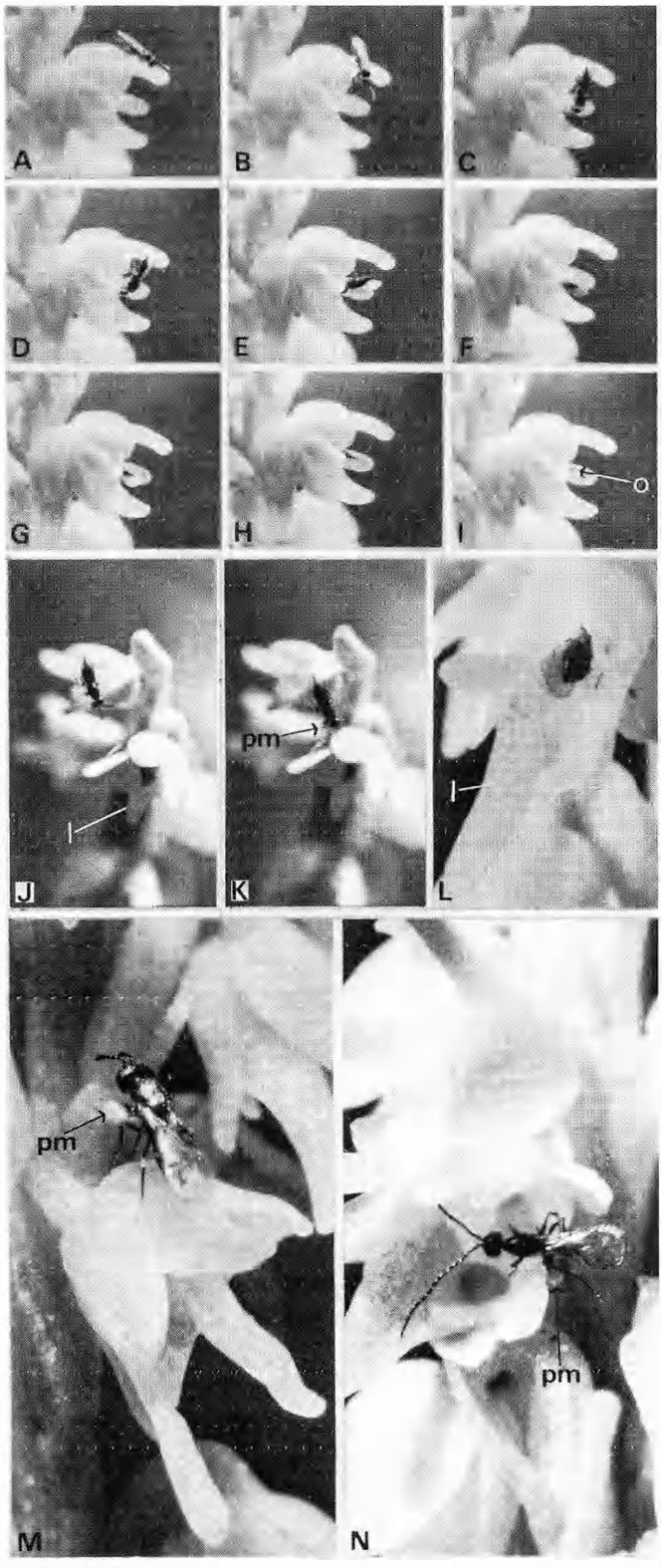

Fig. 4. Parasitic wasps visiting the flowers of *Herminium monorchis*. – A–I: Chalcid entering a flower in the top of the inflorescence. – J–K: One chalcid feeding inside the spur while another one carrying a pollinarium crawls to the same flower. – L: Chalcid feeding and with its back turned to the labellum. – M: Chalcid, which has got a pollinarium on its front femur, grooms on a flower. – N: Eucoilid wasp crawling between flowers. Note the pollinarium attached to the middle leg. – Abbreviations: l labellum, o ovipositor, pm pollinarium.

than two localities, e.g. *Trachysiphonella* spp., *Oscinimorpha sordissima, Swammerdamella brevicornis, Telenomus nitidulus* and several *Tetrastichus* spp. *Tetrastichus pausiris* and *T. leucone,* however, were found only at B but there they were frequent. Several *Tetrastichus* species and some other chalcids were recorded only in Skåne (G).

During the preparation of this paper the author received 26 specimens of insects visiting *H. monorchis* in Denmark collected by Bernt Løjtnant, Aarhus. They had been collected in a natural population at Nørholm Enge (15 visitors) and on cultivated plants at Gjedved (11 visitors), Jylland in 1970. The specimens have not yet been definitely determinated but belong to *Tetrastichus* (8), other Chalcidoidea (5), Proctotrupoidea (3), Eucoilidae (5), *Oscinella* Beck. (3) (Chloropidae) and *Saltella* R.-D. (1) (Milichiidae). At Nørholm 7 of the visitors were *Tetrastichus*.

Pollen vectors

Pollinaria were mainly transported by *Tetrastichus* spp. which together carried 65% of all pollinaria (Fig. 3, right bars). In this genus females carried 95% of the pollinaria. Other important vectors were Scatopsidae (7.8%), *Torymus* (6.1%), *Kleidotoma* (6.1%) and other small parasitic wasps (together carrying 12.2%). Although very frequent as visitors (38%) Chloropidae only had 2.6% of the pollinaria. In the Danish material 5 pollinaria were found (3 on *Tetrastichus*).

Behaviour of visitors

Chalcids and other insects normally alighted in the middle or at the top of the inflorescences on protruding floral parts, i.e. on sepals and petals inclusive labella. Alighting frequently occurred on the top of the flower. Thereafter the visitors crept between individual flowers, entering them from above or laterally between the apices of the perianth (Fig. 4 A–I). As noted by Darwin, small wasps finally orient their backs directly or obliquely towards the labellum i.e. they move into the nectary more or less in an inverted position (Fig. 4 J–L). In a few cases visits took place also with the wasp's venter turned towards the labellum but the results of these visits are unknown.

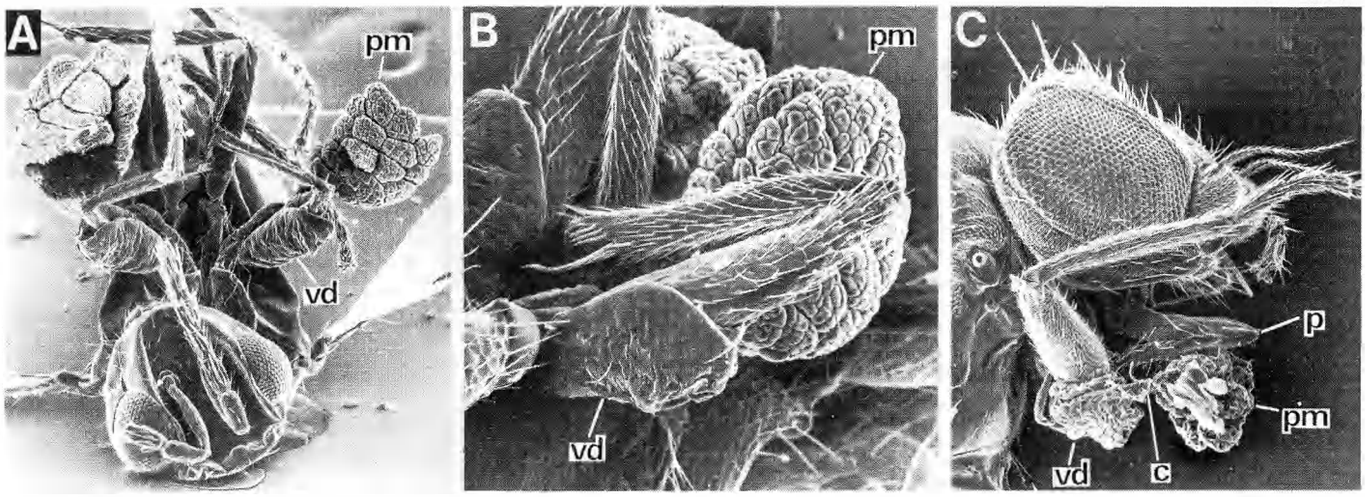

Fig. 5. Scanning electron micrographs of pollinaria attached to flower-visitors of *Herminium monorchis*. – A: *Tetrastichus conon* ♀ with one viscidium on each front femur (55×). – B: *Torymus ventralis* ♂ with viscidia attached to the base of the front femora (110×). – C: *Trachysiphonella ruficeps* ♀ with viscidium on the base of front femur (70×). Note the elongated, angled proboscis. – Abbreviations: c caudicle, p proboscis, pm pollinium, vd viscidium.

The wasps obviously try to reach as deep as possible into the short spur with the anterior part of the body. During this operation only the end of abdomen and the outer part of the wings can be seen from the outside (Fig. 4 I, o). The front legs are stretched forward past the position of the viscidia.

Darwin (1869) mentions that sucking the nectar takes about two or three minutes whereafter the wasp retreats. In the present study the process was regularly carried out within one minute but the time varied greatly probably due to the amount of nectar in the individual flower. For example once a *Tetrastichus* female crawling in a spike was seen to make 18 visits ranging from 6 to 71 seconds ($\bar{x} = 23$ seconds). On the other hand the duration of a wasp's stay in an inflorescence often was considerable. The female mentioned above spent at least 45 minutes in the same spike. On another occasion a *T. leucone* female was observed for two hours making repeated visits to the flowers of one single inflorescence. Between visits the wasps spend much time grooming (Fig. 4 M), resting, attempting to scrape off the pollinia or creeping around among the flowers. During the visit of an inflorescence wasps often crept repeatedly from one end of the spike to the other revisiting the same flowers. Obviously, these habits will cause frequent geitonogamy.

Pollen vectors, e.g. chalcids, Scatopsidae and Chloropidae, regularly fed on the nectar. Once a female of Sciaridae (Dipt. Nematocera) was observed to probe the labellum and the other petals. The two specimens of Lepidoptera probed into the nectary with their proboscis. *Meligethes aeneus* (Col. Nitidulidae) could not reach the nectar but fed on the pollinia.

Visitors which had received two pollinaria on their legs showed difficulties to synchronize their movements and could often not walk properly. The inconvenience was shown by intense grooming movements to get rid of the load. On one occasion a *Swammerdamella brevicornis* which had got one pollinarium on each front femur, acted so violently that it lost its grip and fell backwards from the flower into the grass below.

The flower-visitors were normally abundant in sunny weather although remarkably frequent visits by small parasitic wasps were noted during dull but warm days.

Functional morphology

The distance from the outer surface of the column to the posterior corner of the spur is c. 1.2 mm ($n = 10$) and the width of the entrance is c. 0.9 mm ($n = 10$). Consequently, the width of the thorax in visiting wasps ($\bar{x} = 0.34$ mm) normally allows them to slip through the entrance easily, while the length of the body ($\bar{x} = 1.27$ mm) makes it possible for them to advance so deep into the flower that both head and thorax get past

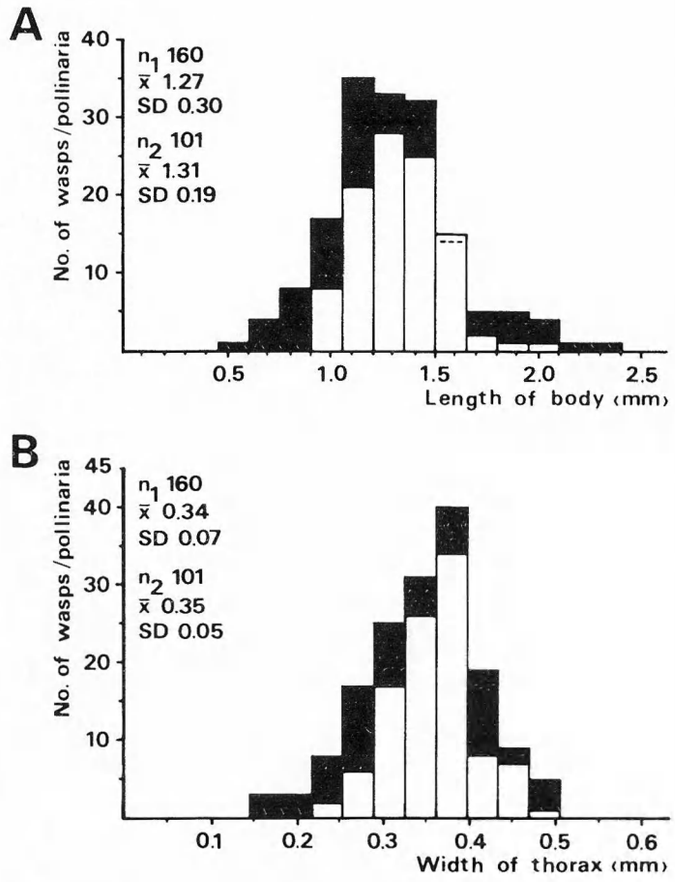

Fig. 6. Size in wasps (Chalcidoidea, Eucoilidae and Proctotrupoidea, filled bars from the base line) visiting the flowers of *Herminium monorchis* and the occurrence of pollinaria (unfilled bars from the base line). – A: Length of body (ovipositor excluded). – B: Width of thorax.

the position of the viscidia (cf. Fig. 6). In most cases, when the wasps enter upside down, the viscidia will normally become attached dorsally and somewhat transversally on the front femora with the pollinia projecting outwards and about posteroventrally (Fig. 5 A, B). Optimally, a viscidium attaches only to the surface of the femur leaving free the basal segments of the legs as well as the knee. In the slightly larger wasps the pollinaria tend to become attached towards the base of the femur and on the connecting segments up to the coxa (Fig. 5 B). The pollinia are carried beneath the femora which certainly makes it easier for the wasps to use their legs in a normal way. If wasps would enter flowers in a "normal" position the viscidia would probably become attached so that the caudicles were directed upwards. The added weight of the pollinia would then likely twist the legs and cause difficulties for the wasps to walk and to disperse the pollen. In dipterous visitors as Scatopsidae and *Trachysiphonella* the viscid discs were also glued to the base of the front femur but the direction of the pollinium was sometimes different (Fig. 5 C). Only once a wasp was observed, which carried a pollinarium on its middle legs (Fig. 4 N). In 99% of the cases the pollinaria were carried on the front legs.

A majority of the vectors (68%) had only one pollinarium. Two pollinaria were carried by 28% while one single specimen (1.3%) was found with three viscidia attached. Only two vectors (2.3%) had two viscid discs on the same femur. Attachment to front tibia was found once (0.9%).

The minute parasitic wasps, Scatopsidae and Sciaridae, have very short mouthparts and lick up the nectar. To reach the food they must therefore bodily enter the spur. In some Chloropidae, e.g. *Trachysiphonella,* the mouthparts are elongated (Fig. 5 C, p). Obviously, these flies do not need to force themselves into the short spur to get access to the nectar. This seems to explain why they so rarely receive pollinaria despite their frequency.

A certain strength is needed to remove the pollinaria. Already Darwin (1869) found visitors which had become permanently glued to the viscidia. On Öland 0.4% of the flowers were occupied by victims towards the end of anthesis in 1977 (Table 5). The lower limit for wasps to become vectors seems to be c. 1.0 mm in length (ovipositor not included) and 0.23 mm in width (Fig. 6). The optimal adaptation, indicated by the frequency of pollinaria, occurs with wasps c. 1.30 mm long and 0.35 mm wide (Fig. 6). The frequency of pollinaria on various groups of visitors indicates that Torymidae and Eulophidae, closely followed by Eucoilidae and Pteromalidae are the best pollinators (Table 2). Diptera, exclusive Scatopsidae, and other groups do not interact successfully with the flowers.

Pollination is effected when a vector advances deep into the spur and operates its front femur under the stigma lobes rubbing some of the massulae on to the sticky surface.

Importance of fragrance

Inflorescences from which the flowers have been cut away lack the characteristic honey-like

odour. Five days of experiments with tape-traps show that such spikes completely lose their attraction to small parasitic wasps (Table 3).

Wasps and chloropids were more often trapped over intact plants. Several of the trapped wasps carried pollinaria and belonged to the genus *Tetrastichus*.

Entomogamy contra possible autogamy

If inflorescences are isolated throughout anthesis no fruits are produced – a fact which can be compared with the very high fruit set of natural plant populations (Tables 4, 5). Anthesis in a greenhouse or even indoors does not at all exclude pollination by external agents because small insects are regularly present also in this environment. Since wasps often stay long in the same spike a single chalcid is enough to produce a clear increase in fruit set. Once in the greenhouse on Öland a *Tetrastichus* female was observed working the flowers of uncovered inflorescences.

During the final part of anthesis the pollinia in unvisited flowers tend to shrink within their pockets and the folds enclosing them dry and become brownish. The pollinaria then fall out easily on to the labellum or further down to the ground. It was never observed that they spontaneously came in contact with the stigma. Since the majority of the pollinaria in natural populations are removed by insects also the possibilities for autogamy by self-pollination are rather small (cf. Table 5).

From the numbers of pollinaria attached to vectors and those removed from flowers it can be estimated how many vectors had been active in the 100 inflorescences in Table 5. The removal of 2043 (58.9%) out of 3468 pollinaria indicate that some 1600 vectors had been present, i.e. c. 16 vectors per spike.

Anthecological status

In the ordinary association of plants where *H. monorchis* occurs the pollinating insect species were not found on any other concurrently blooming plants. The visiting fly *Herina frondescentiae* (Otitidae) is a regular visitor also to *Epipactis palustris* (L.) Cr. (Orchidaceae) (Nilsson 1978 b). At locality B assemblages of *Pastinaca sativa* L. (Apiaceae) grow along a roadside 5–15 m from the population of *H. monorchis* and some of the vector species were found taking nectar from this plant, i.e. *Tetrastichus leucone* (♀♀ frequently), *T. pausiris* (♀♀ frequently), *Pirene penetrans* (Pteromalidae) (♂ once), *Euderus albitarsis* (Eulophidae) (♀ once) and *Swammerdamella brevicornis* (♂♂, ♀♀ several). Along the borders of the damp meadows at A and C scattered specimens of *Listera ovata* (L.) R. Br. (Orchidaceae) occur and may occasionally attract the same visitor species as *H. monorchis*. Species recorded on *L. ovata* were *Tetrastichus pausiris* (♀ once), *T. leucone* (♀ once) and *Trachysiphonella ruficeps* (♂ once). Thus, the pollination system of *H. monorchis* seems to practically lack competition from other entomogamous plants, except in border situations.

Table 2. The frequence of pollinaria on different groups of visitors to the flowers of *Herminium monorchis*.

Insects	Visitors carrying pollinaria (%)	Pollinaria per visitor (mean)
Torymidae	86	1.2
Eulophidae	54	0.71
Eucoilidae	50	0.58
Pteromalidae	43	0.57
Scatopsidae	30	0.45
Chloropidae	2.3	0.02
Proctotrupoidea	.	.
Coleoptera	.	.
Lepidoptera	.	.

Table 3. Tape-trap catches of insects over intact spikes and over spikes having excised flowers. On each occasion 18 traps were used, 9 over each category of spikes. The experiments were carried out at locality A during 5 days in July 1978.

Insects	Catch over intact spikes. No. with pollinaria within parenthesis	Catch over spikes with excised flowers
Hym. Parasitica	17(5)	1
Chloropidae	5	2
Sepsidae	1	.
Scatopsidae	1(1)	.
Thysanoptera	30	1
Aphidoidea	.	1

Table 4. Fruit set in *Herminium monorchis* under various conditions. – * The tallest spike was bent by the screen which caused self-pollination in one of the top-flowers. – ** At S. Baspunkten of the Great Alvar.

Conditions	No. of plants	No. of flowers	No. of fruits	Fruit set per specimen (%)
Isolated throughout anthesis	4	119	1*	0.6
Isolated shortly after beginning of anthesis	2	38	2	4.8
Anthesis in greenhouse	6	161	32	20
Natural population B, 1976	17	278	248	90
Natural population B, 1977	13	265	202	76
Natural population C, 1977	7	132	93	69
Natural population**, 1978	42	853	812	96

Table 5. Removal of pollinaria, pollinated flowers and insects stuck in the flowers in 5 populations of *Herminium monorchis* on Öland 1977. – * Sciaridae 3, Hym. Parasitica 2, Chloropidae 1 and Araneida 1 specimen.

Locality	Date	No. of plants	No. of flowers	Flowers with one pollinarium removed (%)	Flowers with both pollinaria removed (%)	Pollinaria removed (%)	Pollinated flowers (%)	No. of insects stuck
F	1977 07 05	20	369	39	39	59	65	4
E	1977 07 05	20	306	24	58	70	79	1
D	1977 07 08	20	282	44	31	53	71	1
C	1977 07 12	20	375	35	30	48	64	.
A	1977 07 15	20	402	36	48	65	69	1
A–F		100	1734	35.4	41.2	58.9	69.0	7*

Fruit set

Natural populations have a very good fruit set, viz. c. 70–95% (Table 4). These values are a little higher than the records of insect-pollinated flowers (Table 5), which is to be expected since the presence of massulae on stigmas were investigated before the anthesis was completely finished.

Discussion

Darwin's observations in Britain and the records here presented from Öland, Skåne and Denmark show that although many co-pollinators/co-visitors occur *H. monorchis* is mainly pollinated by *Tetrastichus* spp. In this genus, females strongly dominate as pollinating agents. Nectar is secreted and concealed in a short spur. That the nectar is "well exposed" (Proctor & Yeo 1973) or that the flowers lack spurs (Ziegenspeck 1936, Sundermann 1975) is not supported (cf. also Vermeulen 1976).

Experiments indicated that the powerful fragrance is essential for the attraction of pollinators. The fragrance obviously has a remarkable capability to stimulate a wide range of unrelated small wasps to visit the orchid. As flower-visitors this group of insects is regularly found on umbellifers, e.g. *Angelica* (Hedqvist 1963), *Heracleum* and *Daucus* (Hassan 1966) and *Pastinaca* (see above). The compound which gives *H. monorchis* its characteristic scent reminds of the spicy fragrance of some umbellifers such as anise etc. Related or identical volatile compounds are present in these scents. Reasonably, the scent of *H. monorchis* releases both positive chemotaxis and feeding reactions in the pollinators.

In tests Göttsche (1977) found that unfed *Megastigmus bipunctatus* Swed. have a spontaneous reaction towards yellow and that

the flowers of *Pastinaca sativa* are very attractive to this wasp. This chalcid has also been observed to visit *P. sativa* in nature (own observation, Öland). It is likely that the yellow-green colour of the inflorescence of *H. monorchis* stimulates optical near-by orientation in small wasps.

The very striking presence of Chloropidae on *H. monorchis* at all localities suggests that these flies may play a part in the pollination system although they seldom act as pollinators. Unfortunately nothing is known about the insect parasites or biology of *Trachysiphonella* spp. (H. Andersson, pers. comm.). Related genera of Chloropidae e.g. *Oscinella* develop in grasses. Many of the visiting chalcids are parasites on hosts living in galls (K.-J. Hedqvist, pers. comm.). According to Clausen (1940) many *Tetrastichus* are hyperparasites. The chloropid flies are perhaps the hosts, or in the case of hyperparasitism, the hosts for the hosts of many of the pollinators. With such links, attraction of the flies to the growing site supports the abundance of these parasitic wasps in the vicinity of *H. monorchis*.

Results of the present study indicate that *H. monorchis* is strictly entomogamous which contrasts with previous opinions (e.g. Kirchner 1922, Hagerup 1952). Hagerup (1952) writes that: "When the plant is shaken by wind, the pollen falls down from the anther ... inevitably hitting the stigmas". However, it seems very unlikely that wind velocities around such a low plant (often less than 10 cm) growing among grass would play any role for autogamy. Hagerup continues: "Autogamy is so effective that nearly all flowers are pollinated, even if they are cut away and put under glass or in a room". If not extraordinary arrangements are made, however, the minute size of the pollinators and their presence almost everywhere would easily cause that the plant is visited even under such conditions. That autogamy does not take place is evident also from the observation that in certain regions *H. monorchis* rarely seeds (Camus & Camus 1928). Occurrence of intraspecific autogamous varieties seems improbable.

Frequency of removal of pollinaria, pollinated stigmas, fruit set and abundance of visitors all indicate that cross-pollination is very successful. The number of potential vector species among small parasitic Hymenoptera of about the right size is extensive. Of the genus *Tetrastichus* alone there are about 200 species in Sweden (K.-J. Hedqvist, pers. comm.). Thus, under normal circumstances shortage of vectors is probably not a limiting factor in reproduction, especially as competition from concurrently blooming plant species seems practically non-existant. Since each individual vector transports a very small number of pollinaria, seldom more than two, the system seems adapted to ready availability of vectors. It may also be suspected that the small wasps hardly can function properly as vectors with more than one pollinarium on each front femur. Their activity on the flowers both in sunny and dull days is probably advantageous for the plant.

Hagerup (1952) interpreted the flowers of *H. monorchis* as primitive and even thought that the viscidia are transformed stamens demonstrating a link between Basitonae and Acrotonae. Vermeulen (1955) gave some evidence which strongly contradicts this hypothesis. Pijl (1966) propounded that reversion from another type of pollination to wasp pollination seems improbable in *Herminium* and that the adaptation to wasps should be considered primordial. However, the present study has shown that both a spur and a spur-nectary exist. The aggregation of nectar secreting tissues into two rounded swellings seems to be only a slight modification of the common, elongated nectary present in related, principally moth-pollinated genera such as *Habenaria* Willd. and *Platanthera* Rich. The large majority of species within the subtribe Orchidinae hitherto investigated deposit the pollinaria on the mouthparts or other parts of the pollinators' heads. In fact, the position of the viscidia on the column and the morphology of the pollinaria in *H. monorchis* are rather similar to that found in related species having such methods of deposition. Vermeulen (1976) has pointed out that *Herminium* and *Habenaria* show various intermediate forms and are often difficult to separate.

In addition to nectar, adult chalcids are known to feed on the body-juices of their hosts (Marchal 1905), honeydew (Györfi 1951) and on plant-tissue (Quayle 1910). In contrast to their often extreme host specialization these wasps have poorly developed mouthparts for anthophilous habits. On the other hand, their minute size permits access not only to superficial nectar but

also to hidden supplies in spurs etc. Since chalcids obviously use several kinds of food-sources, their relationship with *H. monorchis* is hardly a result of coevolution but the plant has one-sidedly adapted to the wasps. The close relationship with *Habenaria,* the presence of a spur-nectary and the floral morphology suggest that *H. monorchis* has evolved from more long-spurred ancestors adapted to strictly anthophilous pollen vectors. Since the scent emission is so very important for the attraction of wasps, it is possible that an evolutionary shift has been induced by an accidental chemical change in the ancestor's fragrance. The richness in species and individuals of small wasps, their odour-controlled orientation, the feeding habits of chalcids, their capability to penetrate bodily to nectar positions originally adapted to the elongated mouthparts of larger insects, as well as their habits to revisit flowers of the same inflorescence indicate that the new evolutionary course could have been established rather rapidly and even in a sympatric situation. Meanwhile, probably, deposition of pollinaria on the proboscis of larger vectors (e.g. moths) have been shifted against attachment to the legs of the new vectors which correspond in body-size with the mouthparts of the former group. Reasonably, the shift was followed by selection producing various anthecological adaptations to the new vector group. Concerning its pollination system *H. monorchis* appears to be a rather advanced species within the subtribe Orchidinae.

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Fimicolous myxomycetes

Uno Eliasson and Nils Lundqvist

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Thirty-four species of fimicolous myxomycetes are reported, the vast majority from moist chamber cultures. *Physarum spinisporum* U. Eliass. & Lundq., sp. nov., is described. A further nine species are reported for the first time as fimicolous: *Perichaena syncarpon, Arcyria incarnata, Stemonitis pallida, Macbrideola cornea, Leocarpus fragilis, Physarum nutans, P.* cf. *ovisporum, Didymium anellus* and *D. verrucosporum. Physarum apiculosporum* and *Badhamia semiannulata* are regarded as conspecific and the new combination *Badhamia apiculospora* (Härk.) U. Eliass. & Lundq. is proposed. Previous literature records of fimicolous myxomycetes are listed. Some 80 species in 23 genera have been recorded on dung. Common coprophilous species are *Perichaena* cf. *liceoides, Arcyria cinerea, Stemonitis fusca, Badhamia apiculospora, Didymium difforme,* and *D. squamulosum.* The exclusively or preponderatingly coprophilous species are few, constituting less than 2% of the known species. Among these are *Licea alexopouli, L. fimicola, Perichaena* cf. *liceoides,* and *Calonema luteolum.* Regarding the type of dung, substrate preferences can be traced in some species. Thus e.g. *Perichaena* cf. *liceoides* seems to prefer dung from domestic animals, while *Stemonitis fusca* has only been found on dung from forest animals. The majority of the fimicolous myxomycetes are presumed to be secondary inhabitants on dung. No obvious adaptations to endocoprophily have been found.

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While the myxomycete flora on decaying wood or bark can be regarded as relatively well-known, few comprehensive studies have been made on that on other kinds of substrate. Thus, surveys of the coprophilous myxomycete flora are lacking, even though some authors, e.g. Jahn (1916), Hertel (1962), and Keller & Anderson (1978), have shown an interest in the coprophily of these organisms. The majority of the literature records are fairly recent and none is known to us from the 18th century, the oldest being Schumacher's (1803) report of *Physarum fimetarium,* a dubious name, the explanations may be that the interest in coprophilous fungi did not boom until the 1860's, and that the moist chamber method did not come into common use until 40 years later (Lundqvist 1972 pp. 41, 43).

The aim of the present paper is to give a general idea about which species may occur on dung and whether certain taxa could be regarded as predominantly or exclusively coprophilous. We report finds on dung for 34 species. Nine of these have not previously been reported from this substrate, while one species is described as new. We also summarize available records from the literature. Since several specimens were found to deviate from the normal range of variation and since so many problems are unsolved regarding the delimitation of several myxomycete taxa, it proved necessary to include short descriptions and taxonomic comments and discussions in some cases.

Material and methods

The new finds represent over 160 samples; the majority were taken by Lundqvist during 1959–1978 using the moist chamber technique described in Lundqvist (1972 p. 12). Eliasson is responsible for the identification of the material and for the descriptions and taxonomic comments. Most literature records are excerpts from an index of coprophilous fungi started by Lundqvist and continuously kept up to date. Lundqvist is responsible for all historical records included and has compiled the section on 'Additional species reported from dung'. Unless otherwise stated the photos have been taken by Eliasson.

All collections studied are represented in UPS; incomplete series are in GB and in N. E. Nannenga-Bremekamp's private herbarium in Doorwerth, the Netherlands (N-B). Unless otherwise stated the collections originate from moist chamber cultures.

Development in cultures

The specimens in our cultures always developed late, usually after 3 weeks or more, when the dung and the underlying filter paper had become considerably decomposed. This behaviour is common among myxomycetes, as they feed on bacteria and other microorganisms, which abound in decaying substrates. Large, spreading plasmodia could often be seen on the dung or the filter paper if the moisture was optimum. Too high a moisture, however, hampers the development of fruit-bodies and normal spores. One month or more is probably a normal period of time for a life-cycle (cf. Mock & Kowalski 1976, Mulleavy 1977, Faurel & Schotter 1965 b, c, 1966).

We consider that the moist chamber culture method is efficient on the whole and that the majority of species present actually fructificate under these conditions, a conclusion also reached by Keller (1971) for the genus *Perichaena*. Some myxomycete species, however, do not appear in moist chamber cultures (Gray & Alexopoulos 1968), also a phenomenon known for the coprophilous species of true fungi.

Substrate preferences

In our material, cow dung is the most favoured substrate (55 myx. coll.), followed by dung from hares (5 species) 23, horse 21, rabbit 18, elk and moose 14, roe deer 7, goat 5, sheep 5, capercaillie 3, donkey 3, camel 2, lemming 2, grouse 2, buffalo, deer, dik-dik, duiker, eland, omnivore, black grouse, and caterpillar, a total of 25 animal species. Although this distribution primarily reflects that some substrates are more frequently collected than others, substrate preferences can be traced for some myxomycete species. About 80% of all our finds of *Perichaena* cf. *liceoides* are on cow dung, and this species seems to prefer the dung from domestic animals (cow, horse, donkey, sheep; 32 samples). *Didymium difforme* has also often been recorded on cow dung (38%) but has a wider range (9 "host" species). *Arcyria cinerea* is not uncommon on horse dung (50%, 6 "hosts"). *Stemonitis fusca* has only been collected on dung from forest animals (elk, roe deer, hare; 10 finds), a phenomenon known in some coprophilous species of true fungi as well (Lundqvist 1972 pp. 21–27). When the published finds of the species mentioned here are also taken into account, their habitat range appears somewhat broadened, but their substrate preference not necessarily so. *Perichaena chrysosperma,* however, which in our material is mainly found on dung from lagomorphs, does not show any distinct substrate preference when other published records are included. No distinct trends can be recognized where the common coprophilous species *Badhamia apiculospora* and *Didymium squamulosum* are concerned. To obtain a complete picture of the ecological demands of fimicolous myxomycetes, naturally finds on substrates other than dung must also be taken into consideration, but that is beyond the theme of this paper.

A total of over 80 species in 23 genera of myxomycetes have been recorded on dung, viz. c. 15% of the currently accepted species. However, only a limited number can be regarded as common on this substrate. The seven species mentioned in the preceding paragraph belong here. In fact, most myxomycetes found on dung are more frequently recorded on other substrates. Very few seem to be exclusively or preponderatingly coprophilous. Good examples are *Licea alexopouli, L. fimicola, Calonema luteolum,* and *Badhamia apiculospora* ('*B. ovispora*'). This category constitutes less than 2% of the total number of species.

Some species which have been described on samples from dung (field samples or moist chamber collections) are, so far, known only from one or two collections. Naturally in these

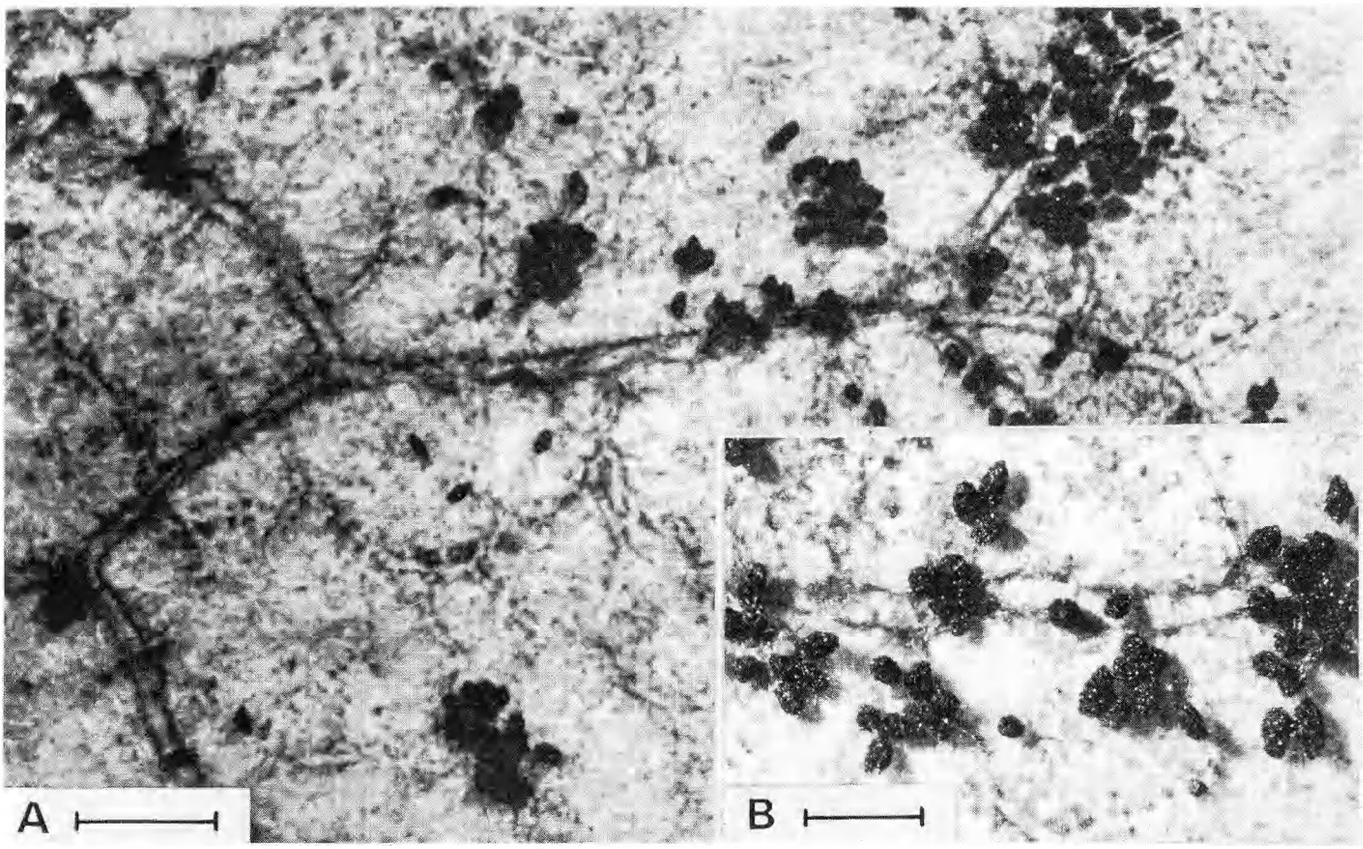

Fig. 1. *Licea fimicola,* sporangia on filter paper in moist chamber culture on dung (Ahti 26567-d). – A: Sporangia and tracks of the phaneroplasmodial veins. – B: Portion of A further enlarged. – Scales: A 1 mm, B 0.5 mm.

cases it is impossible to state whether or not they might be preponderatingly coprophilous. *Arcyria elaterensis, Trichia fimicola, Macbrideola coprophila, Squamuloderma nullifila,* and *Didymium rugulosporum* belong to this category. Some fimicolous species have been grown on artificial media. Among these are *Licea alexopouli* (Mock & Kowalski 1976), *L. fimicola* (Keller & Anderson 1978), *Arcyria elaterensis* (Mulleavy 1977), and *Squamuloderma nullifila* (Kowalski 1973).

Spore dispersal

The question of ecological specialization in the coprophilous myxomycetes brings up the problem of their spore dispersal. Are there any true endocoprophilous species among them or do they only inhabit the dung secondarily? We are not aware of any investigations on the subject, and the very few students who have examined the fungus flora of gut and stomach contents taken from butchered animals and placed in sterilized moist chambers have not reported myxomycetes in their material (Massee & Salmon 1902, Schmidt 1913, Larsen 1971). We presume that the majority of the fimicolous myxomycetes are only secondary inhabitants on dung. Their spores are dispersed by wind or insects, generally epizoochorously. Non-stipitate species without a capillitium, such as *Liceae,* are not adapted to wind-dispersal, and some of them seem to be strictly coprophilous. If they are endocoprophilous, their spores would be expected to show adaptations for dispersal to the surrounding vegetation to be eaten and spread by the vectors, but such adaptations are not known.

Keller & Smith (1978) found that the spores of an undescribed species of *Didymium* were eaten by the acarid mite *Tyrophagus putrescentiae* (Shank). The spores were observed passing through the digestive tract of the mite. When fragments of fecal pellets were suspended in sterile water as hanging drop cultures, intact spores were found to be viable and germinate.

List of animals referred to

Artiodactyls: Barbary sheep (*Ammotragus lervia*), "biche harnachée" (probably bush buck, *Tragelaphus scriptus*), bison (*Bison bison*), buffalo (*Syncerus caffer*), deer (indet.), dik-dik (*Rhynchotragus*), duiker (*Cephalopus*), eland (*Taurotragus oryx*), elk (*Alces alces*), fallow deer (*Dama dama*), gazelle (in N Africa probably *Gazella dorcas*), moose (*Alces alces gigas*), nilgai (*Boselaphus tragocamelus*), pronghorn (*Antilocapra americana*), red deer (*Cervus elaphus*), roan antelope (*Hippotragus equinus*), roe deer (*Capreolus capreolus*).

Hyracoids: Dassie (in N Africa *Procavia antineae*, in Tanzania *Procavia, Heterohyrax* or *Dendrohyrax*).

Rodents: "Goundi" (*Massoutiera harterti*), lemming (*Lemmus lemmus*), mouse (indet.), porcupine (*Erethizon dorsatum*), "sand rat" (*Psammomys algiricus*).

Lagomorphs: Hare (indet. *Lepus*), black-naped hare (*Lepus nigricollis*), blue hare (*L. timidus*), Cape hare (*L. capensis*), European hare (*L. europaeus*), Kabylian hare (*L. kabylicus*), rabbit (in Europe, N Africa and the Canary Islands *Oryctolagus cuniculus*, in North America *Lepus* and *Sylvilagus*).

Bats: Flying fox (*Pteropus medium*).

Marsupials: Kangaroo (indet.).

Birds: Bird (indet.), bird of prey (indet.), black grouse (*Lyrurus tetrix*), capercaillie (*Tetrao urogallus*), goose (*Anser?*), grouse (*Lagopus*), rock dove (*Columba livia*).

Insects: Caterpillar (*Hyponomeuta*).

Domestic herbivores mentioned are cow, yak, horse, donkey, mule, goat, sheep, camel, reindeer, Indian elephant.

Abbreviations

EXS ined. = an unissued exsiccata of fimicolous fungi.

Lqt Lundqvist, S Santesson.

Abbreviations of herbaria follow Holmgren & Keuken (1974).

Swedish provinces: *Sk* Skåne, *Bl* Blekinge, *Öl* Öland, *Gtl* Gotland, *Ög* Östergötland, *Vg* Västergötland, *Hl* Halland, *Bh* Bohuslän, *Srm* Södermanland, *Upl* Uppland, *Vsm* Västmanland, *Dlr* Dalarna, *Gstr* Gästrikland, *Hls* Hälsingland, *Ång* Ångermanland, *Hrj* Härjedalen.

The provinces are cited roughly from south to north. The smallest locality unit listed is usually a parish or similar area. Extra-Swedish localities are mostly given more accurately.

Licea alexopouli Blackw. – Fig. 2 A

Kenya: *Rift Valley,* Nakuru, 10 km E of Londiani (cow) Lqt 6514-g – Tanzania: *Arusha,* Mt Meru (buffalo) Lqt 6480-k; SW of Oldonyo Sambu (cow) Lqt 6511-h (GB, N–B) – USA: *California,* Los Angeles Co., Santa Catalina Isl. (cow) S 17297-u (GB, N–B) – New to the Old World.

Literature records: USA: (bison, cow, horse) Blackwell 1974, Mock & Kowalski 1976, Keller & Anderson 1978.

Licea cf. **belmontiana** Nann.-Brem.

Sweden: *Bh,* Marstrand (hare) Nordin 4547-c – Norway: *Finnmark,* Nord-Varanger par., Fossefjellet (blue hare) Lqt 4965-h – Spain: *Canary Islands,* Tenerife, Anaga Peninsula, San Andrés (rabbit) S 19304-k (GB).

Sporangia gregarious or scattered, hemispheric, 0.05–0.15 mm in diam., olivaceous brown, slightly shiny; peridium yellowish brown in transmitted light, with some refuse matter included, peridial platelets obscure; spores olivaceous brown in transmitted light, dark brown in mass, 10.5–11 μm in diam., smooth or almost smooth, with a thinner and paler area on one side.

The spores are slightly smaller than hitherto described for *L. belmontiana* (Nannenga-Bremekamp 1966, 1974), but the material is closer to this species than to other taxa so far recognized in the genus.

Licea fimicola Dearn. & Bisby – Fig. 1

Mongolia: *Central Aymag,* 145 km W of Ulan Bator (cow or yak) Ahti 26567-d – Kenya: *Mandera,* S of Banissa (dik-dik) Thulin 2686-g – New to the Old World.

Literature records: Canada: (horse) Bisby et al. 1929 – USA: (cow, pronghorn) Angel & Wicklow 1975, Keller & Anderson 1978.

So far this species has only been found on dung. Although rarely collected in the field (Martin & Alexopoulos 1969), it has been found several times in moist chamber cultures (Keller & Anderson 1978). The species may well be more common than the field collections would suggest, as the sporangia, because of their peculiar appearance (Fig. 1), can be mistaken for droppings of insects or insect larvae.

Keller & Anderson (1978) pointed out that *L. fimicola* has a phaneroplasmodium, a condition that is also apparent from Fig. 1, where tracks of the plasmodial veins are visible on the substrate. This is of interest as species of *Licea* normally have protoplasmodia and the plasmodium type is considered to be of taxonomic importance. The other two known exceptions of a protoplasmodium in *Licea* are *L. retiformis* Nawavi

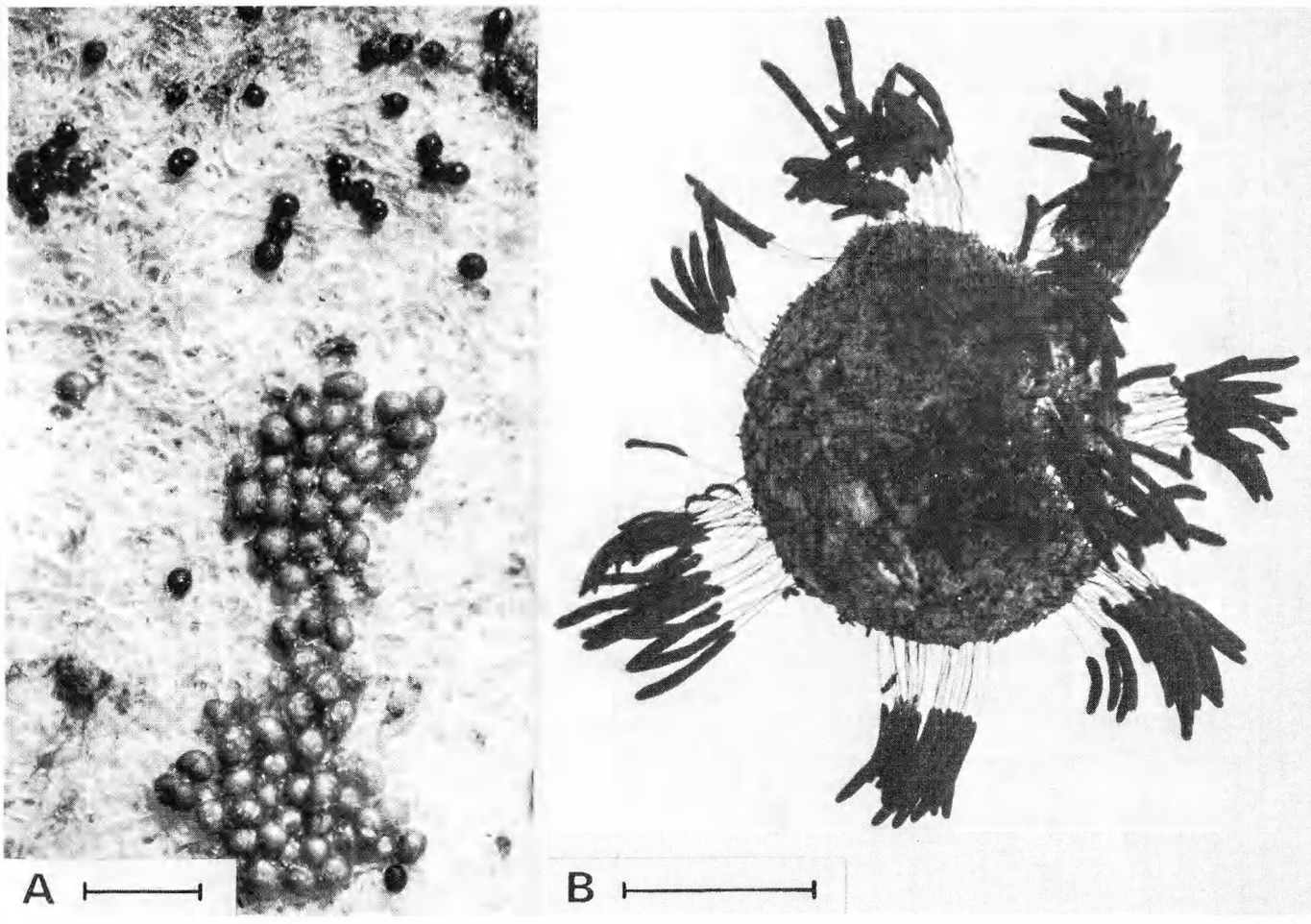

Fig. 2. A: *Licea alexopouli* (shining black sporangia) and *Perichaena* cf. *liceoides* on filter paper in moist chamber culture on dung (Lqt 6511-g). – B: *Stemonitis fusca,* sporangia on dropping of hare, moist chamber culture (Lqt 5906-g). – Scales: A 0.5 mm, B 5 mm.

and *L. variabilis* Schrad., both of which possess a plasmodium of the trichiaceous kind. In these two species there is probably a relationship with *Perichaena* (Alexopoulos 1976, Eliasson 1977), but in the case of *L. fimicola* the affinity is clearly far from this.

Licea pusilla Schrad.

Sweden: *Upl,* Söderby-Karl par., Brölunda (horse) Lqt 2514-b.

Literature record: Norway: (mouse) Moravec 1968.

Perichaena chrysosperma (Currey) A. Lister

Sweden: *Gtl,* Gotska Sandön Isl. (hare) Tibell 2195-p, 2196-s; Östergarn (rabbit) Lqt 2110-p. *Hrj,* Storsjö par., Mt Helagsfjället, 1400 m (lemming) K. & L. Holm 21.VIII.1967 (slide) – Spain: *Canary Islands,* Tenerife, Anaga Peninsula, San Andrés (rabbit) S 19304-q (GB, N-B) – USA: *California,* Los Angeles Co., Santa Catalina Isl. (cow) S 17297-f (GB, N-B) – Ecuador: *Los Ríos,* Salinas (donkey) Martin 3.IX.1945 (GB).

Literature records: Poland: (red deer) Schmidt 1912 (as *Cornuvia circumscissa* var. *spinosa*) – Hungary: (cow) Tóth 1963; (deer) Tóth 1965 (as *Ophiotheca c.*) – Sri Lanka (elephant) Lister 1925 – Tanzania: (mule) Schmidt 1913.

In the material studied the fructifications are sporangia or short plasmodiocarps, never elongated or reticulate plasmodiocarps as often seen in *P. vermicularis* (Schw.) Rost. The spores are generally 8.5–10 μm, and in some fructifications up to 11 μm. The papillose inner peridium was considered by Keller (1971) to be a characteristic feature in *P. vermicularis*. In the specimens cited the inner peridium is faintly papillose in some sporangia, smooth in others. The distinction is not clear and the ornamentation is so faint in some cases that the peridium could be regarded as almost smooth. The capillitium is generally conspicuously spiny, but there are great differ-

ences even between adjacent fructifications or between capillitial parts within one fructification. In duplicate specimens of S 19304-q a large part of the capillitium is completely spineless, while some capillitial parts within the same fructification have conspicuous spines. One of the collections studied (Lqt 2110-p) has (at least in the two sporangia investigated) large spores, 12–13.5 μm in diam. This is outside the variation range normally ascribed to *P. chrysosperma*, and the specimen would key to *P. vermicularis* in e.g. Martin & Alexopoulos (1969) and Keller (1971). However, it agrees with *P. chrysosperma* in other characteristics, and could probably correctly be accommodated within this taxon.

Perichaena corticalis (Batsch) Rost.

USA: *California*, Los Angeles Co., Santa Catalina Isl. (cow) (with *Didymium difforme*) S 17297-k. *Colorado*, Boulder Co., Mt Steamboat (cow) S 18499-E.

Literature records: Hungary: (hare) Tóth 1963; (cow, deer, goose) Tóth 1965, 1967 – Algeria: (donkey, camel, Barbary sheep) Faurel & Schotter 1965 c – Tchad: (goat, gazelle) Faurel & Schotter 1966 – Congo: (gazelle) Faurel & Schotter 1965 d – Chile: (cow) Spegazzini 1921 (as *P. populina*).

Despite the widely scattered sporangia lacking circumscissile dehiscence, the specimens cited are best included in *P. corticalis*. The spores are c. 12 μm in diam., and the capillitium is devoid of spines. Where fructifications of *P. corticalis* and *P. chrysosperma* occur together the different colour of the spore masses is often striking, that of *P. chrysosperma* generally being a brighter yellow than that of *P. corticalis*.

Perichaena depressa Libert

Sweden: *Gtl*, Gotska Sandön Isl. (hare) Tibell 2201-z – Tanzania: *Kilimanjaro*, Mt Kilimanjaro, 3500 m (eland) Lqt 6407-f.

Literature records: Hungary (cow, deer, hare) Tóth 1963, 1965, 1967.

Perichaena cf. **liceoides** Rost. – Figs. 2 A, 3

Sweden: *Bl*, Kristianopel (horse) Lqt 3360-d (EXS ined.) (GB), (cow) Lqt 3364-j (GB, N-B). *Öl*, Räpplinge (horse) Lqt 2301-e, (cow) Lqt 2302-d; Resmo (cow) S 19615-f. *Gtl*, Lilla Karlsö Isl. (sheep) Jacobson 16.V.1970; Östergarn (horse) Lqt 2104-j. *Srm*, Aspö (cow) Lqt 2022-n, 2454-d. *Upl*, Älvkarleby (horse) Lqt 4210-e (GB, N-B). Ärentuna (cow) Lqt 11864-c; Bälinge (cow) Lqt 2804-b (GB); Häverö (horse) Lqt 10223-c; Läby (cow) Lqt 4074-c; Nysätra (cow) Lqt 2009-d. *Vsm*, Svedvi (cow) Lqt 2357 – France: *Bouches-du-Rhône*, le Pèbre (cow) Lqt 9658-b. *Corsica: Ajaccio* (cow) Lqt 4409-f. *Belgodere* (cow) Lqt 4485-h. *Bonifacio* (cow) Lqt 4425-m (GB), 4427-e (GB), (donkey) Lqt 4428-e (GB), (cow) Lqt 4435-d. *Porto-Vecchio* (cow) Lqt 4448-d (GB). *Sartène* (cow) Lqt 4423-d – Yugoslavia: *Croatia*, Velebit Mts, near Mandekić (cow) Lqt 7578-f – Mongolia: *Central Aymag*, 145 km W of Ulan Bator (cow or yak) Ahti 26567-e – Sri Lanka: *Matale*, Dambulla (cow) Lqt 9164-n. *Monaragala*, W of Wellawaya (cow) Lqt 11398-f – Tanzania: *Arusha*, SW of Oldonyo Sambu (cow) Lqt 6511-g (GB, N-B) – Madagascar: *Tamatave*, Île S:t Marie, Ampanihy Forest (cow) Jonsson 1033-e (GB) – USA: *California*, Los Angeles Co., Santa Catalina Isl. (cow) S 17297-t. *Colorado*, Boulder Co., Mt Steamboat (cow) S 18499-D (GB).

Literature records: Denmark: (fallow deer) Lister 1925 – Germany: (dung) Jahn 1916 – Morocco (cow, horse) Malençon & Bertault 1968 – USA: (cow) Keller & Anderson 1978.

Sporangia (Figs. 2 A, 3 A) globose, sessile, 0.1–0.2 mm in diam., scattered or gregarious; peridium yellowish brown to darker brown, if yellowish brown, translucent and generally separated from the spore mass, if darker, less translucent (or nontranslucent) and with varying amounts of refuse matter included, inner surface of peridium almost smooth to faintly papillose; capillitium lacking or present, rarely well-developed and of *Perichaena*-type (Fig. 3 B), sometimes consisting of short threads, sometimes appearing as simple outgrowths from the inner surface of the peridium; spore mass yellow, spores 9.5–12 μm in diam., smooth or very faintly warted.

The description given here may appear rather expansive. An aggregate of yellowish brown sporangia (Fig. 2 A) with translucent peridium may seem very different from scattered, dark brown fructifications (Fig. 3 A) with nontranslucent peridium. However, specimens exhibiting the extremes as well as a series of transitional forms do exist (e.g. Lqt 4448-d). The ornamentation of the inner surface of the peridium may be relatively prominent and reminiscent of that figured by Keller & Brooks (1977) for *Licea scyphoides* Brooks & Keller, but may in other sporangia be much fainter and sometimes hardly distinguishable. Also intergradations occur where the amount of capillitium and size of spores are

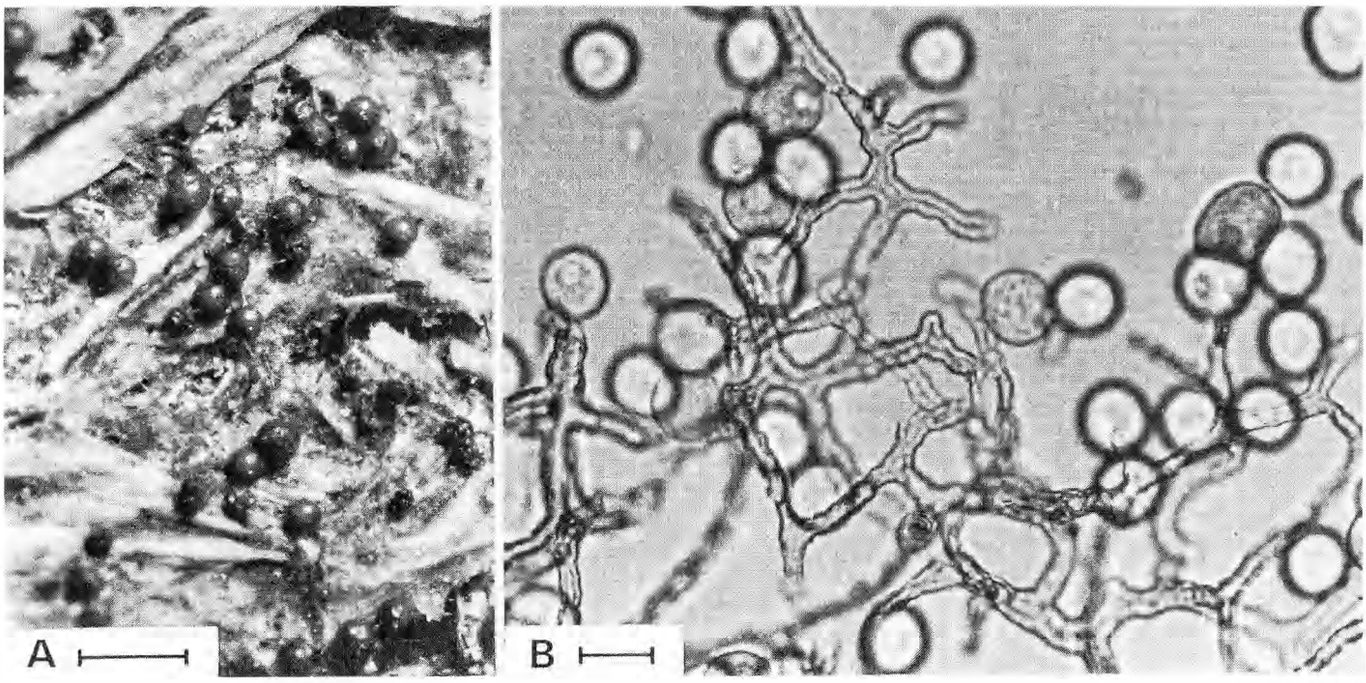

Fig. 3. *Perichaena* cf. *liceoides*, a specimen with well-developed capillitium, moist chamber culture on cow dung (Lqt 7578-f). – A: Sporangia. – B: Capillitium and spores. – Scales: A 0.5 mm, B 10 μm.

concerned. Some specimens have spores 9.5–10.5 μm in diam., others 11.5–12 μm. It has not been possible to correlate e.g. spore size with other characteristics in the same sporangium.

Most of the sporangia studied lack a distinct capillitium and would key to *Licea tenera* Jahn in determination literature (cf. Santesson 1964). However, the spore wall is uniform in thickness and colour, while the spores of *L. tenera* have (ex char.) a thinner and paler area on one side. Moreover, some sporangia have a relatively well-developed capillitium, and there are transition forms to sporangia without a capillitium. For this reason the specimens could hardly be accommodated in *Licea*, at least not as long as the absence of a capillitium is maintained as an important characteristic of this genus. However, the presence or absence of a capillitium as a generic character has been questioned (Alexopoulos 1976, Eliasson 1977).

The specimens studied show a variation, the background and pattern of which can probably only be traced by culture studies. Keller, who kindly examined some of the specimens, wrote (pers. comm.): "Probably the best identification for your specimens with capillitium is *Perichaena liceoides*". Considering the transition forms mentioned, all the material is here tentatively referred to this taxon. Kowalski (pers. comm.), who examined a specimen (Lqt 7578-f; Fig. 3) with a well-developed capillitium, regarded it as close to *Calonema luteolum* Kow. although different in colour. However, as the collection seen by Kowalski is connected by transition forms to specimens better identified as *P.* cf. *liceoides*, it is here cited under this taxon.

Nannenga-Bremekamp (pers. comm.) has pointed out that *Licea tenera* has been misinterpreted in recent literature. The true *L. tenera* differs in some morphological characters to the description given by e.g. Martin & Alexopoulos (1969) and is a species probably restricted to wood or bark.

Perichaena quadrata Macbr.

USA: *Iowa*, Iowa City (rabbit) Martin III.1935.

Most monographers, including Martin & Alexopoulos (1969), have placed *P. quadrata* in synonymy with *P. depressa*, but Keller (1971, 1973) claims that they are autonomous species.

Perichaena syncarpon T. E. Brooks – Fig. 4

Tanzania: *Arusha,* SW of Oldonyo Sambu (cow) Lqt 6511-f.

The collection comprises scattered fructifications occurring together with *P.* cf. *liceoides* and *Licea alexopouli*. The pulvinate sporangia resemble specimens cited in the present paper as *P. corticalis*. However, the spores adhere in clusters (Fig. 4 B) as characteristic in *P. syncarpon*. The peridium appears to be scanty, having been observed only as short, simple or forked outgrowths from the inner peridium (Fig. 4A). First record on dung.

Calonema luteolum Kow.

France: *Corsica: Bonifacio* (cow) Lqt 4425-q, 4427-f. *Porto-Vecchio* (cow) Lqt 4448-h – Spain: *Asturias,* Cabo Peñas (cow) Lqt 1908-g (GB) (IA as *Perichaena vermicularis*).

Literature records: Scotland: (sheep) Rammeloo 1978 – USA: (cow) Kowalski 1969 b.

So far this species is known only from dung. The specimens studied match perfectly (also in colour) the typical fruitings kindly sent by Kowalski for comparison. The species was previously known only from California and Scotland (Rammeloo 1978; a somewhat deviant collection).

Arcyria cinerea (Bull.) Pers.

Sweden: Bl, Kristianopel (horse) Lqt 3360-c (GB). *Gtl,* Gotska Sandön Isl. (hare) Tibell 2195-t (IMI, L). *Ög,* Kisa (horse) Lqt 3351-a. *Srm,* St. Malm (elk) Lqt 3344-c. *Upl,* Älvkarleby (capercaillie) Lqt 4604-e; Danmark (elk) Lqt 4216-f; Läby (cow) Lqt 4074-h; Lena (horse) Lqt 10530-a. *Vsm,* Rytterne (hare) Nordin 2932-y. *Gstr,* Österfärnebo (horse) Lqt 3488-f. *Hls,* Mo (horse) Lqt 2786-h. *Ång,* Ytterlännäs (horse) Lqt 3379-b – Norway: *Nord-Tröndelag,* Hegra par., Einang (horse) Lqt 3431-b (BPI, GB, PAD, PRM, TNS) – Canada: *Ontario,* Rondeau Govt. Park (deer) Cain 14.VIII.1938 (field coll.).

Literature records: Denmark: (dung) Hansen 1876 (as *Lachnobolus arcyrella*) – Finland: (dung) Karsten 1879 – Germany: (dung) Jahn 1916 – Spain: (cow, horse) Moreno & Barrasa 1977 – India (flying fox) Massee & Salmon 1902 (as *A. albida*) – Algeria: (horse) Durieu de Maisonneuve 1849; (camel, rabbit) Faurel & Schotter 1965 c, Faurel et al. 1966.

All material investigated by us is uniform and typical.

Arcyria incarnata (Pers.) Pers.

Sweden: *Hls,* Söderhamn Archipelago, Enskär Isl. (horse) Lqt 3199-b.

First record on dung.

Arcyria sp.

Sri Lanka: *Nuwara Eliya,* Horton Plains, World's End (black-naped hare) Moberg 2579-f.

Fructifications in small clusters, 1.5–1.8 mm tall, bright brick-red; stalks 0.2–0.3 mm long; sporangia subcylindrical, 0.3–0.4 mm wide, basal cups well defined; capillitial threads in upper part of the sporangium 2.0–2.5 μm thick (excl. spines), densely spiny with short blunt spines (ornamentation reminiscent of that in *A. cinerea*); spores 8.0–8.5 μm in diam., very faintly warted.

Apparently closely related to *A. cinerea,* and despite the colour and spore size perhaps possible to accommodate within this variable taxon.

Stemonitis fusca Roth – Fig. 2 B

Sweden: *Ög,* Väversunda (elk) Nordin 4234-d. *Boh,* Säve (roe deer) Nordin 4675-c. *Upl,* Ärentuna (hare) Lqt 5906-g, (roe deer) Lqt 5923-e (GB); Bälinge (elk) Lqt 9532-e; Jumkil (elk) Lqt 3821-e. *Vsm,* Ängsö (hare) Nordin 2983-k, (roe deer) Lqt 6258-d (slide); Rytterne (hare) Nordin 2932-x – Norway: *Finnmark,* Berlevåg par., Mt Tuva (blue hare) Lqt 5132-b.

Literature record: Tanzania: (dassie) Schmidt 1913.

The material studied is very uniform. The sporangia occur in small tufts, (3–)4–5(–6) mm tall (Fig. 2 B). With the exception of one aberrant collection (Lqt 3821-e) with probably premature sporangia, the spores have the characteristic ornamentation of *S. fusca* var. *fusca*.

Stemonitis pallida Wingate

Sweden: *Dlr,* Garpenberg, Lake Pålsbenningsjön (elk) Lqt 8689-e.

Sporangia in small groups, c. 3 mm tall, dull brown; stalk c. one third of total height; columella tapering upwards, dissipating below apex; capillitial net appearing persistent also in upper part, bearing short spines, capillitial meshes 5–15 μm; spores finely warted, 7–7.5 μm in diam.

First record on dung.

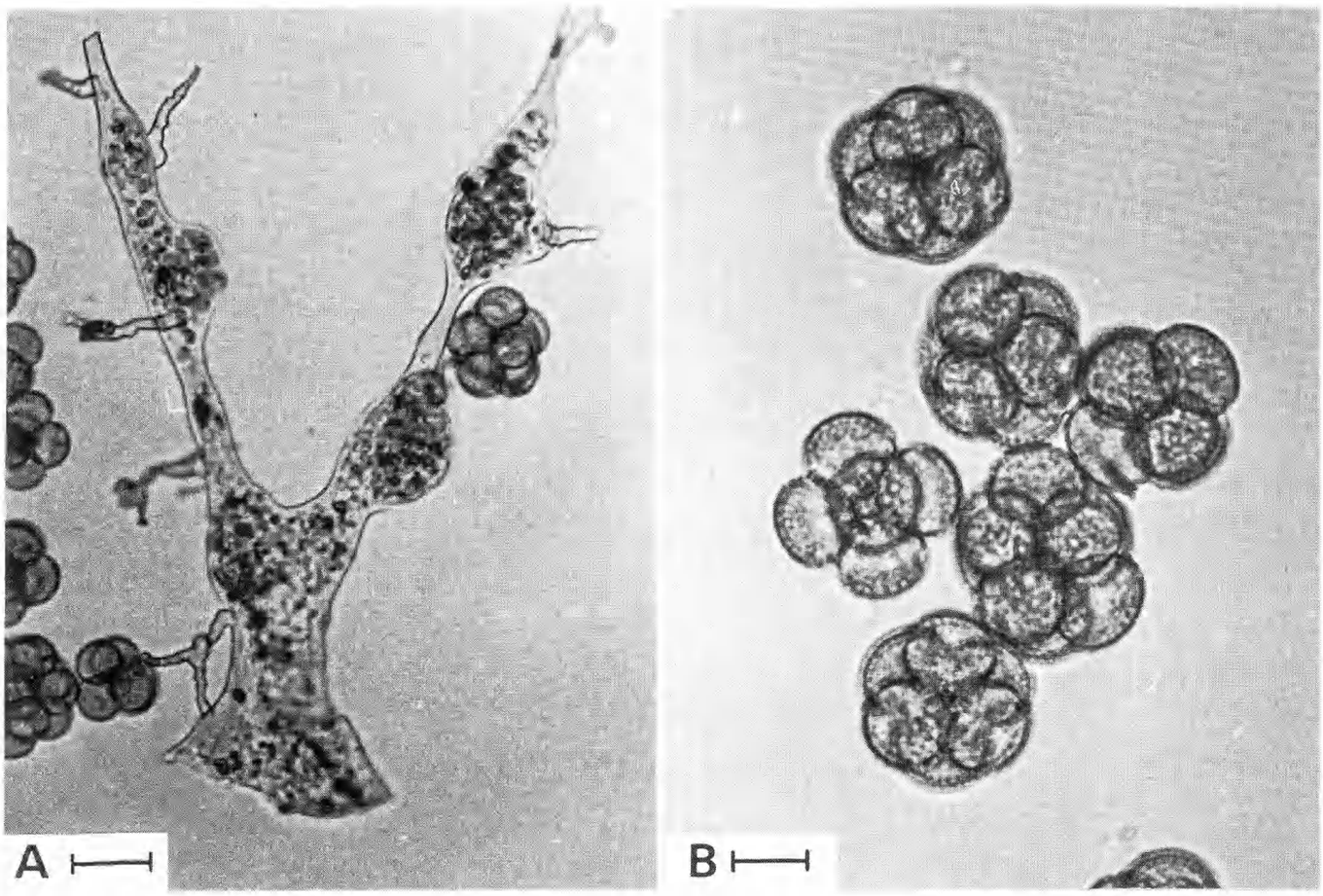

Fig. 4. *Perichaena syncarpon* (Lqt 6511-f). – A: Portion of peridium with capillitial outgrowths and spore clusters. – B: Spore clusters. – Scales: A 20 μm, B 10 μm.

Macbrideola cornea (G. Lister & Cran) Alexop. – Fig. 5

Sweden: *Hrj,* Storsjö par., Mt Helagsfjället, 1400 m (lemming) K. & L. Holm 21.VIII.1967.

First record on dung. The collection comprises a few globose sporangia 0.1–0.2 mm in diam. (Fig. 5 A). The capillitium (Fig. 5 B) consists of robust strains, which originate at the tip of the columella, fork repeatedly, but remain almost even in width close to the periphery, where they end in short, diverging branchlets. The spores are 9.5–11 μm in diam.

Except for spore size the collection fits the description of *M. cornea* given by Alexopoulos (1967). According to Alexopoulos the spores are 8.5–9.5 μm, but Nannenga-Bremekamp (1971) has described a var. *macrospora* with spores 12–14 μm in diam. The collection cited above bridges the gap between var. *cornea* and var. *macrospora* as far as spore size is concerned.

Lister (1925) noted that the stalk consists of a "smooth thick-walled tube enclosing a central strand of parallel brown fibres". The parallel "fibres" appear clearly in the columella (Fig. 5 B, C) in the collection cited above when seen in transmitted light. The fibres continue from the columella out into the capillitium. Peripheral parts of the capillitium contain two fibres (Fig. 5 D) or perhaps sometimes only one. Although it has not been possible to follow individual fibres further than between two or perhaps three ramification points of the capillitium, it seems as if the fibres themselves are not forked, but that each individual fibre is continuous from the peripheral part of the capillitium into the columella (and perhaps the stalk). However, this remains to be demonstrated. A sheath-like structure surrounds the fibre bundle and appears clearly in transmitted light in the columella and in the lower ramification points of the capillitium (Fig. 5 C). The stalk, columella, and capillitium in this species and also perhaps in related species merit ultrastructural studies.

Leocarpus fragilis (Dicks.) Rost.

Sweden: *Gstr,* Österfärnebo, Mattön Isl. (horse) Lqt 3488-e.

First record on dung.

Badhamia apiculospora (Härk.) U. Eliass. & Lundq., comb. nov.

Basionym: *Physarum apiculosporum* Härkönen 1978 p. 24.
Badhamia semiannulata Raub & Keller in Raub et al. 1979.

Sweden: *Sk,* Trollenäs (cow) Lqt 2395-b. (Santesson 1964 as *B. ovispora,* det. Lqt). *Öl,* Vickleby (sheep) Lqt 7285-e. *Upl,* Älvkarleby (elk) Lqt 4602-f; Ärentuna (hare) Lqt 4823-f; Haga (hare) Gunnerbeck 1401-h, 1402-a, 1412-c (BR, GB) (EXS ined.). *Vsm,* Rytterne (hare) (with *Stemonitis fusca)* Nordin 2932-x – France: *Corsica: Calenzana* (cow) Lqt 4498-e; *Nonza* (rabbit) Lqt 4474-k – Poland: *Silesia,* Tamsel (roe deer) Vogel 13.III.1935 (field coll.?) – USSR: *Sibiria,* Irkutsk (goat) Olsson 15.VIII.1968 – Egypt: *Giza,* 40 km WNW of Cairo (goat) Lqt 5621-a (PAD as *B. ovispora*).
Literature records (as *B. ovispora*): Germany: (rabbit) Jahn 1916, 1919 – England: (dung) Jahn 1919 – Canada: (dung) Hagelstein 1944.

This species has generally been wrongly identified as *Badhamia ovispora* Racib. Keller et al. (1975) drew attention to the fact that Raciborski's original description was incomplete and inaccurate as regards the spore characteristics. The true *B. ovispora* is apparently a rare species, probably restricted to decaying wood or bark, while the coprophilous species commonly misidentified as *B. ovispora* was recently described (Raub et al. 1979) as *B. semiannulata.*

Härkönen (1978) described *Physarum apiculosporum* on material obtained on *Hordeum* seeds in a moist chamber culture. She noted that the spores were similar to those of *B. ovispora* sensu Martin & Alexopoulos (1969), but that the new material differed in having "clearly physaroid capillitium, dark spores and a single peridium".

After having studied a relatively large material (listed above) of *B. semiannulata* and compared it with isotype material of *P. apiculosporum,* we feel convinced that the two are conspecific. The shape, structure and colour of the spores agree perfectly in the two taxa and the spore type is unique among myxomycetes (Raub et al. 1979, Härkönen 1978). It is true that the capillitium in the type material of *P. apiculosporum* is physaroid but the capillitium of *B. semiannulata* is rather variable and may often be physaroid, as noted by us as well as by Raub et al. (1979). The single peridium assigned to *P. apiculosporum* may be a doubtful character, since, in some of the material of *B. semiannulata,* poorly lime-encrusted specimens may appear as having a single wall-layer, and from cultivation of other *Badhamia* species it is known that the great variation in peridium structure may be due to external conditions. Finally, the two taxa seem to have similar ecological demands. *P. apiculosporum* was obtained on *Hordeum* and *Avena* in a moist chamber. *B. semiannulata* is often encountered in moist chamber cultures on straw and dung of herbivorous animals. Raub et al. (1979) reported abundant fruitings on hay mulch in greenhouses.

The specimens studied are referred to *Badhamia* because of the predominantly badhamioid capillitium. The inclusion of *P. apiculosporum* in *B. semiannulata* necessitates the new combination *B. apiculospora.* The delimitation of the genera *Physarum* and *Badhamia* is not altogether satisfactory and *B. apiculospora* is one of several species that make the borderline disputable.

Fuligo cinerea (Schw.) Morgan – Fig. 6

Spain: *Canary Islands,* Tenerife, San Andrés (rabbit) S 19304-m (with *Didymium dubium*).
Literature record: Martin & Rickett 1949.

This appears to be the minute distinct form of *F. cinerea* mentioned by Martin & Alexopoulos (1969) as sometimes developing in moist chambers. The plasmodiocarpous strands are convoluted or gyrose and closely massed (Fig. 6 A). The spores agree with those of *F. cinerea* in size and markings (Fig. 6 B, C).

Physarum cf. **bitectum** G. Lister

Norway: *Troms,* Tromsøysund par., Mt Fløjfjeldet (grouse) S 20108-c (GB).
Literature record: Hungary: (deer) Tóth 1965.

In the shape of the fructifications as well as in the size and ornamentation of the spores, this collection appears intermediate between *P. bitectum* and *P. bivalve* Pers. The plasmodiocarps are compressed, sometimes strongly so, generally curved, sometimes branched, in some cases annulate.

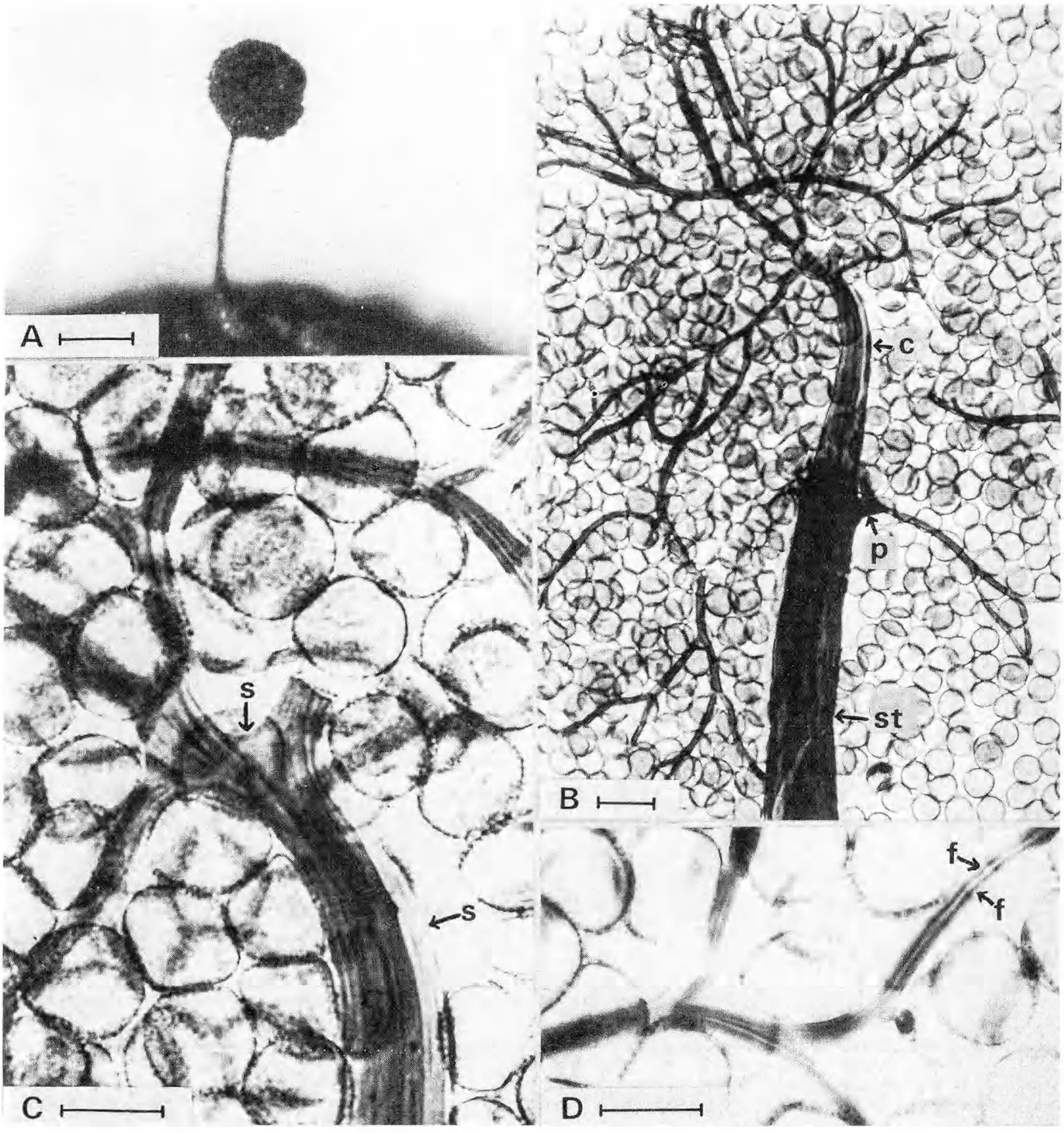

Fig. 5. *Macbrideola cornea,* specimen developed in moist chamber on dung from lemming (K. & L. Holm 21.VIII.1967). – A: Small-sized sporangium. – B: Crushed sporangium seen in transmitted light. The capillitium originates at the tip of the columella but some segments have loosened during mounting. c columella, p peridial collar, st stalk. – C: Upper part of columella with capillitium. The columella consists of a sheath (s) enclosing a central fibre bundle. The sheath is evident at several ramification points of the capillitium. – D: Peripheral part of capillitium. Single fibres (f) are distinct in transmitted light. – Scales: A 0.1 mm, B 20 μm, C, D 10 μm.

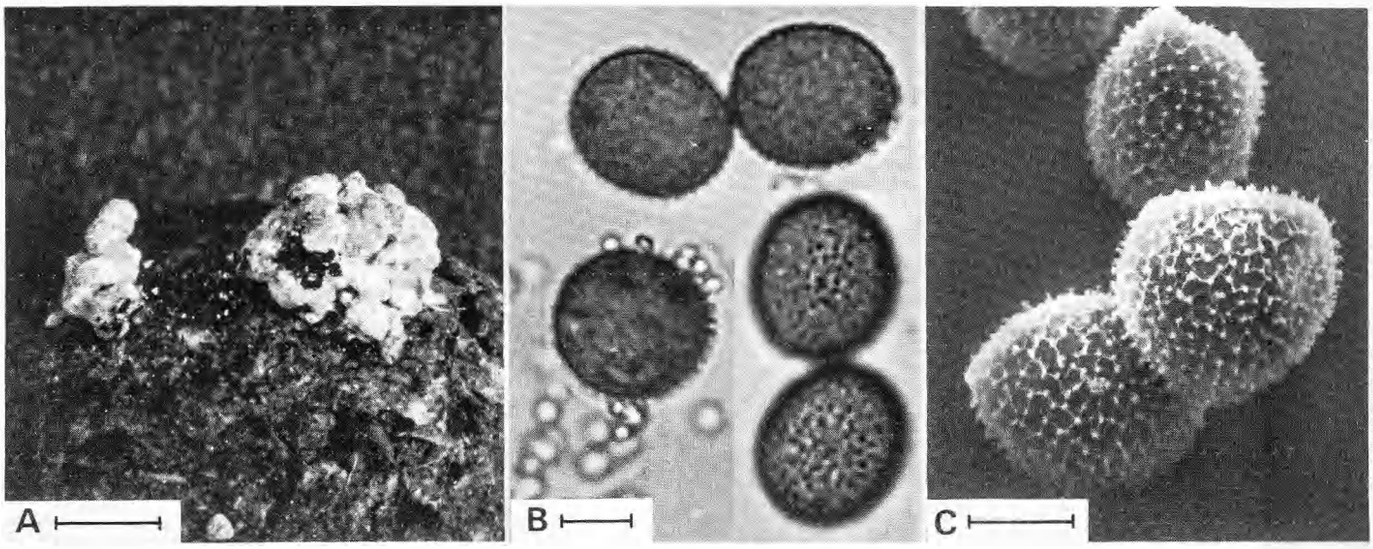

Fig. 6. *Fuligo cinerea,* a minute fimicolous form (S 19304-m). – A: Fructifications on rabbit dung, moist chamber culture. – B: Spores seen with the light microscope. – C: SEM picture of spores. – Scales: A 1 mm, B, C 5 μm.

Physarum confertum Macbr.

Sweden: *Upl,* Vänge par., Fiby Forest (capercaillie) Lqt 1823-b (Santesson 1964).

Physarum mucosum Nann.-Brem.

Sweden: *Mpd,* Borgsjö, SW of Hallsta (horse) Lqt 2779-g.

This specimen has previously been cited as *P. mucosum* from Sweden (Santesson 1964). It is, however, very close to *P. contextum* (Pers.) Pers. The recognition of *P. mucosum* as a distinct species is questioned (cf. Eliasson & Strid 1976).

Physarum nutans Pers.

Sweden: *Bl,* Åryd (rabbit) Nordin 1280-i (Santesson 1964 as *Didymium iridis* det. Lqt). *Vg,* Magra (horse) Lqt 3131-g. *Upl,* Harbo (sheep) Lqt 9364-e.

First record on dung.

Physarum cf. **ovisporum** G. Lister

S Africa: *Cape Province,* Namaqualand, 30 km N of Kamieskroon at Buffelsrivier (donkey) Nordenstam 26.X.1962 (GB, N-B).

Sporangiate to plasmodiocarpous, fructifications scattered or aggregated in pairs or small groups; sporangia globose or subglobose, 0.4–0.5 mm wide, sessile on a constricted base; plasmodiocarps short, elongated or annulate; hypothallus not evident; peridium single, slightly iridescent, densely white-flecked with lime; capillitium irregularly branched, the nodes small, rounded, elongated or irregular, sometimes tending to form a pseudocolumella; spore mass deep brown, shining; spores spherical, 11–12 μm in diam. (excl. ornamentation), spinulose, brown in transmitted light, paler and less spiny on one side.

The specimen is tentatively referred to *P. ovisporum,* a species which – despite the specific epithet – may well have globose spores (Martin & Alexopoulos 1969). Farr (1976) included *P. ovisporum* in *P. vernum* Somm., thus giving a very wide circumscription to the latter. Certainly the collection cited comes within the limits of this wide variation range. *P. ovisporum* has not previously been recorded as fimicolous.

Physarum pusillum (Berk. & Curt.) G. Lister

Scotland: (rabbit) Martin 20.VIII.1964.

Literature records: Pakistan: (dung) Lodhi 1951 – Tchad: (goat, "goundi") Faurel & Schotter 1966 – Congo: ("biche harnachée") Faurel & Schotter 1965 d.

Physarum cf. **pusillum**

Egypt: *Giza,* 40 km WNW of Cairo (camel) Lqt 5620-h, (goat) Lqt 5621-b – USA: *California,* Los Angeles Co., Santa Catalina Isl. (cow) S 17297-e.

Sporangia 0.4–0.5 mm in diam., stalked; stalks 0.1–0.5 mm, brown, thickened and blackish at

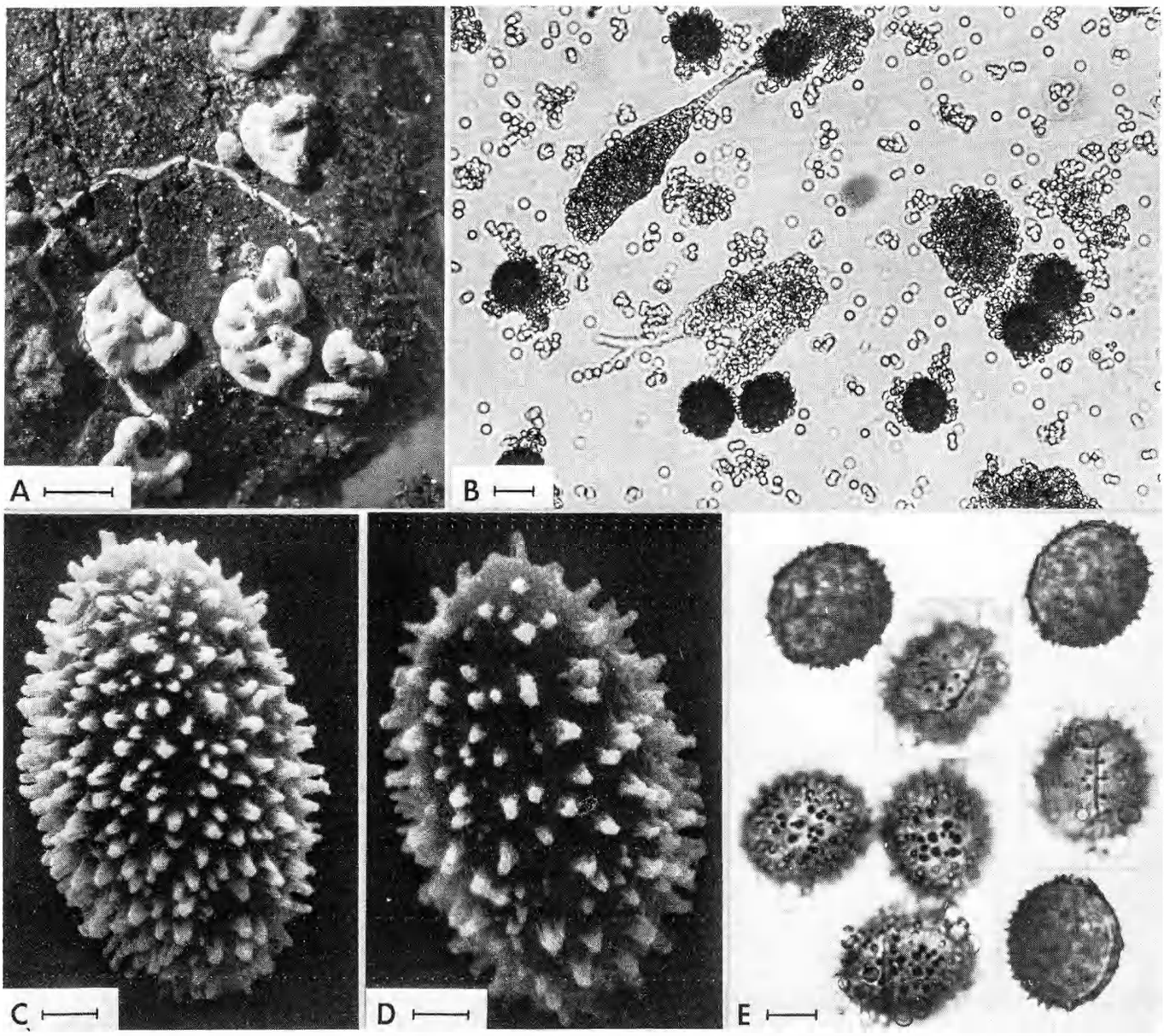

Fig. 7. *Physarum spinisporum* (Lqt 10617-b, holotype). – A: Fructifications on goat dung, moist chamber culture. – B: Capillitial nodes, spores and lime granules. – C, D: SEM pictures of spores. – E: Spores as seen with the light microscope. – Scales: A 1 mm, B 10 μm, C, D 2 μm, E 5 μm.

base; spores dark brown in mass, pale brown in transmitted light, spinulose, 11–12 μm in diam.

Deviant from typical specimens in spore markings and very short stalks (in S 17297-e not exceeding 0.1 mm). Yet it appears closer to *P. pusillum* than to any other species in the genus.

Physarum spinisporum U. Eliass. & Lundq., sp. nov. – Fig. 7

Holotypus: Lundqvist 10617-b (UPS).
Spain: *Canary Islands,* Tenerife, the SE coast, Barranco del Río, at the motorway (rabbit) Lqt 9295-e, (goat) Lqt 10617-b – Ethiopia, *Harar,* Afdem, 1100 m (camel) Thulin 2507-k.

Plasmodiocarpi leviter applanati vel teretes–lateraliter compressi, plerumque 0.3–0.4 mm lati, curvati vel irregulariter ramosi et reticulati, tota fructificatione ad 2.5 mm extensa, saepe 1 mm vel minus; hypothallus non evidens; peridium subfuscum–albidum, bistratum, stratis arcte associatis, exteriore strato calce valide incrustato, interiore strato tenui, membranaceo; nodi capillitiales albi, elongati vel irregulares, nonnumquam ex parte badhamioides, parte centrali plasmodiocarpi saepe aggregati in pseudocolumellam; sporae in acervo nitide atrae, luce transmissa badiae, ambitu plerumque ovales, 12–14.5 × 11–12 μm (spinis omissis), spinae longitudine ad 1 μm accedentes, sub microscopio luce instructo acutae apparentes, obtusae per microscopium electronicum inspectae, sporae pariete altera parte tenuiore et minus spinoso, hac parte (dumtaxat sporis in solutione KOH diluta inspectis)

crista longitudinali prominenti praedita, nonnumquam etiam cristis minus prominentibus (forsitan contractione effectis).

Plasmodiocarps (Fig. 7 A) curved or irregularly branched and netted, strands varying from slightly flattened or round in transection to laterally compressed, generally 0.3–0.4 mm wide, the whole fructification up to 2.5 mm in extent, often 1 mm or less; hypothallus not apparent; peridium dull greyish brown to white, 2-layered, but the layers closely associated, outer layer strongly encrusted with lime, inner layer thin, membranous; capillitial nodes white (Fig. 7 B), elongated or irregular, sometimes partly appearing badhamioid, tending to be aggregated into a pseudocolumella in the central part of the plasmodiocarpous strand; spores shining black in mass, reddish brown in transmitted light, preponderantly oval in outline (Fig. 7 B–E), 12–14.5 × 11–12 μm (excluding spines), spines approaching 1 μm in length (Fig. 7 C. D), appearing pointed in the light microscope, blunt when studied in scanning electron microscope, spore wall thinner and less spiny on one side, this side (at least when the spores are seen in a weak KOH solution) has a prominent longitudinal ridge (Fig. 7 E), sometimes also has less prominent ridges (shrinkage effects?).

Physarum spinisporum has some characters in common with *Badhamia apiculospora,* viz. the plasmodiocarpous fructifications and the predominantly oval spores with a longitudinal ridge. *P. spinisporum* differs in the prominent spines on the spores. Resemblances to the minute form of *Fuligo cinerea* (Fig. 6) also exist, but the spores of the latter lack a longitudinal ridge and the spines are shorter and interconnected by a network of low ridges (Fig. 6 C).

Didymium anellus Morgan

Spain: *Canary Islands,* Tenerife, the SE coast, Barranco del Rio, at the motorway (rabbit) Lqt 8322-m.

First record on dung.

Didymium clavus (Alb. & Schw.) Rabenh.

Sweden: *Upl,* Börje (cow) Lundell, Stordal & Eriksson 12.VIII.1948 (field coll.); Lena (horse) Lqt 7217 (field coll.).

Literature record: Venezuela: (cow) Dennis 1960.

Didymium difforme (Pers.) S. F. Gray

Sweden: *Sk,* Ravlunda (rabbit) Nordin 2517-y. *Bl,* Jämshög (cow) Lqt 3369-f (EXS ined.) (GB). *Öl,* Bredsätra (cow) Lqt 2289-c. *Gtl,* Östergarn (rabbit) Lqt 2110-n; Slite (rabbit) Nordin 1226-h. *Ög,* Grebo (roe deer) Lqt 3350-h. *Srm,* Aspö (cow) Lqt 2022-k, 2023-k. *Upl,* Bälinge (cow) Lqt 2801-c (PAD); Dalby (hare) Lqt 2329-c; Jumkil (elk) Lqt 3821-f; Söderby-Karl (cow) Lqt 2515. *Vsm,* Ängsö (hare) Nordin 2983-e. *Ång,* Nätra (black grouse) Lqt 10257-d. *Hrj,* Tännäs, Mt Ramundberget (elk) Nordin 3352-g – Norway: *Finnmark,* Nord-Varanger par., Vestre Jakobselv (sheep) Lqt 5004-j – Finland: *Kuusamo,* Kuusamo par., Juuma (capercaillie) Lqt 11754-d. *Lapponia inarensis,* Utsjoki par., Utsjoki (grouse) Lqt 4925-f (GB) – Germany: Berlin (roe deer) Sydow VI.1887 (Sydow: Mycotheca Marchica No. 1497, 1887, as *Chondrioderma d.*) (UPS) – France: *Aveyron,* Chaos de Montpellier-le-Vieux (rabbit) Lqt 10164-n. *Bouches-du-Rhône,* les Baux (rabbit) Lqt 9688-f. *Corsica: Bonifacio* (cow) Lqt 4427-m – Tanzania: *Arusha,* Ngurdoto National Park, Lake Kusare (Cape hare) Lqt 6456-g – USA: *California,* Los Angeles Co., Santa Catalina Isl. (cow) S 17297-k (GB). *Colorado,* Boulder Co., Mt Steamboat (cow) S 18499-v (GB).

Literature records: Germany (dung) Jahn 1916 – Poland: (dung) Schmidt 1912 – Hungary: (cow, hare) Tóth 1965, 1967 – Algeria: (rabbit) Faurel et al. 1966 – Canada: (horse) Bisby et al. 1929 – USA: (cow) Keller & Anderson 1978.

Didymium dubium Rost.

Norway: *Finnmark,* Nord-Varanger par., Fossefjellet (blue hare) Lqt 4967 (field coll.) – France: *Bouches-du-Rhône,* les Baux (rabbit) Lqt 9688-g – Spain: *Canary Islands,* Tenerife, San Andrés (rabbit) S 19304-m (with *Fuligo cinerea*).

Literature record: Scotland: (bird) Dennis 1975.

Didymium iridis (Ditm.) Fries

Sweden: *Upl,* Vassunda, Ragnhildsvik (elk) Nordin 269-c (Santesson 1964).

Literature records: France: (manure) Cailleux 1973 (as *D. xanthopus*) – Algeria: (camel, goat) Faurel et al. 1966 – Tchad: (camel) Faurel et al. 1966 – Mauritania: (gazelle, goat, mule) Faurel et al. 1966.

The specimen is referred to this species because of the predominantly upright sporangia. The spores have conspicuous clusters of warts, which is reminiscent of *D. verrucosporum* Welden. In fact, in Farr (1976) the specimen would key to the last-named species. *D. iridis* and *D. verrucosporum* are closely allied, and the distinction between them is not altogether satisfactory.

Didymium squamulosum (Alb. & Schw.) Fries

Sweden: *Sk,* Jonstorp (rabbit) Junell 1664-r. *Bl,* Åryd (rabbit) Nordin 1868-v. *Öl,* Böda (hare) Lqt 3103-e. *Hl,* Fjärås (cow) Lqt 3120-b. *Srm,* Aspö (caterpillars on *Prunus spinosa*) Lqt 2473. *Upl,* Bälinge (cow) Lqt 2802 (GB); Jumkil (elk) Lqt 3821-d, (horse) Lqt 2340-g; Tensta (roe deer) Nordin 230-e; Uppsala (horse) Lqt 2322-b; Vassunda (elk) Nordin 269-e (PAD). *Vsm,* Kila (elk) Nordin 1477-b. *Hls,* Järvsö (horse) Lqt 2787-a – Sri Lanka: *Matale,* Dambulla (omnivore) Kers 8.IV.1973 – Canada: *Alberta,* Oldman River Watershed, Mt Pasque, 2450 m (moose) Tibell 4891-c.

Literature records: Germany: (dung) Jahn 1916 (as *D. effusum*) – Hungary: (cow, deer, hare) Tóth 1965, 1967 – Bulgaria: (cow) Khinkova & Ivanova 1965 – Algeria: (rabbit) Faurel & Schotter 1965 a – Canada: (horse) Bisby et al. 1929 – USA; (cow, rabbit) Angel & Wicklow 1975.

Didymium trachysporum G. Lister

Spain: *Mallorca,* Torrent de Pareis (sheep) Tibell 5861-d.

Literature records: England: (manure) Lister 1925 – Germany (deer, rabbit) Lister 1925 – Spain: (rabbit) Moreno & Barrasa 1977.

Didymium verrucosporum Welden

Tanzania: *Kilosa,* Ukaguru Mts, Mt Matandu (duiker) Thulin & Mhoro 2972-h.

First record on dung.

Additional species reported from dung

The records cited are unverified and their accuracy is sometimes questionable.

Arcyodes incarnata (Alb. & Schw.) O. F. Cook – Chile: (cow) Spegazzini 1921 (as *Lachnobolus incarnatum*).

Arcyria elaterensis Mull. – USA: (horse) Mulleavy 1977.

Arcyria pomiformis (Leers) Rost. – Canada: (cow) Wehmeyer 1950.

Arcyria stipata (Schw.) A. Lister – Norway: (reindeer) Moravec 1968 (as *Hemitrichia stipata* var. *fusca*). – The position in *Arcyria* is preliminary as we have not seen authentic material.

Badhamia macrocarpa (Ces.) Rost. – Morocco: (cow) Malençon & Bertault 1968.

Colloderma oculatum (Lippert) G. Lister – England: (rabbit) Harper & Webster 1964 – Tchad: (dassie, goat) Faurel & Schotter 1966.

Comatricha mirabilis R. K. Benj. & Poitras – USA: (goat) Benjamin & Poitras 1950.

Comatricha nigra (Pers.) Schroet. – Algeria: (Barbary sheep) Faurel & Schotter 1965 c – Tchad: (Barbary sheep) Faurel & Schotter 1966.

Comatricha pulchella (Bab.) Rost. – Algeria: (Barbary sheep) Faurel & Schotter 1966.

Craterium leucocephalum (Pers.) Ditm. – Algeria: (camel) Faurel & Schotter 1965 c – Canada: (horse) Bisby et al. 1929.

Diderma applanatum Fr. – Hungary (deer) Tóth 1965.

Diderma effusum (Schw.) Morgan – Germany: (dung) Jahn 1916 – Hungary: (hare) Tóth 1965.

Diderma globosum Pers. – Hungary: (cow, deer) Tóth 1965.

Diderma niveum (Rost.) Macbr. – Argentina: (horse) Spegazzini 1912 (as *Chondrioderma niveum*).

Diderma simplex (Schroet.) G. Lister – Algeria: (Kabylian hare) Faurel & Schotter 1965 c – Tchad: (Barbary sheep, goat, sheep, camel, gazelle, "goundi") Faurel & Schotter 1966.

Diderma testaceum (Schrad.) Pers. – Hungary: (horse) Tóth 1965 – Canada: (porcupine) Wehmeyer 1950.

Didymium melanospermum (Pers.) Macbr. – Germany: (horse) Opiz 1816 (as *Physarum farinaceum*) – Hungary: (deer) Tóth 1965.

Didymium nigripes (Link) Fr. – Germany: (dung) Jahn 1916.

Didymium quitense (Pat.) Torrend – India (kangaroo, Delhi Zoo) Nannenga-Bremekamp et al. 1979.

Didymium rugulosporum Kow. – USA: (cow) Kowalski 1969 a.

Didymium vaccinum (Dur. & Mont.) Buchet – Germany: (rabbit, dung) Jahn 1916, 1919 (as *D. trochus*) – Hungary: (deer) Tóth 1965 – Canada: (cow) Bisby et al. 1929.

Fuligo septica (L.) Wigg. var. *rufa* (Pers.) R. E. Fr. – Yugoslavia: (dung) Schulzer von Müggenburg 1866 (as *Aethalium rufum*).

Lepidoderma chailletii Rost. – Hungary (cow) Tóth 1967.

Licea cf. *tenera* Jahn – Pakistan: (dung) Ahmed & Asad 1970 – USA: (sheep) Kowalski & Curtis 1968; (cow, pronghorn, rabbit) Angel & Wicklow 1975 – Brazil: (dung) Hagelstein 1944 – The records may refer to another species (see Kowalski & Curtis 1968 and the discussion under *Perichaena* cf. *liceoides*).

Licea variabilis Schrad. – Bulgaria: (horse) Khinkova & Ivanova 1965 (as *L. flexuosa*).

Macbrideola coprophila Nann.-Brem., Mukerji & Singh – India: (nilgai) Nannenga-Bremekamp et al. 1979.

Oligonema schweinitzii (Berk.) Martin – Germany: (dung) Jahn 1916 (as *O. nitens*).

Perichaena pedata (A. Lister) G. Lister – Germany: (rabbit) Jahn 1919.

Physarum compressum Alb. & Schw. – Algeria: (camel) Faurel et al. 1966 – Mauretania: (goat) Faurel et al. 1966 – Tchad: (camel, gazelle, goat, Barbary sheep, sheep, donkey, dassie, Kabylian hare, "goundi", bird of prey, rock dove) Faurel & Schotter 1966 – Congo: ("biche harnachée", gazelle, roan antelope) Faurel & Schotter 1965 d – Gabon: (buffalo, goat, sheep) Faurel & Schotter 1965 d.

Physarum contextum (Pers.) Pers. – Germany: (dung) Jahn 1916.

Physarum didermoides (Pers.) Rost. – Germany: (dung) Jahn 1916 – Hungary: (cow, horse, hare) Tóth 1965, 1967 – Algeria: (camel, goat, dassie, "sand rat") Faurel & Schotter 1965 b, c.

Physarum fimetarium Schum. – Denmark: (cow)

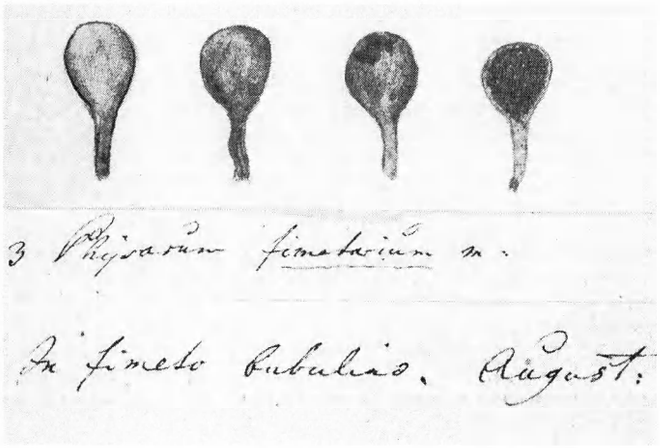

Fig. 8. Photograph of the illustration of *Physarum fimetarium* in Schumacher's unpublished *Flora hafniensis fungi delineati,* Vol. I, p. 71 (herbarium C).

Schumacher 1803 – Belgium: (rabbit) Marchal 1895 – Germany: (cow) Wallroth 1833.

The figures of *P. fimetarium* in Schumacher's *Flora hafniensis fungi delineati* (Vol. 1, p. 71), an unpublished work in three volumes (at C) with descriptions and hand-painted illustrations of some of the fungi described in his flora of 1803, show four yellowish-brown, stipitate fruit-bodies at various stages of development, but no microscopic details (Fig. 8). The published diagnosis runs as follows:

"Sparsum, primo fluxile album deinde subalutaceum pyriforme substipitatum, demum peridio obovato vertice lacero dilute purpurascenti-umbrino; capillitio compacto pulvereque fusco, stipite breve subflexuoso superne paululo incrassato colore peridii. In fimeto bubulino. August. viget."

The paintings are accompanied by a hand-written, partly illegible description that deviates somewhat from the published one (Schumacher 1803 p. 205). We find, however, that the descriptions and illustrations are of no help for the identification of this fungus, neither to species, nor to genus. Since type material is also lacking (Dr H. Knudsen, Copenhagen (C) in litt.), we reject *P. fimetarium* as a nomen dubium.

Physarum leucopus Link – Algeria: (camel) Faurel & Schotter 1965 b, c.

Physarum nucleatum Rex – Algeria: ("goundi") Faurel & Schotter 1965 c.

Squamuloderma nullifila Kow. – USA: (cow) Kowalski 1973.

Trichia contorta (Ditm.) Rost. – Germany: (dung) Jahn 1916.

Trichia fimicola (March.) Ing – Belgium: (rabbit) Marchal 1895 (as *T. varia* var. *fimicola*). – Scotland: (rabbit) Ing 1967.

The following species have been reported without indication of country or kind of dung. Only species not listed above are included.

Martin & Rickett 1949: *Arcyria leiocarpa* (Cooke) Martin & Alex. (as *Hemiarcyria leiocarpa*), *Didymium ochroideum* G. Lister, *Echinostelium minutum* de Bary, *Lamproderma scintillans* (Berk. & Br.) Morgan, *Perichaena minor* (G. Lister) Hagelst.

Hertel 1962: *Cribraria violacea* Rex, *Physarum cinereum* Schum., *Trichia varia* (Pers.) Pers.

Keller 1971: *Perichaena vermicularis* (Schw.) Rost.

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Studies in the lichen family Collemataceae

IV. Collema fecundum, a new species from North America

Gunnar Degelius

Degelius, G. 1979 11 15: Studies in the lichen family Collemataceae. IV. Collema fecundum, a new species from North America. *Bot. Notiser 132:* 569–572. Stockholm. ISSN 0006-8195.

Collema fecundum Degel., a new species from the west coast of N America is described. It is closely related to the New Zealand species *C. novozelandicum* Degel., from which it differs in, i.a., lack of isidia. Taxonomical and ecological data are given.

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In my monograph on the extra-European species of the genus *Collema* (Degelius 1974 p. 83) I mentioned several collections of a probably new species from Queen Charlotte Islands (British Columbia), related to the New Zealand species *C. novozelandicum* Degel. Later on I got more, very good, material, and I can now state that it is a new species; it is described below.

Collema fecundum Degel., sp. nov.

Holotype in Herb. Degel.: Canada, southwest British Columbia, Narvaez Bay, Saturna Island, sandstone boulders along beach (non-calcareous sandstone), altitude 0–2 m, 13.VI.1974 J. Coursley & W. J. Noble (n. 1579), as *Collema cristatum* (L.) Wigg.

Thallus parvus vel mediocris vel sat magnus, foliaceus, ± tenuis, ± adnatus, lobatus (lobis elongatis vel rotundatis; lobulis sat paucis, angustis vel sat latis, saepe ± concavis et margine saepe undulatis), non isidiatus, vulgo obscure olivaceus. Apothecia vulgo numerosa, minuta, sessilia, plana vel concava, immatura saepe subglobosa, epruinosa, margine thallino saepe evanescente (apothecia "subbiatorina"); excipulum thallinum vulgo non pseudocorticatum; excipulum proprium normaliter subparaplectenchymaticum vel euparaplectenchymaticum cellulis sat parvis; sporae vulgo 8:nae, mediocres, ellipsoideae, submurales (vel eumurales). Saxicola (ad saxum vulgo non calcareum).

Thallus up to 6 cm diam. in material studied (though usually a few cm only), foliose, ± rounded, adnate or a little ascending or loosely attached, ± thin (see below), deeply and broadly lobate (see below), dark olive-green (or sometimes lighter; lower surface often somewhat paler), matt or a little glossy, epruinose, not isidiate, smooth. Lobes ± extended and radiating or rounded, repeatedly furcate or rather irregularly branched or (small specimens) less branched; lobules = secondary lobes rather few, rounded to extended, usually 1–3 mm broad, free or contiguous or imbricate, flattened or often distinctly concave (owing to the ascending margin which is often coarsely undulate, entire or a little incised, not swollen). Sometimes accessory lobules occur (flattened, small, usually marginal). Lower surface of thallus with ± scattered, rounded hapters of the common *Collema* type.

Thallus (lobes) (45–)60–130(–170) μm thick (when moist). *Hyphae* loose or rather dense, especially vertical and horizontal ones distinct, not very much branched, 1–4.5 μm thick. A typical (sometimes a primitive) pseudocortex often occurring at both surfaces of thallus or at lower surface only (often several layers of isodiametric or extended, thin-walled cells); parts of thallus may be paraplectenchymatous

throughout. *Nostoc* cells spread in the whole thallus, in chains or in small lumps or free, usually globose (3–6 μm), heterocysts 5–8.5 μm; gelatine I–.

Apothecia usually numerous, often dense or crowded, superficial (also submarginal), flattened (often subglobose when young), soon sessile with constricted base, generally very small (0.2–0.6 mm diam.). *Disc* plane to somewhat concave (in younger apothecia more pronouncedly concave, in very young ones punctiform), usually dark red (sometimes very dark, but at times lighter red), matt or somewhat glossy, epruinose, smooth. *Margo thallinus* ± thin (mature apothecia), entire, smooth, often a little glossy, not rarely disappearing. *Margo proprius* in some specimens very distinct, thin, pale, sometimes predominant ("subbiatorine" apothecia). Margo somewhat prominent or not so.

Apothecia c. 250–365 μm thick when moist. *Excipulum thallinum* rather thin (± disappearing in "subbiatorine" apothecia), without pseudocortex or sometimes with a rather badly developed one especially at base of apothecia, I–. *Excipulum proprium* subparaplectenchymatous (hyphae usually up to 6.5 μm thick) or – particularly in central part (45–110 μm or more) – euparaplectenchymatous with ± small, thin-walled cells (4.5–10.5 μm or in some apothecia up to 13 μm), rarely in part euthyplectenchymatous, colourless or yellowish, I–; in "subbiatorine" apoth., euparaplectenchyma often reaching surface of apothecium. *Subhymenium* 30–70 μm thick, pale or colourless, I+ constantly blue. *Hymenium* 95–170 μm high, in uppermost part yellowish or reddish, for the rest colourless and I+ rapidly and constantly blue. *Paraphyses* simple or somewhat branched (and anastomosing), rather stiff or somewhat flexuose, 1.5–2(–3) μm thick (KOH), irregularly thickened at apices (3–6.5, rarely 8.5 μm). *Asci* clavate to subcylindrical, 65–105 × 15–24 μm, wall towards apex thickened. *Spores* 8 (or 4–6) per ascus, monostichous or distichous, rarely polystichous, usually imbricate, ellipsoid with obtuse or acute ends, occasionally globose to subglobose, submuriform with 3(–5) transversal septa, more rarely eumuriform with 2 longitudinal septa, sometimes constricted at septa, colourless, (18–)20–28 × 8.5–10.5(–15) μm.

Pycnidia in some collections hardly rare, superficial (laminal), immersed or slightly prominent, globose, c. 130 μm or more diam., pale within, from outside visible as small pale dots on both surfaces of thallus. *Pycnoconidia* rather rare, straight, slightly swollen towards the ends, c. 4–4.5 × 1–1.2 μm.

Taxonomical remarks

The most important characteristics of this species are the foliose, small to rather large, ± thin thallus with narrow to rather broad, often ± concave and undulate lobules, without isidia; the usually numerous and very small apothecia, the normally not (pseudo) corticate excipulum thallinum, the subparaplectenchymatous to ± small-celled euparaplectenchymatous excipulum proprium, and the ellipsoid and muriform spores.

C. fecundum belongs to the *crispum* group and is closely related to *C. novozelandicum* Degel., also saxicolous, from New Zealand (see Degelius 1974 p. 83). It differs from that species and the other two species of this group first and foremost in the lack of isidia. The thallus is, on the whole, somewhat thinner than in *C. novozelandicum,* and the apothecia are a little smaller, often very numerous and dense. There are also some differences in the anatomy of the apothecia: *C. novozelandicum* has more highly developed excipulum thallinum (a distinct, rather thick pseudocortex outside the algal tissue), but a more primitive, euthy- to subparaplectenchymatous excipulum proprium.

Distribution and habitat ecology

C. fecundum is only known from the Pacific coast of Canada (British Columbia) and the United States (Washington State). In the areas mentioned it seems not to be rare on or near the seashore. (The two very uncertain collections from the West Indies mentioned by Degelius 1974 p. 83 are disregarded here.)

This new species is saxicolous, grows on sandstone, conglomerate, serpentine, igneous rock, etc., rarely on calciferous rock. Occasionally, one may find *C. fecundum* on mosses on rocks. The substrate of the related *C. novozelandicum* is usually calciferous.

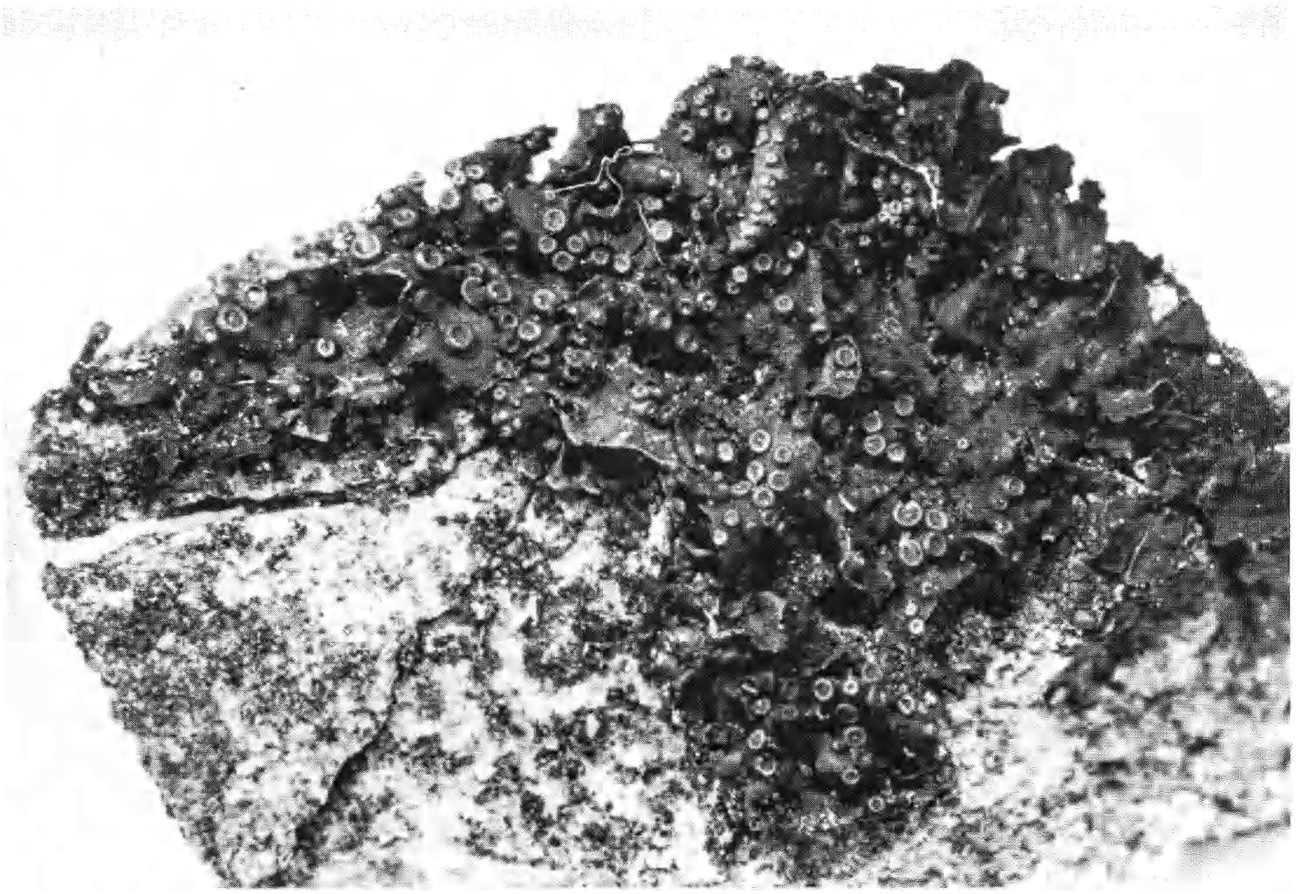

Fig. 1. *Collema fecundum* (part of the holotype). Thallus with apothecia. ×6.25. – Photo Dan Nilson.

According to our present knowledge, *C. fecundum* is thus a marine and maritime (aërohaline) lichen (following the terminology in Degelius 1939 p. 25). The occurrence in this type of habitat is unique within the genus, although some other species occasionally grow on the seashore. Mrs Noble writes (letter 13.VII.1978) that the species is in SW British Columbia (Vancouver Island, etc.) "rather common in the area just above the intertidal zone usually on noncalcareous rocks (since calcareous substrates are not common)". According to Mr Ryan (letter 5.II.1979), the species is in Washington State (NW part of Fidalgo Island, serpentine rock) "strongly associated with, but not confined to, gently sloping (5 to 30°), north-facing rock surfaces exposed to moderate freshwater seepage"; among other lichens at the site he mentions *Verrucaria maura* (often overgrown by *C. fecundum*), several *Leptogium* species, and *Spilonema revertens*. See further *Localities* below, and forthcoming works on rocky seashore vegetation by the two scientists cited.

Accompanying plants in herbarium collections (from different areas) seen by me include, i.a., Musci, *Caloplaca* sp., *Leptogium lichenoides, Physcia caesia, Verrucaria* spp.; sometimes *Collema fecundum* is the only plant occurring.

Localities

The information on the herbarium labels is somewhat abbreviated here, the most important facts only being related.

Canada. British Columbia. Queen Charlotte Islands: Graham Island, Seal Inlet in Rennell's Sound, volcanic sea stacks and surrounding spruce-alder forest, lower aërohaline, 1967, Brodo 10311 (CAN). – Do.: Graham Island, Skidegate Landing at Haida Point, coastal rocks, 1967, Brodo 11723 (CAN, Degel.). – Do.: Graham Island, Tow Hill, slopes at summit (357 ft), 1967, Brodo 9918 (CAN). – Do.: Huxley Island, off E coast of Moresby Island N of Burnaby Island, N shore, calciferous and volcanic rock, mostly shade, forming rocky points and high wet rock walls, on shoreline

rocks – *Coccotrema* zone, 1971, Brodo 17513 (CAN). – Do.: Moresby Island, N shore of Copper Bay, rocky shore, lower aërohaline, 1971, Brodo 17262 (CAN). – Do.: Skidegate Inlet, Torrens Island, 1/2 mile SE of Skidegate Mission, basaltic and breccia rock knoll and headland with *Thuja–Picea* forest, rock of hygrohaline above *Verrucaria* zone, 1971, Brodo 17363 (CAN).– SW British Columbia: Galiano Island, Galiano Way, sloping sandstone terraced beach, 0–2 m, 1974, Coursley & Noble 1113 (UBC). – Do.: Galiano Island, Whaler Bay, sloping sandstone beach, 0–2 m, 1974, Coursley & Noble 937 (UBC, Degel.). – Do.: Mayne Island, Dinner Point, conglomerate beach (shaded), 0–2 m, 1974, Coursley & Noble 1919 (UBC). – Do.: Saturna Island, Narvaez Bay (holotype). – Do.: Thetis Island, Pilkey Point, sandstone beach, 0–2 m, 1974, Coursley & Noble 3167 (UBC, Degel.). – Do.: Vancouver Island, 1 km N of Neck Point, just N of Nanaimo, igneous rocky beach, 0–3 m, 1975, Crane & Noble 5191 (UBC). – Do.: Vancouver Island, Swartz Head, 1 km E of Swartz Bay, on shale (shaded crevices), 0–2 m, 1975, Crane & Noble 3947 (UBC). – Do.: Vancouver Island, Bare Point, Chemainus, conglomerate beach, 0–2 m, 1975, Crane & Noble 4642 (UBC). – Do.: Vancouver Island, Metchosin, cove beside Pamir Road, vertical igneous cliff (shaded), 0–2 m, 1975, Crane & Noble 4188 (UBC). – Do.: Vancouver Island, Mermaid Cove, 2 km N of Yellow Point, sandstone beach, 0–2 m, 1975, Crane & Noble 4562 (UBC, Degel.).

USA. State Washington. Co. Skagit: NW part of Fidalgo Island, serpentine rock, supralittoral (shaded), 1978, Ryan 3621 a (Degel.). – Do.: about the same loc., 4.3 m, 1978, Ryan 4266 (Degel.). – Do.: about the same loc., lower supralittoral, seepage area, 3.5 m, 1978, Ryan 4287 (Degel.).

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Degelius, G. 1974: The lichen genus Collema with special reference to the extra-European species. *Symb. Bot. Upsal. 20 (2).*

Botanical literature

Stafleu, F. A. & Cowan, R. S. 1979: *Taxonomic literature*. A selective guide to botanical publications and collections with dates, commentaries and types. 2nd ed. Vol. 2: H–Le. XVIII + 991 pp. Regnum vegetabile Vol. 98. Bohn, Scheltema & Holkema, Utrecht. ISBN 90313 0343 7. Price (bound) DFl. 264.

Vol. 1 of the second edition of this monumental bibliography (cf. review in *Bot. Notiser 130* (1977) p. 349) has been succeeded by a second volume in less than three years. The scope of the work is still expanding as new collections, libraries and other sources have become available. Three further volumes, two more than were earlier planned, and a supplement to Vols. 1–5 are now announced.

The entire work will be a much enlarged edition of the *Taxonomic literature* of 1967 (by Stafleu only) which, according to its subtitle, was modestly introduced as a "selective guide". Almost all fields of plant taxonomy are now well surveyed. The majority of the works quoted fall between the years 1753 and 1940; a few earlier authors have also been included. Some authors who commenced publishing before 1940 have been incorporated, including their recent major publications. Very few botanists still alive (and hardly any one active) are recorded.

It must have been necessary to apply some selectivity to the number of entries, enforced by the enormous quantity of data assembled and the limited space available. Thus several minor or otherwise less important works have been omitted, especially those printed in periodicals. Nevertheless, even the most critical reader will be satisfied by the mine of information in this volume, often obtained from sources very difficult of access. Among the many merits of the work should be emphasized the detailed comments on actual dates of publication. This is especially useful for books which were issued in fascicles. In such cases, many botanists have often quoted in error the year printed on the title-page believing this to be valid publication date for the whole work.

Dissertations from Swedish universities have been quoted as issued on the day when these were publicly defended. This date is often printed on a detached "dissertation title page". However, according to regulations which have existed in Sweden for at least a hundred years, a thesis must be printed and available, not only to the opponents, but also for sale at book sellers, three weeks before the day indicated on this title page. Generally the real publication date will be 20–30 days earlier than the date printed.

The following remarks may be of some use for the forthcoming supplement:

Hellbom, Per Johan. "Herbarium and types unknown". H.'s main collection (incl. types) is at GB. An important part of his herbarium, including the material for his *Nerikes lafflora* (Lichen flora of the province of Närke) is in the school (now "Karolinska skolan") at Örebro where he was a teacher. The material for *Lichenaea neo-zelandica* (collected by S. Berggren) is at S. Under the entry *Nerikes lafflora* is recorded another work by H., *Om Nerikes lafvegetation* (On the lichen vegetation of Närke). However, this is not, as stated, a review ("Ref.") of the *lafflora* but a different work intended for a wider public. Although the contents are partly the same, the *lafvegetation* has additional chapters on ecology and distribution, and Latin diagnoses of several species described in Swedish in the *lafflora;* the latter work was published earlier in the same year (1871).

Hultén, Eric. His well-known *Flora of Alaska and neighboring territories* (1968) can be regarded as a second, condensed edition, illustrated with drawings and distribution maps, of his *Flora of Alaska and Yukon,* Vols. 1–10, Lund 1941–1950 (*Lunds Univ. Årsskrift N.F. Avd. 2, 37(1)–46(1)).* This basic work of 1902 pp. contains much information on nomenclature, synonymy, and distribution including all locality records for each species, which is not repeated in the manual of 1968. The first version ought to have been mentioned as his comprehensive floras of Kamtchatka and of the Aleutian Islands are recorded in detail.

König, Johann Gerhard. "Herbarium and types BM". Important material is at LD and/or C, including types of many species described by A. J. Retzius. An additional entry to the bibliography and biography of König is that of Fischer, C. E. C., *Kew Bull. 1932:* 49–76 (pr. 1933). Fischer had the König collection at Lund sent on loan to Kew in 1929. He determined the material according to modern nomenclature and selected several lectotypes (marked with bold type in his paper). It is evident, however, that he did not see the whole collection. In fact, many of the 33 König species (described by Retzius), which Fischer recorded as lacking, are still extant at Lund. Retzius, A. J., *Observ. bot., 4:* 5–6; 1786 gives a short account of K.'s travels. In the same series (*6:* 41–66; 1791) R. published a posthumous work by K., *Descriptiones Epidendrorum in India orientali factae".* The material for this paper, which should only be ascribed to K., is at C.

Kylin, Harald. "Herbarium and types LD". This is true with regard to the major part of the material collected after 1920 when he moved from Uppsala to Lund. The type material for his thesis *Studien über die Algenflora der schwedischen Westküste* (1907) is at UPS, isotypes at LD. The major part of the material for *Zur Kenntnis der subantarktischen und antarktischen Meeresalgen. II. Rhodophyceen* (1919; co-author C. Skottsberg) is at UPS, not at S as stated in the preface. In several cases the specimens are represented only as slide preparations, and are not in the Herbarium. No type material seems to be extant for some of his species. *Die Florideenordnung Rhodohymeniales* is an inadmissable changed spelling. Like other phycologists Kylin wrote *Rhodymeniales.* To his "eponymy" (i.e., genera commemorating him) should be added *Haraldia* Feldmann (1939).

Lehmann, Johann Georg Christian. "Herbarium and types: The greater part at S." An important part (probably the first set, according to Australian botanists), including many types, of the material quoted in his *Plantae Preissianae* (1844–1848) is at LD.

The Swedish reader will appreciate the detailed accounts of the many editions of our well-known floras Hartman, *Handbok i Skandinaviens flora* and Krok & Almquist, *Svensk flora för skolor.* To the comments on part II. *Kryptogamer* of the latter work can be added that Ed. 6 (1947, 2nd printing, somewhat amended 1957) has drawings by the co-authors E. von Krusenstjerna (mosses) and O. Almborn (lichens). Ed. 7 (1962), amended reprint 1969) has also drawings by the co-author T. Willén (algae). The statement that "figures by C. A. M. Lindman" were included in ed. 7 of the cryptogamic part is not correct.

There is an above average number of misprints; as in Vol. 1; it is surprising to find the genus *Oenothera* consistently misspelt without the first e throughout, even in the index.

The present volume concludes, as did Vol. 1, with two indexes, one to titles of works quoted and abbreviated "short titles" such as *Fl. Kamtchatka* (Hultén), *Fl. Kamtschatka* (Komarov), and the other to persons and generic names commemorating persons. It should be noted that both indexes include some direct references to entries in Vol. 1, which, for some reason, were omitted there.

This "adventurous odyssey through the history of plant taxonomy" is a milestone in botanical literature. All of us await the forthcoming volumes with keen anticipation.

Ove Almborn