Santessonia, a new lichen genus from Southwest Africa

Mason E. Hale, Jr. and Gernot Vobis

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The genus *Santessonia* Hale & Vobis is proposed as new. The only known species, *S. namibensis* Hale & Vobis, is fruticose and has buellioid apothecial characters, placing it in the family Physciaceae. It occurs in the coastal fog zone on rocks and shrubs.

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The discovery of a new genus of lichens is not a common event. It was surprising, therefore, to receive for identification a conspicuous fruticose specimen from the Namib coast of Southwest Africa which could not be compared with any known genus. One might have presumed that such a large showy lichen would already have been collected by the German botanists in the 19th century even along the little-known Namib coast. Superficially the plant seems to resemble *Roccella* in the flat, strap-shaped lobation (Fig. 1 A), but the lack of a dense, fastigiately arranged cortex and the apothecial characters rule this out at once. The apothecia and spores are typically buellioid, yet we have seen no reports of anything but crustose or at most primitively squamulose members of *Buellia* or *Diploicia*. The chemistry (norstictic acid), however, would be considered normal for *Buellia*.

This lichen, then, appears to be a fruticose relative of *Buellia* in the family Physciaceae, falling in the series *Buellia* (crustose) – *Pyxine* (foliose) – *Santessonia* (fruticose). It would be comparable, for example, to fruticose *Teloschistes* in the series *Caloplaca* (crustose) – *Xanthoria* (foliose) – *Teloschistes* (fruticose). The correspondence is not perfect, obviously, since *Teloschistes* and *Xanthoria* have highly developed cortical tissues.

The genus, quoting from data provided by the collector, Mr E. R. Robinson, occurs on shrubs and metamorphic rock outcrops (dolomite and marble) along the Namib coast about 200 km south of Walvis Bay, from 25° 10' S to 25° 50' S. Photographs provided by Mr Robinson show the thalli, both erect and pendulous, moderately covering large boulders. The most outstanding climatic feature of the habitat is the persistent coastal fog and mist which occurs on 150–200 days of the year and contributes 3–5 mm of precipitation each month. The thalli are actually very brittle when dry, an expected consequence of the lack of well developed supporting tissues.

We are dedicating the genus to Dr Rolf Santesson, who has contributed so much fundamental work to lichenology at the generic level.

Santessonia namibensis Hale & Vobis, gen. et sp. nov. – Fig. 1 A

Thallus fruticosus, semi-erectus vel pendulus, crassus, fragilissimus, cinereo-albus, 2–4 cm altus, lobis elongatis, planis vel apicem versus plus minusve radialibus, integris, 5–9 mm latis vel apice pro parte ramosis, ramis ca. 1 mm diametro, recurvis, ca. 250–300 µm crassis, stratis corticalibus parce evolutis, strato gonidiali distincto; alga chroococcoides; apothecia numerosa, terminalia, 1.5–2 mm diametro, sporis octonis, fuscis, 2-loculatis, 7–8 × 10–14 µm; pycnidia immersa, conidiis 1 × 5–6µm.

Chemistry: Norstictic and connorstictic acids (determined with thin-layer chromatography).

Type. Southwest Africa. Spencer Bay, North Head (14° 52–1/2' E, 25° 35' S), about 117 km N of Lüderitz Bay, growing on a *Lycium* shrub and rocks close to the sea at 15 m above s.l., 1971, E. R. Robinson (holotype in US, isotypes in LD, UPS).

Other collections. Southwest Africa. Saddle Hill (14° 55' E, 25° 50' S), about 89 km N of Lüderitz Bay, growing on metamorphic rocks at 10–100 m above s. l., 1971, E. R. Robinson (US).

Thallus morphology

The thallus is flattened and quite variable in width toward the central older parts but narrows and becomes more or less radially symmetric at the tips (Fig. 1 A). It is not dorsiventral and the two surfaces are identical (Fig. 1 C, D). The surface of the thallus (Fig. 1 B) consists of loosely packed hyphae with considerable interstices. No dense polysaccharide layer or epicortex are present. In cross section the cortical layer appears as a loosely aggregated layer with many dead cells interspersed with branched living hyphae (Fig. 1 E–G). Algal layers are found on both surfaces just below this cortical layer (Fig. 1 E), clearly visible in stained sections but seen only as hollowed out pockets in scanning electron microscope sections (Fig. 1 D). The medullary hyphae are rather dense and irregularly arranged in the flattened part of the thallus (Fig. 1 C, D). Toward the lobe ends they are thick walled and more or less prosoplectenchymatously arranged, running parallel to the surface (Fig. 2 A, B). The surfaces of the hyphae in the various layers are covered with the rather amorphous crystalline accretions of norstictic acid.

Apothecia

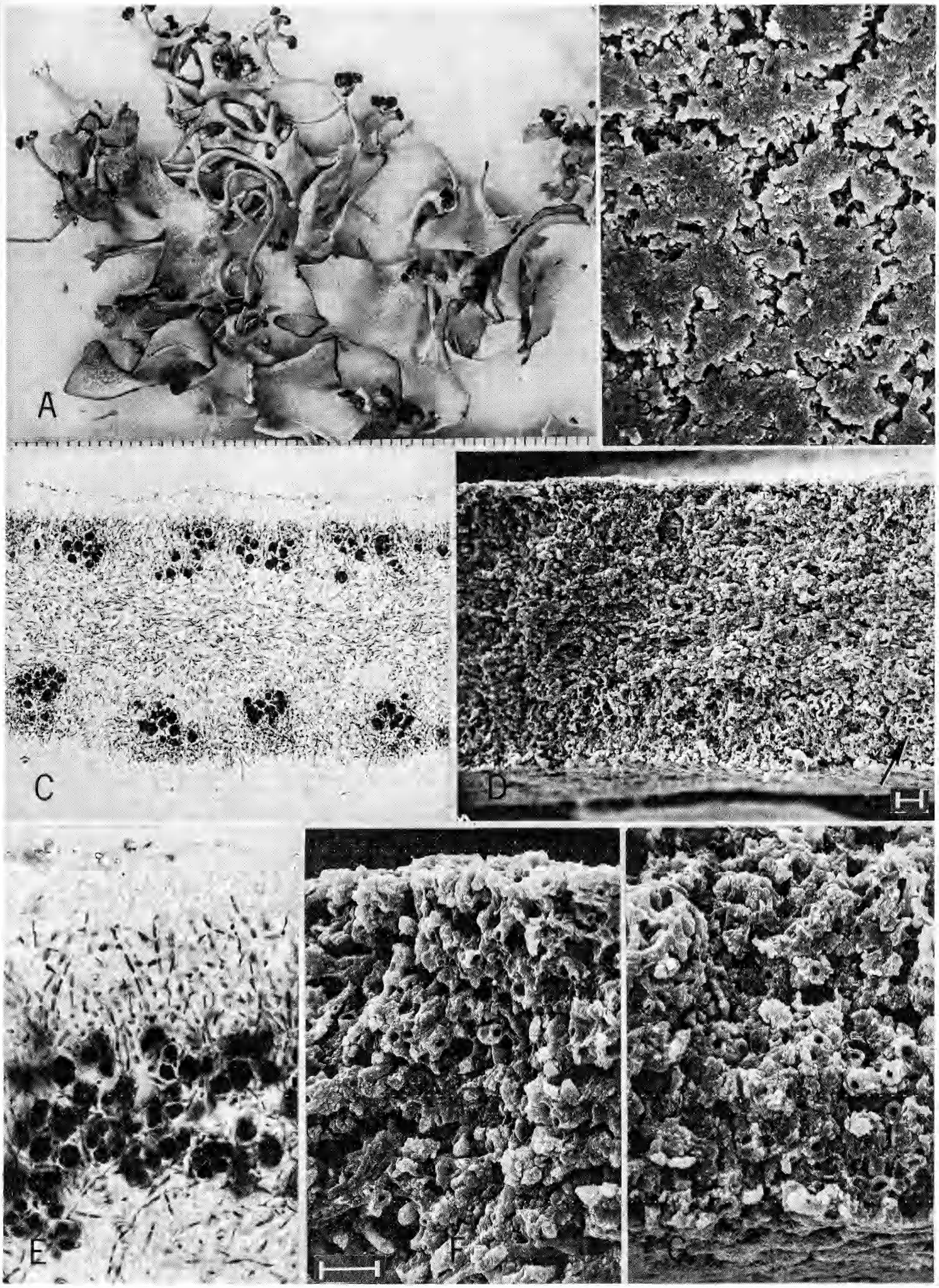
The apothecial primordia are located laterally on the flattened part of the thallus, appearing as brownish areas caused by darkening of the cell walls. The generative tissue is comparable to that of *Buellia wahlenbergii* (see Lamb & Henssen 1968). Although ascogones and trichogynes could be observed only in a degenerated condition (Fig. 2 C), it appears that the apothecial "stroma" is raised up from the vegetative tissue below by spreading (comparable to pseudopodial formation in *Thysanothecium* according to Jahns 1970). The unoriented medullary hyphae in the flattened part of the thallus maintain their orientation parallel to the surface at this time. If several "stromata" are present they are manifested by further growth of the thallus part. Mature apothecia are located on branched pseudopodetia (Fig. 3).

The apothecia are hemispherical and delimited by a weakly developed exciple (Fig. 2 D). The hymenium stains deep blue in Lugol's solution. It is about 100 µm high with a dark subhymenium about 110 µm thick (Fig. 2 E). The paraphyses are branched and anastomosing (Fig. 2 F) and their tips are capitately thickened with brown cells as in *Buellia*. The ascus apex stains blue in iodine. There are 8 spores, 7–8 × 10–14 µm, ovoid to elliptical at maturity and 2-celled with a dark roughened wall (Fig. 2 I). Spores that have not been ejected were observed in the hymenium and in the subhymenium (as in *Buellia wahlenbergii*).

Pycnidia

Pycnidia are produced mostly terminally at the lobe ends, more rarely on the margins. They are immersed in the thallus and aggregated (Fig. 2 G). They vary from elongate to pear-shaped, spherical, or conical. Size varies from 65–80 (rarely 120) µm wide and 120–170 µm long. The pycnidial wall consists of the basal cells of the conidiophores (Fig. 2 H). The ostiole, which is

Fig. 1. *Santessonia namibensis*. – A: Habit of plant from Saddle Hill. – B: Scanning electron microscope view of thallus surface (× 450). – C: Stained cross section of flattened part of thallus (same scale as D). – D: Scanning electron microscope view of cross section of flattened part of thallus (scale = 20 µm) (arrow points to area of algal colony). – E: Stained section of cortical area (×450). – F: Scanning electron microscope view of upper cortical area (scale = 10 µm). – G: Scanning electron microscope view of lower cortical area (same scale as F).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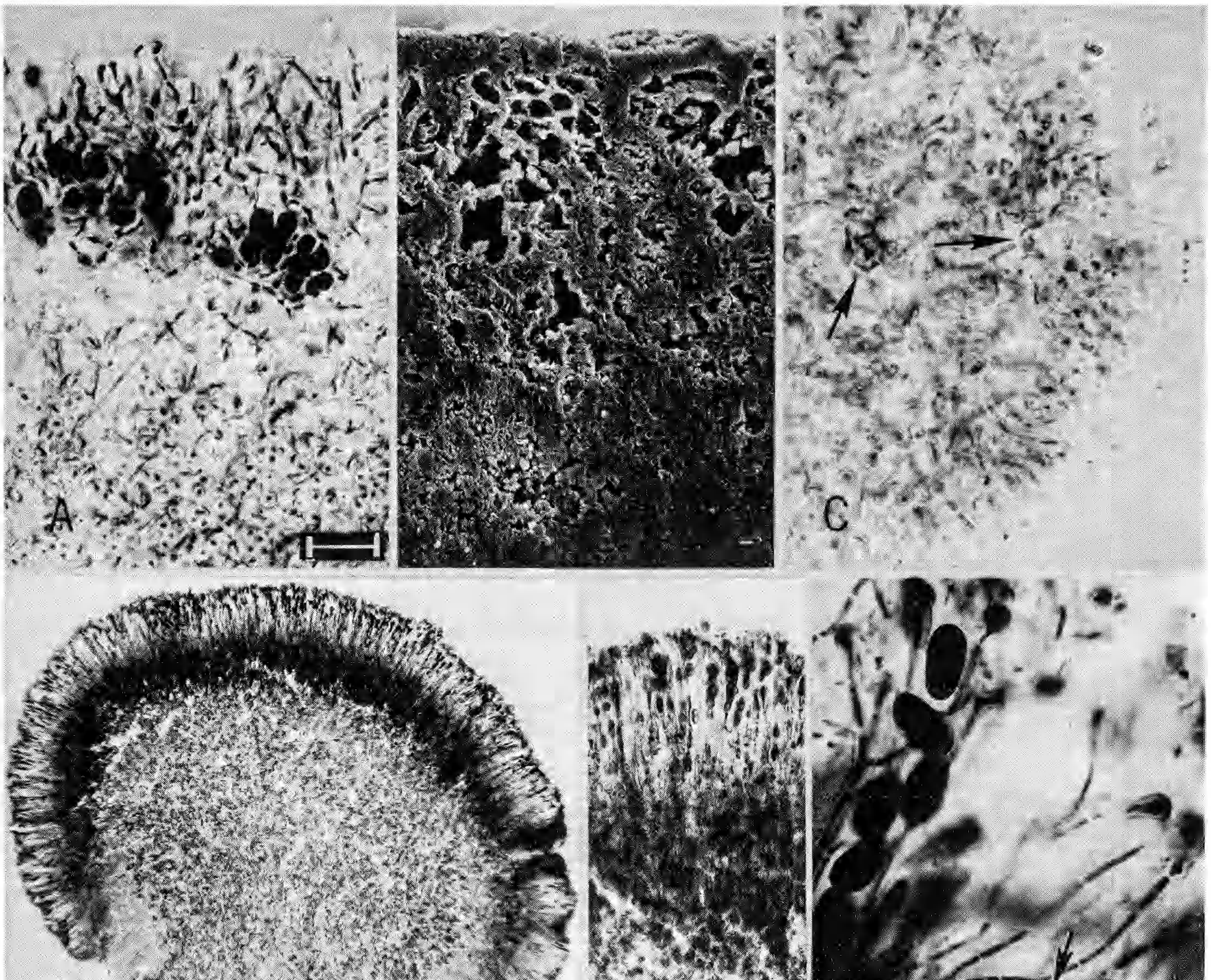
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open when the conidia are mature, has very dark cell walls, making the surrounding area appear black. Conidiophores are made up of several conidiogenous cells arranged in a series of 3–5 cells. They branch frequently. Conidia are formed terminally from apical conidiogenous cells or laterally on conidiophore cells below. The formation of conidia follows the phialid pattern. At maturity the conidia are elongate and cylindrical, 1 × 5–6 μm.

Acknowledgments. We wish to thank Dr Ove Almborn and Dr Aino Henssen for comments on this paper.

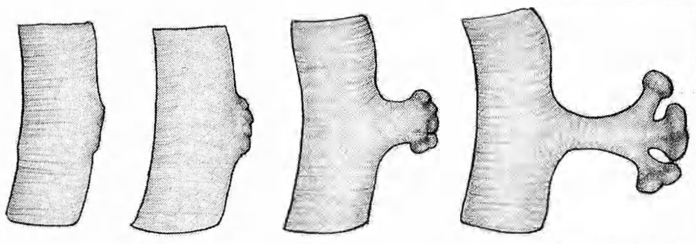

Fig. 3. Stages in development of apothecia (stage shown in second from left illustrated in Fig. 2 C).

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Fig. 2. *Santessonia namibensis.* – A: Stained cross section of upper cortical area at lobe tip (scale = 20 μm). – B: Scanning electron microscope view of a cross section of cortical area at lobe tip (same scale as A). – C: Ascogone (left arrow) and trichogyne (right arrow) (same scale as A). – D: Vertical cross section of apothecium (× 50). – E: Portion of the hymenium (× 180). – F: Paraphyses with arrow pointing to anastomosing group (× 800). – G: Clump of pycnidia (× 180). – H: Single pycnidium (same scale as A). – I: Ascospores (× 1000).

Bark culture Myxomycetes new to India

S. S. Dhillon

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Licea castanea G. Lister, *L. testudinacea* Nannenga-Bremekamp, *Cribraria minutissima* Schw. and *Didymium sturgisii* Hagelst. are reported as new to India. The plasmodium of *D. sturgisii* is light brown, that of *L. testudinacea* is at first colourless, later light brown.

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A large number of Myxomycetes has been obtained by culturing bark samples from living trees from NW Himalayas, by the moist chamber culture technique (Gilbert & Martin 1933). The following four species are new to India. The author's collections do not differ in any important respects from the descriptions given in Martin & Alexopoulos (1969).

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Licea castanea G. Lister, J. Bot. 49: 61 (1911).

Matured from bark of *Aesculus indica* Colebr., collected from Jagat Sukh, Manali, Himchal Pradesh, India, 29.9.1971, Dhillon 1830 (PAN, herb. Nannenga-Bremekamp).

Licea testudinacea Nann.-Brem., Acta Bot. Neerl. 14: 141 (1965).

Matured from bark of *Abies* sp., collected from Manali, Himachal Pradesh, India, 27.6. 1971, Dhillon 1844 (PAN, herb. Nannenga-Bremekamp).

Previously known only from the type (Netherlands, Angiosperm tree bark). The plasmodium is at first colourless, becoming light brown before fruiting. The spores of the Indian collection are smaller (9.5–10.8(–12.2) μm) than those of the type (up to 15 μm).

Cribraria minutissima Schw., Trans. Am. Phil. Soc. II, 4: 260 (1832).

Matured from bark of *Picea* sp., collected from Pulga, Kulu, Himachal Pradesh, India, 20.9.1971, Dhillon 1832, 1834 (PAN).

The spores are larger in both the Indian collections (8–9.5 μm) than previously reported (up to 8 μm).

Didymium sturgisii Hagelst., Mycologia 29: 397 (1927).

Matured from bark of *Pinus* sp., collected from Nainital, Uttar Pradesh, India, 15.8.1973, Dhillon 14029 (PAN, herb. Nannenga-Bremekamp).

The plasmodium is light brown in colour. The spores are more prominently sculptured than previously reported.

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Floristic reports from the high mountains of Sterea Ellas, Greece 1

Lars-Åke Gustavsson

Gustavsson, L.-Å. 1978 03 31: Floristic reports from the high mountains of Sterea Ellas, Greece 1. *Bot. Notiser 131:* 7–25. Stockholm. ISSN 0006-8195.

Notes on 55 species are given. One new species, *Veronica oetaea* L.-Å. Gustavsson, is described. The following 4 species are new to Greece: *Geum heterocarpum* Boiss., *Plantago reniformis* G. Beck, *Seseli libanotis* (L.) Koch and *Trollius europaeus* L. 39 taxa are reported for the first time from the mountains investigated. One new combination, *Linum punctatum* Presl ssp. *pycnophyllum* (Boiss. & Heldr.) L.-Å. Gustavsson is proposed. Chromosome numbers are given for 19 of the taxa, 12 of which have previously not been counted.

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This article deals mainly with the alpine flora of mountains in Sterea Ellas, SC Greece. The mountains investigated are shown in Fig. 1 (geographical names according to Atlas of Greece 1965).

The highest mountains, viz. Mt Parnassos (2457 m), Mt Giona (2510 m), Mt Vardousia (2484 m), Mt Iti (2152 m) and Mt Timfristos (2315 m), have been visited by a number of botanists. The southern slopes of Mt Parnassos are among the most frequently visited localities in Greece. The lower mountains, however, viz. Mt Kokkinari (1911 m), Mt Oxia (1926 m), Mt Yiorla (1924 m), Mt Chelidon (1975 m) and Mt Kaliakouda (2101 m), have previously been little explored or not at all. Among the most important publications dealing with the flora of this part of Sterea Ellas can be mentioned Halácsy (1888), Heldreich (1890), Maire & Petitmengin (1907, 1908), Rechinger (1936), Regel (1944), Quézel (1973) and Quézel & Contandriopoulos (1965 a). Much unpublished and even undetermined material collected by many botanists in Sterea Ellas and other parts of Greece is preserved in a number of herbaria in Greece and other European countries. I have not yet been able to study these collections.

More than 7000 collections, almost entirely from the alpine zone, were made during 22.7.–2.8.1970 (no. 183–610), 20.6.–4.8.1972 (no. 611–2104), 15.5.1973 (no. 2213–2271), 1.7.–1.9.1973 (no. 2285–4395), 11.5.–25.7.1975 (no. 4396–7254) and 21.7.–4.8.1976 (no. 7255–7388).

If not otherwise stated the nomenclature follows Tutin et al. (1964–1976). All my collections are preserved at LD (not marked in the collection lists). Some duplicates are also in the Goulandris Museum, Kifissia (ATH) and/or Copenhagen (C). Aldén's material (marked A) is at LD while that of Strid and Hartvig is preserved in Copenhagen. The main works consulted for information on general distributions are Tutin et al. (1964–1976), Meusel et al. (1965), Davis (1965–1975) and Hess et al. (1967–1972).

Chromosome counts – material and methods

Plants were raised from seeds and bulbs collected in the area and kept in cultivation in the experimental greenhouses at the Lund Botanical Garden. Young plants were kept overnight at a temperature of c. 4° C. Root tips were then fixed in the Svalöv modification of the Navashin-Karpechenko fixative, sectioned with a microtome and stained with crystal violet.

PTERIDOPHYTA

Aspidiaceae

Dryopteris villarii (Bellardi) Woynar ex Schinz & Thell. ssp. **villarii**

Collections: Mt Parnassos, c. 6 km N of Arachova, 2100–2200 m, G 4317 – Mt Giona, 4 km ENE of Lefkadition, c. 2350 m, G 2037; c. 2.5 km ESE and E of Sikea, c. 2450 and 2200 m, G 3800 and G 6963; 8 km NW–WNW of Prosilion, c. 1840 m, G 6984 – Mt Vardousia, c. 5 km NE of Dafnos, 2100–2300 m, G 3112; c. 6 km E–ESE of Artotina, 2100–2300 m, G 3217; c. 7 km W of Athanasios Diakos, c. 2000 m, G 3616.

New to Sterea Ellas. This taxon has previously been reported only once from Greece, viz. Mt Olympos (Stojanov & Jordanov 1938, as *Nephrodium rigidium* Desv.). In Jalas & Suominen (1972) this locality is, however, omitted, but another locality, probably Mt Kajmakčalan, on the border between Greece and Jugoslavia is marked. However, I have seen no record in the literature from that area. Strid has recently collected this subspecies from several places on Mt Olympos (Strid 1492, 9357, 9732, 11578 and 11878, all unpublished).

The plants from Sterea Ellas have lanceolate and dull green leaves 6–30 cm long and densely glandular above. The pinnae are up to 4.5 cm long. G 6984, growing at the bottom of a shady doline with precipitous walls at a lower altitude than usual, is an exception. The leaves of these specimens are up to 50 cm long with pinnae up to 9 cm long. Much longer (c. 15%) stomata indicate that they may be tetraploid.

In Sterea Ellas *D. villarii* ssp. *villarii* inhabits only damp cliff ledges and crevices and moist ground at the base of cliffs at 1840–2500 m. *D. villarii* ssp. *pallida* (Bory) Heywood, distributed in the Mediterranean area, is fairly common in dry stony places on most mountains visited. Apart from morphological characters these subspecies are thus also ecologically well separated. Some authors treat these taxa at the species level.

General distribution: C, S and NW Europe eastwards to the Caucasus and Afghanistan; NW Africa.

Aspleniaceae

Asplenium cuneifolium Viv.

Collection: Mt Oxia, 6.5 km SSW of Gardikion, 1800–1920 m, G 6318.

New to the area. *A. cuneifolium* is previously known from a few localities in N Greece and on Evvoia (cf. Jalas & Suominen 1972). It grows mostly on serpentine, but on Mt Oxia it was found in sandstone rocks.

General distribution: S and C Europe and Turkey (map in Meusel et al. 1965).

Asplenium septentrionale (L.) Hoffm.

Collections: Mt Iti, 5 km SSE of Ipati, c. 1950 m, G 4801 – Mt Oxia, 6 km SSW of Gardikion, 1875–1900 m, G 6276 – Mt Yiorla, 3 km W–WSW of Lampirion, 1700–1800 m, G 5995 – Mt Chelidon, 3 km WSW of Mikro Chorio, c. 1900 m, G 5429.

New to Sterea Ellas. The species is previously known from many localities in Macedonia and Thrace but in other parts of Greece it is rare (cf. Jalas & Suominen 1972). Apart from the mainland it also occurs on Samothraki (Rechinger 1943) and Thasos (Stojanov & Kitanov 1950). In Jalas & Suominen (1972) it is, probably erroneously, marked for the part of Aetolia-Akarnania which includes Mt Oxia. *A. septentrionale* is reported by Halácsy (1904) from Mt Oxya in Pindhos, but as this locality is omitted on the map the two mountains have probably been confused.

A. septentrionale was found inhabiting sandstone and schist rocks between 1700 and 1950 m, often together with *Polypodium vulgare* L.

General distribution: Eurasia, N Africa, Japan and N America (map in Meusel et al. 1965).

Athyriaceae

Athyrium filix-femina (L.) Roth

Collections: Mt Oxia, 6.5 km SSW of Gardikion, 1800–1920 m, G 6287 – Mt Timfristos, 6 km ENE of Karpenision, c. 1450 m, G 5073.

New to the area. *A. filix-femina* is scattered throughout Greece, but no published locality from the area is known to me. A dot on the map in Aetolia-Akarnania in Jalas & Suominen (1972) may depend on confusion with Mt Oxya in Pindhos from where the species was reported by Halácsy (1904). This locality is, however, not marked on the map.

A. filix-femina was found in wet places along rivulets.

General distribution: Europe, Asia, NW Africa and N and S America (map in Meusel et al. 1965).

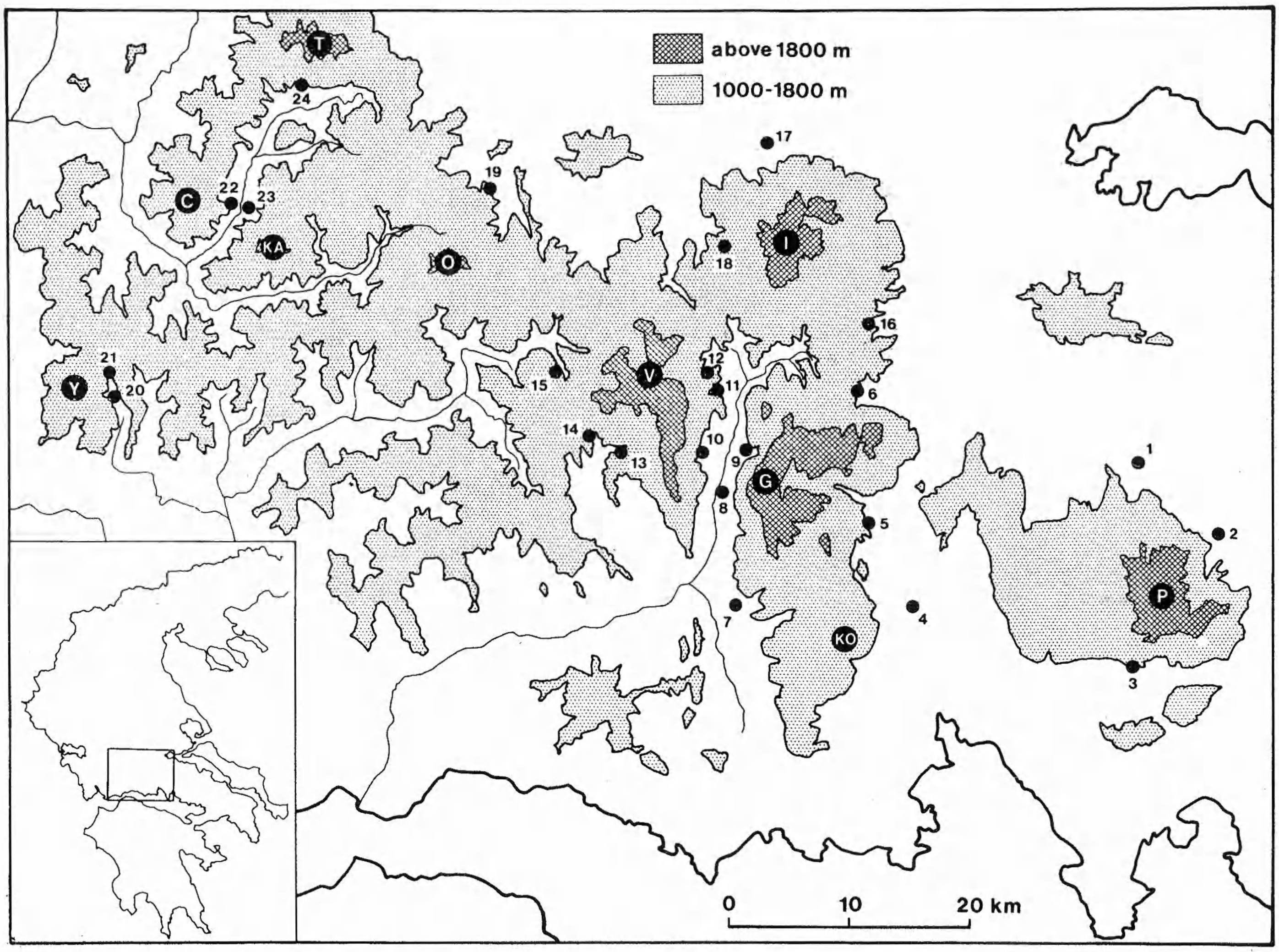

Fig. 1. The area investigated.

Mountains:	
Parnassos	P
Kokkinari	KO
Giona	G
Vardousia	V
Iti	I
Oxia	O
Yiorla	Y
Chelidon	C
Kaliakouda	KA
Timfristos	T

Towns and villages:	
Amfiklia	1
Amfissa	4
Arachova	3
Artotina	15
Athanasios Diakos	12
Dafnos	13
Dichorion	14
Gardikion	19
Ipati	17
Kaloskopi	6
Karpenision	24
Kato Lampirion	20
Kato Mousounitsa	11
Koniakos	10
Lampirion	21
Lefkadition	8
Lidorikion	7
Megalo Chorio	23
Mikro Chorio	22
Neochorion	18
Pavliani	16
Prosilion	5
Sikea	9
Titorea	2

Ophioglossaceae

Ophioglossum vulgatum L.

Collection: Mt Iti, 4.5 km E of Neochorion, c. 2000 m, G 6693.

New to Sterea Ellas. On the Greek mainland previously known from the extreme NW, some mountains in Pindhos, Mt Athos and some of the Aegean islands (cf. Aldén 1976, Jalas & Suominen 1972).

On Mt Iti only some 10 specimens were found in a wet pasture close to a spring.

General distribution: Eurasia, NW Africa and N America (map in Meusel et al. 1965).

Polypodiaceae

Polypodium vulgare L.

Collections: Mt Iti, 5 km SSE of Ipati, c. 1950 m, G 4802 – Mt Yiorla, 3 km W–WSW of Lampirion, 1700–1800 m, G 5997 – Mt Chelidon, 3 km WSW of Mikro Chorio, c. 1900 m. G 5430 – Mt Timfristos, 4 km N of Karpenision, c. 1950 m, G 5125.

New to the area investigated but otherwise known to occur in most parts of Greece (cf. Jalas & Suominen 1972).

As it inhabits very dry rocks at high altitudes the leaves of most of the specimens found are only 4–13 cm long with 5–10 pairs of pinnae.

The species was found in rock crevices of sandstone and schist from 1700–1950 m.

General distribution: Europe eastwards to Iran and W Siberia (map in Meusel et al. 1965).

SPERMATOPHYTA

Apiaceae

Peucedanum longifolium Waldst. & Kit.

Collections: Mt Chelidon, c. 3 km W of Mikro Chorio, 1725–1900 m, G 2346 – Mt Kaliakouda, c. 3.5 km SE of Megalo Chorio, 1800–1850 m, G 2847 (C); 3.5 km SSE of Megalo Chorio, 1800–1850 m, G 5200 – Mt Timfristos, c. 5 km NE of Karpenision, 1800–1900 m, G 4076 (ATH).

New to Sterea Ellas. This species is very rare in Greece where it has been reported from Mt Falakron (Kitanov 1943, Quézel & Contandriopoulos 1968), Mt Vourinos (Goulimis 1960) and from several mountains in S and C Pindhos (Aldén 1976).

Except for the narrower, keeled leaves and the shorter pedicels *P. longifolium* is very close to *P. officinale* L. The material from Sterea Ellas has leaves that are 0.5–1.0(–1.3) mm broad and fruit about equalling pedicels (in one specimen in G 4076, however, some pedicels are 2–3 times as long as the immature fruits).

In Sterea Ellas *P. longifolium* has only been found on N-facing slopes where it inhabits stony ground and meadows on rock ledges from 1725 to 1900 m.

General distribution: Balkan peninsula from Bosna and C Romania southwards to SC Greece.

Peucedanum oligophyllum (Griseb.) Vandas ssp. **oligophyllum**

Collections: Mt Vardousia, c. 4 km W of Athanasios Diakos, c. 1750 m, G 3686 – Mt Iti, 6.5 km SE–SSE of Ipati, 1850–1950 m, G 1877 (ATH); c. 7 km SSE of Ipati, 1850–1900 m, G 4217; 6.5 km SSE of Ipati, 1850–1900 m, G 6483 – Mt Oxia, 7 km SSW of Gardikion, 1800–1900 m, G 6249 (C) – Mt Timfristos, 3.5 km N of Karpenision, 1850–1950 m, G 1570; c. 4 km NNW of Karpenision, 2050–2100 m, G 4119.

New to Sterea Ellas. Neither Hayek (1927) nor Tutin et al. (1968) mention this species from Greece though it has in fact previously been found there. Rechinger (1936) reported it from Mt Kajmakčalan and recently it was recorded from Mt Pangeon (Markgraf-Dannenberg 1976 p. 103). According to a sheet at LD it also occurs on Mt Lisia in Thessaly (Sintenis 1896 no. 1610, as *Seseli oligophyllum* Griseb.). Morphologically my collections agree well with material seen from outside Greece.

P. oligophyllum is not uncommon in subalpine meadows and pastures on sand and schist.

Chromosome number: $2n = 22$ (G 4217). No previous count.

General distribution: Albania, S Jugoslavia and N and C Greece.

Seseli libanotis (L.) Koch

Collections: Mt Giona, 6 km SW–SSW of Kaloskopi, c. 2150 m, G 7270; 5.5 km SW of Kaloskopi, c. 1900 m, G 7300.

New to Greece. Nearest localities are in Bulgaria and Montenegro.

S. libanotis shows a considerable variation in leaf-dissection, shape of the lobes and in the indumentum. According to Tutin et al. (1968) leaf-dissection and shape of the lobes shows an east-west cline, plants with the most dissected leaves and narrowest lobes occurring in W Europe. Glabrous fruits occur mainly in the S half of the range of the species. It is thus surprising that the plants from Mt Giona have 2- to 3-pinnate levaes with acute, linear to lanceolate lobes and pubescent fruits. Many local taxa are described on combinations of these characters. Of the two subspecies accepted in Tutin et al. (1968) the Greek plants belong to ssp. *libanotis*.

On Mt Giona *S. libanotis* grows in small grassy patches on damp N–NE-facing cliff ledges.

General distribution: Europe, Turkey, Caucasus, Iran and Siberia.

Seseli parnassicum Boiss. & Heldr.

Collections: Mt Parnassos, 5.5 km NE of Arachova, c. 1600 m, G 4401; 5 km NE–ENE of Arachova, c. 1650 m, G 7023 – Mt Giona, 5.5. km SW of Kaloskopi, c. 1900 m, G 7296 – Mt Yiorla, c. 3 km WSW of Lampirion, 1850–1920 m, G 3441 (C) – Mt Timfristos, c. 5 km NE of Karpenision, 1800–1900 m, G 4077 (ATH).

A rare Greek endemic species, previously recorded from Mt Parnassos (e.g. Heldreich 1890, Quézel & Contandriopoulos 1965 a) and Mt Giona (Quézel & Contandriopoulos 1965 a). Zaganiaris (1940) reported it from near Krania in Macedonia. A dubious determination of a non-flowering collection from Mt Gionscala in Pindhos (Sintenis 1896 no. 1205) has been checked and is correct. It has recently also been collected on Mt Tzoumerka in C Pindhos (Aldén 2739, unpublished).

S. parnassicum grows in crevices, on rock ledges and among blocks of hard limestone.

General distribution: Endemic to Greece.

Asteraceae

Achillea barbeyana Heldr. & Heimerl

Collection: Mt Vardousia, 4 km SW–WSW of Athanasios Diakos, 2350–2450 m, G 7245 (ATH, C).

This Vardousian endemic has previously only been reported in connection with the type description.

It has been found only in the summit area above 2350 m of what the local inhabitants as well as previous collectors call Mt Korax, the highest peak just SW of Athanasios Diakos. (In Atlas of Greece (1965) this name, however, has been used for quite another part of the Vardousia massif).

It grows in stony soils often in semi-shaded places.

Chromosome number: 2n = 18 (G 7245). No previous count.

General distribution: Endemic to Mt Vardousia.

Aster alpinus L.

Collection: Mt Giona, c. 2.5 km ESE of Sikea, c. 2450 m, G 3806(C).

New to Sterea Ellas. An arctic-alpine species, in Greece previously reported from Mt Killini and Mt Chelmos on Peloponnisos (Halácsy 1902, Maire & Petitmengin 1908) and Mt Bela Voda and Mt Kajmakčalan in Macedonia (Zaganiaris 1940).

Aster alpinus is extremely polymorphic. Local taxa have been distinguished, so also in Greece where the plants from Mt Killini were described as *A. cylleneus* by Boissier & Orphanides. It was separated from *A. alpinus* s.str. on the shorter stems and smaller leaves, both with a greyish-white pubescence, the smaller capitula, obtuse involucral bracts and pale violet ligules. In comparison with the plants from Mt Killini the specimens from Mt Giona differ in the following characters: Stems somewhat longer (up to 10 cm), leaves larger (basal spathulate and up to 4 cm, cauline lanceolate and up to 4.5 cm) and moderately pubescent with more or less patent hairs mixed with short-stalked glands, involucral bracts obtuse to acute and ligules bright violet-blue. These populations fall well within the total variation of *A. alpinus* s.lat. Material from Macedonia has not been seen.

A few individuals have been observed in two adjacent localities on the summit ridge of Mt Giona, where it was found on damp limestone rock ledges and in crevices at 2100 and 2450 m.

General distribution: S, C and NE Europe, W and C Asia to Siberia and Kamtschatka and NW America.

Filaginella uliginosa (L.) Opiz

Gnaphalium uliginosum L.

Collection: Mt Iti, 7 km SSE of Ipati, c. 1850 m, G 4264.

New to Sterea Ellas. The species is very rare in Greece. In Halácsy (1901) there is only one early report from Peloponnisos by Sibthorp. Hayek (1931) mentioned the species as also occurring in Thrace and Macedonia. Only one exact locality, near Chryssoupolis in Macedonia (Zaganiaris 1940), has been seen.

The plants from Mt Iti have hairy achenes, thus according to Tutin et al. (1976) they should be referred to *Gnaphalium uliginosum* L. ssp. *pilulare* (Wahlenb.) Nyman.

On Mt Iti *F. uliginosa* was found in the bare clay of a dried-up melt-water pool, together with *Corrigiola litoralis* and *Eleocharis palustris*.

General distribution: Most of Europe eastwards to Japan; introduced in N America.

Helichrysum plicatum DC.

Collection: Mt Timfristos, 6 km ENE of Karpenision, 1700–1850 m, G 338 (ATH, C).

New to Sterea Ellas. In Greece previously reported from several mountains in Pindhos and

Macedonia (e.g. Halácsy 1902, Quézel & Contandriopoulos 1965 b, Regel 1941, Zaganiaris 1938).

According to Davis (1975) the material collected is referable to ssp. *plicatum*.

The species was found in subalpine pastures in a limited area on a NE-facing slope.

General distribution (ssp. *plicatum*): S part of the Balkan peninsula, Anatolia, Lebanon, N Iraq and Caucasus.

Leontodon hellenicus Phitos

Collections: Mt Chelidon, 3.5 km W of Mikro Chorio, 1750–1850 m, G 5417 (ATH, C) – Mt Kaliakouda, 4 and c. 4.5 km SE of Megalo Chorio, c. 1850 and 1900–2000 m, G 5287 and G 2690.

This very rare, only recently described species (Phitos 1966), was previously only known from the type collection (Mt Kaliakouda, Phitos 4394).

It inhabits subalpine crevices in hard limestone.

General distribution: Endemic to Mt Chelidon and Mt Kaliakouda.

Omalotheca hoppeana (Koch) Schultz Bip. & F. W. Schultz

Gnaphalium hoppeanum Koch

Collections: Mt Vardousia, 5 km NNE of Dafnos, c. 2000 m, G 2965; c. 5 km NE of Dafnos, 2100–2300 m, G 3123; 3 km SW–WSW of Athanasios Diakos, c. 2100 m, G 7234; 3.5 km SW–WSW of Athanasios Diakos, 2100–2200 m, G 7244.

New to Sterea Ellas. In Greece it has previously been reported from Mt Olympos and several mountains in Pindhos (Quézel & Contandriopoulos 1965 b, Aldén 1976). The species is not mentioned from Greece in Tutin et al. (1976).

O. hoppeana is sometimes difficult to distinguish from *O. supina* (L.) DC. They are best separated on the hairs on the achenes which in *O. hoppeana* are rounded at the apex while those of *O. supina* are bifid. It can perhaps also be confused with a dwarf alpine variant of *O. sylvatica* (L.) Schultz Bip. & F. W. Schultz which in Sterea Ellas has been found growing together with *O. hoppeana*. This variant has a stem 0.5–4 cm long with 4–8 capitula and leaves which are sometimes only 1–3 mm broad and greyish-tomentose. It is, however, distinguished on the lighter involucral bracts and connate pappus hairs.

O. hoppeana grows in grazed pastures above 2000 m.

Chromosome number: $2n = 28 + 2B$ (G 7234). No previous count.

General distribution: C Europe, from the Alps to the Carpathians, C Italy and the Balkan peninsula.

Senecio scopolii Hoppe & Hornsch. ex Bluff & Fingerh.

Collections: Mt Chelidon, c. 3 km W of Mikro Chorio, 1725–1900 m, G 2403; 3.5 km W of Mikro Chorio, 1700–1900 m, G 5364 – Mt Kaliakouda, 3.5 km SSE of Megalo Chorio, 1800–1850 m, G 5170 (ATH); 3.5 km SE–SSE of Megalo Chorio, 2050–2100 m, G 5267.

New to Sterea Ellas. From Greece it is known from four previous localities, Mt Tzoumerka, near Mandra Hodza in Thessaly, Siatista in Macedonia (all as *S. arachnoideus* Sieber ex DC.) and Mt Smolikas (as *S. lanatus* Scop.) (Halácsy 1902, Zaganiaris 1939, Phitos 1962). Aldén has recently collected the species in the following localities in C Pindhos: Katara (A 1256), Mt Baros (A 3066), Mt Kakarditsa (A 3508) and Mt Tringia (A 354), all unpublished.

S. scopolii belongs to the critical *S. doronicum* group and is most closely related to *S. doronicum* (L.) L. from which it can generally be distinguished on the thinner and softer leaves. In Hayek (1931) none of these species were mentioned from Greece but they appear in Tutin et al. (1976).

In Sterea Ellas it inhabits stony pastures, mostly just above the timber-line, but it has also been found in the summit area of Mt Kaliakouda.

General distribution: C and N Italy and the W part of the Balkan peninsula.

Boraginaceae

Anchusa phocidica L.-Å. Gustavsson

Collection: Mt Giona, 4 km SW–SSW of Kaloskopi, c. 1960 m, G 7329.

A. phocidica was previously only known from the type collection from another part of the Giona massif (cf. Gustavsson 1976).

These newly discovered plants, some 50 were observed, agree well morphologically with the type collection. They were found growing among limestone boulders. The species is thus not a strict chasmophyte as was suggested in Gustavsson (1976).

General distribution: Endemic to Mt Giona.

Macrotomia densiflora (Ledeb. ex Nordm.) Macbride

Collection: Mt Giona, 8 km WNW of Prosilion, c. 1900 m, G 7273.

New to Sterea Ellas. In Greece previously known only from Mt Chelmos (cf. Halácsy 1902 sub *M. cephalotes* (A. DC.) Boiss.).

My specimens differ somewhat from the plants on Mt Chelmos, particularly in the stem which is 6 cm long(not 15–20), the basal leaves which are up to 11 mm broad (not 20) and the cauline leaves which are up to 3 mm broad (not 10). The corolla tube of *M. densiflora* is about as long as the calyx (cf. Tutin et al. 1972).

On Mt Giona only one clump with a single flowering stem was found in a crevice in a NE-facing limestone cliff, but as the area is rocky and difficult of access further finds are to be expected. Its occurrence in Greece is of phytogeographical interest. As the species is mainly Anatolian its occurrence here indicates a former connection with Asia Minor.

General distribution: S and SC Greece and Anatolia.

Myosotis refracta Boiss.

Collections: Mt Kokkinari, 6 km WSW of Amfissa, c. 1900 m, G 5639 – Mt Giona, 6 km ENE of Lidorikion, c. 1750 m, G 4544; 7 km N of Prosilion, c. 1800 m, G 4642; 4.5 km E–ENE of Sikea, c. 2150 m, G 6927 – Mt Vardousia, 3.5 km W of Athanasios Diakos, 1850–1950 m, G 1263 and G 1343; 5–6 km WNW of Athanasios Diakos, 1850–1950 m, G 4940; do, c. 1900 m, G 4951 – Mt Iti, 6 km SE–SSE of Ipati, 1850–1950 m, G 6546 – Mt Chelidon, 3.5 km W of Mikro Chorio, c. 1900 m, G 5320 – Mt Kaliakouda, c. 4 km SE of Megalo Chorio, c. 1700 m, G 2763; 3.5 km SSE of Megalo Chorio, c. 1800 m, G 5230 – Mt Timfristos, 3.5 km N–NNE of Karpenision, 1900–2000 m, G 5141.

Previously reported from Mt Parnassos (Maire & Petitmengin 1908), Mt Giona (Quézel & Contandriopoulos 1965 a) and Mt Timfristos (Rechinger 1936). Outside the area investigated it is known from scattered localities on the Greek mainland, Peloponnisos and some of the islands (Halácsy 1902, Hayek 1931, Rechinger 1943, 1961).

Most collections are typical ssp. *refracta*. In the hairiness of the calyx, however, some specimens are intermediate between ssp. *refracta* and ssp. *paucipilosa* Grau in having very few hooked hairs in the lower 1/3 of the calyx tube. Other specimens, growing in moist situations, have slender flexuous stems and somewhat broader leaves, characters distinguishing the Cretan endemic ssp. *aegagrophila* Greuter & Grau. The reflexed calyces, appressed almost to the stem, do not, however, agree with those of the Cretan subspecies.

M. refracta is not uncommon in dry stony places, but it can also be found in moist, sometimes sheep-manured soil, mainly up to 1900 m. On Mt Parnassos it was observed but not collected at c. 2450 m.

Chromosome number: $2n = 44$ (G 1263 and G 1343), which agrees with previous counts (Fedorov 1969).

General distribution: Spain, Jugoslavia, Greece, Turkey, Krym, Iraq and Iran.

Rindera graeca (A. DC.) Boiss. & Heldr.

Collections: Mt Parnassos, 6.5 km WSW of Titorea, 1850–1900 m, G 614 and G 662 (C) – Mt Giona, 6 km NW of Prosilion, 1900–2000 m, G 4659 (ATH); 8 km WNW of Prosilion, c. 1900 m, G 7274 – Mt Vardousia, c. 4.5 km NE of Dichorion, 2050–2200 m, G 2933; 4 km N of Dafnos, 1700–1800 m, G 3093 (seed collection).

A Greek endemic species previously reported from Mt Parnassos and Mt Vardousia (Halácsy 1902, Quézel 1973). Outside the area investigated it is also known from the higher mountains on Peloponnisos, Mt Cithaeron on Attica, Mt Dirphys, Mt Timphi and Mt Grammos and the island of Poros (Halácsy 1902, Zaganiaris 1940).

On the mountains visited *R. graeca* inhabits crevices of subalpine and alpine limestone outcrops and bare stony ground.

Chromosome number: $2n = 24$ (G 3093). No previous count.

General distribution: Endemic to Greece.

Caryophyllaceae

Arenaria conferta Boiss.

Collections: Mt Parnassos, 5.5 km NE–ENE of Arachova, c. 2100 m, G 7265 (ATH, C) – Mt Giona, 8 km NNE of Lidorikion, c. 2000 m, G 1039; 3.5 km ENE of Lefkadition, 2250–2300 m, G 2026; 7 km NW of Prosilion, 2050–2100 m, G 6798; 6 km W–WNW of Prosilion, c. 2175 m, G 7351 – Mt Vardousia, 7 km W of Athanasios Diakos, c. 1950 m, G 3635.

New to Sterea Ellas. *A. conferta* is previously known from a number of mountains in NW Greece southwards to Mt Olympos and S Pindhos (Halácsy 1901, McNeill 1963).

According to Balkan floras *A. conferta* has an eglandular, greyish pubescence. Nevertheless all specimens from Sterea Ellas have both eglandular and glandular hairs on sepals, pedicels, upper leaves and upper parts of the stem. Such glandular plants have been found in other parts of Greece, too. In one collection from Mt Timphi (Rechinger 21570, LD) all specimens have both types of hairs and in one collection from Mt Katafili in C Pindhos (Aldén 4648, unpublished) there are plants either with or without glandular hairs. Hayek (1928) described these glandular plants as f. *glandulosa,* while Stojanov & Jordanov (1938) accorded them varietal status. There is also considerable variation in length of the pedicels and shape and size of the leaves and sepals. The species is in need of detailed study.

In Sterea Ellas *A. conferta* has been found only on mobile screes of hard limestone above 1950 m.

Chromosome number: 2n = 20 (G 1039 and G 2026). No previous count.

General distribution: SC to NW Greece; Albania and SW Jugoslavia.

Cerastium cerastioides (L.) Britton

Collection: Mt Vardousia, 6 km WSW of Athanasios Diakos, c. 2000 m, G 1444.

New to Sterea Ellas. This arctic-alpine species is apparently very rare in Greece. It has previously been recorded from Mt Tzoumerka (Halácsy 1901), Mt Timphi (Phitos 1962, Quézel & Contandriopoulos 1965 b), near Samarina (Mt Smolikas) (Zaganiaris 1940) and Mt Kajmakčalan (Strid 1977). Apart from my collection it has also been observed in the summit area of Mt Korax (see under *Achillea barbeyana*) at 2400–2450 m.

On Mt Vardousia *C. cerastioides* grows in grazed pastures, often below large snow patches, between 2000 and 2450 m.

Chromosome number: 2n = 38 (G 1444), which agrees with most previous counts. 2n = 34, 36 and 40 are also known (Fedorov 1969, Tutin et al. 1964).

General distribution: Eurasia, NW Africa, NE America and Greenland (map in Meusel et al. 1965).

Corrigiola litoralis L.

Collection: Mt Iti, 7 km SSE of Ipati, c. 1850 m, G 4263.

New to the mountains investigated. According to Halácsy (1901) a rare species in Greece. Scattered localities are, however, known from most parts of the country including Crete and some Aegean islands.

C. litoralis is a predominantly lowland to montane species, previously not known to occur in the alpine zone. On Mt Iti it was found growing in the bare clay of a dried-up melt-water pool. Associated species were *Filaginella uliginosa* and *Eleocharis palustris.*

General distribution: W, C and S Europe, Asia Minor to Syria; N And C Africa; introduced in S Africa and America (map in Meusel et al. 1965).

Dianthus pinifolius Sibth. & Sm. ssp. **serbicus** Wettst.

Collections: Mt Yiorla, c. 3 km WSW of Lampirion, 1850–1920 m, G 3411 – 7.5 km WSW of Karpenision, c. 1200 m, G 1499 (ATH).

New to Sterea Ellas. In Greece this taxon has previously been reported from Mt Smolikas (Halácsy 1901), Mt Vermion (Ganiatsas 1939), Mt Olympos (Zaganiaris 1939) and Mt Athos and Samothraki (Rechinger 1943).

My plants are closest to ssp. *serbicus* but they are not typical, especially G 1499, which has slightly shorter and paler bracts than usual.

D. pinifolius ssp. *serbicus* was found in stony pastures.

General distribution: SW Romania and Balkan peninsula southwards to Sterea Ellas.

Silene barbeyana Heldr. ex Boiss.

Collections: Mt Parnassos, c. 6 km N–NNE of Arachova, 2100–2150 m, G 4332 – Mt Giona, 2–2.5 km ESE–E of Sikea, 2200–2450 m, G 3816, G 3952 and G 6962 (ATH) – Mt Vardousia, c. 6 km E–ESE of Artotina, 2100–2300 m, G 3225.

The species is endemic to Mt Parnassos, Mt Giona and Mt Vardousia. It has previously been reported only from the last two mountains (Halácsy 1901). Apart from the collections mentioned above the species has also been observed in abundance in the summit area ot Mt Korax (see under *Achillea barbeyana*) at c. 2450 m.

S. barbeyana is a rare species inhabiting small crevices in almost vertical, often semi-shaded, limestone cliffs above 2100 m. On Mt Parnassos it is associated with *Oxyria digyna* while on Mt Giona it often grows together with *Omphalodes luciliae* and *Saxifraga spruneri*.

Chromosome number : 2n = 24 (G 3816 and G 3952). No previous count.

General distribution: Endemic to Sterea Ellas.

Convolvulaceae

Convolvulus libanoticus Boiss.

Collection: Mt Giona, 6 km SW–SSW of Kaloskopi, c. 2130 m, G 7323 (ATH, C).

New to Sterea Ellas. In Greece previously reported only from Crete (cf. Greuter 1973) and Mt Killini (Halácsy 1902, as *C. radicosus* Heldr. & Sart.).

C. libanoticus is a dwarf, loosely caespitose and hirsute plant with procumbent to ascending stems up to 10 cm (because of grazing it is mostly acaulescent on Mt Giona), lanceolate to narrowly obovate, green leaves with glabrous upper surface and pink corolla with deep purple spots at the base.

It has been found in grazed pastures on bauxite. As this mineral is heavily exploited on Mt Giona, often by strip mining, many localities will soon be destroyed and *C. libanoticus* is therefore threatened with extinction on this mountain.

General distribution: S and SC Greece, Crete and SW Asia.

Crassulaceae

Jovibarba heuffelii (Schott) Á. & D. Löve

Collection: Mt Timfristos, c. 4 km NE of Karpenision, 1950–2100 m, G 4052.

New to Sterea Ellas. A rare species in Greece, previously reported from Macedonia, Mt Olympos and Mt Ossa (Halácsy 1901, Zaganiaris 1940, as *Sempervivum patens* Griseb., Hayek 1927, 1928 as *Sempervivum heuffelii* Schott). It has recently been collected by Aldén on the following mountains in Pindhos: Mt Korouna (A 1998 1/2), Mt Trapos (A 3885) and Mt Katarraxias (A 5286), all unpublished.

On Mt Timfristos it grows in a steep, stony pasture on a SE-facing slope.

General distribution: E Carpathians and the Balkan peninsula (map in Meusel et al. 1965).

Euphorbiaceae

Euphorbia capitulata Reichenb.

Collection: Mt Giona, 3 km E of Sikea, c. 2300 m, G 6996 (ATH).

New to Sterea Ellas. In Greece previously known only from Mt Olympos (e.g. Halácsy (1904).

E. capitulata is a very characteristic species with short more or less procumbent stems and a solitary cyathium.

On Mt Giona it was found on stabilized scree and in crevices at the bottom of a small limestone ravine on the eastern slope of the summit ridge.

General distribution: Balkan peninsula.

Gentianaceae

Gentiana lutea L. ssp. **lutea**

Collections: Mt Giona, 5.5 km SW of Kaloskopi, c. 1900 m, G 7302 – Mt Iti, 6.5 km SSE of Ipati, 1850–1900 m, G 6452.

The following collections can be determined only as *G. lutea* s. lat. (see below): Mt Giona, 2.5 km E of Sikea, c. 2200 m, G 6965 – Mt Vardousia, c. 7 km WNW of Athanasios Diakos, 2000–2200 m, G 7211 – Mt Iti, 5.5 km ENE of Neochorion, c. 2100 m, G 4806.

According to Tutin et al. (1972) *G. lutea* is divided into two subspecies: ssp. *lutea*, with free anthers and ssp. *symphyandra* (Murb.) Hayek in which the anthers are connate in a tube. The latter is distributed in the Balkan peninsula westwards to the SE Alps, while ssp. *lutea* is said to occur in the rest of the distributional area of the species.

G. lutea ssp. *symphyandra* has been reported from the following localities in Greece: Mt Iti (Halácsy 1902), Mt Giona (Quézel & Contandriopoulos 1965 a) and Edessa in Macedonia

(Zaganiaris 1939). From Mt Vermion (Ganiatsas 1939) and Mt Bela Voda (Zaganiaris 1940) *G. lutea* is reported without stating the subspecies. *G. lutea* ssp. *lutea* was recently found for the first time on the Balkan peninsula (Mt Smolikas, Hartvig 1977). Three of my collections (G 4806, G 6965 and G 7211) cannot be determined at subspecies level as only sterile leaf rosettes were found. The other two, G 6452 from Mt Iti and G 7302 from Mt Giona, have flowers with the anthers completely free and thus they also belong to ssp. *lutea*. So far it has not been possible to check whether the previous records of ssp. *symphyandra* from Sterea Ellas have been correctly determined.

On Mt Iti *G. lutea* ssp. *lutea* and *G. lutea* s. lat. grows in abundance on sand and schist in openings in the upper *Abies cephalonica* woodland. On Mt Giona and Mt Vardousia it was found in pastures on stabilized screes and on rock ledges.

General distribution: C and S Europe and Asia Minor.

Linaceae

Linum aroanium Boiss. & Orph.

Collections: Mt Timfristos, 6 km ENE of Karpenision, 1700–1800 m, G 377; c. 5 km NE of Karpenision, 1700–1850 m, G 4095.

New to the area. Mainly a montane species which in Greece has previously been reported from a few mountains on Peloponnisos, Mt Dirphys on Evvoia and S and C Pindhos (Halácsy 1901, Quézel & Contandriopoulos 1965 b). Zaganiaris (1940) reported it from near Katafigi in Macedonia.

L. aroanium was found growing in steep, almost ungrazed pastures on slopes facing N.

Chromosome number: 2n = 36 (G 4095). No previous count.

General distribution: Greece, Turkey, Syria and N Lebanon.

Linum punctatum Presl ssp. **pycnophyllum** (Boiss. & Heldr.) L.-Å. Gustavsson comb. nov.

L. pycnophyllum Boiss. & Heldr. in Boiss., Diagn., Ser. II(1): 97 (1853) – *L. alpinum* Jacq. var. *pycnophyllum* (Boiss. & Heldr.) Boiss., Fl. Or. 1: 865 (1867) – *L. alpinum* Jacq. ssp. *pycnophyllum* (Boiss. & Heldr.) Maire & Petitmengin, Bull. Soc. Sc. Nancy 1908: 199 (1908).

Collections: Mt Iti, c. 5 km E of Neochorion, 1900–2000 m, G 4151 (ATH) and G 4840 b.

New to Sterea Ellas. Outside the area investigated this taxon is known from the following Greek localities: Mt Killini (locus classicus), Mt Chelmos (Bornmüller 1928, Goulimis no. 1949–33 (K), Persson no. 3322 and no. 3511 (GB)), Mt Timphi (Goulimis 1954), Mt Smolikas (Quézel & Contandriopoulos 1965 b, Baldacci no. 1896-227 (K, W), Balls and Balfour Gourlay no. B 3440 (E)) and Mt Grammos (Zaganiaris 1939).

L. punctatum ssp. *punctatum* is endemic to Sicily (early records from N Africa have not been confirmed and no material from that area has been seen).

The Greek plants have obtuse, sometimes shortly acute leaves while those from Sicily are almost consistently acuminate. Sicilian specimens also have more pointed sepals. The size of the seeds has been measured on all available material (5 collections from Sicily and G 4840 b from Greece). The length of the seeds from the Sicilian collections varies between 3.7 and 4.6 mm while the plants from Mt Iti have distinctly longer seeds, 4.9–5.0 mm. Furthermore there is a marked difference in the shape (Fig. 2).

The morphological differences do not justify separating them into two distinct species but nor should all collections be regarded as conspecific as in Tutin et al. (1968). On the basis of morphology and geographical disjunction a treatment at subspecific level seems most reasonable.

In addition to the European material Davis and Polunin found closely related plants in Kurdistan. They have been described as *L. pycnophyllum* Boiss. & Heldr. ssp. *kurdicum* Davis (1957) merely because of the marked geographical disjunction (1800 km). Morphologically the Kurdish material agrees well with that from Greece with the possible exception of the capsule. Davis (1957) reports that the capsule of ssp. *kurdicum* is shorter than that of *L. punctatum,* 5–6 instead of 6–8 mm. This refers to a single collection (Davis 22835) in which the fruits are probably not fully developed. No fruit of any Greek collection agreeing with *L. punctatum* in this character was seen by Davis. As there is little or no morphological difference between the Greek and Kurdish plants the latter should be included within ssp. *pycnophyllum*.

On Mt Iti *L. punctatum* ssp. *pycnophyllum* grows in open schist ground associated with *Astragalus baldaccii, A. creticus* ans *A. parnassi* at 1900–2000 m. In the other Greek localities it has been found between 1650 and 2565 m. One collection from lower altitudes, 1000–1100 m, on Mt Chelmos (Maire & Petitmengin 1906 no. 918) deviates in several respects. More material must be collected before its status can be better understood.

Chromosome number: 2n = 18 (G 4151). No previous count for *L. pycnophyllum*, but for *L. punctatum* the same chromosome number has previously been found (Fedorov 1969).

General distribution: Greece and Kurdistan.

Lythraceae

Lythrum thymifolia L.

Collections: Mt Iti, 7 and 6 km SE–SSE of Ipati, c. 1850 and c. 1950 m, G 1959 and G 7307.

New to Sterea Ellas. An imperfectly known species which has often been confused with *L. hyssopifolia* L. *L. thymifolia* is not mentioned in Halácsy (1901) whereas Hayek (1927) reports it from Thrace, the Ionian Islands, C Greece and Peloponnisos, Kikladhes and Crete. In Tutin et al. (1968) it is mentioned from Greece only with a mark of interrogation.

The specimens found on Mt Iti can be up to 5 cm high. They have 4-merous flowers with (1–)2(–3) stamens and leaves c. 1 mm broad. The species grows in abundance in small melt-water pools.

General distribution: S Europe eastwards to Turkestan and Siberia; Algeria.

Onagraceae

Epilobium anagallidifolium Lam.

Collection: Mt Vardousia, c. 3 km SW–WSW of Athanasios Diakos, 2050–2200 m, G 3746.

New to Sterea Ellas. This arctic-alpine species is previously known only from one locality in Greece, viz. Mt Kajmakčalan (Rechinger 1936).

On Mt Vardousia it was found on N–NE-facing moss-covered cliff ledges kept damp by seepage water. Apart from the above-mentioned collection the species has also been observed in two adjacent localities.

General distribution: Eurasia and N America (map in Hultén 1958).

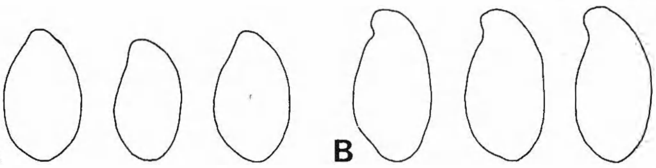

Fig. 2. Seeds of *Linum punctatum*. – A: ssp. *punctatum*. – B: ssp. *pycnophyllum*.

Plantaginaceae

Plantago reniformis G. Beck

Collection: Mt Timfristos, 4 km N of Karpenision, 1800–1900 m, G 6158 (ATH, C).

New to Greece. The nearest localities are in N Albania.

The plants from Mt Timfristos agree well morphologically with specimens seen from outside Greece.

P. reniformis grows on Mt Timfristos in wet pastures close to springs and along rivulets in a limited area on a N-facing slope.

General distribution: SW Jugoslavia, N Albania and SC Greece.

Polygonaceae

Oxyria digyna (L.) Hill

Collections: Mt Parnassos, c. 6 km N–NNE of Arachova, 2100–2150 m, G 4334 (ATH) – Mt Vardousia, 3.5 km SW–WSW of Athanasios Diakos, 2100–2200 m, G 7239.

New to Sterea Ellas. *Oxyria digyna* is one of the few arctic-alpine species occurring in Sterea Ellas. It is very rare in Greece and has previously been reported only from Mt Smolikas (Halácsy 1901, Quézel & Contandriopoulos 1965 b). It is not mentioned from Greece in Tutin et al. (1964). In addition to the localities given above it has also been observed on Mt Parnassos, 6 km NE–NNE of Arachova at c. 2300 m.

In Sterea Ellas *O. digyna* grows on shaded, N–NE-facing rock ledges kept damp by seepage water.

Chromosome number: 2n = 14 (G 4334), which agrees with previous counts (Fedorov 1969).

General distribution: Eurasia, Greenland and N America (map in Meusel et al. 1965).

Rumex kerneri Borbás

Collections: Mt Giona, 5 km E of Sikea, c. 1950 m, G 6838 – Mt Iti, 7 km SSE of Ipati, c. 1800 m, G 1856; 6.5 km SSE of Ipati, 1850–1900 m, G 6518 and G 7312 – Mt Yiorla, 3 km W–WSW of Lampirion, c. 1750 m, G 5929 – Mt Timfristos, 5 km NE of Karpenision, c. 1900 m, G 6079 (det. K. H. Rechinger).

New to the area. The species has previously been reported from only a few localities in N and C Greece (Rechinger 1933, 1939), but as *R. kerneri* in most older floras was not distinguished from the closely related *R. patientia* L. some records of the latter, i.e. from Mt Giona by Maire & Petitmengin (1907) and Quézel & Contandriopoulos (1965 a), may be referable to *R. kerneri*. Aldén has collected the species at Katara (A 1399), between Mt Boustagani and Mt Boutaia (A 3230), on Mt Plastaria (A 4253), Mt Kouziakas (A 1575) and Mt Karava (A 4348) in Pindhos, all unpublished.

In Sterea Ellas it has been found mainly in damp subalpine pastures.

Chromosome number: 2n = 80 (G 1856). No previous count. For *R. patientia* 2n = 40 and 2n = 60 have been reported (Fedorov 1969).

General distribution: From Hungary and Romania southwards to SC Greece (map in Rechinger 1933).

Rumex obtusifolius L.

Collection: Mt Oxia, 6 km SSW of Gardikion, 1750–1850 m, G 6367 (det. K. H. Rechinger).

New to the area. Outside the mountains investigated the species is reported from a few localities on the Greek mainland, Peloponnisos and some of the islands (Halácsy 1904, Rechinger 1932, 1939, 1943, Hayek 1928, Zaganiaris 1939, 1940, Kitanov 1945). In Pindhos it has recently been collected by Aldén between Mt Trapos and Mt Peristeri (A 3919), on Mt Katarraxias (A 5362) and Mt Kakarditsa (A 3775), all unpublished.

R. obtusifolius in mainly a lowland to montane species but on Mt Oxia it grows in damp subalpine pastures.

General distribution (*R. obtusifolius* s. lat.): Europe and W Asia; introduced in E Asia, N and S America, S Africa and Australia (Rechinger 1949). In Hess et al. (1967) it is also reported from NW Africa (map in Rechinger 1932 p. 131).

Rumex scutatus L.

Collections: Mt Vardousia, c. 5.5 km NNE of Dafnos, 2100–2300 m, G 2996; 5 km NNE of Dafnos, c. 2000 m, G 3023; c. 7 km W of Athanasios Diakos, c. 2000 m, G 3607.

New to the area. The species is not common in Greece but is known from localities both N and S of the area and the islands of Milos and Samothraki (e.g. Halácsy 1904, Rechinger 1943, Quézel & Contandriopoulos 1965 b).

R. scutatus was found on stony ground, on rock ledges and on screes.

General distribution: C and S Europe eastwards to Caucasus and N Iran; NW Africa (map in Meusel et al. 1965).

Ranunculaceae

Actaea spicata L.

Collection: Mt Giona, 8 km NW–WNW of Prosilion, c. 1840 m, G 6982 (ATH).

New to Sterea Ellas. In Greece previously known from mountains in Pindhos (Aldén 1976), Mt Peristeri and Mt Timphi (Quézel & Contandriopoulos 1965 b, Mt Vermion (Quézel & Contandriopoulos 1968), Mt Olympos (Hayek 1928), Mt Bela Voda (Quézel 1969), Mt Cholomon on Chalkidhiki (Zaganiaris 1939), Mt Lailias (Voliotis 1976), Mt Falakron (Kitanov 1943) and it has been reported once from Peloponnisos by Sibthorp (in Halácsy 1901).

A. spicata was found at the bottom of a deep doline with precipitous walls near the katafigion on Mt Giona.

General distribution: Temperate Eurasia (map in Meusel et al. 1965).

Delphinium fissum Waldst. & Kit.

Collections: Mt Giona, 8 km WNW of Prosilion, c. 1900 m, G 7283 – Mt Vardousia, 3 km W of Athanasios Diakos, c. 1750 m, G 7252 (ATH) – Mt Chelidon, 3.5 km W of Mikro Chorio, 1700–1850 m, G 5401 – Mt Kaliakouda, c. 3.5 km SE of Megalo Chorio, 1800–1850 m, G 2861 (C) – Mt Timfristos, 5 km NE of Karpenision, 1700–1900 m, G 6097.

New to Sterea Ellas. The first Greek locality, Mt Chortiatis near Thessaloniki, was reported by Regel (1941). It has since been recorded from a few other localities by Goulimis (1954, 1956), viz. Mt Chelmos, Mt Timphi, Mt Athos and Mt Falakron.

My plants of this polymorphic species have the following morphology with regard to the most variable characters: Stem glabrous below, densely pubescent with golden-yellow to white hairs above. Leaf segments linear to linear-lanceolate. Lower bracts trisect or entire and linear like the upper ones, pubescent. Flowers patent-pubescent, spur more or less horizontal. Follicles densely pubescent.

In Sterea Ellas *D. fissum* has been found in stony pastures between 1700 and 1900 m.

General distribution: S Europe from France to C Ukraine.

Myosurus minimus L.

Collection: Mt Iti, 6 km SE–SSE of Ipati, c. 1950 m, G 4736 and G 6588.

New to Sterea Ellas. Apparently a very rare species in Greece, formerly reported by Hayek (1927) as occurring in Macedonia and Thrace. No exact Greek locality is known to me.

On Mt Iti it grows in a small melt-water pool associated with *Limosella aquatica, Lythrum thymifolia* and *Veronica oetaea*.

Chromosome number: $2n = 16$ (G 6588), which agrees with most previous counts. $2n \approx 28$ has also been reported (Fedorov 1969).

General distribution: Most of Europe eastwards to C Siberia; on Cyprus, in Syria, Iran, NW Africa and N America; introduced in Australia (map in Meusel et al. 1965).

Ranunculus brutius Ten.

Collection: Mt Iti, 6 km NNW of Pavliani, 1660–1700 m, G 4858 (C).

New to Sterea Ellas. *R. brutius* is very rare in Greece. Only three localities have previously been reported: Mt Kyllene, Mt Mikrigura in Pindhos and Siatista in Macedonia (Halácsy 1901, Zaganiaris 1939).

On Mt Iti it was found growing in rather damp *Abies* woodland.

General distribution: Italy, Balkan peninsula, Anatolia, Caucasus and N Iran.

Ranunculus ficaria L.

Collection: Mt Timfristos, 3 km NNE of Karpenision, c. 1800 m, G 5104.

The species has not previously been reported from the mountains investigated but otherwise scattered localities are known all over the Greek mainland and on many islands (e.g. Halácsy 1901, Rechinger 1943).

It is a predominantly lowland to montane species, but on Mt Timfristos it occurs in subalpine pastures far above the present timberline.

General distribution: Most of Europe eastwards to W Siberia and C Asia; N Africa; introduced in N America (map in Meusel et al. 1965).

Ranunculus ficarioides Bory & Chaub.

Collection: Mt Vardousia, 5.5 km W of Athanasios Diakos, c. 1600 m, G 4957 (ATH, C).

New to Sterea Ellas. In Greece previously reported from Mt Kalilimni on Karpathos (Rechinger 1943) and mountains on Peloponnisos, viz. Mt Taygetos, Mt Killini, Mt Chelmos and Mt Panachaicon (Halácsy 1901). The occurrence on Karpathos is of phytogeographical interest in that it links the Greek localities and those of Asia.

It is a distinct species separated from *R. ficaria* on the deeply crenate and cordate leaves.

R. ficarioides was found on damp, stony ground by a rivulet.

General distribution: S and SC Greece, Karpathos, Anatolia, Lebanon and Transcaucasia (map in Meusel et al. 1965).

Trollius europaeus L.

Collection: Mt Iti, 7.5 km SSE of Ipati, c. 1800 m, G 1808.

New to Greece. In 1977 it was collected by Hartvig et al. on Mt Smolikas at c. 1450 m (Hartvig et al. 7361, unpublished).

The specimens from Mt Iti has 5-lobed leaves, with the lobes themselves lobed and with acute-serrate margins. The follicles are 8–10 mm long with a beak 1–1.5 mm long.

T. europaeus was found in a damp pasture by a spring.

Chromosome number: 2n = 16 (G 1808), which agrees with previous counts (Fedorov 1969).

General distribution: Temperate Eurasia (map in Meusel et al. 1965).

Rosaceae

Geum heterocarpum Boiss.

Collection: Mt Vardousia, 6 km WNW of Athanasios Diakos, c. 1850 m, G 4950 (C).

New to Greece. The nearest locality is in Albania.

G. heterocarpum belongs to subgen. *Orthostylus* (Fisch. & C. A. Meyer) F. Bolle. Gajewski (1957) split Bolle's subgenus into two new subgenera and placed *G. heterocarpum* in subgen. *Orthurus* (Juz.) Gaj. which, however, is an illegitimate name. He later used the name *Orthostylus* in Tutin et al. (1968) where, however, this subgenus is wrongly characterized: "Style long, persistent in its entirety, the distal part with stiff, deflexed bristles." In all material available to me the distal part of the style is deciduous, glabrous or with long, soft, ascending hairs. The proximal part of the style is covered with stiff, deflexed hairs at the apex but is glabrous in the basal part (cf. Gajewski 1957).

The plants from Mt Vardousia have the following morphology: Whole plant hairy. Stems 20–30 cm long. Basal leaves 2–4-pinnate, the terminal leaflets 3–5-lobed, c. 3 × 3–4 × 4 cm, more or less cordate at base. Inflorescence 3–7-flowered with 1–3 cymes. Calyx lobes 9–12 mm and epicalyx lobes 5–8 mm, both linear to lanceolate. Petals obovate-cuneate, pale yellow, 1/2–2/3 as long as calyx lobes. Achenes 9–15. Style as described above.

On Mt Vardousia *G. heterocarpum* was found on moist, stony ground on a W-facing slope, just above the timber-line.

General distribution: *G. heterocarpum* has a remarkable distribution which is more or less continuous from SE Spain to NW Africa and from Anatolia and Syria eastwards to Tien-Shan. Between these areas isolated localities are known in SE France, C. Italy, Albania and SC Greece (map in Gajewski 1957 p. 77).

Potentilla kionaea Halácsy

Collections: Mt Giona, 4 km ENE of Lefkaditiοn, c. 2350 m, G 2040 (C); 2 km SE and 2.5 km E of Sikea, 2350–2400 and c. 2450 m, G 3962 (seed collection) and G 6997; 4 km SW–SSW of Kaloskopi, c. 2050 m, G 7334 (ATH).

The species is endemic to Mt Giona. In addition to the original collection it has been reported again by Maire & Petitmengin (1907) and Quézel & Contandriopoulos (1965 a) as ssp. *kionaea* (Hal.) Maire & Petitmengin of *P. apennina* Ten.

The species seems to be restricted to altitudes above 2000 m. Outside the summit ridge, where it is fairly abundant in rock crevices and among blocks and stones of hard limestone especially from c. 2300 m to the summit, it has been observed in only one locality (G 7334).

Chromosome number: 2n = 14 (G 3962). No previous count.

General distribution: Endemic to Mt Giona.

Saxifragaceae

Saxifraga exarata Vill.

Collection: Mt Iti, 6 km SE–SSE of Ipati, 1850–1950 m, G 6551 (ATH, C).

New to the area. Halácsy (1901) reported *S. exarata* from Mt Olenos, Mt Killini, Mt Dirphys, Mt Olympos and Mt Smolikas, Maire & Petitmengin (1908) from Mt Chelmos, Zaganiaris (1940) from Mt Grammos, Beauverd (1941) from Mt Kajmakčalan (as *S. adenophora* C. Koch var. *Humbertiana* Bvrd.) and Quézel & Contandriopoulos (1968) from Mt Bela Voda and Mt Falakron. The closely related *S. moschata* Wulfen was reported from Mt Falakron by Kitanov (1945) and from Mt Olympos by Stojanov & Jordanov (1938). Plants collected on these mountains by Strid (pers. comm.) and by me on Mt Falakron (G 109) also agree with *S. moschata*. This species is best separated from *S. exarata* on the dull yellow or cream-coloured petals. Halácsy (1901) and Hayek (1927) did not mention *S. moschata* from Greece but as both species occur in the country and they are difficult to determine all Greek collections should be controlled.

S. exarata is morphologically very variable. Intraspecific taxa have been distinguished. The plants from Mt Iti have fairly densely imbricate leaves 8–14 mm long with 3–5 lobes. The petals are white, 4.5–5.5 mm long and 2–2.5 times longer than the sepals. My plants combine the leaf size of var. *exarata* with flower characters

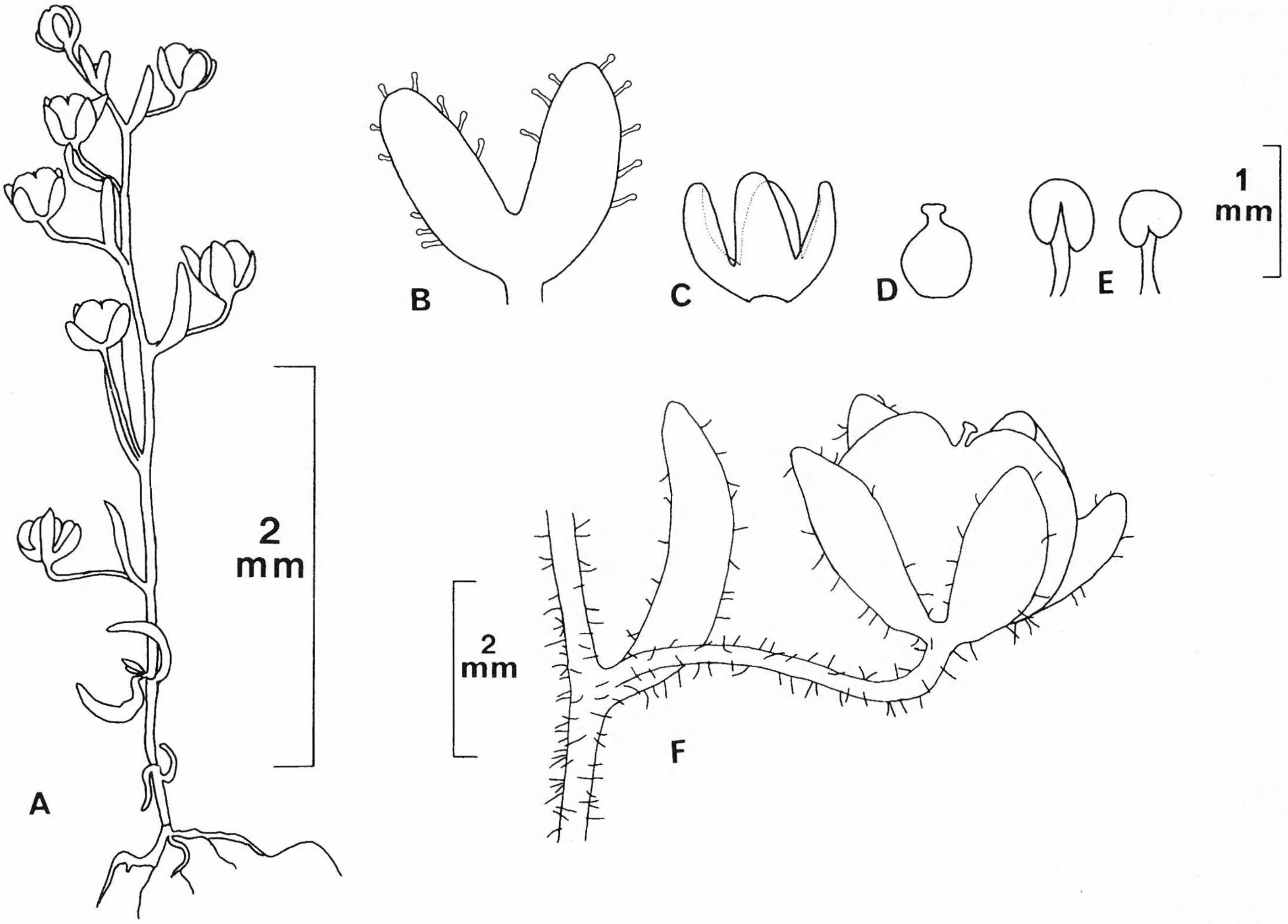

Fig. 3. *Veronica oetaea*. – A: Habit. – B: 2 sepals. – C: Corolla. – D: Young gynoecium. – E: Stamens. – F: Mature capsule. – A, F: Gustavsson 7305. – B–E: Gustavsson 4737 (at anthesis).

of var. *adenophora* (C. Koch) Engler & Irmscher according to Davis (1972). Hayek (1927) places all Greek material within ssp. *adenophora* (C. Koch) Hayek.

On Mt Iti *S. exarata* grows on damp N-facing cliff ledges and in crevices of hard limestone.

General distribution: S & C Europe, Turkey, Caucasus and N Iran (map in Meusel et al. 1965).

Scrophulariaceae

Limosella aquatica L.

Collection: Mt Iti, 6 km SE–SSE of Ipati, c. 1950 m, G 6590.

New to Sterea Ellas. The species has only recently been found in Greece. It was first reported from Mt Timphi by Quézel & Contandriopoulos (1965 b) both as *L. aquatica* and *L. tenella* Quézel & Contandr. It has since also been found on Mt Karava by Aldén (1976) and on Mt Annitsa, SW of Mt Smolikas by Hartvig et al. (no. 5205, unpublished). On the status of *L. tenella* see Aldén (1976).

The specimens found on Mt Iti have long-petiolate and spathulate to short-petiolate and linear leaves.

On Mt Iti *L. aquatica* grows in a small melt-water pool together with *Lythrum thymifolia*, *Myosurus minimus* and *Veronica oetaea*.

General distribution: Eurasia, N Africa, Greenland and N America (map in Hultén 1958).

Verbascum reiseri Halácsy

Collections: Mt Vardousia, 5 km NNE of Dafnos, c. 2000 m, G 3020 and G 3169; c. 6 km E–ESE of Artotina, 2050–2150 m, G 3197; 7 km W of Athanasios Diakos, c. 1950 m, G 3633.

Apart from the type description of this Vardousian endemic no other report is known to me.

It grows mainly in stony pastures and on stabilized screes between 1900 and 2450 m. It is scattered throughout most parts of the Vardousia massif but never occurs in great numbers.

Chromosome number: 2n = 32 (G 3633). No previous count.

General distribution: Endemic to Mt Vardousia.

Veronica oetaea L.-Å. Gustavsson sp. nov. – Fig. 3.

Collections: Greece, Phthiotis: Mt Iti, 6 km SE–SSE of Ipati, in a small melt-water pool, c. 1950 m, 25.7.1976, G 7305 (LD holotype; ATH, G, UPA, W isotypes); do, G 4737 (LD) and G 6589 (LD).

Herba annua, glanduloso-pubescens. Caulis erectus, 1–5 cm altus, simplex vel ramo solitario basali provisus. Folia integra, sessilia, anguste ovata ad lanceolata, ad 6,7 mm longa, 1,9 mm lata, pubescentia. Inflorescentia racemosa, 1–11-flora. Bracteae lanceolatae ad lineari-lanceolatae, ad 6,1 mm longae, 1,1 mm latae, glanduloso-pubescentes. Pedicelli ad 6 mm, bracteis aequilongi vel leviter longiores vel breviores, patentes ad erecto-patentes, in statu maturali saepe sub capsula sursum distincte curvati, glanduloso-pubescentes. Segmenta calycis ovata ad elliptica, capsula aequilonga vel breviora, 1,6–2,9 mm longa, 0,7–1,4 mm lata, sparse glandulosa. Corolla c. 1 mm longa, ad 4/5 divisa, tubo latiore quam longo, colore ignoto (verisimiliter pallido). Capsula sparse glandulosa, compressa, 1,8–2,6 mm longa et 1,8–3,1 mm lata, ut longa quam lata vel brevior quam lata, sinu acute-anguloso, 1/8–1/5 longitudinis capsulae. Stylus 0,2–0,4 mm longus, sinu paullo brevior vel aequilongus. Semina plerumque 40–60 pro capsula, elliptica ad ovata, 0,5–0,6 × 0,3–0,4 mm, pro ratione crassa, laevia ad leviter tuberculata, dorso convexo, superficie chalazali plana, chalaza centrali.

Glandular-pubescent annual. *Stems* 1–5 cm, erect, simple or rarely with one basal branch. *Leaves* entire, sessile, narrowly ovate to lanceolate, up to 6.7 × 1.9 mm, pubescent. *Inflorescence* racemose with 1–11 flowers. *Bracts* lanceolate to linear-lanceolate, up to 6.1 × 1.1 mm, glandular-pubescent. *Pedicels* up to 6 mm, equalling or slightly shorter or longer than bracts, patent to erecto-patent, when mature often distinctly curved upwards below the capsule, glandular-pubescent. *Calyx* segments ovate to elliptic, shorter to equalling capsule, 1.6–2.9 × 0.7–1.4 mm, sparsely glandular-hairy. *Corolla* c. 1 mm long, divided to c. 4/5, tube wider than long, colour not known (probably pale). *Capsule* with few glandular hairs, compressed, 1.8–2.6 mm long and 1.8–3.1 mm broad, as long as to shorter than broad, sinus acute-angled, 1/8–1/5 as long as the capsule. *Style* 0.2–0.4 mm, slightly shorter than to equalling sinus. *Seeds* mainly 40–60 per capsule, elliptic to ovate 0.5–0.6 × 0.3–0.4 mm, relatively thick, smooth to slightly tuberculate with convex back, flat chalazal face and central chalaza.

V. oetaea belongs to subsection *Acinifolia* (Römpp) Stroh of section *Alsinebe* (Griseb.) Lehmann in Stroh (1942) or section *Pocilla* Dumort in Tutin et al. (1972). Only two of the species belonging to subsect. *Acinifolia* occur in Europe. *V. acinifolia* L. is widespread in S, SC and W Europe while the recently described *V. bozakmanii* M. Fischer is known from a single locality in C Pindhos (Katara near Metsovo). All the other species of the subsection are distributed in Asia (cf. Fischer 1972).

V. oetaea is very characteristic. It deviates from all other species of the subsection in a number of respects: absence of crispate hairs, smaller capsule with different shape and shallow sinus with an acuter angle and many more much smaller seeds per capsule. Its closest affinity is probably with *V. glaberrima* Boiss. & Bal., *V. hispidula* Boiss. & Huet and *V. nudicaulis* Kar. & Kir. They are dwarf, alpine species occurring in the Taurus Mountains in Turkey, in Lebanon and Armenia eastwards to Pakistan.

V. oetaea was found at the bottom of two small melt-water pools on Mt Iti, at c. 1950 and 1850 m respectively. The plants had already reached anthesis while there was still water in the pools. Associated species in the first pool were *Limosella aquatica*, *Lythrum thymifolia* and *Myosurus minimus* (Fig. 4). In the lower locality it grew together with *Lythrum portula (Peplis portula)*, *L. thymifolia*, *Myosurus minimus* and *Ranunculus lateriflorus*.

In recent years roads have been built only a few metres from both pools and this may influence water conditions. The slopes near the upper pool are rich in bauxite, which in Greece is subject to heavy exploitation often by strip mining. If this was the reason for making the roads the locality will very soon be destroyed.

General distribution: Endemic to Mt Iti.

Veronica praecox All.

Collections: Mt Kokkinari, 6 km WSW of Amfissa, 1850–1910 m, G 5780 – Mt Giona, 6 km NE–NNE of Lidorikion, 1750–1900 m, G 869; 6 km ENE of

Fig. 4. Mt Iti: Dried-up melt-water pool with *Limosella aquatica*, *Lythrum thymifolia*, *Myosurus minimus* and *Veronica oetaea*.

Lidorikion, c. 1750 m, G 4525 – Mt Iti, 4–4.5 km E–ESE of Neochorion, 2000–2050 m, G 6661.

New to Sterea Ellas. Only a few previous localities from N to C Greece, Thasos, Corfu and Crete are known to me (Halácsy 1902, Zaganiaris 1940, Rechinger 1943).

V. praecox grows in dry, stony places up to 2050 m.

Chromosome number: 2n = 18 (G 869), which agrees with previous counts (Fedorov 1969, Fischer 1969).

General distribution: S, C and W Europe, extending northwards locally to SE Sweden; Anatolia, Caucasus and NW Africa.

Veronica verna L.

Collections: Mt Kokkinari, 6 km WSW of Amfissa, c. 1900 m, G 5630 and G 5665 – Mt Giona, 6 km NE–NNE of Lidorikion, 1750–1900 m, G 865; c. 2.5 km ESE of Sikea, c. 2400 m, G 3870; 6 km ENE of Lidorikion, c. 1750 m, G 4524 – Mt Vardousia, 6 km WSW of Athanasios Diakos, c. 2000 m, G 1459; 5 km NNE of Dafnos, c. 2000 m, G 2961; 3.5 km W of Athanasios Diakos, c. 1750 m, G 4881; 4 km W of Athanasios Diakos, c. 1850 m, G 4906 – Mt Iti, 7 km SSE of Ipati, c. 1950 m, G 4712; 5.5 km SSE of Ipati, 1850–1900 m, G 4768; 5 km SSE of Ipati, c. 1900 m, G 4796 – Mt Oxia, 7 km SSW of Gardikion, 1800–1900 m, G 5489 and G 6208; 6 km SSW of Gardikion, c. 1900 m, G 6363 – Mt Yiorla, 3 km W–WSW of Lampirion, 1800–1850 m, G 6012 – Mt Chelidon, c. 3.5 km W of Mikro Chorio, 1725–1900 m, G 2545; do, c. 1900 m, G 5326 – Mt Kaliakouda, 3.5 km SSE of Megalo Chorio, c. 1800 m, G 5251; 3.5 km SE–SSE of Megalo Chorio, 2050–2100 m, G 5266 – Mt Timfristos, 3.5 km NNW of Karpenision, 2000–2100 m, G 4107.

New to Sterea Ellas. Certainly an overlooked species in many parts of Greece. A few scattered localities from Peloponnisos in the S to Mt Falakron in the N and the islands of Corfu and Samothraki have been recorded (Halácsy 1902, Rechinger 1939, 1943, Zaganiaris 1940, Kitanov 1943). Aldén has collected the species on Mt Tringia (A 283, A 365 and A 426), Mt Spilea (A 2885), Mt Karava (A 972) and Mt Kazarma (A 656) in Pindhos, all unpublished.

In Sterea Ellas the species is fairly common in dry, stony places up to 2400 m. It has been found on all mountains visited except on Mt Parnassos.

Chromosome number: 2n = 16 (G 865), which agrees with one of the two previously reported counts (Fedorov 1969). Fischer (1969) reported 2n = 14.

General distribution: Most of Europe, W and C Asia and NW Africa; introduced in N America.

Violaceae

Viola poetica Boiss. & Spruner

Collections: Mt Parnassos, 6.5 and 7 km NNE of Arachova, 2300–2457 m, G 531 and G 561; 6 km SW of Titorea, 2100–2140 m, G 763 – Mt Giona, 3 km E of Lefkadition, c. 2150 m, G 1053; 7 km NE–NNE of Lidorikion, c. 1900 m, G 1114; 2.5 km ESE of Sikea, c. 2450 m, G 3830 (seed collection) – Mt Vardousia, c. 6 km E–ESE of Artotina, 2100–2300 m, G 3236; c. 5.5 km NNE of Dafnos, 2100–2300 m, G 2995 – Mt Iti, 4 km E of Neochorion, 1950–2000 m, G 4841.

This charming violet has been collected by several botanists on Mt Parnassos, Mt Giona and Mt Vardousia while the locality on Mt Iti is new. *V. poetica* is endemic to these mountains.

It is scattered and not uncommon in hard limestone crevices at 1900–2500 m.

Chromosome number: 2n = 12 (G 3830). No previous count.

General distribution: Endemic to Sterea Ellas.

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Typification of Atriplex alaskensis

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Gustafsson, M.: 1978 03 31: Typification of Atriplex alaskensis. *Bot. Notiser 131:* 26. Stockholm. ISSN 0006-8195.

Atriplex alaskensis S. Wats., an annual hexaploid belonging to the section *Teutliopsis* Dumort., is typified.

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Atriplex alaskensis S. Watson

Proc. Am. Acad. 9 p. 108 (1874). – *A. patula* L. ssp. *alaskensis* (S. Wats.) Hall & Clements 1923 p. 253. – Original material: Alaska, Barlows Cove, Kellogg 176, sheet no. 48457 (US lectotype, US, GH isotypes).

The halophytic species *Atriplex alaskensis* S. Wats. is distributed along the coasts of the NW parts of N America, from British Columbia to the Aleutians (Hultén 1968). It is one of the very few hexaploid species in sect. *Teutliopsis* Dumort. (Bassett & Crompton 1973) and like all the others it is monoecious and annual. *A. alaskensis* seems to be most closely related to the diploids *A. glabriuscula* Edmondst. and *A. franktonii* Tasch., as indicated by the spongy basal inner layer of the bracteoles, the rather large, mostly dull-brownish seeds and by the laterally-situated, erect radicle. *A. alaskensis* is well isolated geographically from the two other species. No typification of the species has been made, although it has been discussed by Hall & Clements (1923), Hultén (1968) and Bassett & Crompton (1973). From the two sheets present at US representing material seen by Watson, no. 48457 is here selected as lectotype.

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The biology of Pippenalia delphinifolia (Compositae)

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Correa, S. & Pippen, R. W. 1978 03 31: The biology of Pippenalia delphinifolia (Compositae). *Bot. Notiser 131:* 27–30. Stockholm. ISSN 0006-8195.

Pippenalia delphinifolia (Rydb.) McVaugh is endemic to a portion of the Pine Oak zone of the Sierra Madre Occidental of western Mexico in a region phytogeographically known as Nueva Galicia. Populations are comprised of small groups of c. 15–20 individuals. The species exhibits low seed productivity although large amounts of pollen grains per anther and ovules per capitulum are formed. The chromosome number, n = c. 30, is reported.

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Pippenalia delphinifolia (Rydb.) McVaugh (Compositae) is a little known and poorly understood plant with large delphinium-like basal leaves and bright yellow flower heads much like those of a sunflower. It is endemic to a restricted region of western Mexico (Fig. 1) where it occurs in usually locally abundant populations in the herbaceous layer of some high elevation oak communities in the Pine-Oak forest zone. This study is an attempt to gain some insight into the life history and general ecology of this species. Essentially nothing is known about this plant except its taxonomic description (Rydberg 1924, McVaugh 1972 b). Apparently this plant has evolved as a single species within the genus and there are no closely related genera. Robinson & Brettell (1973 a, b) treated the genus *Pippenalia* in the 'Cacalioid' complex of the tribe Senecioneae. Nordenstam, according to Keil & Stuessy (1977) considers the genus more closely allied to *Senecio*. The chromosome number of n = c. 30 reported here and confirmed by Keil & Stuessy (1977) certainly would strengthen the position of *Pippenalia* within the tribe Senecioneae but the reported meiotic irregularities and variable fertility data would support the possibility of a hybrid origin.

Material and methods

Three populations of *Pippenalia delphinifolia* were studied by the senior author in the field during the summers of 1975 and 1976. Herbarium specimens, material for cytological studies and living rootstocks were collected. Morphological and floral biology studies were made in the laboratory from a total of 98 herbarium specimens collected by the senior author. Chromosome numbers were obtained by the standard acetocarmine squash technique of pollen mother cells fixed in Newcomer's solution from individuals in two populations. Voucher specimens are indicated by an (*) in the following list of collections. Pollen for stainability was stained with acetocarmine. Voucher specimens are indicated with (**) in the following list of collections. Leaf clearings in NaOH, stained with aniline blue were made to observe the internal anatomy of the leaves. Plants growing in association with *P. delphinifolia* were collected and identified. Specimens collected by the senior author are deposited in the Hanes Herbarium of Western Michigan University (WMU).

Collections. Aguascalientes, Sierra del Laurel SW of Calvillo: Correa 1, 18.7.1975 (WMU)**; Correa 2, 4.8.1975 (WMU); Correa 4, 29.7.1975 (WMU); Correa 5, 29.7.1975 (WMU); Correa 186, 25.7.1976 (WMU); Correa 194a, 4.7.1976 (WMU)*; McVaugh 18427, 26–28.8.1960 (MICH) – Durango, E of La Ciudad: Roberts and Keil 10289, 27.6.1974 (MICH) – Jalisco, Las Vidrieras, Rzedowski 26183, 1.9.1969 (MICH) – Cerro Viejo near Cujutlan: Rzedowski 27565, 16.8. 1970 (MICH); Diaz-Luna 1857, 9.8.1970 (MICH) – Zacatecas, Near Palos Altos, on Sierra de Cicacalco: Correa 191, 23.7.1976 (WMU); Correa 194b, 7.1976

(WMU) – Sierra de Morones along the Jalpa–Tlaltenango road: Correa 3, 22.7.1975 (WMU)**; Correa 26, 22.7.1975 (WMU)**; Correa 189, 20.8.1976 (WMU); Correa 190, 23.7.1976 (WMU); Correa 192, 20.8.1976 (WMU); Correa 188, 20.8.1976 (WMU); 193, 27.7.1976 (WMU)*; Correa 195, 24.7.1976 (WMU); McVaugh 25633, 23.12.1970 (MICH); Rzedowski & McVaugh 978, 21–23.10.1973 (WMU) – Sierra de los Huicholes, SW of San Juan Capistrano; McVaugh 25741, 12–13.1.1975 (MICH), Rose 2390, 19.8.1897 (GH, US).

Geographic locations and habitat description

Pippenalia delphinifolia is endemic to a relatively small portion of the Pine-Oak zone in the highlands of the Sierra Madre Occidental in western Mexico. It is essentially part of the novo-galician flora (McVaugh 1972 a) but it transcends the northern border of Nueva Galicia into Chihuahua, Zacatecas and Durango. The mountains of the Sierra Madre Occidental primarily originated from the Middle and Upper Cenozoic and are composed of rhyolites, andesites and basaltic forms; other metamorphic rocks like acid extrusive formations are also prominent (CETENAL 1974). Generally the Pine-oak forests of these mountains form an extensive and very heterogeneous group of vegetational associations and the following habitat description pertains only to those areas where *P. delphinifolia* has been collected.

Altitude and area. The upper and lower limits of *P. delphinifolia* are respectively 3000 m and 2450 m. However, the majority of the sites are above 2650 m. The northern limit is near La Ciudad, Durango; represented by a young specimen collected by Keil and Roberts. This location is about 200 km north of any other known site for this taxon. The highland forests of the coastal side of Sierra Madre Occidental should form the western limit because of the altitude and vegetational composition, although no collections have been reported from there.

Substratum. The soils of this area are generally of red clay and classified as mostly eutric regasols, cambisols and occasionally chromic luvisols (CETENAL 1974) with the soil texture ranging from medium to fine. The upper 50 cm layer is usually lithic having boulders of a diameter greater than 7 cm on or near the surface which ordinarily is covered with 1–1.5 dm humus layer. Soils are shallow ranging from slightly acidic to neutral. For the most part the soils are well drained; occasionally, however, when there is a pronounced slope, the horizons are thinner and at times there is a partial exposure of the soil profile facilitating erosion. Commonly, *P. delphinifolia* is found in very irregular terrain; occurring in greater numbers on steep forested slopes, rocky hills, mountain sides and ravines. It is found much less frequently on flatlands but never in open areas.

Climate. The climate is typical of that found in most of Meso-america where there are essentially alternating wet and dry seasons. In this area over 90 percent of the rain occurs between the months of May and October; followed by a 5–8 months interval of almost no precipitation. The total rainfall may range from 400 mm to 1500 mm annually (Rzedowski & McVaugh 1966), however, most of the regions accumulate more than 1000 mm a year. The rain usually comes in brief, sudden and torrential showers occurring generally in the afternoons. The temperature ranges between 5° and 25°C. (Rzedowski & McVaugh 1966) with minimal temperatures always greater than 0°C; the lowest temperatures occur in January while the highest readings are reached in May or June, just prior to the rainy season.

General description of the forest. The forest is 10–15 m tall but at times the canopy can be as low as 8 m. It is composed mainly of three basic formations: pine stands, oak stands and mixed pine-oak stands. The majority of the stands are mixed and most of these intermediate conditions are oak dominated with various degrees of intensity although there are stands composed almost entirely of *Arctostaphylos* species. The following species of trees (in decreasing order of abundance) are usually found in the forest communities where *Pippenalia delphinifolia* occurs: *Quercus rugosa, Q. resinosa, Q. crassifolia, Q. coccolobifolia, Q. candicans, Q. castanea.* Present to a much lesser extent are: *Arctostaphylos pungens, Pinus lumholtzii, Pinus* sp. and *Prunus serotina.*

Many species occur in the ground cover stratum of the forest with various degrees of intensity depending upon the composition of the arboreal stratum. This layer is herbaceous, rarely shrubby, and about 30 cm tall. A relatively more herbaceous component is found primarily under the stands of shorter trees and stands of mixed tree species, while under the almost pure or pure oak stands *P. delphinifolia* appears to be the most common and more abundant form of the herbaceous stratum. Some herbaceous species tend to be more frequent under a particular type of stand than under others. The following species are the most common components of the herbaceous layer: *Asclepias linaria, Tradescantia crassiflora, Tagetes lucida, Salvia heterotrichia, Oxalis decaphylla, Geranium* sp., *Pinguicula* sp., *Psacalium megaphyllum, Cologonia angustifolia, Castilleja* sp. and *Commelina* spp.

Occasionally there are small clearings where grasses are dominant separating woodland areas and they are possibly the result of natural fire or human disturbance. On these scattered clearings *P. delphinifolia* is never present. Besides several species of grasses the following species are frequent: *Aneilema* sp., *Oxalis decaphylla, Bessera* sp., *Milla biflora, Odontotrichum amplum, Salvia heterotrichia* and *Asclepias curassavica*.

Population biology

Each of the populations of *Pippenalia delphinifolia* visited occupied an area of about 8–10 km^2 throughout pine-oak forests. In a given forest the population was divided into large aggregates which were present wherever oak stands occurred. Within a particular oak area each aggregate was further divided into isolated groups of individual plants, the number of groups varied depending upon the size of the area covered by the oak stand. The groups usually consisted of about 15–20 members and individual plants were ordinarily spaced 30–35 cm apart. There is no evidence for the existence of any method of vegetative propagation. Frequently the more homogeneous an oak stand, the greater the abundance of *P. delphinifolia* and the fewer the number of other kinds of plants. The size of a population appeared to remain stable although it was observed that sometimes *P. delphinifolia* was chewed upon by grazing livestock.

Floral biology

The flowering period begins in the early part of July and ends in the latter part of August. Shortly after the onset of the rainy season the flowering stalk begins to develop rapidly and when it is about 20 cm long the solitary head starts to open while the stem continues to grow to an average height of 35 cm. Plants rarely flower the first or second year but older plants appear to flower every season. The capitula are usually 1.5–2 cm in diameter producing 12–18 pistillate ray florets and 180–230 disc florets. The corollas of the ray-floret are golden yellow, of the disc florets yellow. Although no pollination studies *per se* were made several types of insects, mostly coleopterans and dipterans were observed visiting the flowers. The flowering period is relatively short and practically all the plants flower within a period of about two weeks. By the middle of August, almost all of the disc and ray florets have disarticulated and fallen while the floral stem dries and remains erect throughout the dry season. The older leaves die and fall to the ground with their bases remaining attached to the caudex. The achenes mature within the head during November and December. Since neither a pappus nor any other obvious morphological adaptation for dispersal is present, the means of seed dispersal is not well understood. It is possible that small animals such as rodents or ants might aid in seed dispersal or perhaps the seeds may be carried away from the parent plant by runoff water during the following rainy season. No studies have yet been done to verify this speculation.

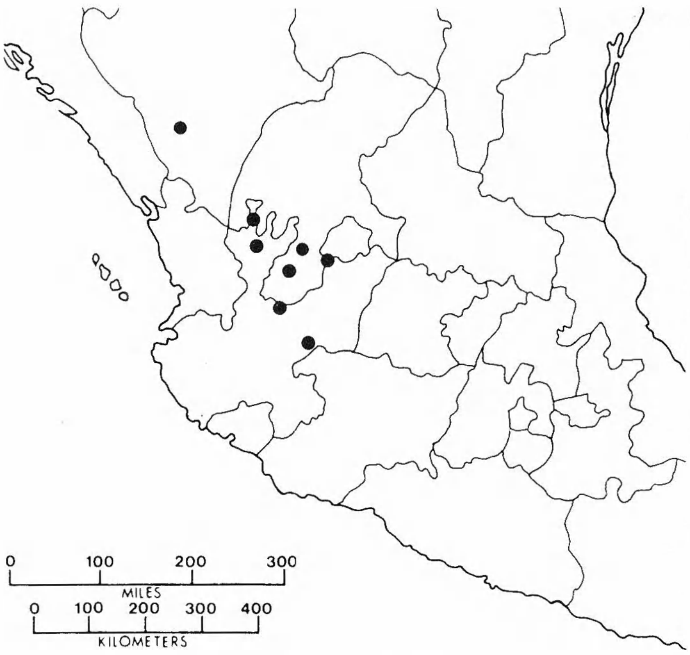

Fig. 1. Known distribution of *Pippenalia delphinifolia*. The map shows the central parts of Mexico.

Observations of older plants in all three populations in the field suggest that only about 10–15 mature achenes are produced per capitulum. It is curious that so few seeds develop (less than 10 percent of the available fertile florets apparently set seed) from so many florets per head. Counts of pollen indicate that between 960 and 1000 pollen grains are produced per anther (sample of five florets from each of 10 heads). We obtained a chromosome number of n = c. 30 from pollen mother cells. The number is not precise due to what appears to be meiotic irregularities in the chromosome pairing with apparently some univalents and tetravalents mixed with the bivalents. This has recently been confirmed by Keil & Stuessy (1977). Pollen stainability in acetocarmine was variable: 97.5 percent (Correa 1, 1996 pollen grains), 93.5 percent (Correa 26, 2301 pollen grains) and 54 percent (Correa 3, 3876 pollen grains) stained pollen. These data, along with Keil & Stuessy's (1977) report of 75 percent pollen stainability and the peculiar meiotic formations suggest that there may be a degree of sterility which could possibly explain the low seed production and support the suggestion of Keil & Stuessy (1977) that this taxon may have been derived from hybrid origin. Without a doubt more field and cytological studies on this monotypic genus are urgently needed.

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A hitherto un-named form of Cyathus olla (Nidulariaceae)

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Brodie, H. J. 1978 03 31: A hitherto un-named form of Cyathus olla (Nidulariaceae). *Bot. Notiser 131:* 31–34. Stockholm. ISSN 0006-8195.

Cyathus olla (Batsch) ex Pers. f. *lanatus* Brodie, a distinct form from the semi-arid Owyhee Mountains of Idaho, USA, is described and illustrated. It differs from common forms of *C. olla* by having a peridium, shaggy or woolly on the outside, a markedly fimbriate lip, wrinkled peridioles which are smaller than those of *C. olla*, a peridium marked by internal concentric grooves, and a stout, short funiculus.

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An interesting semi-arid area in NW United States comprising the Owyhee Mountains and adjacent regions of Idaho, Oregon and Nevada has yielded a large number of unusual macrofungi including many previously undescribed species. Knowledge of the fungus flora of the Owyhee Region is due largely to the studies of Ellen Trueblood (Mrs T. Trueblood) of Nampa, Idaho, assisted by Dr Alexander Smith of the University of Michigan.

Trueblood (1975) gave an account of the physiographic features of the area and commented on about sixty of the most important macrofungi found in the Owyhee Region. A region where precipitation is very scanty (5–60 mm annually, 25 mm only over much of the area) and irregular might be considered to be "a hostile environment for fungi. This impression plus poor roads is probably why the region was previously unexplored mycologically. However, a surprising number of species are adapted to the various ecological niches of mountains and plains" (Trueblood 1975 p. 315).

I have been privileged to examine numerous collections of the Nidulariaceae from the Owyhee Region thanks to the generosity of Mrs Trueblood. *Cyathus pygmaeus* Lloyd was found to be abundant (Brodie 1966) although it had not been recognized since Lloyd described it in 1906. A very small *Crucibulum* was also found to be common in the area. This fungus, although closely related to *C. laeve* (Huds. ex Rehl.) Kambly & Lee, was believed to be distinct and was described under the name *C. parvulum* Brodie (1970).

Cyathus olla (Batsch) ex Pers. also occurs rather widely in the Owyhee Region. However, almost all collections of this species from the region differ strikingly from the common form of *C. olla* from other parts of North America (and from the European forms) to such an extent that I have several times doubted that the Owyhee fungi should be identified with *C. olla*. Some collections are very small for the species and are often short, thick-walled and so bleached that, at first glance, they might easily be mistakenly identified as *Crucibulum laeve*. The difficulty is increased by the fact that the tunica of the dry land specimens of *Cyathus olla* is commonly as thick and tough as is the tunica of *Crucibulum*. Moreover, the funiculus of some specimens is of such construction that one needs to look closely to be convinced that one is seeing a *Cyathus* funiculus and not that of *Crucibulum*.

Cyathus olla, like a few other species of the genus, exists in many variations, which differ greatly from one another, especially in size and shape. When I dealt with *C. olla* in my monograph (Brodie 1975) I decided that, because few, if any, of these 'forms' are geographically or ecologically circumscribed, it would be unwise to recognize them as discrete taxonomic entities. The only exception made was the recognition of the very large and distinct f. *anglicus* Lloyd.

Among the Trueblood collections of *C. olla* which I have examined, one 'form' now appears to me to be worthy of note and to be best dealt with as a form in the taxonomic sense. The variant herewith described as *C. olla* f. *lanatus* is so unlike most specimens of *C. olla* known to me that it could easily be misidentified or not identified at all by persons resorting to the usual descriptions of *C. olla*. For that reason, it seemed that it might be helpful to mycologists to publish it under a form name.

Cyathus olla f. **lanatus** Brodie f. nov. – Fig. 1 A–C

Holotype: USA, Idaho, Owyhee County, Reynold's Creek, on dead twigs of *Artemisia* sp., 4.11.1976, Trueblood 6112 (Herbarium of H. J. Brodie [no. 77002]), Victoria, B. C., Canada – Paratype: USA, Idaho, Owyhee County, West Rabbit Creek, on dead twigs of *Sarcobatus vermiculatus*, 2.11.1969. Trueblood 2978 (MICH).

Peridium griseopallidum aut bubalino-pallidum, late obconicum, in quarta parte superiore repandum, ad basin non valde decrescens et basi bulbosa late affixum, 5–6 mm latum, 5–8 mm altum, basi globosa excepta; labium distincte fimbriatum. Peridium extus non plicatum, tomento fasciculisque pilorum longiorum erectorum vel radiantium obtectum; peridium intus non plicatum sed sulcis latis, concentricis distincte notatum, album aut bubalinum, nitidum. Peridiola 2–3 mm lata, asymmetrica, nitida, grisea vel bubalina, rugata. Tunica crassa (60 µm) nitida, bubalina, albescens. Cortex simplex (60–80 µm crassum). Sporae plerumque late ellipsoideae sed variabiles, hilo instructae; 7.5–9 µm × 12–15 µm, pariete crassa. Funiculus crassus, brevis et asymmetricus. Epiphragma tenax, alba.

Peridium light grey or light buff, broadly obconic, flaring out somewhat towards the mouth, not tapering abruptly near base and broadly attached to a firm emplacement; 5–6 mm wide at mouth, 5–8 mm high exclusive of emplacement; lip distinctly fimbriate. Peridium outside not plicate, covered with a fine tomentum and with tufts of conspicuous longer hairs which are arranged in upward-pointing tufts or in radiate tufts; inside not plicate but distinctly marked transversely with wide concentric grooves, white or pale buff, shiny. Peridioles 2–3 mm in diameter, irregular in outline, shiny, grey to light buff, irregularly wrinkled. Tunica thick (up to 60 µm), shiny, pale buff fading to white. Cortex a single layer (60–80 µm thick). Spores mostly broadly ellipsoid but variable in shape, provided with hilum, 7.5–9 µm wide, 12–15 µm long, rather thick-walled. Funiculus stout, short and irregular in form. Epiphragm tough, whitish (having the appearance of bleached kid).

Cyathus olla f. *lanatus* grows on pieces of dead desert plants and soil.

The epithet *lanatus* alludes to the conspicuously hairy appearance of the external surface of the peridia and to the markedly fimbriate lip.

Discussion

That *C. olla* f. *anglicus* is properly regarded as a form of *C. olla* is a position which was strengthened by the demonstration (Brodie 1952) that some degree of fertility is manifested between mycelia of those two taxa. Unfortunately no test of possible fertility between f. *lanatus* and *C. olla* has been carried out up to the present because all attempts to germinate spores of f. *lanatus* have been unsuccessful.

At first, I believed that f. *lanatus* could be separated from *C. olla* in that the basidiospore of the former possesses a hilum which can easily be discerned in most spore samples. However, examination of spores of several collections of *C. olla* revealed that a hilum is also present, at least on spores of some collections. According to Martin (1927), a hilum can be discerned on spores of *C. olla* soon after they are separated from basidia, though it may not be visible by ordinary light microscopy when spores are older. Although I have not studied the type material of *C. olla* with regard to the matter of hilum, it seems that the presence of a hilum (Martin used the broader term 'apiculus') cannot, by itself, be used as a distinguishing feature of *C. olla* f. *lanatus*.

The form *lanatus* is readily recognized, first by its tufted tomentum and upward-pointing hairs which are much more conspicuous than in any other specimens of *C. olla* which I have ever examined. The clearly fimbriate lip is also distinctive; it should be noted that in typical *C. olla*, the lip of young specimens is often beset with

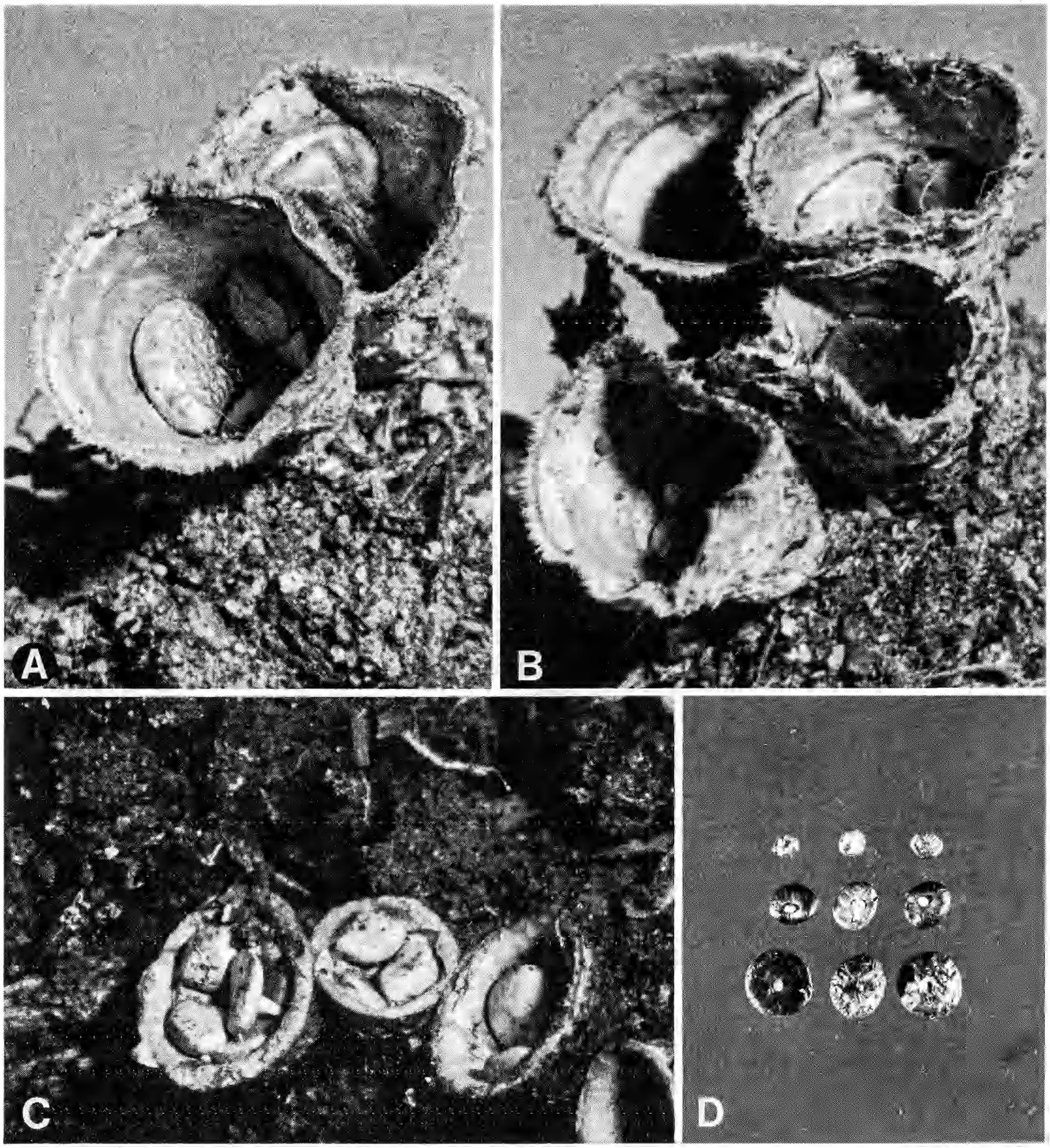

Fig. 1 A: *Cyathus olla* f. *lanatus;* holotype specimens showing fimbriate lip of peridium, internal transverse ridges and wrinkled peridioles. ×7. – B: Same collection as in A; fimbriate lip is shown in lower lefthand specimen and woolly exterior in both righthand specimens. ×7. – C: Paratype (Trueblood 2978) showing short, thick funiculus in lefthand specimen. The very strongly developed tunica is apparent on the peridioles of these specimens though the peridioles are less wrinkled than in the holotype specimens. ×5.5. – D: Peridioles of three related *Cyathus* (all of which occur in the Owyhee region): upper row, *C. pygmaeus,* lower row, *C. olla*, middle row, *C. olla* f. *lanatus*. ×3.5.

irregular fragments of the epiphragm but that condition is not comparable to the regularly-disposed hairs around the lip in *C. olla* f. *lanatus* which are clearly shown in Fig. 1 A, B. The concentric grooves that mark the interior surface (Fig. 1 A, B) are striking in f. *lanatus;* faint concentric sulcation is occasionally seen in typical *C. olla*, but the lines or zones are never as distinct as they are in f. *lanatus*. The peculiar thick, stubby funiculus (Fig. 1 C) is an additional diagnostic character. Further, in my experience, peridioles of the common forms of *C. olla* are usually plump and smooth and only rarely wrinkled when fresh. In contrast, peridioles of f. *lanatus* are mostly rather flat and usually wrinkled (Fig. 1).

Although less than 40 specimens in all are at present referred to f. *lanatus,* it may nevertheless be worthy of note that the peridioles are, on the average, considerably smaller than those of *C. olla*. Peridioles of C. *pygmaeus,* a species common in the Owyhee area and also related to *C. olla*, are invariably much smaller than those of *C. olla* f. *lanatus* (Fig. 1 D).

The holotype consists of 20 specimens of which 6 are immature. The paratype consists of 6 specimens, mostly older and more weathered than the holotype. The paratype material (Fig. 1 C) in general resembles the holotype closely except that the peridium mouth is less obviously fimbriate, peridia are considerably darker in colour, and the funiculus is even stubbier.

Acknowledgments. I am indebted to Mrs T. Trueblood for permitting me to examine her collections as cited above and for providing the photographs (Fig. 1 A–C). Dr Alexander Smith kindly loaned to me Mrs Trueblood's collection No. 2978 from the Herbarium of the University of Michigan. To Mr H. F. Dietrich, University of Victoria, who provided the photograph of peridioles (Fig. 1 D) and prepared photographic prints for publication, I also express my thanks.

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Pollination ecology and adaptation in Platanthera chlorantha (Orchidaceae)

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Observations mainly from the island of Öland, southern Sweden, on relationships between insects and *Platanthera chlorantha* (Cust.) Rchb. are reported. Twenty-eight species of Lepidoptera were found as pollen-vectors. The most important pollinators were species of *Autographa, Apamea, Deilephila* and *Polia* together with *Cucullia umbratica* and *Diachrysia chrysitis*. On Öland these moths transported about 97% of the pollinaria. Morphological comparisons between flowers and vectors revealed special adaptation to a group of medium-sized moths. The behaviour of moths on flowers and the function of the pollination system are described. Selective mechanisms controlling adaptation between the plant and its pollen-vectors are elucidated. Emission periodicity of the floral fragrance was demonstrated by gas chromatography. Its chemical composition was analysed with gas chromatography-mass spectrometry and some of the components have been tentatively identified. In experimental tests with moths the floral fragrance was shown to provoke alighting on artificial flowers and feeding reactions. Available information indicates great similarities of the pollinator fauna of *Platanthera chlorantha* in different parts of Europe. Morphological uniformity among pollinator-species is suggested responsible for the small variation in flower morphology observed.

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The polymorphic and closely related genera *Platanthera* L. C. Rich. and *Habenaria* Willd. include approximately 800 species which are native mainly of the warmer regions of the world. Most of them are considered adapted to be pollinated by Lepidoptera (Pijl & Dodson 1966). Thus nectar is normally abundant in the flowers, deeply hidden in narrow tubes (spurs) and available only for long mouth-parts. In most species the pollinaria are deposited on the proboscis or other parts of the head of the insect. However, peculiar methods of deposition on moths such as sternotribic and on front legs are known e.g. from South African species of *Habenaria* having elongated stigmatic projections (Vogel 1954). Flowers of species affixing pollinaria to the eyes of moths or butterflies generally have a well developed column with lateral protrusions carrying rather widely separated viscidia and long-caudicled pollinia. In a classical work on orchid pollination Darwin (1862) drew attention to such adaptation in *Platanthera chlorantha* (Cust.) Rchb. Attachment to eyes of Lepidoptera has later been found in North American species viz. *P. hookeri* Torr. ex Gray and *P. orbiculata* (Pursh) Torr. (Gray according to Darwin 1877, Gray 1880). Obviously it also occurs in *P. blephariglottis* (Willd.) Lindl. and *P. ciliaris* (L.) Lindl. (Smith & Snow 1976). Similar adaptations probably also exist in *P. grandiflora* (Bigel.) Lindl., *P. peramoena* Gray and perhaps *P. leucophaea* (Nutt.) Gray (Stoutamire 1974). In *P. obtusata* (Pursh) Lindl. viscidia attach to the eyes of mosquitoes or geometrid moths (Stoutamire 1968, Thien 1970). The flower morphology of *P. oligantha* Turcz., a rare species in northern Europe, suggests deposition on the eyes of an insect.

Anthecological information on *Platanthera chlorantha* is still fragmentary. That two larger nocturnal Lepidoptera were pollen-vectors in Britain was reported by Darwin (1862). The first record of a pollinator, however, had obviously already been made in France (Robin 1853). Among insects carrying pollinaria of *"Ophrys"* reported by Robin, a "Bombyx d'espèce indéterminée" is reproduced on a coloured plate. Without any doubt the excellent drawing shows *Deilephila porcellus* (L.) (Sphingidae) and affixed pollinaria of *P. chlorantha*. Onwards only a few reliable records of moths bearing evidence of visitation have been presented. Although the pollinaria differ considerably from those of other European orchids, both in morphology and mode of attachment on vector, confusions have evidently occurred e.g. with *Dactylorhiza maculata* (L.) Soó (Meldola 1909, Stewart 1910). It seems that no one has hitherto witnessed a pollinator in action.

The greenish-white and resupinate flowers of *Platanthera chlorantha* develop in a loose raceme. The front view of a flower appears cross-like from the positions and shapes of the sepals and petals (Fig. 1 A). Intercellular spaces in flower tissues produce strong light-refraction making the inflorescence conspicuous especially in darkness. The petal forming the labellum is elongated backward into a slender nectar-tube which is somewhat flattened laterally. Among minute hairs in the ventral furrow or accumulated towards the apex of this spur, nectar is abundant up to about two-thirds of the spur-length (Ziegenspeck 1936). The column is laterally expanded and curved forward thus producing a semi-circular cavity in front of the spur-mouth. The two ventrally diverging anther-cells enclose long-caudicled pollinia (Fig. 1 B) which lie inclined backwards. Each caudicle is twisted and rather stiff and, just before prolonging into a little tip, distally united to a subcircular disc of cells (viscidium) whose exterior surface is converted into viscid matter. The two viscid discs face each other. The connection between caudicle and disc consists of a hygroscopic cell mass (stipes) which contracts after removal from its embedded environment in the column.

After the viscid disc has been deposited on a pollinator, contraction slowly rotates the caudicle downwards–inwards moving the pollinium into proper position for the stigma of another flower (Darwin 1862) (Fig. 1 C). Darwin propounded that the time required to produce the movement was sufficient to prevent geitonogamy as a visitor probably leaves the inflorescence before rotating is completed. Since neither self-pollination nur fruit-setting without pollination has been observed, visiting by moths is expected necessary for production of seed. As in several other orchids, however, apomictic formation of embryos occurs from some of the ovula in an ovarium receiving pollen-tubes (Hagerup 1947).

The flowers emit a sweet but faint scent and as it is most easily perceptible to man shortly after dusk, emission periodicity is suggested (Vogel 1963, Kugler 1970). The theory that certain epidermal leucoplasts in the labellum are concerned with the synthesis of fragrance compounds (Germ 1947, Vogel 1963) could not be verified (Heinrich 1973).

Material and methods

The studies were mainly performed on Central Öland in Torslunda and Gårdby parishes in June–July 1972–75. A few observations were also made at Stenshuvud, Svaneholm and S. Sandby in Skåne and at Häverö in Uppland in 1976. During two earlier visits to Öland in 1969 and 1970 a few pollinators were found which have been added to the material collected in the present investigation.

Flower visitors were collected with a net. To catch a larger number of pollen-vectors in 1972 and 1973 a method was applied similar to that used by Frost (1965) to record pollinators of *Asclepias*. A 250 W mercury vapor lamp was placed in the vicinity of assemblages of *Platanthera chlorantha* and the attracted moths examined for pollinaria. Vectors were killed, determined and their numbers of pollinaria counted. Length of proboscis, width of head across compound eyes and distance between frontal eye-edges were measured.

Behaviour of visitors was observed from dusk. A torch covered with red paper was sometimes used to enhance ability for observation.

Selected flower characters considered of special functional importance for pollination, such as spur-length and distance between viscidia were measured. Depth from spur-mouth to the accumulation of nectar (Fig. 1 A) was investigated in the day on flowers which showed no sign of having been visited i.e. undisturbed pollinaria and no scales or massulae on sticky surfaces. As preliminary measurements showed that variation of characters within the same inflorescence was very small if the top-flowers were excluded, the mean value of two randomly selected flowers below the top was taken as representative for each plant. Nectar was withdrawn from spurs with a longneedled 5 µl syringe and further secretion observed.

To check if autogamy occurred, a number of inflorescences in bud were enclosed with net bags to exclude pollinators and observed daily throughout the flowering. A few experiments with artificial cross- and

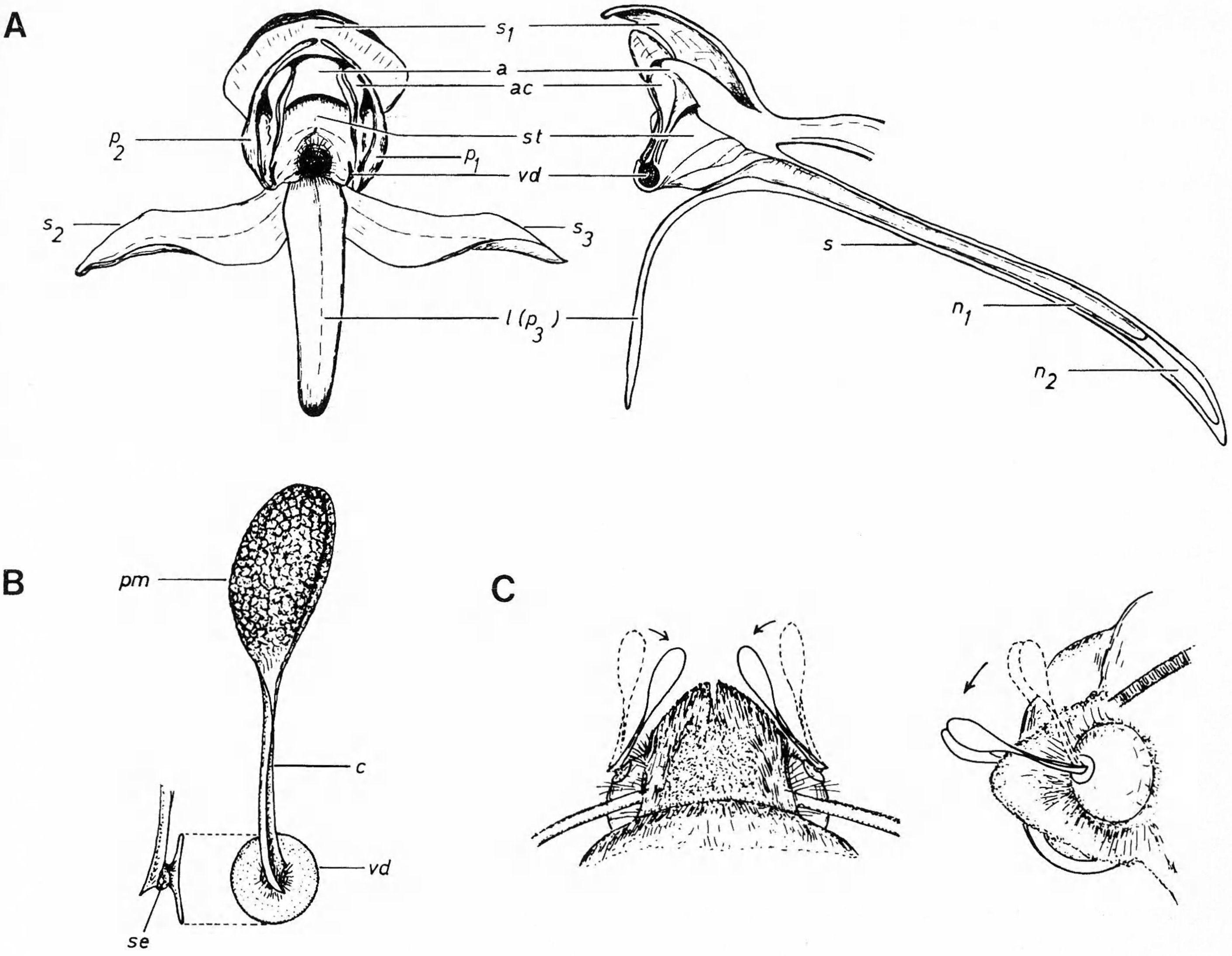

Fig. 1. A: Front view and longitudinal section of flower of *Platanthera chlorantha* (3 ×). – B: Pollinarium (12 ×). – C: Movements of pollinia after deposition on moths. Dorsal and lateral view. – Abbreviations: a anther, ac anther-cells, c caudicle, l labellum, n_1 nectar in ventral furrow, n_2 accumulated nectar, p_1–p_3 petals, pm pollinium, s spur, s_1–s_3 sepals, se stipes (hygroscopic cell mass), st stigmatic surface, vd viscidia.

self-pollination were carried out. In some localities fruit set was counted in the autumn.

The Lepidoptera deposited in the Swedish Museum of Natural History, Stockholm were examined for pollinaria of *P. chlorantha*.

The floral fragrance and the suggested emission periodicity were analysed in 1974–75 by gas chromatography (GC) and combined gas chromatography-mass spectrometry (GC-MS) at the Ecological Station of Uppsala University, Ölands Skogsby. The instruments, Perkin-Elmer 900 and LBK 9000 respectively, were equipped with all-glass capillary intake systems (Ställberg-Stenhagen 1972). Fragrance compounds were isolated by collection in pre-column tubes (cf. Silverstein & Rodin 1966). Fresh inflorescences on root or cut were placed inside a glass-tube (L 20 cm, ID 4 cm). A pre-column (L 40 mm, ID 4 mm) made of glass was packed with scent-collecting materials, Chromosorb G 60–80 mesh treated with 10 % silicone grease or Porapak Q 50–80 mesh, that were sufficiently conditioned before usage (Bergström 1973). It was then vertically coupled to the top of the glass-tube and with its other end to a flow indicator connected with a pump. Air-borne scent was slowly drawn through the packed pre-column for a few hours or up to two days. Regular runs without flowers controlled that additional compounds from the air were absent or did not interfere on the results. After finished collection the pre-column tube was directly placed into the GC inlet and heated to 150°C for 20 minutes while the analytical column (LKB OV 101, 25 m glass) was cooled. After removal of the pre-column tube the capillary analytical column was programmed from 25° to 225°C at 4° or 8° per minute. Mass-spectra and retention indices were easily obtained for fragrance compounds which had been transferred from the collecting materials and were compared with published data (mainly Stenhagen et al. 1974) and model compounds.

Details in the behaviour of pollinators on flowers were studied in 1975 with captive moths in a cage (1 × 1 × 0.6 m). All moths used were captured in the

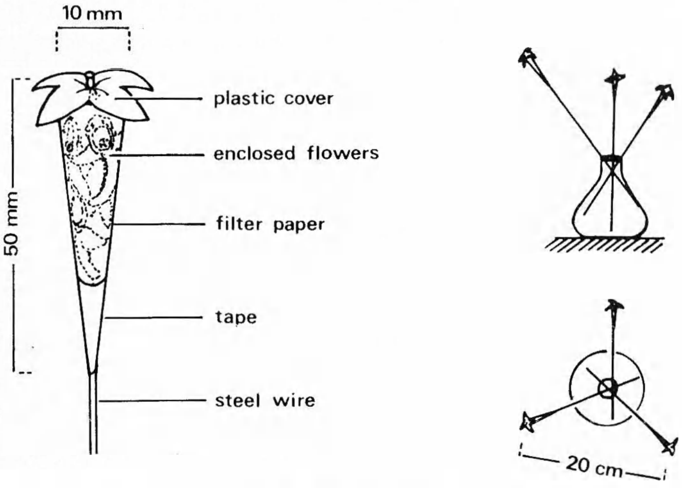

Fig. 2. Artificial "flower" hiding cut natural flowers. Arrangement in experiments to the right.

field with a lamp the night before. Undamaged specimens only were introduced into the cage together with fresh flowers and observed during the evening. Before usage moths in an inactive state were kept individually in glass bottles under a lamp. Lowering of light intensity normally caused an almost immediate warming up for flight.

Importance of the scent for alighting and feeding reactions was investigated in some experiments with artificial white models into which intact cut flowers could be placed (Fig. 2). Scent then emanated through and along the upper margin of a cone made of filter paper while the true source of scent was invisible. Three models of which one contained 4 flowers were placed 2 dm apart forming an equilateral triangle in the middle of the cage (Fig. 2). A few experiments were also carried out with two inflorescences and one white plastic imitation placed in the same way. Species tested were *Autographa bractea* (Den. & Schiff.), *A. gamma* (L.), *Cucullia umbratica* (L.) and *Apamea lateritia* (Hufn.).

Only observations on typical specimens of *Platanthera chlorantha* are presented here. Intermediates to *Platanthera bifolia*, not too rare and probably of hybrid origin, have been excluded. The nomenclature used for Lepidoptera agrees with Karsholt & Schmidt Nielsen (1976).

Variation in flower morphology

Measurements of flower characters in populations on Öland show approximate Gauss distributions. As no discrepancies were found which might indicate genetical differences between local populations, all data were lumped (Fig. 3 A, D). Plants growing in shade seem to develop somewhat bigger flowers than those in exposed sites but this most probably phenotypical variability was small. A maximum of 3.5 mm difference was found in mean spur-length between populations in shady wood biotopes and on open ground. Specimens studied in Skåne and Uppland fall within the variation range of the material from Öland. Herbarium material in UPS from other parts of Sweden and northern Europe (233 specimens), suggests homogeneity. For Britain 19–28 mm spur-length is reported (Percival 1965). Available data thus indicate that geographically restricted intraspecific flower-types of any greater morphological significance do not occur in this area.

Nectar

Prior to anthesis fluid is present in the spur. Usually when the flower opens, 2–4 mm nectar is accumulated towards the apex. If the spur is emptied by a syringe further fluid is first noticed in the ventral furrow of the spur and later on a free nectar surface will arise. It seems likely that secretion is connected with the hairs occurring along the furrow. The nectar is held by capillarity between these short hairs but as secretion continues it apparently flows down and will accumulate from the apex of the spur. The time of secretion could not be determined because of the unknown influences of air humidity. In emptied spurs fluid reappeared along the bottom during the afternoon which might reflect a secretion phase. During damp night conditions nectar was sometimes observed reaching the spur-mouth, which certainly was the result of a considerable water uptake from the air. In the day the upper surface of the accumulation of nectar was seldom found to reach above 15 mm from the spur-mouth (Fig. 3 B). However, the ventral furrow yields nectar higher up usually within 7–10 mm from the entrance. If the needle of the syringe was inserted into the furrow in this upper part of the spur it was possible to lower the surface of the accumulated nectar whereby most of the nectar could be withdrawn from the spur. Evidently the furrow is refilled from below with nectar mostly by capillary attraction. Accordingly, insects with relatively short proboscises are able to reach the food and remove it.

Floral fragrance

Capillary GC on scent collected in pre-columns revealed that clear emission differences exist

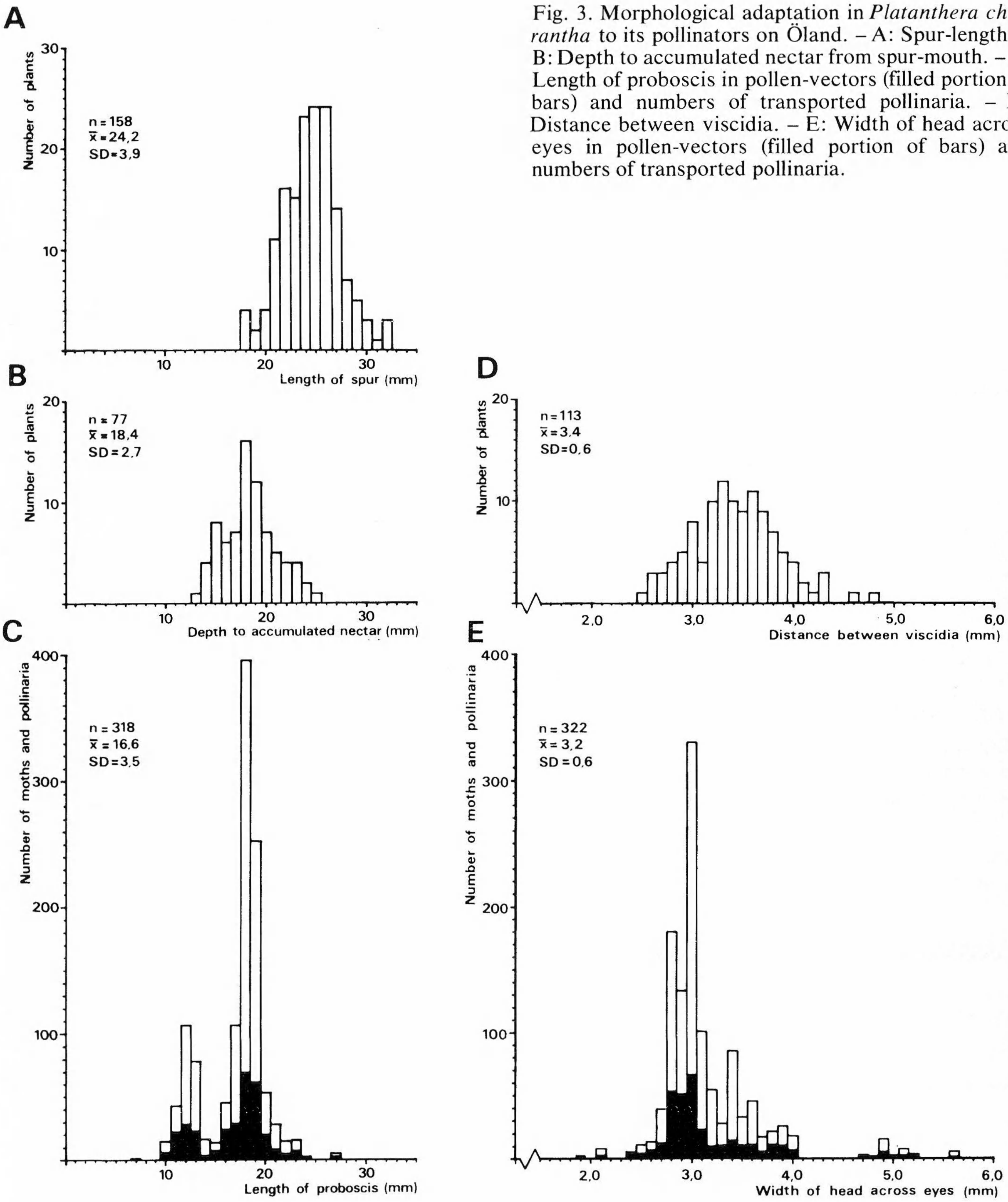

Fig. 3. Morphological adaptation in *Platanthera chlorantha* to its pollinators on Öland. – A: Spur-length. – B: Depth to accumulated nectar from spur-mouth. – C: Length of proboscis in pollen-vectors (filled portion of bars) and numbers of transported pollinaria. – D: Distance between viscidia. – E: Width of head across eyes in pollen-vectors (filled portion of bars) and numbers of transported pollinaria.

between day and night (cf. Fig. 4 A, B). At least 11 fragrance compounds were detected, of which some have been tentatively identified. Some of the compounds appear to emanate continuously, while others show distinct periodicity. This explains, at least partly, why the scent has been differently experienced by human olfaction. In daytime-collections caryophyllene dominates (Fig. 4 A), but in collections after dark more low-molecular compounds appear on the chromatograms, especially methyl-benzoate and monoterpenes (Fig. 4 B). The sesquiterpenes seem to have no pronounced periodicity. According to the chromatograms and compared

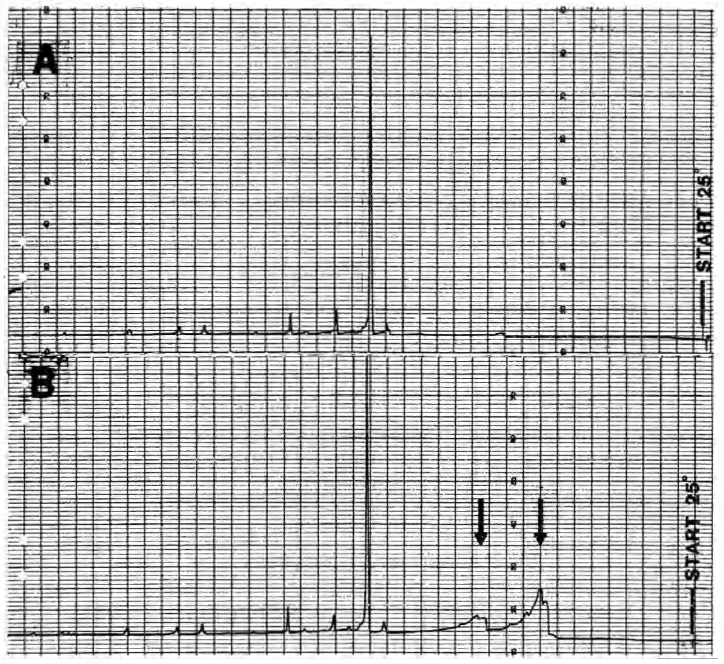

Fig. 4. Scent-emission in *Platanthera chlorantha* demonstrated by gas chromatography of pre-column collections on silicone-chromosorb. – A: Three-hour collection from one inflorescence with 20 flowers during the day, 10.00–13.00. – B: Same plant and conditions but collection after dusk, 21.00–24.00.

with more fragrant species e.g. *Platanthera bifolia,* the amounts of periodically emitted compounds must be considered low. Collection during longer time showed higher amounts of compounds with larger molecules such as benzyl-benzoate. That the applied techniques approximately reflect the real output of scent is supported by human perception of the scent of the compounds in question, which were studied as references.

Pollinators and visitors

Insects of several orders and some other animals visit the inflorescences. Spiders occasionally stay among the flowers in ambush or when constructing webs. Adults and larvae of *Taeniothrips picipes* (Zett.) (Thysanoptera) are sometimes common in flowers and, since they are often creeping into spurs, obviously feeding on nectar. However, only Lepidoptera were found to transfer pollen. On Öland a total of 333 specimens of 28 species carrying pollinaria were collected (Table 1). In addition one *Autographa jota* carrying one pollinarium was found at Svaneholm in Skåne. Moths netted on flowers were of the same species as those found attracted to light. In the vector-material Noctuidae dominate with 22 species followed by Sphingidae three, Geometridae two and Hesperiidae with one species. *Autographa* spp., *Apamea* spp., *Deilephila* spp., *Cucullia umbratica, Polia* spp. and *Diachrysia chrysitis* together transport ap-

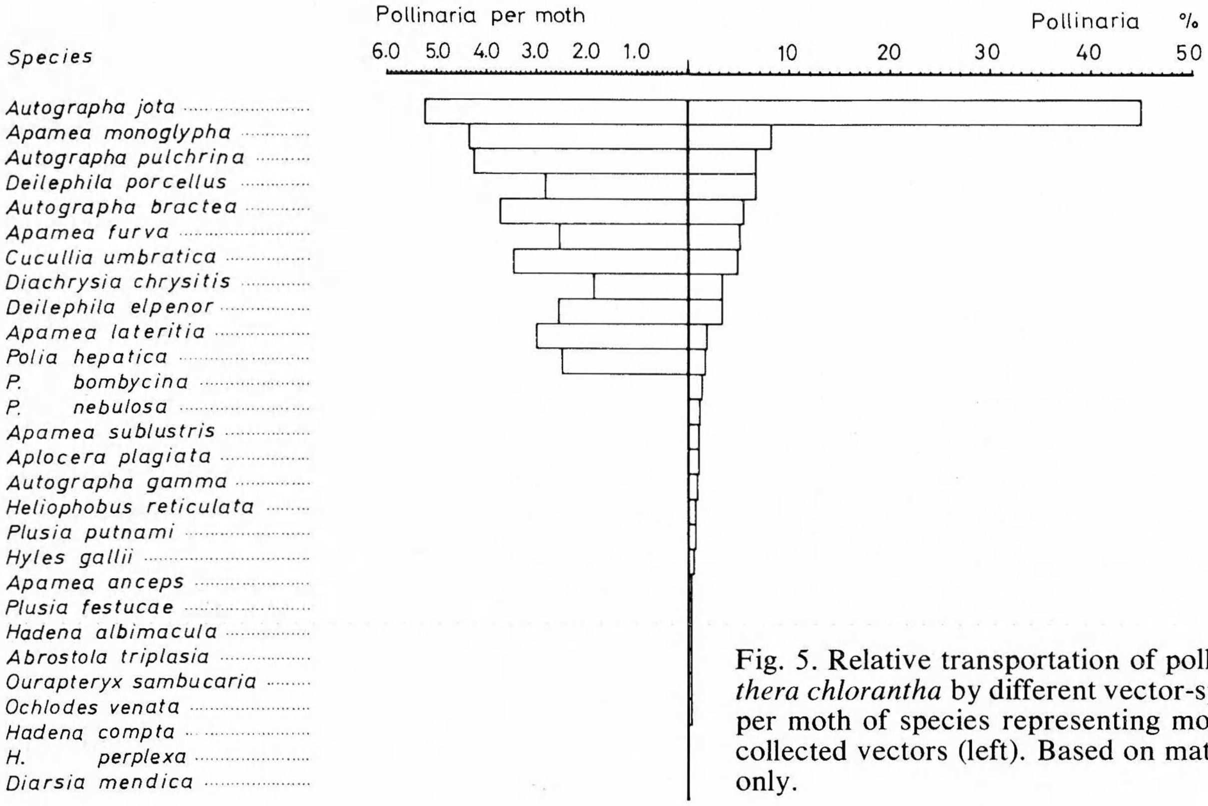

Fig. 5. Relative transportation of pollinaria of *Platanthera chlorantha* by different vector-species (right) and per moth of species representing more than 1.5 % of collected vectors (left). Based on material from Öland only.

Table 1. Pollen-vectors of *Platanthera chlorantha* recorded on Öland and the morphology of moths.

Species	Total vectors found. Females within brackets	Attaced pollinaria	Morphology of moths. Number measured within brackets		
			Length of proboscis. Range (mm)	Width of head across eyes. Mean (mm)	Distance between frontal eye edges. Mean (mm)
Hesperiidae					
Ochlodes venata (Brem. & Grey)	1 (1)	2	10.5–16.0 (6)	3.0 (1)	1.4 (1)
Geometridae					
Aplocera plagiata (L.)	4	11	12.0–13.0 (3)	2.0 (3)	0.7 (2)
Ourapteryx sambucaria (L.)	1	2	10.5 (1)	2.6 (1)	0.7 (1)
Sphingidae					
Hyles gallii (Rott.)	1 (1)	6	23.5–27.0 (4)	5.6 (1)	2.6 (1)
Deilephila elpenor (L.)	16 (1)	41	21.0–25.0 (27)	4.9 (14)	1.7 (7)
D. porcellus (L.)	29 (2)	81	16.0–20.0 (75)	3.9 (29)	1.4 (5)
Noctuidae					
Diarsia mendica (F.)	1	1	7.0 (1)	2.4 (1)	0.8 (1)
Polia bombycina (Hufn.)	4	16	12.5–14.0 (5)	3.3 (4)	1.1 (3)
P. hepatica (Cl.)	8 (2)	20	11.5–12.5 (7)	3.0 (6)	1.1 (5)
P. nebulosa (Hufn.)	4	13	11.0–13.5 (12)	3.4 (3)	1.0 (3)
Heliophobus reticulata (Goeze)	4	9	10.5–12.5 (9)	3.0 (4)	1.0 (3)
Hadena perplexa (Den. & Schiff.)	1	1	12.0–14.5 (12)	2.6 (1)	0.8 (1)
H. compta (Den. & Schiff.)	1	1	15.0–16.0 (4)	2.6 (1)	0.9 (1)
H. albimacula (Bkh.)	1	2	15.5 (1)	2.8 (1)	0.9 (1)
Cucullia umbratica (L.)	17 (6)	59	18.5–21.0 (18)	3.4 (16)	1.1 (6)
Apamea monoglypha (Hufn.)	23 (10)	100	10.5–13.5 (25)	3.5 (22)	1.2 (5)
A. sublustris (Esp.)	7 (3)	12	9.5–11.0 (7)	3.0 (7)	1.1 (5)
A. lateritia (Hufn.)	7 (1)	21	10.0–13.0 (9)	3.2 (7)	1.1 (5)
A. furva (Den. & Schiff.)	25 (9)	63	10.0–12.0 (23)	2.9 (21)	1.0 (7)
A. anceps (Den. & Schiff.)	2	3	9.5–11.0 (3)	2.9 (2)	1.1 (2)
Diachrysia chrysitis (L.)	22 (10)	41	14.5–16.5 (30)	2.8 (22)	0.9 (5)
Plusia festucae (L.)	1	3	13.5–16.0 (6)	2.5 (1)	0.8 (1)
P. putnami (Grote)	3	8	12.0–14.0 (9)	2.5 (3)	0.8 (2)
Autographa gamma (L.)	6	10	15.5–17.5 (9)	2.9 (6)	1.1 (2)
A. pulchrina (Hw.)	19 (3)	81	15.5–18.0 (25)	2.7 (19)	1.0 (5)
A. jota (L.)	106 (10)	554	16.0–20.0 (125)	3.0 (106)	1.0 (5)
A. bractea (Den. & Schiff.)	18 (2)	67	17.5–21.0 (19)	2.9 (18)	1.0 (4)
Abrostola triplasia (L.)	1	2	11.5–12.0 (4)	2.6 (1)	0.8 (1)
Total	333 (61)	1230			

proximately 97% of the pollinaria. *Autographa* spp. carry 58% and *Autographa jota* alone no less than 45%. Compared to *A. jota* other species thus disperse a small part of the pollen (Fig. 5). For *A. jota* also the number of transported pollinaria per moth is highest (Fig. 5). The pollen-vectors found were predominantly males. Soon after flowering has begun and until far beyond its end moths carrying pollinaria are abundant as demonstrated with the light trap (Fig. 6). As expected the number attached is highest towards the end of flowering. The specific diversity among the vectors was greater during the first two weeks but as time went by, *Autographa* spp. became more and more dominant in the catch, probably due to greater longevity. As flowering proceeds deposited pollinaria become worn and finally only parts of caudicles and viscid discs are left on the eyes. The last pollinators found in a season are in a very worn condition which indicates that the viscidia often remain affixed until the death of the insect.

In the museum material investigated nine moths representing eight species carried pollinaria (Table 2). The six species collected in

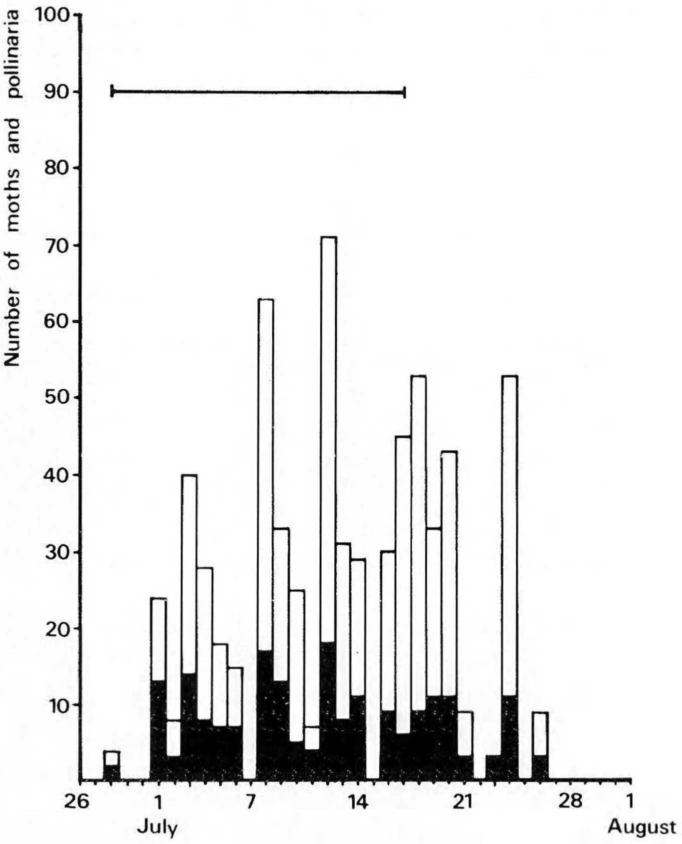

Fig. 6. Abundance of pollen-vecting moths (filled portion of bars) and their attached pollinaria of *Platanthera chlorantha* recorded by a light-trap at Tävelsrum, Öland in 1972. The flowering period is indicated by a horizontal line.

other Swedish provinces are all present in the material found on Öland.

Pollinator morphology

The heads in pollen-vecting species are structurally rather uniform. Frons and regions around the eyes are covered with long hairs and the labial palps, bending upwards on each side of the base of proboscis, are densely scaly or hairy (Fig. 1 C). The only unprotected firm surfaces on the head, except the proboscis, are the velvet compound eyes. Dimensions of head and mouthparts differ much between species (Table 1). About 85 % of the pollinaria were transported by moths whose distance between the frontal eye-edges was 1.0–1.2 mm and 70 % by vectors having width across head 2.7–3.2 mm (Fig. 3 E). Although *Polia* spp. and *Heliophobus reticulata* have 0.2–0.3 mm long erect hairs on their eyes they were often found carrying pollinaria. About 0.1 mm long, curved hairs occur in *Hadena* spp. A histogram of proboscis length in the vectors shows two distinct peaks (Fig. 3 C). The higher peak results from the occurrence of *Autographa* spp., *Deilephila porcellus, Cucullia umbratica* and *Diachrysia chrysitis* and the lower mainly from *Apamea* spp. and *Polia* spp. Moths with proboscises 16–20 mm transported 72 % of all pollinia. Thus, moths with comparatively extreme morphology disperse only a small part of the pollen i.e. geometrids, some species of noctuids and the larger sphingids.

Pollinator behaviour

All visitors found but one are crepuscular or nocturnal insects. The exception was *Ochlodes venata* taken in sunshine not far from flowering *Platanthera chlorantha*. Activity of moths on flowers was seen to begin at dusk around 21.30 and observations so far suggest that visiting frequency is highest during the two following hours. Linear flight-paths between adjacent inflorescences regardless of direction of wind occurred in those few cases which could be observed. That linear approach is possible from a considerable distance was demonstrated by one *D. porcellus* at 22.20 on 8 July 1972. While visiting racemes of *Gymnadenia conopsea* R. Br. (Orchidaceae) the moth came to pass a small *Alnus*-bush behind which a *Platanthera chlorantha* was in flower. Immediately when optical contact was possible the moth was seen to abandon *G. conopsea* and from a distance of approximately 1.5 m fly directly to *P. chlorantha* and visit it. Such behaviour certainly indicates effective visual guidance of pollinators.

Normally visitors first work one of the lowermost flowers and then move upwards on the raceme. Speed of visitation differs greatly between moth-species. Sphingids and *Autographa* spp. are fast, *Apamea* spp. and geometrids much slower on flowers. Moths alight upon the flowers except sphingids which hover all the time while resting their front legs predominantly on the lateral sepals when forcing against the flower. The legs of sphingids are used in a crawling way when moving to the next flower. *Autographa* spp. flutter, "Schwirrenflug" (Schremmer 1941), or walk with vibrating wings on racemes. A similar behaviour as the last mentioned is practised by *Apamea* spp. and other noctuids but often their wings are held quite still in a flat position. Geometrids usually climb inflorescences slowly fluttering or with their wings

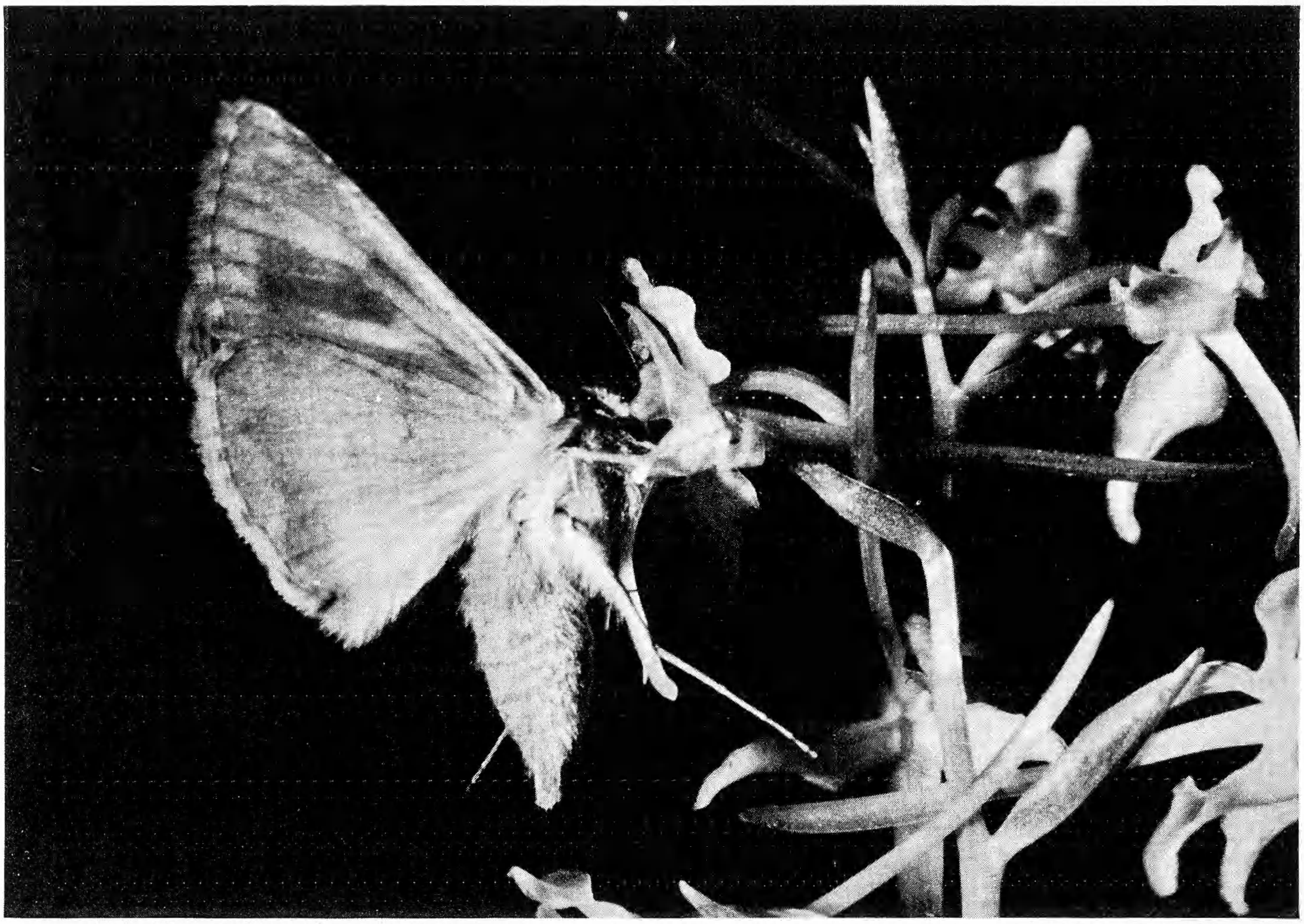

Fig. 7. The noctuid *Autographa gamma* in nectar extracting position on a flower of *Platanthera chlorantha*.

simply in an erect position. Flash photographs revealed that the proboscis is not completely coiled between visits within the same raceme and that its apex rapidly probes various flower surfaces before finding the entrance to the spur. Normally during nectar-sucking the thorax of the moth rests on the basal part of the labellum while the head is filling up the cavity formed by

Table 2. Moths carrying pollinaria of *Platanthera chlorantha* in the material of Lepidoptera deposited in the Swedish Museum of Natural History, Stockholm.

Species	Number of moths. Attached pollinaria within brackets	Province, locality, date and collector
Geometridae		
Aplocera plagiata (L.)	1 ♀ (1)	Gotland, Kyllej, 1954-07-09, E. Kjellander
Sphingidae		
Deilephila elpenor (L.)	1 ♀ (1)	Småland, Gårdsby, 1943-06-26, J. A. Z. Brundin
Noctuidae		
Cucullia umbratica (L.)	1 ♂, 1 ♀ (1, 4)	Småland, Bhn
Apamea monoglypha (Hufn.)	1 ♂ (1)	Öland, Halltorp, 1938-07-06, N. Bruce
Diachrysia chrysitis (L.)	1 ♂ (3)	Småland, Åseda, 1972-07-06, B. Gustavsson
Plusia festucae (L.)	1 ♂ (1)	Södermanland, Sandhamn, 1923-08-06, Ljungdahl
Autographa jota (L.)	1 ♀ (2)	Öland, Halltorp, 1938-07-25, N. Bruce
A. bractea (Den. & Schiff.)	1 ♂ (1)	Östergötland, Ulrika, 1965-07-28, G. Christiansson

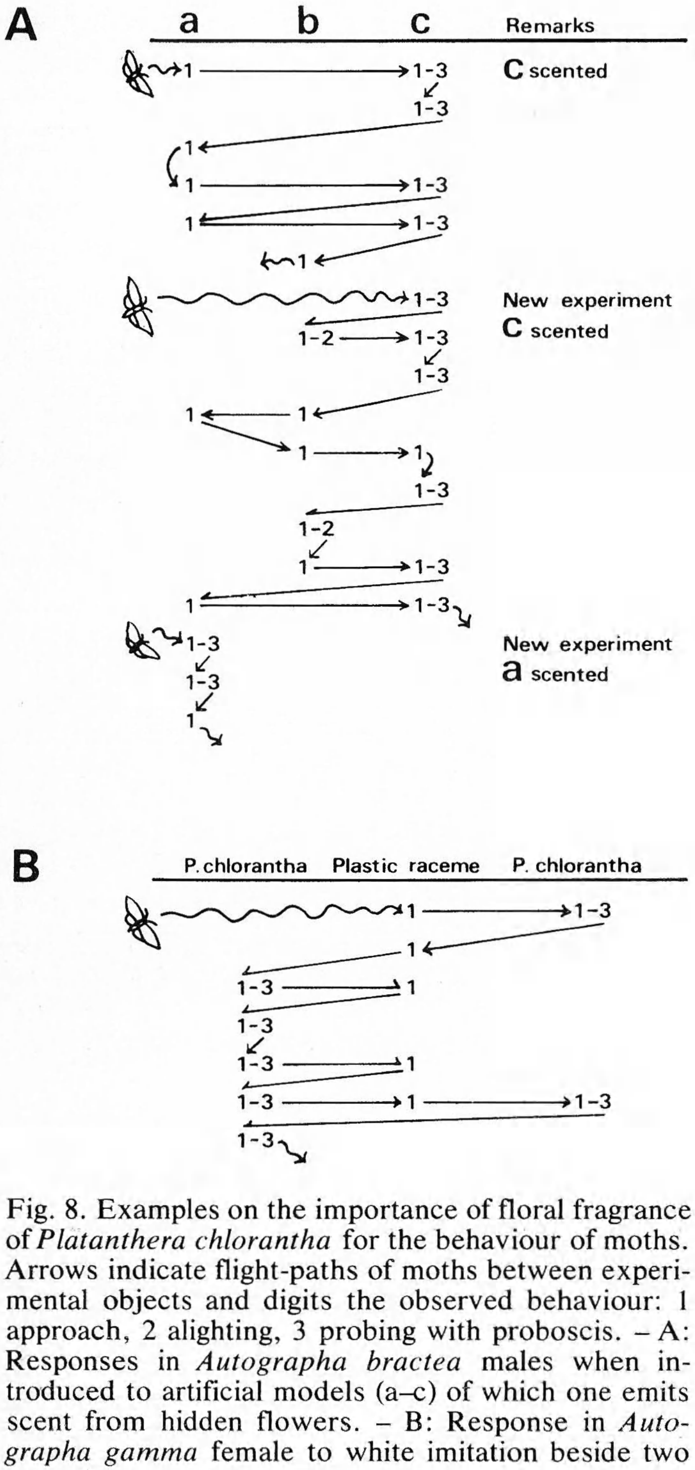

Fig. 8. Examples on the importance of floral fragrance of *Platanthera chlorantha* for the behaviour of moths. Arrows indicate flight-paths of moths between experimental objects and digits the observed behaviour: 1 approach, 2 alighting, 3 probing with proboscis. – A: Responses in *Autographa bractea* males when introduced to artificial models (a–c) of which one emits scent from hidden flowers. – B: Response in *Autographa gamma* female to white imitation beside two natural racemes.

the column (Fig. 7). The statement that in *Platanthera* "the labellum has lost its function as a landing-place and is only a visual aid" (Faegri & Pijl 1966) must then be modified. The frontal part of the head is tightly pressed to the spur-mouth obviously with help of the front legs which grasp behind the edges of the lateral sepals. Meanwhile middle and hind legs grasp the labellum or crawl on the sides for foothold. Sphingids and *Autographa* spp. can practically always be seen to take such proper position on flowers but other moths behave more irrationally. *Apamea* spp., *Hadena* spp. and geometrids often sit on various flower parts inserting their proboscises from the side or even from an upside down position. Normally the head is forced several times against the spur-mouth as if to penetrate deeper for more nectar. A similar pumping against deeply hidden nectar has been observed on *Melandrium album* (Mill.) Garcke visited by *Autographa gamma* (Schremmer 1941) and on *Lonicera periclymenum* L. visited by *Deilephila elpenor* (Brantjes 1973). Activity from *Autographa* spp. causes the flowers of *P. chlorantha* to quiver and vibrate. A violent visiting behaviour is practised by *D. porcellus*. This moth attacks flowers hovering against the spur with all its strength which even results in a swaying of the stalk (cf. Fig. 9 B).

Preliminary experiments show that the floral fragrance provokes behavioural responses in all four tested pollinator species. When offered artificial flowers the unscented were seldom alighted but often approached (Fig. 8 A). On the scented, however, approach was followed by alighting and eager attempts to feed. After landing the moths crept in circles or climbed around probing especially the filter-paper but also surfaces of the plastic with uncoiled proboscis. A scentless imitation of a white raceme was approached but not alighted when standing beside two inflorescences of *P. chlorantha* (Fig. 8 B). So far no behavioural differences between the moths used in tests have been detected.

Pollination and functional morphology

The efficiency of the pollination system in *Platanthera chlorantha* depends upon the behavioural response in visiting moths to the deep-situated food. This response is achieved by a special relation in length between mouth-parts and flower-spurs. According to behaviour observed, moths obviously try to extract as much nectar as possible from each flower. A visitor with a proboscis longer than the nectar tube receives no food stimulation for moving further into the flower as all liquid yet can be easily reached with its head outside (Fig. 9 A). Such visitors will not act as pollinators because of the positions of the reproductive organs of the flower. However, the head of a moth with

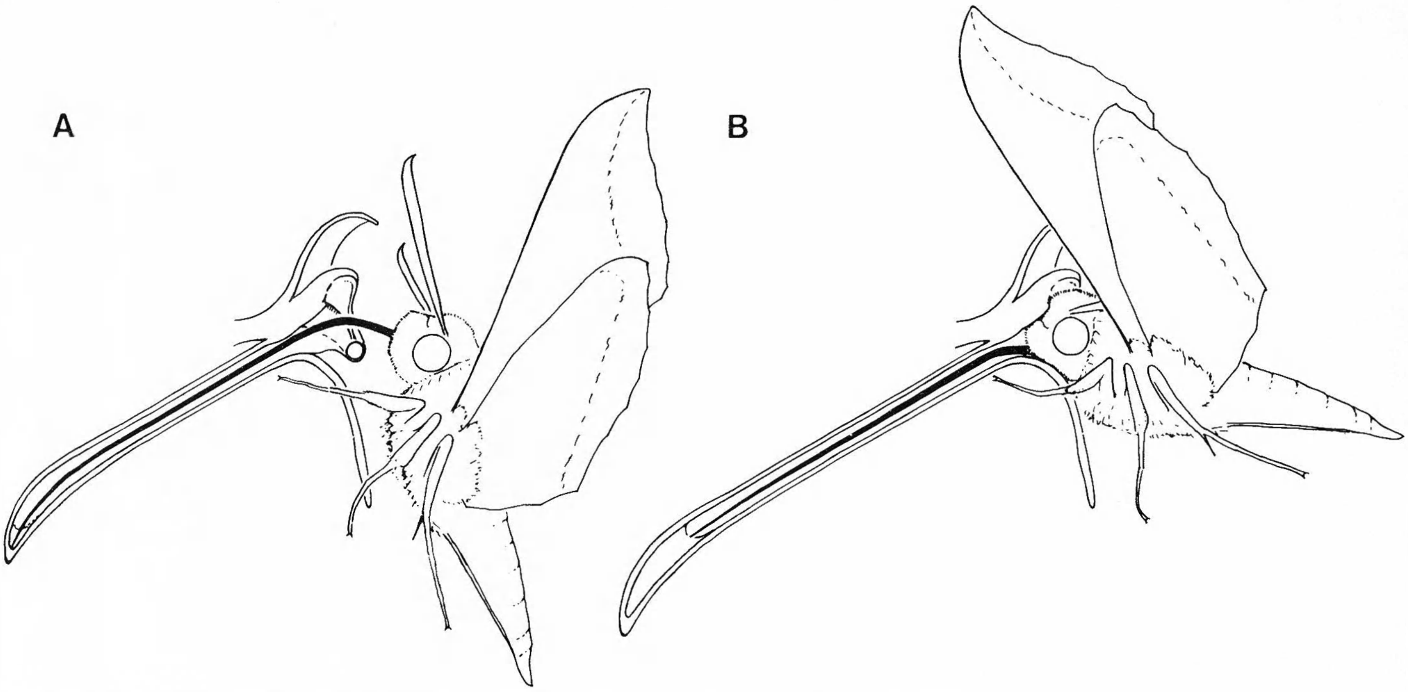

Fig. 9. Model of the functional adaptation mechanism of the flower-spurs in *Platanthera chlorantha* to the morphology and behaviour of the pollinators. – A: In short-spurred forms removal of pollinaria and deposition of pollen on the stigma are decreased as the head of the visitor is outside the flower. – B: Longer spurs induce forcing by the moth against the flower resulting in effective removal of pollinaria and pollination.

shorter proboscis must come into contact with these organs when forced against the spur-mouth (Fig. 9 B). Consequently selection has strongly favoured flower-types with longer spurs than the length of proboscis in the major group of pollen-vectors (cf. Fig. 3 A, C). Meanwhile these moths regularly reach the surface of the accumulation of nectar in the bottom of the spur (cf. Fig. 3 B, C). Moths with still shorter proboscises seldom reach the accumulation but are nevertheless frequent as visitors e.g. *Apamea* spp. Evidently such species are able to extract sufficient amounts of nectar through the ventral furrow in the spur.

When the viscid discs touch the sides of the face of a moth having a suitable proboscis the distribution of the easily detachable hairs and scales covering frontal parts of the head becomes of great importance (Fig. 10). Experiments with dead moths revealed that if the discs touch such surfaces they will not attach effectively. The results are then often displaced or only partly withdrawn pollinaria with numerous hairs or scales left on the discs. Such traces are not seldom seen on flowers in nature. If a pollinarium is all the same removed it is easily scrabbled off by the insect. Pollen-vectors collected never had viscid-discs affixed solely to hairs and only a few times to the outside of the palps. Almost all visitors had them adhered to their eyes or to the surfaces of pollinaria earlier deposited on the same eye. Exceptions were *Hyles gallii* who had 6 cemented on worn parts of its palps, one *Deilephila porcellus* with one dorsally on abdomen and one *Autographa jota* carrying two on its front legs. A comparison between the width across the head of pollinators and the distance between the viscid-discs demonstrates the adaptation of the flowers to the narrow morphologically favourable zone on the head of moths (cf. Fig. 3 D, E). Countings show that moths frequently transport only one pollinarium and that the difference between the number on the eyes of each moth often is one (Fig. 11). Apparently only one viscid-disc in most cases will adhere during a visit. Darwin (1862) came to the same conclusion after counting the number of pollinaria removed from inflorescences. In later visits, viscidia touching the same side of head will be restricted to unoccupied surfaces of the eye or to various parts of previously adhered pollinaria. As the number on a keen visitor increases, deposition occurs more and more irregularly finally with caudicles protruding in all directions. The highest number seen affixed to the same side was 26

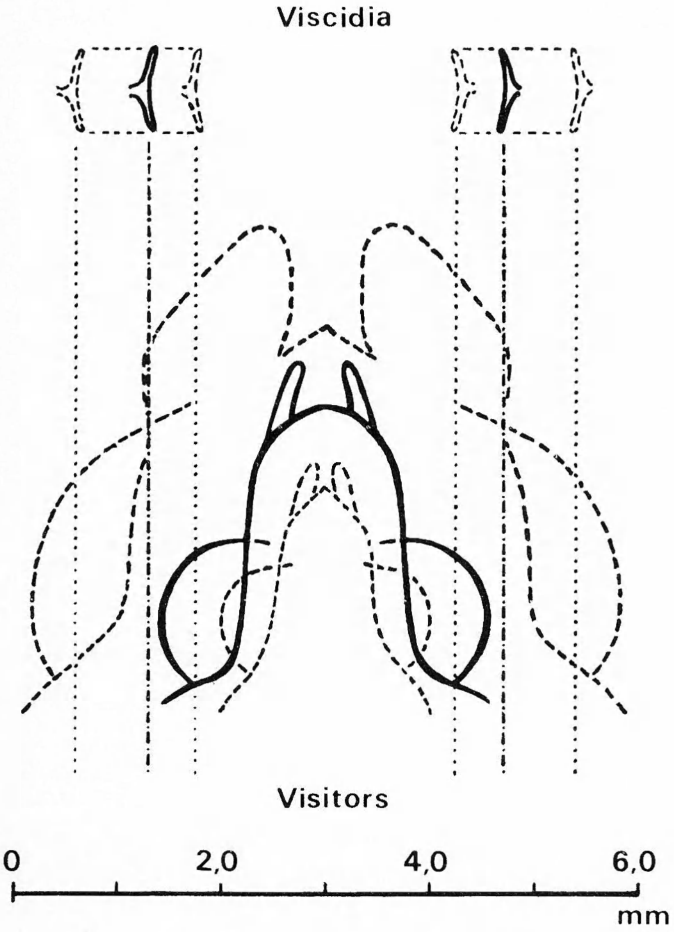

Fig. 10. Adaptation of the distance between viscidia in *Platanthera chlorantha* to the head of visiting moths. Continuous lines indicate mean position of viscidia and the mean dimension of the head of a pollinator (*Autographa* sp.). Lines of short dashes mark the extreme positions of viscidia and the heads of the largest visitor *(Hyles gallii)* and the smallest *(Aplocera plagiata)*. Note that the large sphingid will probably touch the discs with its palps.

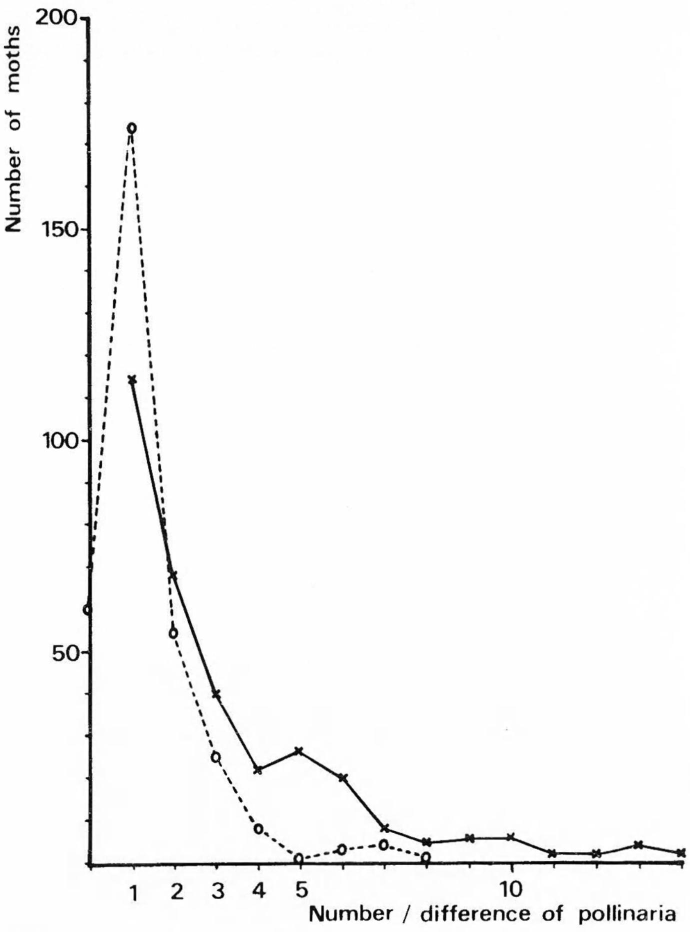

Fig. 11. Number of pollinaria of *Platanthera chlorantha* on moths and differences of numbers between the sides of face (continuous and dotted line respectively). Based on material from Öland only. Extremes are excluded.

and to a single moth 46 (both on *A. jota*). Relatively big-headed visitors as *Deilephila elpenor* receive viscidia on the frontal parts and edges of the eyes. On even larger species e.g. *H. gallii* deposition may occur on the palps (Fig. 10). The attachment found on *Hyloicus pinastri* (Rogenhofer 1890) is in good accordance with these observations. As noted above a good many pollinaria are also transported by moths with hairy eyes. These hairs are not easily loosened but become bent aside as the moth forces against the column. The adhesive matter on the discs may then reach the eye-surfaces between the hairs cementing it all together.

A freshly withdrawn pollinium rotates through an angle of approximately an eighth of a circle in about one minute. Artificial removal of pollinaria using dead moths indicated that pollination can hardly occur before the caudicle has performed most of this movement. As visitors seldom spend more than 30 seconds on the same raceme rotation is not completed before the moth leaves for another plant just like Darwin suggested. However, "abnormal" behaviour of moths and misplaced viscidia may often cause geitonogamy as well as misdirected pollinia that never will effect successful deposition of pollen on a stigma. Thus, in many cases the mechanism may fail.

Application of pollinia on the stigma occurs when the moth forces against the spur-mouth, i.e. only when the proboscis is shorter than the spur (Fig. 9). The adhered layer of massulae appears as a yellow mark on the sticky surface often together with detached hairs and scales from the head of the visitor. Effective deposition is facilitated by the length and stiffness of the caudicles which hold the pollinia just beyond the palps. Their length is obviously adapted for this purpose (x̄ 1.9 mm, SD 0.3 mm, n 126). Comparisons of the caudicle and the sizes of the palps of moths suggest that a good effect is received with most medium-sized moths as vectors.

No spontaneous mechanism accomplishing self-pollination was detected in enclosed flowers (n 76) or otherwise observed.

Fruit set

Development of capsules and seeds occurs only after pollination (n 115). Artificial self-pollination seems to result in normal fruits and embryos (n 23) not differing from those obtained from cross-pollination (n 16). Irregular and incomplete fruit-setting indicates entomogamy exclusively. Further evidence of the effect of visiting insects was the higher fruit set in inflorescences standing free compared with those concealed by surrounding vegetation. Pollinating moths on Öland often produce over 50 % fruits (Table 3). In exposed sites, however, in summers with exceptional drought as 1973, many racemes fade away without developing capsules. In Uppland towards the northern distribution limit of the plant a low value was found which can not be explained by unfavourable weather conditions. Probably it is an effect of lower populations of anthophilous moths compared to Öland.

Table 3. Fruit set of *Platanthera chlorantha*. Calculation represent mean of individual values (no. of capsules/no. of flowers per plant).

Locality	Biotope	Year	No. of plants	Fruit set (%)
Uppland				
Häverö	Deciduous wood	1976	58	30.9
Öland				
Tävelsrum	Deciduous wood	1975	34	78.3
Tävelsrum	Deciduous wood	1976	23	47.8
Tävelsrum	Slope with *Juniperus*	1973	43	30.8
Tävelsrum	Slope with *Juniperus*	1976	59	68.9
Ullevi	Glades among *Corylus*	1975	24	78.1
Skogslund	Coniferous wood	1976	28	40.6
Halltorp	Deciduous wood	1976	27	55.7

Discussion

The pollinators found belong to the most common anthophilous moths not only on Öland but in Scandinavia and western Europe. Except *Hada nana* and *Hyloicus pinastri* the species reported from other areas take part in pollination of the plant also on Öland. *Deilephila porcellus*, earlier found in France and Norway (Table 4), and *Cucullia umbratica* and *Autographa pul-*

Table 4. Previously reported pollen-vectors of *Platanthera chlorantha*. Asterisks refer to observations of pollinaria not attributed by the authors to *Platanthera chlorantha* but probably derived from this species.

Species	Number of moths	Remark on pollinaria	Author	Country
Geometridae				
Aplocera plagiata (L.)*	1	Two on eyes, "d'un *Platanthera*"	Girard (1864)	France
Sphingidae				
Hyloicus pinastri (L.)*	1	Sticking to palps	Rogenhofer (1890)	Germany
Deilephila porcellus (L.)*	1	Several sticking to eyes	Robin (1853)	France
D. porcellus	1	One affixed to eye	Mehl (1972)	Norway
Noctuidae				
Hada nana (Hufn.) (*Hadena dentina* (Den. & Schiff.))	1	"one eye blinded by a disc"	Darwin (1862)	Great Britain
Cucullia umbratica (L.)	7	Attached to eyes	Marshall (1872)	Great Britain
*C. umbratica**	1	One affixed to eye	Meldola (1909)	Great Britain
C. umbratica	1	One on each eye	Mehl (1972)	Norway
Plusia festucae (L.)*	2	Photograph showing one on eye	Stewart (1910)	Great Britain
Autographa pulchrina (Hw.) (*Plusia v-aureum* (Hb.))	1	One adhered to edge of eye	Darwin (1862)	Great Britain
A. pulchrina	3	Eight sticking to eyes	Mehl (1972)	Norway

chrina, recorded in Britain and Norway, regularly act as pollinators. All observations indicate that noctuids and perhaps small sphingids play the major role in the dispersal of pollen. Evidently, the same species are involved. During the flowering period numerous anthophilous species are in flight and will co-operate to a high pollination rate. The dominance of *Autographa jota* as a vector on Öland may be a matter of local occurrence limited to this island. However, a comparison between the distribution areas of *P. chlorantha* and *A. jota* in the Nordic countries reveals a striking resemblance (cf. Hultén 1971 and Nordström et al. 1969). Moreover, flowering and flight period coincide in southern Sweden. These facts may suggest some degree of coevolution or dependence between the two. As the plant obviously is strictly entomogamous the production of fruits probably reflects the total effect of the pollinating insect-fauna. Consequently, as the number of anthophilous moth-species decreases towards the north in Europe, fruit set should follow the same pattern. From Germany 72 and 80 % and from Switzerland 89.4 % capsules have been reported (Detto 1905). This together with data presented here support the expected trend.

Morphological comparisons between the plant and its pollinators illustrate the stabilizing selection of flower structures which is effected by a group of mainly medium-sized nectar-competing moths having proboscis about 16–20 mm long, viz. *Autographa* spp., *Diachrysia chrysitis*, *C. umbratica* and *D. porcellus*. Of these moths, the last species is by far the heaviest and probably requires a relatively high energy intake from nectar offering plants for its life-processes. However, the competing capability of *D. porcellus* is certainly high owing to a pronounced early flight after sunset. Thus the crepuscular visiting of various species of flowering plants by this moth may be regarded as an adaptation to efficient utilization of the available resources.

Morphology itself excludes only the largest European sphingids from being effective pollinators of *P. chlorantha* but not from consuming its nectar. Despite their strong potential ability in extracting nectar the plant has not adapted to these moths which is worth special attention as regular visiting by them would disturb constancy (restricted visits to a single plant-species) in smaller moths and favour evolution of strictly sphingophilous flower-types. On Öland, for example, the very common *Sphinx ligustri* L. (proboscis 36–42 mm) would certainly be destructive if it were a frequent visitor. Adaptation to this moth would require much larger flowers with spurs approximately 40–50 mm long. It looks therefore as if selection has favoured an anthecological specialization in which such visitors are discriminated. Longevity and reproduction in the larger group of moths with medium-long proboscis are then supported. Such selection of visitors by the plant can be explained if the fragrance does not release behavioural response in the larger sphingids (see below). It is also possible that competition from visitors with longer proboscis is reduced because nectar can be successfully extracted by other moths through the ventral furrow in the spur. Regular food stimulation would then be secured for moths with shorter proboscis and suffice for their continued visiting. In fact this phenomenon seems to be demonstrated by *Apamea* spp. and other visitors with very short proboscis which are frequent despite the dominance of *Autographa* spp. etc. Probably, thus, the presence of the nectar yielding furrow considerably enlarges the number of visiting moth-species and indirectly also the dispersal of pollen. The opinion that the spur-length itself stratifies the visitors (cf. Percival 1965) is not supported.

The observed feeding activity of pollinators during the first hours after dusk is in accordance with that found in hawkmoth pollinated *Oenothera* (Gregory 1963–64). Reasonably the feeding time is determined by the duration of "the feeding mood", a physiological state in the moth when stimuli from specific environmental chemicals or reflected light emanating from food sources dominate the releasing mechanism in the central nervous system for orientation and feeding reactions. As shown by gas chromatography, the scent emission in *P. chlorantha* is probably quantitatively adapted to the feeding time of the pollinators. Energy expenditure in the synthesis of fragrance compounds is then minimized. The functionally important components should probably be looked for among those showing periodicity. As several esters of benzoic and salicylic acid since long have been known for being "attractive" to many species of sphingids in North America (Morgan & Lyon 1928), attention should be directed to these compounds. On Öland *Platanthera bifolia,* which produces relatively much higher amounts of such esters than *P. chlorantha,* is intensely visited by large sphingids especially *S. ligustri* (Nilsson unpubl.). The comparatively low concentration of benzoates emanating from *P. chlorantha* perhaps do not release orientation or visiting behaviour in these moths. This hypothesis has not yet been experimentally verified.

Experiments illustrated that orientation can be visually guided as scentless objects are approached. This is in good accordance with the linear flight of moths between racemes observed in nature. That optical stimuli are important for the visiting of moths is supported also by the lower fruit set noted for concealed racemes of *P. chlorantha.* The colour of the flowers probably favours optical guidance of pollinators over long distances. That light colour in darkness gives the strongest optical stimuli has been shown experimentally with *Hyles lineata* (F.) (Sphingidae) viz. selective visiting occurs to the most contrasting combinations (white on black background) (Knoll 1925). Slow energy-consuming seeking flight is then minimized allowing pollinators to visit many flowers in a short time. However, optical orientation itself might be released and stimulated by scent present. It was early reported that tests with *Deilephila elpenor* suggested specific scents to lower the treshold for release of optically oriented behaviour (Knoll 1927). Later it was demonstrated that not only newly hatched but also experienced but untrained *Autographa gamma* and sphingid-species do not orient to scentless artificial or enclosed natural flowers unless scent is present in the air (Schremmer 1941, Brantjes 1973). Many arguments support that specific odours can act as sign stimuli in the releasing mechanism of the feeding behaviour of the flower visiting sphingids (Brantjes 1973). The floral fragrance of *P. chlorantha* might possess such ability in a restricted number of moth-species. Perhaps, it also releases anemotaxis (orientation to an air current) in specific moths (cf. Kennedy & Marsh 1974).

Experiments furthermore indicated that alighting is released by scent. Since the atmosphere in tests was scented and alighting seldom did occur on unscented "flowers" the moths seem to have ability for successive and simultaneous perception of the gradient in short distances. The landing response appears then to be stimulated by the combined action of visual cues and higher odour concentration as revealed for sex pheromones (Farkas et al. 1974). The number of landings on objects by *Hadena bicruris* (Hufn.) is proportional to the concentration of the volatile constituents in extracts of flowers of *Melandrium album* (Brantjes 1976). Alighting and feeding will probably lead to constancy on the plant. That such acquired behaviour as constancy can be based on scent has been shown with *A. gamma* (Schremmer 1941). According to tests, searching for food after alighting as well as probing with the proboscis seem strongly stimulated by the scent. However, tested moths were taken from the field and might have been experienced on various flowers. Thus it can not be concluded whether the behaviour observed was due to innate capability or learning. In any case the importance of the scent is evident.

To what extent adherence of viscidia affects function of the eyes of pollinators is not known. A fascinating thought is that vectors become more and more restricted to olfaction in locating food sources due to increasing blindness. Finally plants that produce chemical compounds capable of releasing orientational response can be visited only i.e. *P. chlorantha* and perhaps some others. A forced high visiting by those moths carrying much pollen and possessing the acute chemical sense would then arise. In all probability, however, such dependence would have negative consequences for the insects. If viscidia cause considerable behavioural disturbances, selection should favour pollinator unspecificity i.e. exploiting of many moth-species as vectors to disperse the effects. As shown, pollinating species are numerous and deposited pollinaria often few, mostly only one.

The nocturnal chemical and optical stimuli from *P. chlorantha* compete with those from other nectar plants many of which depend on moths for pollination. Especially species of Silenoidae (Caryophyllaceae) are regularly visited by most of the species pollinating the orchid (cf. Wahlgren 1941). On Öland competition from *Gymnadenia conopsea* is evident and rather often pollinaria of the two orchids can be found deposited on the same moth (Nilsson unpubl.)

The small intraspecific variation in *P. chlo-*

rantha is probably a result of morphological uniformity in the pollinating group of moths. The end-products of intraspecific selection would then form not too diverging aggregates. Consequently, local adaptations to specific pollinators, "anthecotypes", can be difficult to detect. Another important factor acting against race formation might be the mobility of pollen-vectors. Some of them are strong flyers and migrate over vast areas, e.g. *A. gamma* (Nordström et al. 1969). Such visitors may facilitate gene-exchange even between distant plant populations.

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Thirteenth International Botanical Congress – preliminary announcement

W. J. Cram

The Thirteenth International Botanical Congress, sponsored by the Australian Academy of Science, will be held in Sydney, Australia, 21–28th August, 1981.

Programme. The programme will consist of twelve sections – molecular, metabolic, cellular and structural, developmental, environmental, community, genetic, systematic and evolutionary, fungal, aquatic, historical, and applied botany. There will be plenary sessions, symposia, and sessions for submitted contributions (papers and posters). Chairman of the Programme Committee: Dr L. T. Evans.

Field trips will include visits to arid and semi-arid regions, eucalypt forest, rain forest, heath, coastal vegetation (e.g. Great Barrier Reef, mangroves) etc., and specialist trips. Chairman of the Field Trips Committee: Prof. L. D. Pryor.

First Circular, containing details, will be mailed in August, 1979. Send your name and full address, preferably on a postcard, to ensure your inclusion on the mailing list.

Enquiries should be sent to the Executive Secretary, Dr W. J. Cram.

Congress address: 13th International Botanical Congress, University of Sydney, N.S.W. 2006, Australia.

Revision of Dorstenia sect. Nothodorstenia (Moraceae)

C. C. Berg

Berg, C. C. 1978 03 31: Revision of Dorstenia sect. Nothodorstenia (Moraceae). *Bot. Notiser 131:* 53–66. Stockholm. ISSN 0006-8195.

The African genus *Craterogyne* Lanjouw has to be united with *Dorstenia* L. Most species of *Craterogyne* can be included in *Dorstenia* sect. *Nothodorstenia* Engl. A revision of this section is presented. 5 species have been accepted, viz. *D. elliptica* Bureau, *D. djettii* J. L. Guillaumet, *D. oligogyna* (Pellegrin) C. C. Berg, *D. africana* (Baillon) C. C. Berg and *D. kameruniana* Engler.

C. C. Berg, Institute for Systematic Botany, State University of Utrecht, Trans. II, Heidelberglaan 2, Utrecht, Netherlands.

In 1875 Baillon described *Trymatococcus africanus* as the second species of a genus established by Poeppig & Endlicher (1838) for material collected in Peru. A few more African species were described in *Trymatococcus* by Engler (1898, 1902), De Wildeman (1903–1906) and Pellegrin (1929). In 1935 Lanjouw set the African *Trymatococcus* species apart in a new genus *Craterogyne,* in which he recognized 4 species. Hallé & Aké Assi (1967) added a fifth species by transferring *Dorstenia djettii* Guillaumet (1965), placed by the author near *Dorstenia elliptica,* the only species classified under *Dorstenia* sect. *Nothodorstenia* Engler.

In a study of African Moraceae (Berg 1977) it proved impossible to maintain *Craterogyne* as a distinct genus. The species of *Craterogyne* should be placed in *Dorstenia* sect. *Nothodorstenia,* with the exception of *C. dorstenioides* (Engl.) Lanjouw which belongs to another group of *Dorstenia* species (cf. Berg & Hijman 1977).

Material from the following herbaria was used: ABI, B, BM, BR, COI, E, FHI, FHO, G, HBG, K, L, LISC, LISU, P, S, U, UPS and WAG.

The collections on which the present study is based are included in an Index of exsiccatae also comprising the collections examined during revisional work of other African Moraceae (Berg 1977). Requests for the index can be sent to the author.

Habit

Most herbaceous to suffrutescent *Dorstenia* species inhabiting the forest floor have creeping rhizomes from which erect or ascending, mostly unbranched twigs with spirally arranged leaves arise. *D. elliptica,* the smallest and the least woody of the five species of sect. *Nothodorstenia* fully matches this habit. The other four species form branched or unbranched shrubs and possibly have rhizomes only when young. *D. africana* and *D. kameruniana* form shrubs with sympodial growth. The medium-sized leaves are arranged in spirals on vertical parts and in two rows on horizontal parts of the stem and on the plagiotropic branches (cf. Hallé & Oldeman 1970). This habit is also found in *D. turbinata* Engl. and allied frutescent species (cf. Berg & Hijman 1977). *D. djettii* and *D. oligogyna* have unbranched stems (in *D. oligogyna* up to 2.5 m tall) bearing relatively large leaves (in *D. oligogyna* up to 50 cm long) in spirals. Because of its manifest monocaul habit *D. oligogyna* can be ranked among the type of rosette trees occurring in the lower stories of rain forests.

Inflorescence

The inflorescences are borne in the axils of the leaves on short-shoots bearing stipules modified into scales, and forming successively or almost simultaneously several inflorescences. The inflorescences bear bracts which in texture and shape are reminiscent of the stipules. These bracts occur in 2–3 rows on the margin of the receptacle, but occur in *D. elliptica, D. djettii* and *D. oligogyna* also lower on the receptacle even onto the peduncle. *D. djettii* is exceptional in *Dorstenia* because of the presence of interfloral peltate bracts. These bracts are caducous and can only be found in young inflorescences.

The inflorescences are bisexual; they have a single pistillate flower in *D. africana, D. kameruniana* and *D. oligogyna,* mostly more than one in *D. djettii,* and always several in *D. elliptica.*

The greater part of the perianth of the pistillate flower is fused with the surrounding tissue which probably consists of fused pedicels of the staminate flowers. As in many *Dorstenia* species of other sections the perianths bear swollen, papilla-like hairs. Such hairs do not occur in *D. djettii.* The stamens are inflexed in the bud. At anthesis, they remain inflexed or straighten gradually. The filaments are short and often basally swollen. *D. djettii* have relatively long and slender filaments.

Fruit

The fruit is more or less distinctly stipitate and has a white fleshy dehiscent exocarp which pushes outward the endocarp body by tearing the upper surface of the infructescence.

The endocarp body is not ejected as in microspermous *Dorstenia* species. In these species the endocarp is often tuberculate. It is smooth in the species with larger seeds. In the microspermous *Dorstenia* species there is usually endosperm and a simple embryo with flat cotyledons and a long radicle. In the large-seeded species of sect. *Nothodorstenia,* endosperm is lacking and the embryo has thick cotyledons unequal in size, and a short radicle. *D. elliptica* with its relatively small seeds is transitional to the microspermous species because of the rather thin cotyledons, the rather long radicle, and the presence of remnants of endosperm.

Distribution

The species of sect. *Nothodorstenia* are components of the undergrowth of forests. *D. africana, D. elliptica* and *D. oligogyna* are confined to the area of rain forests ranging from SE Nigeria to the Lower Congo River (Fig. 1 A–C), in which area most of the rain forest species of *Dorstenia* occur (cf. Berg & Hijman 1977). *D. djettii* is a rather rare species in rain forest areas in West Africa (Fig. 1 A). *D. kameruniana* is the only species of the section which also occurs in drier types of forest. As in many Moraceae adapted to drier conditions, the area of *D. kameruniana* is much more extensive than those of the rain forest species (Fig. 1 D; cf. Berg 1977).

Systematic position and relationships

Engler's (1898) main reason for distinguishing section *Nothodorstenia* was the presence of bracts not only on the margin but also lower on the receptacle of the inflorescences of *D. frutescens (=D. elliptica),* the only species classified under that section since.

This arrangement, and the more advanced situation in which the bracts are placed in several rows on the margin of the receptacle only, is one of the characters uniting the five species here included in sect. *Nothodorstenia.* Not only the arrangement, but also the shape, texture, and venation of the bracts, which still resemble the stipules in these features, are differentiating characters. The predominantly woody habit and the presence of relatively large seeds and the small number of pistillate flowers in the inflorescence are shared with a small group of African *Dorstenia* species comprising, e.g., *D. turbinata* Engl., *D. scaphigera* Bur. and *D. dorstenioides* (Engl.) M. Hijman & C. C. Berg (=*Craterogyne dorstenioides*). In this group, however, the margin of the receptacle bears a single row of appendages which are not reminiscent of stipules.

D. djettii is the least advanced species in the section. *D. oligogyna* is very closely related to *D. djettii.* Without inflorescences one cannot even tell them apart. *D. elliptica* is less closely, yet distinctly related to *D. djettii* (cf. Guillaumet 1965). *D. africana* and *D. kameruniana* can be regarded as the most advanced species in the section.

The presence of interfloral bracts, and, to a lesser degree, the absence of papilla-like hairs on the perianth, and the relatively long stamens

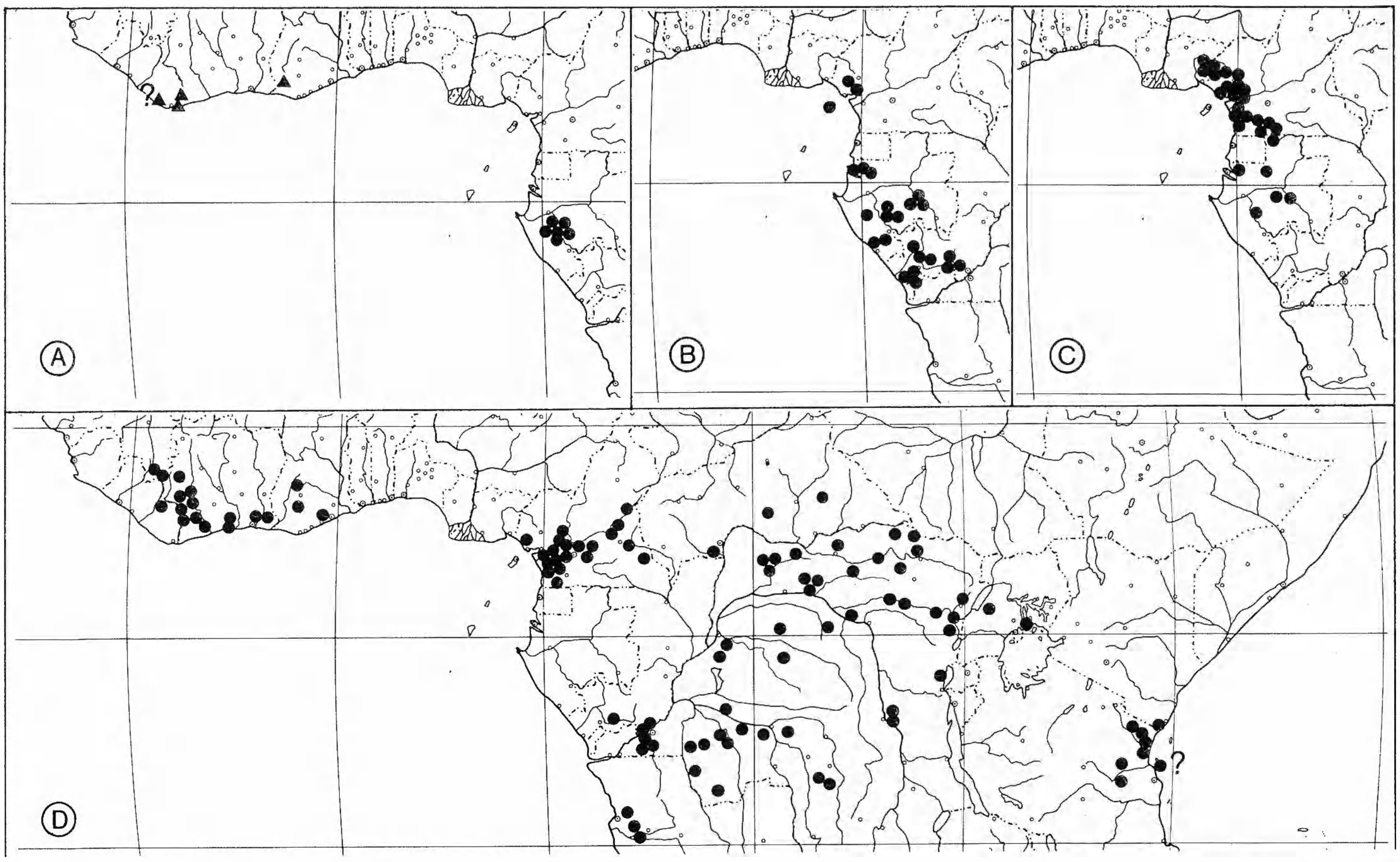


Fig. 1. Distribution of the species of *Dorstenia* sect. *Nothodorstenia*. – A: ▲ *D. djettii*, ● *D. oligogyna*. – B: *D. elliptica*. – C: *D. africana*. – D: *D. kameruniana*.

set *D. djettii* apart in the genus, and, moreover, link *Dorstenia* with other genera of the Dorstenieae sensu Berg (1973). Sect. *Nothodorstenia* appears to contain the morphologically least advanced species of *Dorstenia*.

Dorstenia L. sect. **Nothodorstenia** Engler

Engler, Monogr. Afr. Pfl. 1, Moraceae: 7, 10, 1898; Rendle in Prain, Fl. Trop. Afr. 6 (2): 25, 1916. – Type species: *Dorstenia frutescens* Engler (=*Dorstenia elliptica* Bureau).

Craterogyne Lanjouw, Rec. Trav. Bot. Néerl. 32: 272, 1935. – Type species: *Craterogyne africana* (Baillon) Lanjouw (=*Dorstenia africana* (Baillon) C. C. Berg).

Shrubs or undershrubs with branched or unbranched stems. Leaves in spirals or distichous on branches, pinnately veined; stipules free, semi-amplexicaul or lateral. Inflorescences often in groups on short-shoots in the axils of the leaves, bisexual, rarely only staminate, turbinate to (convexly) discoid, pedunculate; short bracts in 2–3 rows on the margin of the receptacle, sometimes also lower onto the peduncle; staminate flowers numerous; perianth 2–3(–4)-parted, mostly bearing papilla-like hairs; stamens 2–3(–4), inflexed in the bud, at anthesis still more or less bent or curved; anthers latrorse, connective broad to narrow; pistillode lacking or minute; pistillate flowers embedded in the receptacle, solitary in the centre of the receptacle or up to 8; the upper free part of the perianth 2–3-lobed, mostly bearing papilla-like hairs; ovary free, style bifid; in fruit the receptacle enlarged, usually green; exocarp white, fleshy, dehiscent, pushing upward the endocarp body, endocarp body 4–10 mm in diameter, smooth; testa with a thickened vascularized part below the hilum, endosperm mostly absent, cotyledons thick, free, unequal or equal.

Key to the species of Dorstenia sect. Nothodorstenia

1. Stipules subulate, lateral .... 1. *D. elliptica*
– Stipules with a broad base, semi-amplexicaul 2

2. Branched shrubs; leaves on the branches distichous; stipules usually shorter than 10 mm, only with the midrib prominent 3
– Usually unbranched shrubs; leaves on the stems in spirals; stipules usually longer than 10 mm, prominently parallel-veined 4
3. Leaf margin usually entire; inflorescences in groups of 2 or more, turbinate; peduncle 5–27 mm long .... 4. *D. africana*
– Leaf margin usually dentate to lobed; inflorescences often solitary, discoid to broadly turbinate; peduncle 2–9 mm long .... 5. *D. kameruniana*
4. Inflorescences with 1–8 pistillate flowers, (initially) with peltate interfloral bracts; Liberia to Ghana .... 2. *D. djettii*
– Inflorescences with 1 pistillate flower, without interfloral bracts; Gabon .... 3. *D. oligogyna*

1. **Dorstenia elliptica** Bureau – Fig. 2

Bureau in De Candolle, Prodr. 17: 271, 1873; Engler, Monogr. Afr. Pfl. 1, Moraceae: 12, 1898; Rendle in Prain, Fl. Trop. Afr. 6 (2): 31, 1916; Guillaumet, Adansonia Ser. 2, 5: 99, 1965. – Type: Mann 64, Fernando Póo (P; isotype K).

Dorstenia frutescens Engler, Monogr. Afr. Pfl. 1, Moraceae: 12, t. 2B, 1898; Engler, Pflanzenw. Afr. 3 (1): 23, t. 12E, 12F, 1915. – Lectotype: Preuss 384, Cameroun, Barombi (B; isotype K).

Plants up to 1.5 m tall, with a creeping rhizome and erect or ascending stems with a woody base, unbranched or (sometimes?) with spreading branches. Leafy twigs 1.5–4 mm thick, sparsely to rather densely puberulous, partly with uncinate hairs.

Leaves (at least on the stem) in spirals, (elliptic to) oblong to lanceolate, mostly tending to obovate or oblanceolate, (3–)7–28 cm long, (1–)2.5–9 cm broad, chartaceous, acuminate or sometimes tending to obtuse or acute, at the base attenuate to acute; margin entire to faintly repand or faintly dentate, on both sides almost glabrous or, especially at the base, sparsely puberulous with uncinate hairs, glabrescent; (6–)10–16(–19) pairs of secondary veins, without parallel tertiary veins; petioles (2–)5–12(–20) mm long, puberulous with uncinate hairs; stipules subulate, 3–17 mm long, sparsely puberulous with straight hairs to almost glabrous, subpersistent.

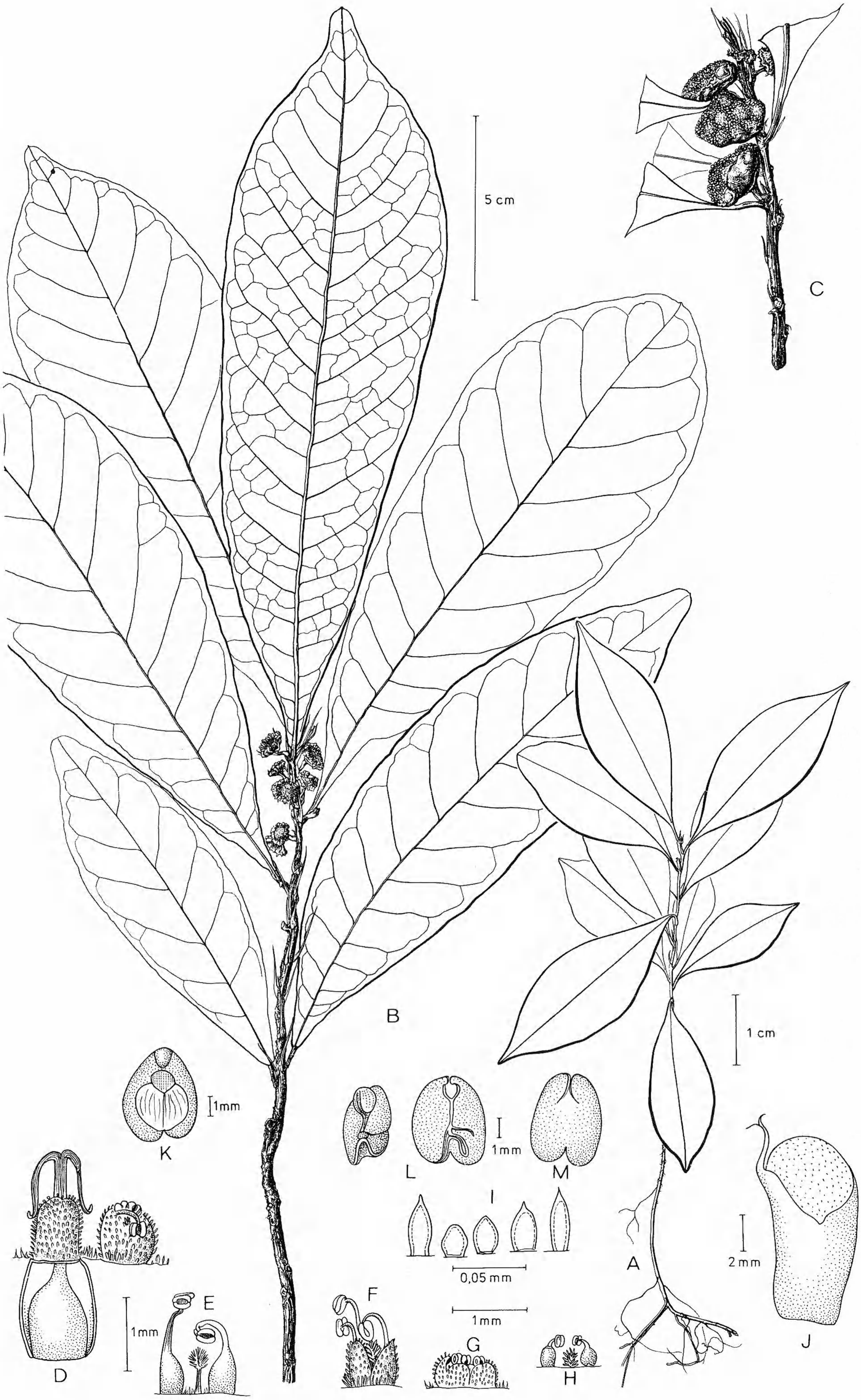
Inflorescences one, two, or occasionally a few simultaneously in the leaf axils, broadly turbinate to discoid, 5–11 mm in diameter, usually brownish to purplish; peduncle 4–6 (in fruit up to 10) mm long, puberulous, partly with uncinate hairs, like the surface of the receptacle; bracts ovate to lanceolate to subulate, up to 3.5 mm long, scattered on the outer surface of the receptacle, on the margin crowded, in c. 2 rows; perianth of the staminate flower (2–)3(–4)-parted, 0.2–0.8(–1.0) mm high, puberulous with minute globose to oblongoid papilla-like hairs; stamens (2–)3(–4), filaments 0.4–1.6 mm long, glabrous, the lower part swollen, anthers 0.1–0.25 × 0.1–0.25, connective narrow; pistillode up to 0.8 mm long, more or less penicillate; pistillate flowers (1?–)3–7; free part of the perianth tubular, 0.4–0.8 mm high, entire to faintly 3–4-lobed, puberulous with minute globose to oblongoid papilla-like hairs; style c. 1.5 mm long, stigmas 0.2–1.0 mm long.

Infructescences broadly turbinate to convexly discoid, 1–2 cm in diameter; fruit ellipsoid, c. 8 × 6 mm; endocarp body subglobose, c. 4–5 × 5–6 mm, endocarp crustaceous (to coriaceous?); seed c. 5 × 4 mm, testa with a thickened but not distinctly vascularized part below the hilum; embryo with rather thin, folded, unequal cotyledons, the inner one almost completely enclosed by the outer one, radicle rather long, curved, remnants of endosperm in the median split of the embryo.

Distribution (Fig. 1 B). From western Cameroun to Angola-Cabinda, and in Fernando Póo; in the undergrowth of rain forests, usually in moist places, often along streams, locally frequent. About 65 collections have been examined.

Flowering probably throughout the year, possibly mainly from September to April. Fructification normal.

Fig. 2. *Dorstenia elliptica.* – A: Leafy stem with rhizome (Le Testu 7490). – B: Leafy stem with inflorescences (Le Testu 1359). – C: Infructescences (Onochie 9301). – D: Pistillate and staminate flower. – E: Stamens and pistillode (Le Testu 1359). – F: Staminate flower (Le Testu 7511). – G: Staminate flower. – H: Stamens and pistillode. – I: Swollen hairs of the tepals. – J: Fruit. – K: Seed. – L, M: Embryo (Daramola 29834).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H

The staminate flowers have somewhat longer perianths and filaments in specimens from Gabon than in specimens from Cameroun.

2. **Dorstenia djettii** J. L. Guillaumet – Fig. 3

J. L. Guillaumet, Adansonia Ser. 2, 5: 99, t. 1, 1965. – *Craterogyne djettii* (J. L. Guillaumet) N. Hallé & Aké Assi, Adansonia Ser. 2, 7: 390, 1967. – Type: Guillaumet 744, Ivory Coast, near Tabou (P; isotype ABI).

Plants up to 1 m tall, with unbranched stems with a woody base. Leafy twigs 2–5 mm thick, almost glabrous, periderm peeling off in ribbon-shaped flakes.

Leaves (at least on the stems) in spirals, tending to obovate, oblanceolate or to subpandurate, 14–26 cm long, 4–8 cm broad, chartaceous to subcoriaceous, acuminate or subacute, at the base truncate, obtuse, acute, or attenuate; margin entire or subentire; on both sides glabrous or with sparse, partly uncinate hairs, glabrescent; 14–12 pairs of secondary veins, without distinct parallel tertiary veins; petioles 4–8 mm long, more or less thickened at the base, sparsely puberulous with partly uncinate hairs; stipules semi-amplexicaul, ovate to lanceolate, 10–16 mm long, coriaceous, apiculate to subaristate, with conspicuous parallel veins, almost glabrous, always ciliolate, subpersistent.

Inflorescences (always?) solitary, broadly turbinate to discoid, c. 1–1.5 cm in diameter; peduncle c. 1 cm (?) long, like the outer surface of the receptacle appressed-puberulous to almost glabrous; bracts appressed-puberulous to almost glabrous, with conspicuous veins, those scattered from the base of the peduncle towards the margin of the receptacle about ovate, those on the margin reniform to subrotundate to oblong, obtuse, up to 3 mm long, and in c. 3 rows; among the flowers peltate to subpeltate bracts up to 1 mm high and up to 1 mm in diameter, at first completely covering the young flowers, caducous; perianth of the staminate flowers c. 1 mm high, 2-parted, segments cucullate, puberulous, at the base with up to 0.5 mm long hairs; stamens 2, filaments 1.5–1.8 mm long, glabrous, at the base somewhat swollen but never cushion-shaped, the upper part more or less tortuous or incurved; anthers 0.15–0.3 × 0.15–0.3 mm, connective rather small; pistillate flowers 1–3 (or more?).

Infructescences broadly turbinate, c. 1–2 cm in diameter; endocarp body subglobose, c. 8–10 mm in diameter, endocarp subcoriaceous; seeds subglobose, c. 7–9 mm in diameter, testa partly with a brown to purple network, below the hilum an ovate, thickened, vascularized part; cotyledons thick, equal, free, radicle apical, very short.

Distribution (Fig. 1 A). The species is known from SE Liberia (Sinoe Coast), Western Ivory Coast (in the region of the Lower Cavally River, from Tabou to Fété), and from Ghana (Ankasa Forest Reserve), in damp places in rain forests.

Collections examined: Liberia: Sinoe Coast, Kulo (Baldwin 11441) – Ivory Coast: near the Néka River, E of Néka, c. 80 km N of Tabou (Debray s.n.); between Fété and the Cavally River (Guillaumet 847); near Pata-Idié, E of Tabou (Guillaumet 744, 1811; Tehe 401) – Ghana: Ankasa Forest Reserve (Hall & Enti 36266; Vigne 3186).

Collections with flowers have been made from November to March.

In the inflorescences examined only 1–3 pistillate flowers were found. According to Guillaumet (1965) the inflorescences may contain up to 8 pistillate flowers.

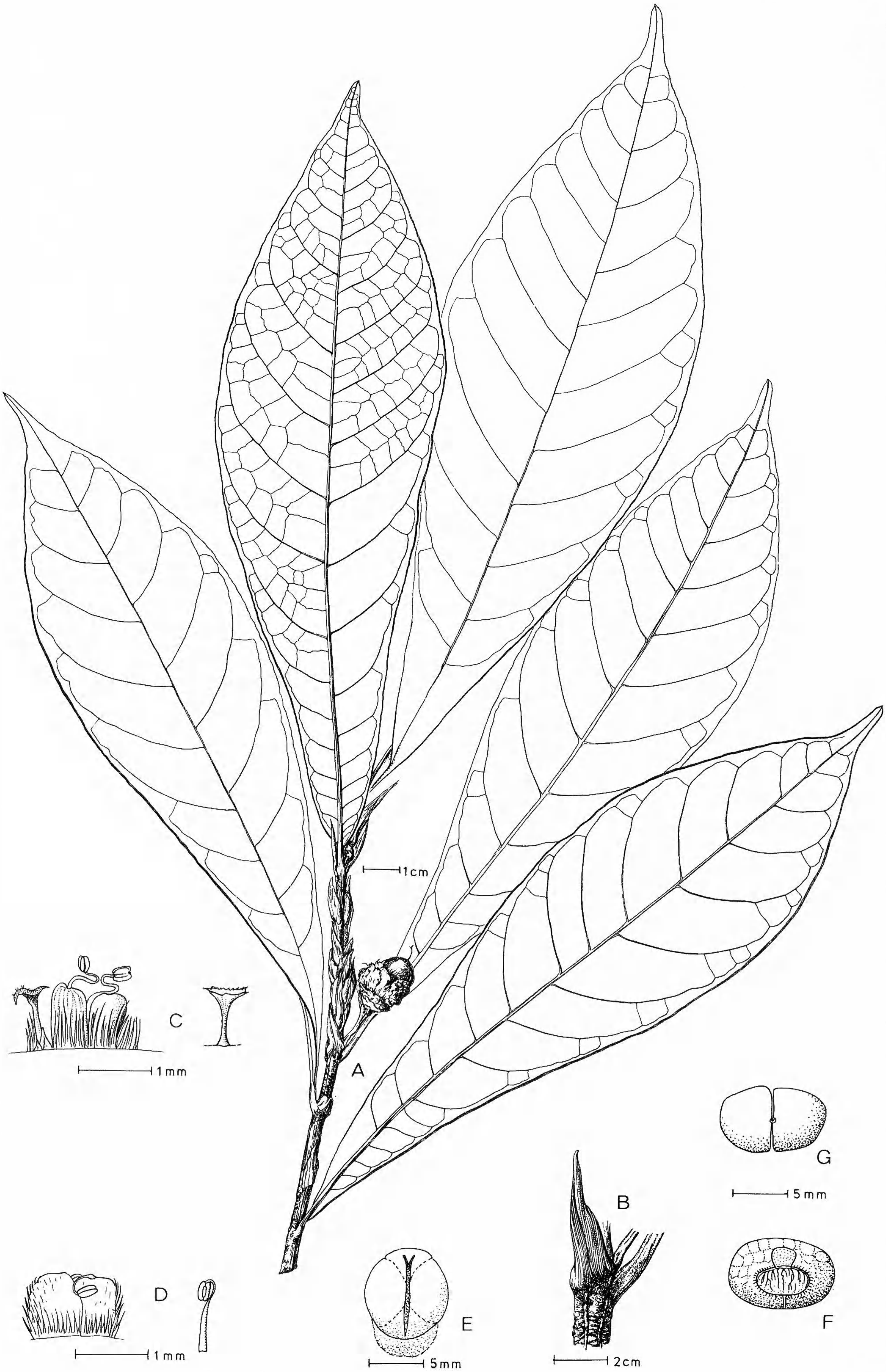
3. **Dorstenia oligogyna** (Pellegrin) C. C. Berg – Fig. 4

C. C. Berg, Adansonia Ser. 2, 16: 422, 1977. – *Trymatococcus oligogyna* Pellegrin, Bull. Mus. Hist. Nat. Paris Ser. 2, 1: 62, 1929. – *Craterogyne oligogyna* (Pellegrin) Lanjouw, Rec. Trav. Bot. Néerl. 32: 277, t. 10, 1935. – Lectotype: Le Testu 2234, Gabon, near Sindara (P; isotypes B, BM, K).

Plants up to 2.5 m tall, with erect, mostly unbranched stems with a woody base. Leafy twigs 3–10 mm thick, sparsely puberulous with straight hairs to almost glabrous.

Leaves (at least on the stem) in spirals, tending to oblanceolate to obovate or sometimes to pandurate, 14–50 cm long, 4–16 cm broad, chartaceous to subcoriaceous, acuminate to

Fig. 3. *Dorstenia djettii*. – A: Leafy part of the stem with infructescence. – B: Stipule (Hall & Enti 36266). – C: Staminate flower and bracts. – D: Staminate flower and stamen (Baldwin 11441). – E: Fruit. – F: Seed. – G: Embryo (Hall & Enti 36266).


1cm
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subacute, at the base truncate, obtuse, acute or attenuate; margin entire or subentire; on both sides (almost) glabrous or often at first with sparse, partly uncinate hairs on the costa beneath; (12–)14–22 pairs of secondary veins, without distinct parallel tertiary veins; petioles 3–14 mm long, sparsely puberulous to almost glabrous, more or less thickened at the base; stipules semi-amplexicaul, lanceolate to ovate, 8–17 mm long, coriaceous, sometimes shortly apiculate, minutely puberulous to almost glabrous, with conspicuous parallel veins, subpersistent.

Inflorescences one, two, or a few simultaneously in the leaf axils, narrowly to broadly turbinate to almost discoid, 4–8 mm in diameter; peduncle 4–10 mm long, peduncle and outer surface of the receptacle sparsely puberulous; bracts ovate to reniform, almost glabrous but always ciliolate, sometimes with some distinct veins, scattered from the base of the peduncle to the margin of the receptacle, there in c. 2 rows; perianth of the staminate flower 0.5–0.7 mm high, 2–3(–4)-parted, puberulous, in the upper part with clavate or oblongoid to globose minute papilla-like hairs; stamens 1–3, mostly 2, filaments 0.7–1.0 mm long, at the base strongly swollen and mostly more or less cushion-shaped, glabrous or nearly so, their upper parts usually incurved, anthers 0.2–0.3 × 0.2–0.3 mm, connective usually broad and more or less swollen; pistillate flowers solitary, the free part of the perianth 0.6–0.8 mm high, 4-lobed, puberulous; style c. 1 mm long, stigmas 0.5–1.5 mm long.

Infructescences c. 1 cm in diameter, broadly turbinate to subglobose.

Distribution (Fig. 1 A). The species has only been collected in the region of the Ngounyé River in Gabon. 8 collections have been examined.

Collections with flowers have been made in September, October and November.

4. **Dorstenia africana** (Baillon) C. C. Berg – Fig. 5

C. C. Berg, Adansonia Ser. 2, 16: 422, 1977. – *Trymatococcus africanus* Baillon, Adansonia 11: 300, 1875; Engler, Monogr. Afr. Pfl. 1, Moraceae: 28, t. 11A, 1898. – *Craterogyne africana* (Baillon) Lanjouw, Rec. Trav. Bot. Néerl. 32: 273, t. 6, 1935. – Type: Mann 723, Cameroun, near Douala ("Cameroons River") (K).

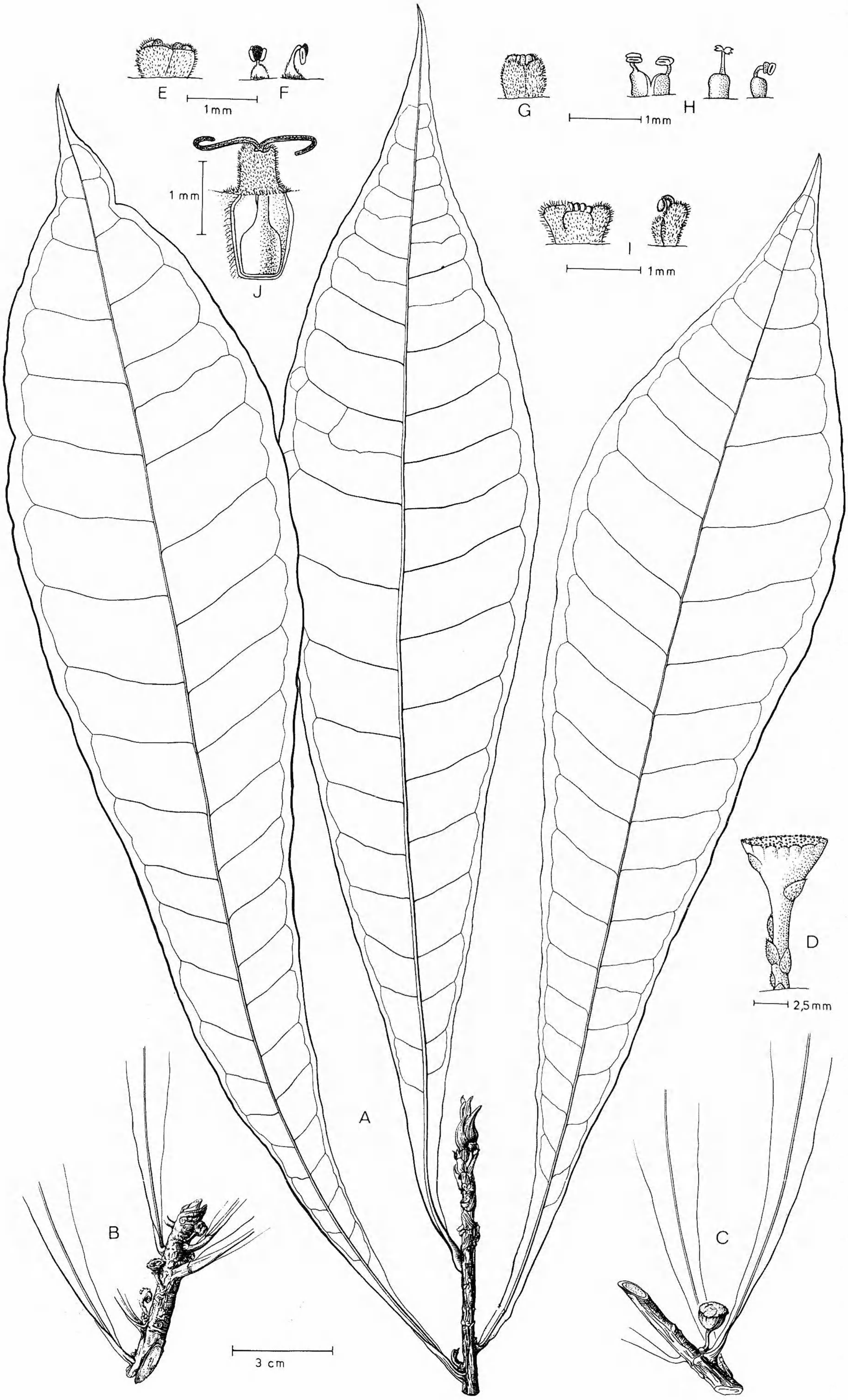
Trymatococcus conrauanus Engler, Bot. Jahrb. Syst. 33: 117, 1902; Lanjouw, Rec. Trav. Bot. Néerl. 32: 273, 1935. – Type: Conrau 130, Cameroun, near Tinto (B).

Shrubs up to 2.5 m tall, with spreading or arching branches, leafy twigs 0.5–3 mm thick, puberulous with very short patent hairs and longer retrorse and usually appressed uncinate hairs.

Leaves (at least on the branches) distichous, oblong to lanceolate, (3–)7–25 cm long, (1.5–) 2.5–11 cm broad, chartaceous, acuminate to subcaudate, at the base obtuse to subacute, sometimes subtruncate to emarginate; margin entire, sometimes subentire to faintly dentate; on both sides sparsely puberulous, usually with appressed and retrorse uncinate hairs, glabrescent; (6–)8–14 pairs of secondary veins arching rather far from the margin, without or with a few parallel tertiary veins; petioles 2–6 mm long, 1–1.5 mm thick; stipules caducous or subpersistent, 3–8 mm long, semi-amplexicaul, sparsely puberulous, costa rather prominent.

Inflorescences (sometimes only with staminate flowers) mostly 2 or more simultaneously in the leaf axils, pendulous, turbinate, 3–7 mm in diameter, mostly bright yellow, hardly to rather distinctly lobed, bearing c. 10–25 reniform to ovate, up to 0.6 mm long bracts in two rows on the margin of the receptacle; peduncle 5–27 mm long, often with a single bract on its lower part or on its base, like the receptacle usually with appressed and retrorse uncinate hairs; perianth of the staminate flower c. 0.5 mm high, 2(–3)-lobed, or sometimes tending to 3-fid or 3-parted, puberulous, especially on the margins with minute clavate papilla-like hairs; stamens 2, occasionally 3, filaments mostly even at anthesis incurved, 0.6–0.8 mm long, the lower part puberulous, at first thickened, later on cushion-

Fig. 4. *Dorstenia oligogyna*. – A: Leafy part of the stem. – B: Inflorescences (Le Testu 5092). – C: Young infructescence. – D: Inflorescence. – E: Staminate flower. – F: Stamens (Le Testu 2234). – G: Staminate flower. – H: Stamens (Breteler 5683). – I: Staminate flowers. – J: Pistillate flower (Le Testu 5575).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shaped, anthers 0.2–0.3 mm long, 0.3–0.4 mm broad, connective rather broad; the free part of the perianth of the pistillate flower 0.5–0.7 mm high, 2-lobed, puberulous, especially on the margins with minute, clavate to globose, papilla-like hairs; style 1–1.5 mm long, stigmas 2, 1–1.2 mm long, of equal or unequal length, straight or twisted.

Infructescences green, subglobose, c. 7 mm, crowned by a disc consisting of the remains of the staminate flowers and bracts; endocarp body subglobose, c. 5 mm in diameter, seeds subglobose to transversely ellipsoid, c. 4–5 × 4.5–3 mm, testa with a slightly thickened and sparsely vascularized part below the small hilum; cotyledons very unequal, radicle short.

Distribution (Fig. 1C). From SE Nigeria (east of the Cross River) to Gabon, in the undergrowth of rain forests, sometimes in secondary forests, often along streams, locally frequent, from sea level to 850 m. About 80 collections have been examined.

Flowering throughout the year, probably mainly from December to April. A low percentage of the inflorescences set fruit.

Except for the differences indicated in the key to the species, *D. africana* differs slightly from *D. kameruniana* in the indumentum (mostly appressed and retrorse, longer, uncinate hairs), the secondary leaf veins (looping rather far from the margin), the smaller connectives of the stamens, and the less deeply divided perianths of the staminate flowers.

5. **Dorstenia kameruniana** Engler – Fig. 6

Engler, Bot. Jahrb. Syst. 20: 142, 1894. – *Trymatococcus kamerunianus* (Engler) Engler, Monogr. Afr. Pfl. 1, Moraceae: 29, t. 11B, 1898; Rendle in Prain, Fl. Trop. Afr. 6 (2): 76, 1916. – *Craterogyne kameruniana* (Engler) Lanjouw, Rec. Trav. Bot. Néerl. 32: 274, t. 7, 8, 1935; Mangenot, Ic. Pl. Afr. IV. No. 83. – Type: Dinklage 232, Cameroun, Lokoundjé (B; isotype HBG).

Trymatococcus kamerunianus (Engler) Engler var. *welwitschii* Engler, Monogr. Afr. Pfl. 1, Moraceae: 29, 1898. – Type: Welwitsch 2594, Angola, Golungo Alto, Sange (B, not seen; isotypes BM, K, LISU, P).

Trymatococcus usambarensis Engler, Bot. Jahrb. Syst. 33: 117, 1902; Lanjouw, Rec. Trav. Bot. Néerl. 32: 274, 1935. – Type: Scheffler 251, Tanzania, Useguha, Makingumbi (B).

Trymatococcus gilletii De Wildeman, Ann. Mus. Congo Ser. 5, Bot. 1: 119, t. 26, 1904; Lanjouw, Rec. Trav. Bot. Néerl. 32: 274, 1935; Hauman, Fl. Congo Ruanda-Urundi 1: 81, 1948. – Type: Gillet 2194, Zaire, Kimuenza (BR).

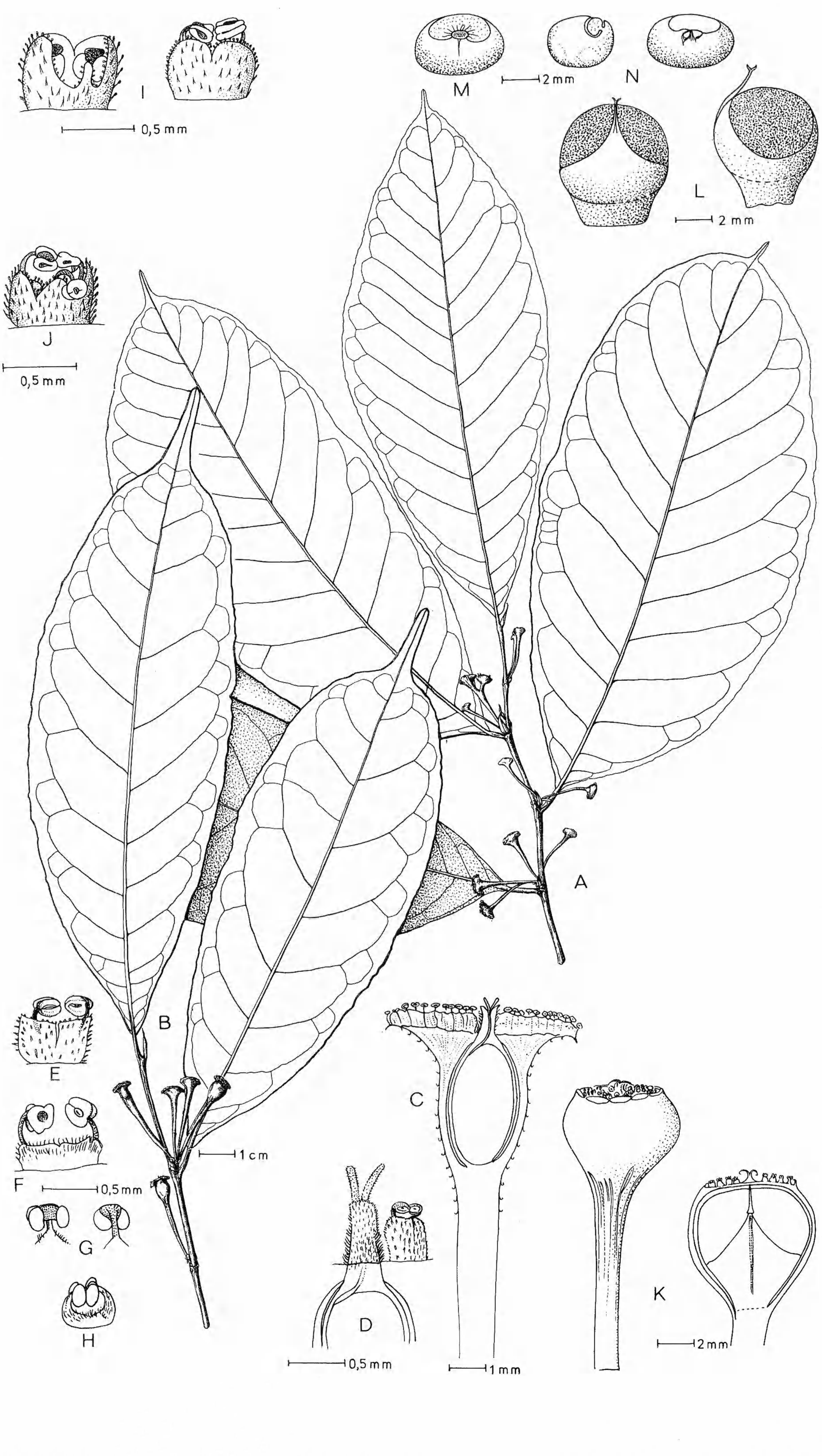
Dorstenia amoena A. Chevalier, Bull. Soc. Bot. France 58, Mém. 8: 208, 1912; Lanjouw, Rec. Trav. Bot. Néerl. 32: 274, 1935. – Type: Chevalier 21528, Ivory Coast, between Diodandougon and Niangouepleu (P).

Shrubs or undershrubs, usually 0.5–3 m, sometimes up to 6 m tall, with few or many stiff or weak branches; latex white or yellowish. Leafy twigs 0.5–2 mm thick, rather densely white or sometimes brownish puberulous to hirtellous to scabrous with very short patent hairs intermixed with mostly (distinctly) longer, (almost) patent, uncinate, near the nodes often straight hairs.

Leaves (at least on branches) distichous, elliptic to lanceolate, or obovate to oblanceolate (3–)7–16(–22) cm long, (1–)2.5–9 cm broad, chartaceous to subcoriaceous, acuminate to subcaudate, often truncate and coarsely dentate (to lobed) towards the apex, at the base usually distinctly inequilateral, acute to obtuse; margin dentate, often coarsely dentate to lobed, sometimes almost entire or entire; on both sides sparsely puberulous to hirtellous with straight and/or uncinate hairs, glabrescent; (4–)6–12(–14) pairs of secondary veins, usually with some parallel tertiary veins; petioles 3–10(–17) mm long; stipules often subpersistent, semi-amplexicaul, 3–11 mm long, sparsely puberulous to substrigulose, costa prominent.

Inflorescences (occasionally entirely staminate with an abortive pistillate flower) often one, sometimes 2–3 or occasionally more simultaneously in the leaf axils, broadly turbinate to discoid, 3–8 mm in diameter, whitish, mostly more or less lobed; peduncle 2–8(–9) (in fruit up to 12) mm long, puberulous with (almost) patent, straight or uncinate hairs; receptacle puberulous with (almost) patent, straight and usually longer and retrorse uncinate hairs, with reniform to ovate bracts in two rows on its margin, sometimes a single bract inserted lower on the

Fig. 5. *Dorstenia africana*. – A: Leafy twig with inflorescences (Zenker 875). – B: Leafy twig with young infructescences (de Wilde 1951). – C: Inflorescence (Zenker 3092). – D: Pistillate and staminate flower. – E: Staminate flower. – F, G, H: Stamens (Zenker 3092). – I: Staminate flowers (Letouzey 1257). – J: Staminate flower (Zenker 170). – K: Infructescence. – L: Fruit. – M: Seed. – N: Embryo (de Wilde 1951).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receptacle; perianth of the staminate flowers c. 0.5 mm high, 2-parted to near the base, often with 3-lobed segments, sometimes 6-parted, at least the upper part puberulous with minute clavate to globose papilla-like hairs; stamens 2, incurved at and after anthesis, filaments 0.5–0.8 mm long, initially with a thickened, later with a cushion-shaped, sparsely puberulous to glabrous base, anthers 0.2–0.3 mm long, 0.4–0.5 mm broad, connective very broad; often a tuft of hairs in the centre of the flower; pistillate flowers 1, occasionally 2, the free part of the perianth 2.5–3.5 mm high, 2-parted, puberulous with clavate to globose minute papilla-like hairs; style 2–2.5 mm long, stigmas c. 1–2 mm long, strap-shaped to filiform, straight or twisted, often unequal in length, puberulous.

Infructescences turbinate to subglobose, c. 7–8 mm in diameter, crowned by a discoid part consisting of the bracts and staminate flowers; endocarp body subglobose, c. 6.5 mm in diameter; seed subglobose, c. 6 mm in diameter, testa with a hardly thickened vascularized part below the small hilum; cotyledons very unequal, radicle short.

Distribution (Fig. 1 D). The main and central part of the disjunct area occupies the central and northern part of Zaire and extends westwards through the Central African Republic to southern Cameroun, southwestwards to Angola (E of Luanda), and eastwards to Uganda. In W Africa the species ranges from SE Guinea (region of Mount Nimba) to SE Ghana. In E Africa the species inhabits some areas in E Tanzania. *D. kameruniana* is a species of the undergrowth of evergreen forests, sometimes of secondary forests; often near streams. In the central part of its area it often occurs in gallery forests. It grows from sea level to c. 1300 m altitude (in Uganda). About 250 collections have been examined.

Flowering throughout the year. Rather few inflorescences set fruit.

The perianth of the staminate flower usually consists of two large segments corresponding to the stamens. These segments are often 3-lobed or 3-fid. The two smaller lateral lobes may even be almost completely separated from the large middle lobe. Sometimes there are 1 or 2 much smaller segments between the large ones. They may be regarded as the reduced third and fourth tepal. Thus, the perianth of the staminate flower is rather variable: with at least 2 large segments, lobed or not, up to at most 6 segments, 4 of which are (very) small.

D. kameruniana is very variable in leaf shape. The variations seem not to be regionally confined, although certain variations seem to occur more frequently in one region than in another. For example, leaves with a truncate apex and coarsely dentate to lobed margin towards the apex are more common in Cameroun than elsewhere.

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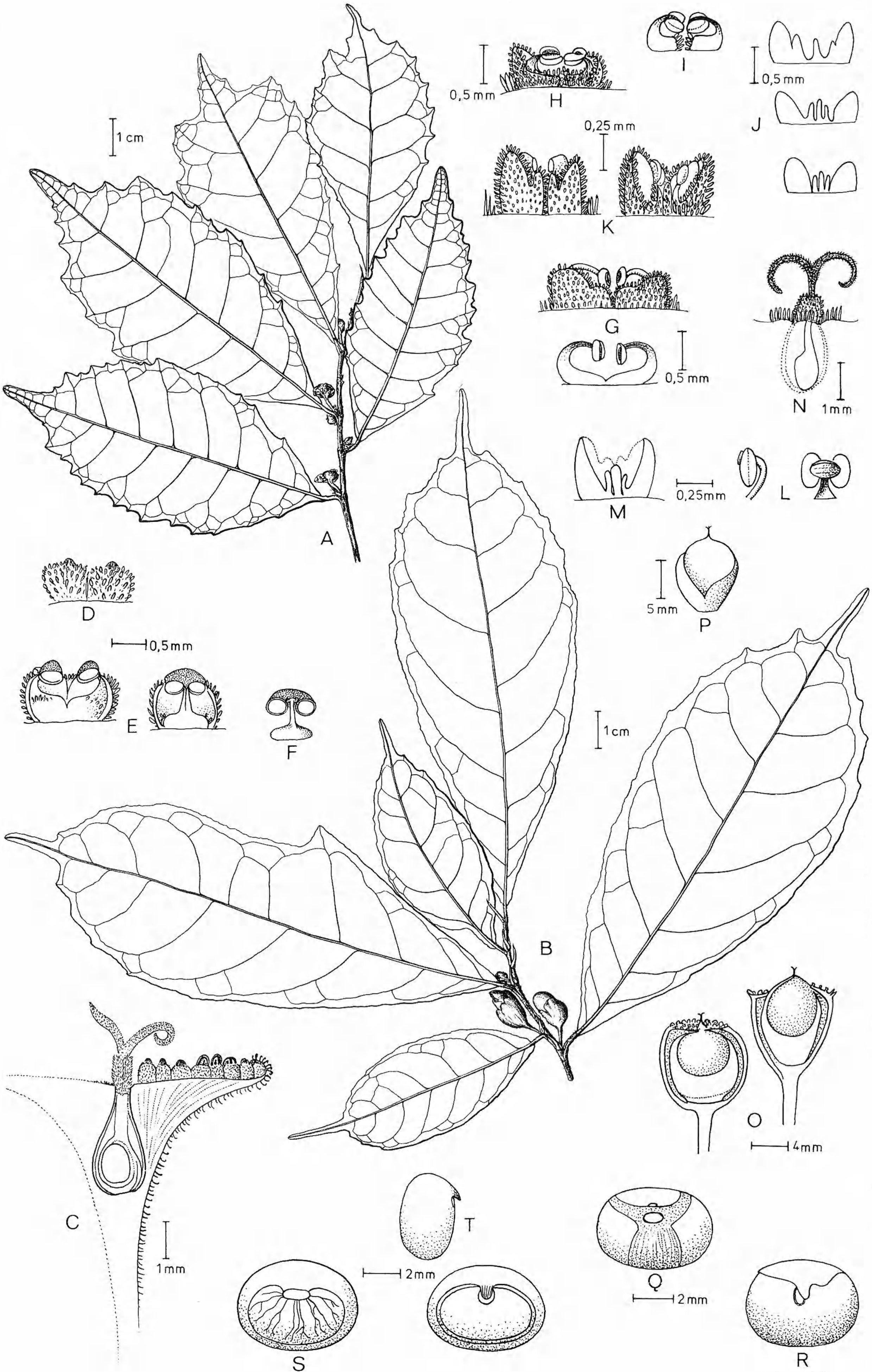
Fig. 6. *Dorstenia kameruniana*. – A: Leafy twig with inflorescences (Proctor 2786). – B: Leafy twig with infructescences (Leeuwenberg 3886). – C: Inflorescence (de Wilde 1638). – D: Staminate flower. – E, F: Stamens (Leeuwenberg 5184). – G: Staminate flower and stamens (Callens 3738). – H: Staminate flower. – I: Stamens. – J: Tepals (Gilbert 2090). – K: Staminate flowers. – L: Stamens. – M: Tepals (Brenan & Greenway 8275). – N: Pistillate flower (Evrard 5736). – O: Infructescences (Tisserant 998). – P: Fruit. – Q: Seed. – R: Embryo (Breteler 1382). – S: Seed. – T: Embryo (Callens 3738).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Wahlenbergia rhytidosperma (Campanulaceae), a new species from Transvaal

Mats Thulin

Thulin, M. 1978 03 31: Wahlenbergia rhytidosperma (Campanulaceae), a new species from Transvaal. *Bot. Notiser 131:* 67–70. Stockholm. ISSN 0006-8195.

The new species *Wahlenbergia rhytidosperma* Thulin, belonging to the *W. madagascariensis* group, is described from Transvaal. By its rugulose, non-reticulate testa it differs from all other African representatives in this group.

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Wahlenbergia rhytidosperma Thulin sp. nov. – Figs. 1–3

Orig. coll.: Galpin 13822, South Africa, Transvaal, Lydenburg Div., upper slopes of Mt Anderson, 29.III.1933 (K holotype, PRE).

Species nova a *W. madagascariensi* A. DC. et speciebus affinibus combinatione seminum rugulosorum cum gynoecio trimero et foliis inflorescentiae plerumque alternis distinguenda.

Probably perennial herb with a taproot and numerous, decumbent, filiform stems up to 15 cm long, glabrous or pubescent. Leaves opposite, except for the inflorescence region where alternate leaves often occur, thin, very narrowly to broadly elliptic, up to 9 mm long and 2–3.2 mm wide, acute at the apex, narrowing at the base into a short petiole, glabrous or pubescent; margin not incrassate, with 1–3 denticles on each side or sometimes entire; midvein somewhat protruding beneath. Inflorescence frondose, one- to few-flowered, with the flowers terminal or in dichotomous forks; pedicels filiform, up to 16 mm long, glabrous or sparsely pubescent. Hypanthium hemispherical or broadly obconical, c. 10-nerved, glabrous or pubescent. Calyx-lobes 0.8–2.4 mm long, narrowly triangular, with hyaline often recurved tips, entire, glabrous or pubescent. Corolla 3.5–6 mm long, lobed to about half the length, white or mauve, glabrous, or pubescent on the outside of the lobes; tube 1.8–3 mm long. Stamens with the filament-bases narrowly dilated or almost linear, sparsely ciliate; anthers 0.7–1 mm long. Ovary semi-inferior, 3-locular. Style about equalling the corolla-tube, eglandular, slightly thickened in the upper part, glabrous below; lobes 3, ±0.5 mm long. Capsule 3-locular, 1.5–2 mm long, c. 10-nerved with 3 valves, 0.5–0.8 mm long. Seeds elliptic to broadly elliptic in outline, 0.5–0.6 mm long; testa rugulose.

Specimens examined

South Africa. Transvaal. 2428 Nylstroom: Warmbaths, Leipoldt in PRE 43508 (PRE). – 2530 Lydenburg: Lydenburg Div., upper slopes of Mt Anderson, 29.III.1933, Galpin 13822 (K, PRE); Belfast Div., Dullstroom, Steenkampsbergen, 12.I.1933, Galpin 13065 (K, PRE); ibid., Slaaihoek road, 27 km from Machadodorp, 14.II.1936, Pole-Evans 3926 (K, PRE); ibid., 15 km W of Slaaihoek, 17.I.1952, Bruce 496 (PRE).

Distribution and habitat

W. rhytidosperma is only known from a small area in C and E Transvaal (Fig. 4) at altitudes between 1200 and 2150 m. Galpin 13822 and Bruce 496 have been collected "under rocks" and the habitat of Galpin 13065 is described as "deep shade under large overhanging rock in moist ground".

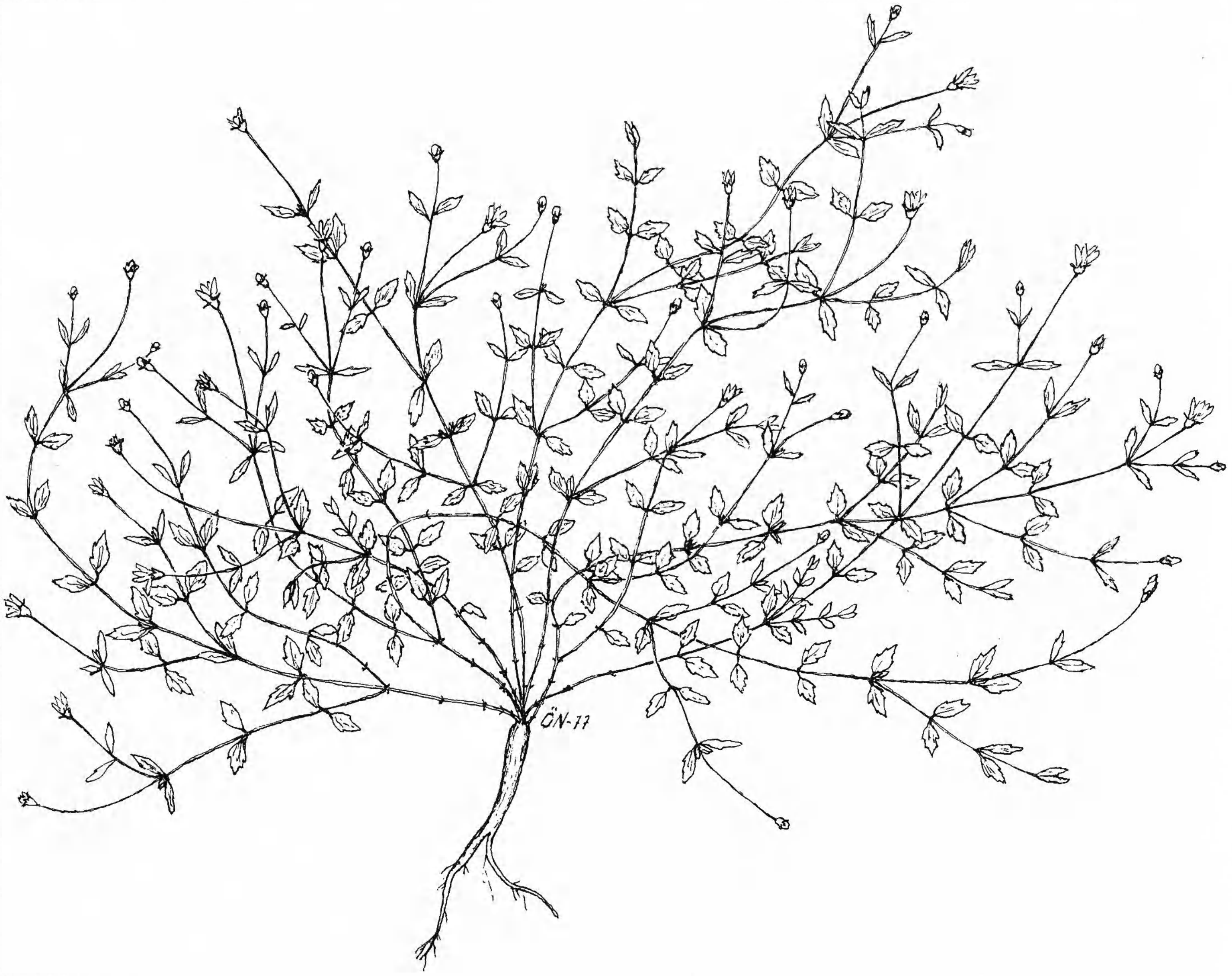

Fig. 1. *Wahlenbergia rhytidosperma,* ×0.6.

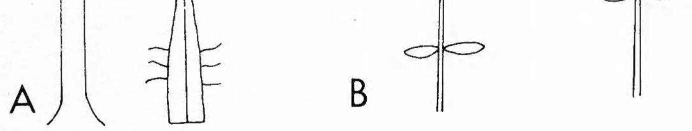

Fig. 2. *Wahlenbergia rhytidosperma.* Semi-diagrammatic drawings. – A: Style and stamen. The dotted area of the style indicates distribution of pollen-collecting hairs. – B: Examples of inflorescences. The figures indicate the order of flowering.

Variation and taxonomic remarks

The few collections seen of *W. rhytidosperma* are on the whole uniform. Galpin 13065 is more pubescent than the others and sometimes has entire leaf-margins.

The species, with its opposite leaves, distinct corolla-tube and eglandular style, clearly belongs to the "*W. madagascariensis* group" which was proposed in my revision of the genus *Wahlenbergia* in tropical Africa and Madagascar (Thulin 1975 p. 105). From the area covered by this revision three species were referred to the group: *W. madagascariensis* A. DC., *W. cerastioides* Thulin and *W. tsaratananae* Thulin. The first-mentioned species is distributed in the E parts of tropical and southern Africa and in

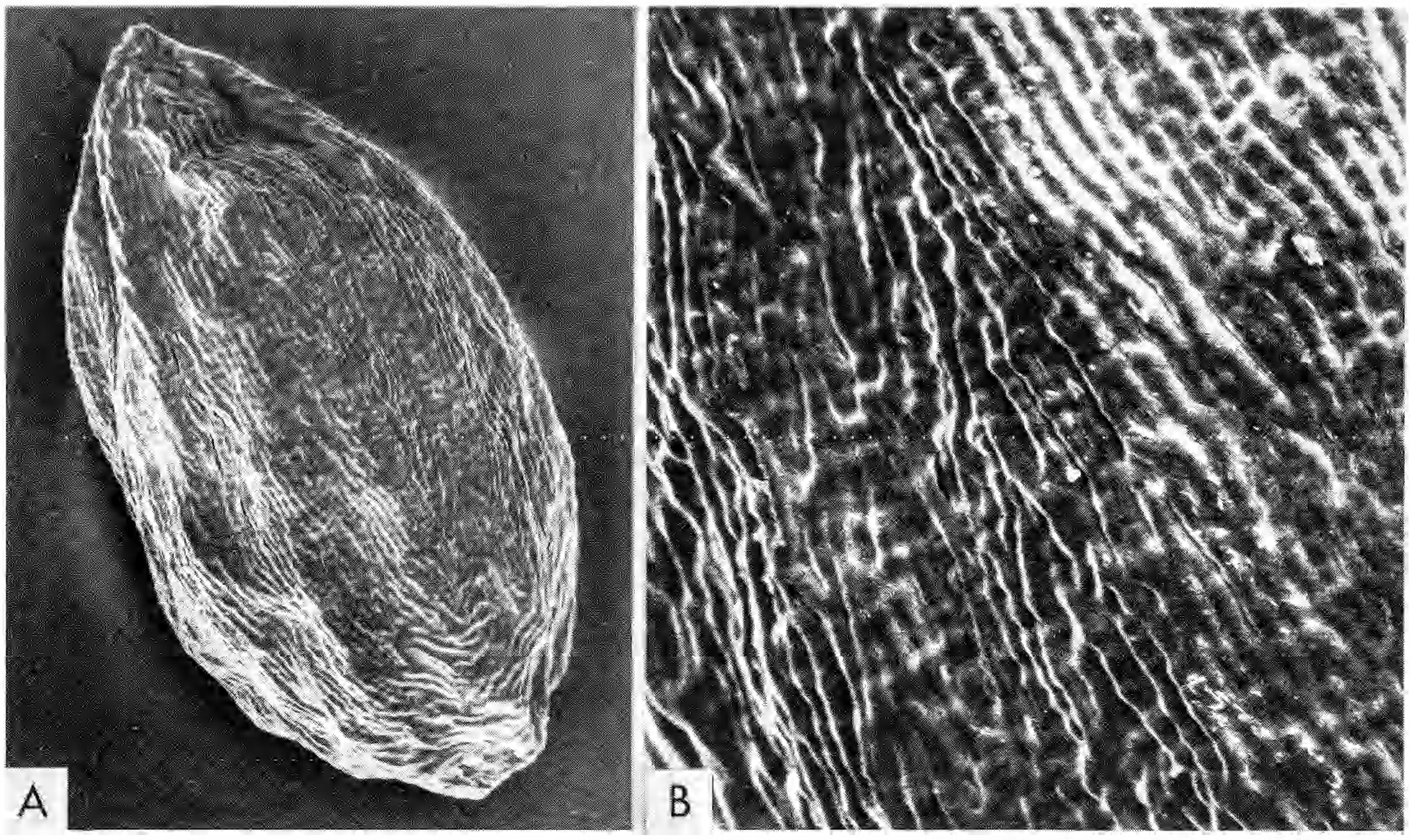

Fig. 3. *Wahlenbergia rhytidosperma*. – A: Seed, SEM × 150. – B: Detail of seed, SEM × 500. – From Galpin 13822 (K).

Madagascar, while the two latter are Madagascan endemics. However, I also pointed out that outside the area of the revision the South African *W. procumbens* (L.f.) A.DC. and the South American *W. schwackeana* A. Zahlbr., among others, also belong here.

W. madagascariensis, *W. cerastioides*, *W. tsaratananae* and *W. procumbens* all have a distinctly reticulate testa, although the reticulation is of a different type in each of these species (see Thulin 1975 Fig. 7 A–H). In *W. rhytidosperma* the seeds are instead rugulose with ± verrucose, close-spaced, mostly longitudinal elevations with hardly any interstices (Fig. 3). The four species mentioned, except for *W. tsaratananae*, also differ from *W. rhytidosperma* in having strictly opposite leaves in all parts of the plant (see Thulin 1975 Fig. 4 A). In *W. rhytidosperma* (Fig. 2 B) as in *W. tsaratananae* (Thulin 1975 Fig. 4 C–E) the leaves are often alternate in the inflorescence region and the flowers usually keep their terminal position without becoming "lateral" by overtopping. Such overtopping is characteristic for example of *W. madagascariensis*. *W. rhytidosperma* also differs from *W. cerastioides* and *W. tsaratananae* in its 3-merous (not 2-merous) gynoecium.

However, judging from morphological comparison, the nearest ally of *W. rhytidosperma* perhaps is *W. schwackeana*, a species only recorded, as far as I know, from Minas Gerais in Brazil. These species are very similar in habit and also agree very well in shape and size of leaves, stamens, style and capsule. Furthermore they both have a 3-merous gynoecium, alternate leaves in the inflorescence region and non-reticulate seeds. Nevertheless the two species

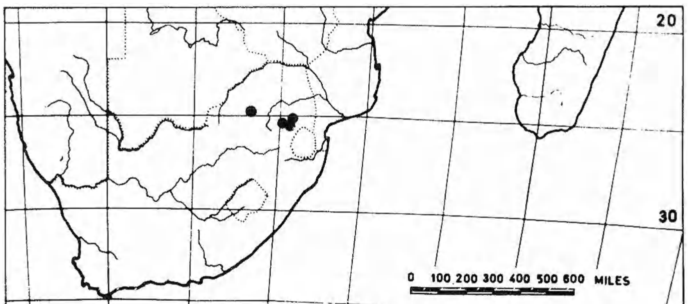

Fig. 4. Distribution of *Wahlenbergia rhytidosperma*.

are quite distinct. The inflorescences of *W. schwackeana* apparently are always one-flowered and the testa is almost smooth. Only at a high magnification short, shallow, mostly longitudinal depressions are visible on the seeds. Furthermore the corolla-tube in *W. schwackeana* is less than 1 mm long and only about a quarter of the length of the corolla (in *W. rhytidosperma* about half the length). A more vague difference is found in the texture of the leaves which are thin and brittle in *W. rhytidosperma* as opposed to the more cartilaginous ones in *W. schwackeana*.

W. rhytidosperma and *W. schwackeana* in their testa ornamentation approaches the "*W. denticulata* group" (Thulin 1975 p. 110). In particular there is a similarity in this regard between *W. rhytidosperma* and *W. capillacea* (L. f.) A. DC. (Thulin 1975 Fig. 7 I–L). However, this similarity is not correlated with other characters and therefore should not be taken as an implication of a close relationship between these two species.

Acknowledgements. I am indebted to the curators at K and PRE for loan of herbarium material, to Dr Ö. Nilsson for the drawing in Fig. 1, and to Mr M. Iwarsson for work at the scanning electron microscope.

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New records of Ethiopian Leguminosae

Mats Thulin

Thulin, M. 1978 03 31: New records of Ethiopian Leguminosae. *Bot. Notiser 131:* 71–74. Stockholm. ISSN 0006-8195.

Nineteen species and one subspecies of Leguminosae subfam. Papilionoideae are reported from Ethiopia for the first time: *Abrus canescens* Welw. ex Bak., *Crotalaria alexandri* Bak. f., *Desmodium schweinfurthii* Schindl., *Indigofera butayei* De Wild., *I. congolensis* De Wild. & Th. Dur., *I. dendroides* Jacq., *I. hirsuta* L., *I. welwitschii* Bak., *I. zenkeri* Bak. f., *Macrotyloma stenophyllum* (Harms) Verdc., *M. tenuiflorum* (Micheli) Verdc., *Rhynchosia nyasica* Bak., *Tephrosia humilis* Guill. & Perr., *T. lortii* Bak. f., *T. nana* Schweinf., *T. reptans* Bak., *T. schweinfurthii* Defl., *Teramnus labialis* (L. f.) Spreng. subsp. *arabicus* Verdc., *Vigna friesiorum* Harms, *V. multinervis* Hutch. & Dalz.

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A field-trip in Ethiopia was undertaken in Aug.–Sept. 1975 in cooperation with the National Herbarium in Addis Abeba. About 1000 collections were made mainly in the Wollega and Gamu-Gofa Regions in the W and S part of the country respectively. Some collecting was also made in the Shoa, Sidamo and Harar Regions. Many of the species collected have proved to be new records for the country and several collections apparently represent undescribed taxa. In this paper 19 species and one subspecies of Leguminosae subfam. Papilionoideae are reported as new to Ethiopia. It is remarkable that 12 of these, as well as several new records in other families, were collected within an area of approximately only one km^2 at about 1300 m altitude in the Didessa River Valley in Wollega. Didessa River is one of the main tributaries to the Blue Nile (Abbai) and these rivers join at about 800 m altitude some 160 km from the Sudan border.

Not much original vegetation seems to remain on the fertile plateau land of Wollega, but the deep Didessa Valley which is ravaged by malaria is still rather unexploited. In the area visited, close to the Nekempt–Gimbi road, much of the valley near to the river is covered by a seemingly uniform tall grass with scattered trees, but in places it is interrupted by basalt pavements, depressions with standing water or steep rock-slopes with waterfalls, altogether forming a mosaic of habitats with a rich and in Ethiopia apparently still largely unrecorded flora with a W African impression. For 8 of the 12 species reported here from the Didessa Valley, this locality is the easternmost known for the species. Probably much the same flora as in this valley is to be found in the uncollected Ethiopian part of the lower Blue Nile Valley and supposedly these valleys have served as migration routes far into the Ethiopian highland for a large number of more or less W African, deciduous woodland species. So, for example, *Anogeissus leiocarpus* (DC.) Guill. & Perr. (Combretaceae), often a dominant tree on clay soils in the deciduous woodlands from Senegal to Sudan (Wickens 1976 p. 16, 98, Map 53) but very little known in Ethiopia, is in fact dominant in places in the Blue Nile Gorge as far E as between Debre Libanos and Debre Markos NW of Addis Abeba.

Using for comparison the new chorological map by White (1976 p. 664), this valley flora seems largely to be an outlier of the Sudanian regional centre of endemism. In the terminology of Wickens (1976 p. 40, Fig. 18) it belongs nearest to the Sudanian Domain of the Sudano-Zambesian phytogeographical Region.

Further collecting in these valleys as well as in other low-lying parts of W Ethiopia seems very desirable and will probably yield a substantial amount of additional new records for the country.

Abrus canescens Welw. ex Bak.

Wollega Region: E slope of Didessa R. valley, c. 9°03'N, 36°11'E, 1300 m, 12.IX.1975, Gilbert & Thulin 741 (EA, ETH, K, MO, UPS, WAG). Up to 6 m long climber in riparian woodland along a small stream.

Abrus canescens mainly occurs in the W parts of tropical Africa and this is the easternmost locality known for the species. The nearest certain localities are in the area just N of Lake Victoria in Uganda and Kenya. Andrews (1952 p. 169) also reports the species from the Equatoria Province of Sudan without citing any specimens. No records from Sudan, however, are given by Breteler (1960).

Crotalaria alexandri Bak. f.

Gamu-Gofa Region: E slope of Gughe highlands above Arba Minch, c. 6°03'N, 37°35'E, 1800 m, 3.IX.1975, Gilbert, Thulin & Aweke 398 (ETH, K, UPS). Rather open grassy slopes with traces of old terraceing.

This is the northernmost record for the species which has its nearest localities in N Uganda and W Kenya.

Desmodium schweinfurthii Schindl.

Locality as for *Abrus canescens,* 11.IX.1975, Gilbert & Thulin 632 (EA, ETH, K, MO, UPS, WAG). In crevices in a level basalt pavement surrounded by tall grass.

This rare little annual is apparently confined to the Sudanian regional centre of endemism (White 1976 p. 664). The locality is the easternmost for the species and the nearest known occurrence is the type locality, Seriba Ghattas in the Ghazal Province of Sudan (Schweinfurth 48 from 1869), which is apparently still the only Sudanese record.

Indigofera butayei De Wild.

Locality and date as for *Abrus canescens,* Gilbert & Thulin 665 (ETH, K, MO, UPS). Along path at the margin of tall grass.

This is the easternmost record for the species. The nearest localities are in N Uganda.

Indigofera congolensis De Wild. & Th. Dur.

Locality and date as for *Abrus canescens,* Gilbert & Thulin 673 (ETH, K, MO, UPS). On clay at margin of tall grass.

This is the easternmost record for the species, which has its nearest localities in C Uganda and NE Zaire.

Indigofera dendroides Jacq.

Locality and date as for *Abrus canescens,* Gilbert & Thulin 673 a (UPS). On clay at margin of tall grass. – Gamu-Gofa Region: 55 km N of Arba Minch, c. 6°23'N, 37°46'E, 1350 m, 29.VIII.1975, Gilbert, Thulin & Aweke 222 b (ETH, K, MO, UPS, WAG). Rocky hill with *Acacia-Balanites* scrub.

The nearest localities are in Sudan and N Uganda.

Indigofera hirsuta L.

Locality as for *Abrus canescens,* 1200 m, 14.IX.1975, Gilbert & Thulin 747 (ETH, K, MO, UPS, WAG). Roadside.

Indigofera hirsuta is widespread in tropical Africa, S Asia, N Australia and is introduced in tropical America (Gillett 1971 p. 310). It is a more or less weedy plant occurring in lowland areas with a comparatively high precipitation. The nearest localities are in Sudan and N Uganda. The Ethiopian record for this species given by Cufodontis (1955 p. 266) is doubtful. It is based on the list by Schweinfurth & Ascherson (1867 p. 257) and no specimen is cited there, nor in the revision by Gillett (1958 a p. 109).

Indigofera welwitschii Bak.

Locality and date as for *Abrus canescens,* Gilbert & Thulin 659 (EA, ETH, K, MO, UPS, WAG). Along path at margin of tall grass.

The nearest localities are in Sudan and N Uganda. The Ethiopian form belongs to var. *welwitschii.*

Indigofera zenkeri Harms ex Bak. f.

Locality and date as for *Abrus canescens*, Gilbert & Thulin 647 (ETH, K, MO, UPS, WAG). Disturbed stony ground in grassland.

The nearest certain localities are in S Uganda and SE Kenya. Also reported from Sudan by Andrews (1952 p. 211), but no specimens are cited and no Sudanese record is given by Gillett (1970 p. 486).

Macrotyloma stenophyllum (Harms) Verdc.

Locality and date as for *Abrus canescens*, Gilbert & Thulin 643 (EA, ETH, K, MO, UPS, WAG). Climbing up grass-stems in tall grass.

The easternmost record for this mainly W African species. The nearest localities are in NE Zaire and W Uganda.

Macrotyloma tenuiflorum (Micheli) Verdc.

Locality and date as for *Abrus canescens*, Gilbert & Thulin 642 (EA, ETH, K, MO, UPS, WAG). On bare ground at the margin of tall grass.

The distribution of *M. tenuiflorum* is very much the same as for the closely related *M. stenophyllum*, and the nearest known localities are also in this case in NE Zaire and W Uganda. The habit of the two plants, however, is very different. While *M. stenophyllum* is a climbing or trailing herb, *M. tenuiflorum* is prostrate and growing completely flat on the ground.

Rhynchosia nyasica Bak.

Gamu-Gofa Region: 30 km N of Arba Minch, c. 6°21'N, 37°46'E, 1300 m, 5.IX.1975, Gilbert, Thulin & Aweke 531 (ETH, K, MO, UPS, WAG). Rocky hillside with *Acacia, Terminalia* woodland.

The nearest localities for the species are in Sudan and N Uganda. The Ethiopian plant is a trailing shrub up to 1.5 m long. According to Verdcourt (1971 p. 736) the species is usually an erect herb or subshrub and trailing forms are said to be rare and only known from Tanzania.

Tephrosia humilis Guill. & Perr.

Locality and date as for *Abrus canescens*, Gilbert & Thulin 646 (ETH, K, MO, UPS, WAG). Stony slope in grassland.

This is the easternmost record for *Tephrosia humilis*. The nearest localities are in Sudan.

Tephrosia lortii Bak. f.

Harar Region: 5 km S of Ourso, c. 9°36'N, 41°38'E, 1350 m, 20.VIII.1975, Gilbert & Thulin 122 (EA, ETH, K, MO, UPS, WAG). Evergreen bushland with *Cadia purpurea* and *Dodonaea viscosa* on a mixture of sandstone and basalt.

Tephrosia lortii is previously known only from N Somalia and from the arid parts of SE Kenya and N Tanzania with a very wide gap in the area of distribution. This gap still remains as the Ethiopian record is from about the same latitude as N Somalia.

Tephrosia nana Kotschy ex Schweinf.

Locality and date as for *Rhynchosia nyasica*, Gilbert, Thulin & Aweke 532 (ETH, K, MO, UPS, WAG). Rocky hillside with *Acacia, Terminalia* woodland.

Tephrosia nana is not with certainty reported from Ethiopia before, but one of the syntypes of the species, Schweinfurth 1871, was collected on the Sudan/Ethiopia border near Gallabat, Matamma (cf. Cufodontis 1955 p. 282, Gillett 1971 p. 208).

Tephrosia reptans Bak.

Gamu-Gofa Region: between Lake Chamo and Lake Abaya, "God's Brigde", 1250–1300 m, 30.VIII.1975, Gilbert, Thulin & Aweke 299 (EA, ETH, K, MO, UPS, WAG). Rocky hillside with regularly burnt *Acacia, Commiphora, Sclerocarya* woodland.

This is the northernmost locality for the species. The nearest localities are in N Kenya. The Ethiopian material belongs to var. *reptans*.

Tephrosia schweinfurthii Deflers

Shoa Region: Blue Nile Gorge, S. side, c. 10°04'N, 38°15'E, 1350 m, 23.IX.1975, Gilbert & Thulin 988 (ETH, K, MO, UPS, WAG). Open bushland with *Boswellia* and *Anogeissus*.

Tephrosia schweinfurthii (= *T. franchetii* Hutch. & Bruce) is previously only recorded from S Yemen (Aden) and N Somalia (British Somaliland) (Gillett 1958 b p. 115).

Teramnus labialis (L. f.) Spreng. subsp. **arabicus** Verdc.

Gamu-Gofa Region: Arba Minch, below the escarpment E of the town, 1250 m, 30.VIII.1975, Gilbert, Thulin & Aweke 291 (ETH, K, UPS, WAG). Climbing in grass and scrub near a track in groundwater forest on the bottom of the Rift Valley.

This taxon is widespread in tropical Africa and also occurs in Arabia, the West Indies and Guyana (see Verdcourt 1970 a p. 273, 1971 p. 537), but there seems to be no previous record from Ethiopia. The altitudinal range for the plant in East Africa given by Verdcourt (1971 p. 538) is 0–870(–1080) m. The closely related *T. labialis* subsp. *labialis* var. *abyssinicus* (A. Rich.) Verdc. is fairly common in the Ethiopian highlands at altitudes at least up to 2300 m.

Vigna friesiorum Harms

Gamu-Gofa Region: 8 km S of Arba Minch, c. 5°58'N, 37°36'E, 1160–1200 m, 30.VIII.1975, Gilbert, Thulin & Aweke 322 (UPS). Hillside with *Acacia* woodland.

This is the northernmost record for *Vigna friesiorum* which has its nearest localities in Uganda and Kenya. Verdcourt (1970 b p. 537, 1971 p. 641) divides the species into three varieties which are all said to grade into each other. Judging from the descriptions the Ethiopian plant is nearest to var. *ulugurensis* (Harms) Verdc., which is also the most widespread of the varieties.

Vigna multinervis Hutch. & Dalz.

Locality and date as for *Abrus canescens*, Gilbert & Thulin 691 (ETH, K, MO, UPS, WAG). Climbing up grass stems in tall grass.

This is the easternmost record for the species which is widely distributed in the Sudano-Zambesian Region with the nearest localities in Sudan and N Uganda.

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Elasmomyces krjukowensis (Fungi hypogaei) found in Sweden

Lars E. Kers

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Elasmomyces krjukowensis (Bucholtz) Sacc. & D. Sacc. (Hydnangiaceae or Asterogastraceae) is reported from E Central Sweden and the island of Gotland in the Baltic. The fungus is new to Scandinavia. It was found under *Corylus avellana* in deciduous woods. The species is not clearly distinguished from *E. mattirolianus* Cav. (typus generis). A survey of the literature dealing with *E. krjukowensis* is presented. The morphological variation of the Swedish material is described. A map with the European records of *Elasmomyces* is presented.

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Some years ago I came across a number of Fungi hypogaei, which were not well-known in Sweden. Ever since then I have kept on looking for this kind of fungi during my excursions. I have also tried to enroll amateur botanists in the hunt for those interesting fungi. In the autumn of 1977 I received an unusually rich collection of hypogeous fungi from Mr Evert Plahn, Stockholm. A most unexpected find was that of *Elasmomyces krjukowensis*. The species had actually been collected once before from Sweden, viz. from the island of Gotland by Mr Gunnar Eriksson.

Swedish material

Gotland, Ekeby parish, Mangsarve. Eriksson 17.8. 1965 (UPS, two collections, det. J. A. Nannfeldt 1969 as *Hydnangium krjukowense*) – *Uppland,* Kulla parish, Nybylund, 1.8 km S of the Kulla church. Deciduous wood close to the lake Mälaren. One specimen. Plahn 12.11.1977 (S) – Husby-Sjutolft parish, 3.1 km W of Ekolsund railway halt and 350 m N of the W end of the Sisshammar inlet of the lake Mälaren. Plahn 21.8.1977 (S); Kers & Plahn 30.8.1977 (S) – Övergran parish, E side of the Ekolsund inlet of the lake Mälaren. Partly 1.1 km SSW and partly 500 m SSW of Segersta manor house. Plahn 2.8.1977 (S); 500 m SSW of Segersta manor house. Kers & Plahn 30.8.1977 (S); 1.1 km SSW of Segersta manor house. Kers & Plahn 30.8.1977 (S, UPS).

Elasmomyces krjukowensis (Buch.) Sacc. & D. Sacc.

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Icon.: Figs. 1–3. – Bucholtz 1902 Table III (same in Bucholtz 1903 Table V and partly in Fischer 1933 p. 112, Fig. 84 and in Greis 1943 Fig. 179), Singer & Smith 1960 p. 112, Fig. 83–85 (spores and cystidia), Gross 1968 p. 29.

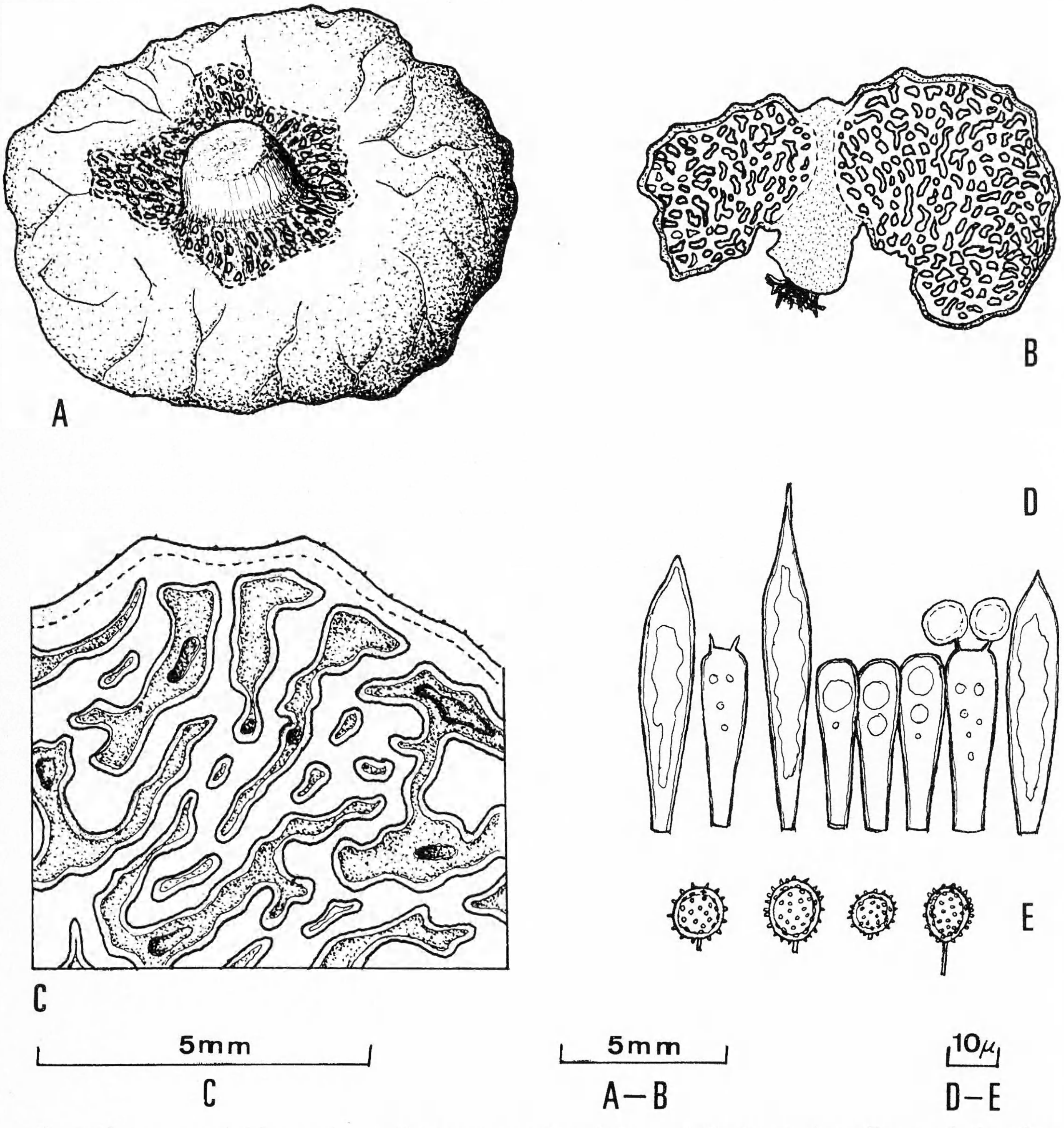

Fig. 1. *Elasmomyces krjukowensis*. – A: Gastrocarp seen from below. – B: Gastrocarp in median, vertical section. – C: Detail of B showing peridium and gleba cavities. – D: Three cystidia, two basidia and three pseudoparaphyses. – E: Spores. – Kers & Plahn 30. VIII.1977 (S).

Description of the Swedish material

Gastrocarps hypogeous, gregarious, depressed globose, up to 3.5 cm broad and 2.5 cm high when fresh, pure white at first, turning yellowish brown to dark brown when dried, peridial surface whitish pruinose, lower side with a central, navel-shaped depression in which the stipe is inserted. *Stipe* solid, short and thick, easily broken, hardly extending beyond the basal depression, straight or curved, free from the lateral peridium or intergrown with this along one side. Stipe with a short mycelial cord to which particles of soil adhere firmly. *Columella* percurrent, white, unbranched or rarely with a few delicate, apical branches, composed of a heteromerous tissue consisting of densely interwoven, narrow hyphae mixed with islands of globose–subglobose cells. *Peridium* non-continuous, elastic–gelified, about 200 μm thick, thinning near the stipe, separable from the gleba in aged specimens, with oleiferous vessels 3–5 μm thick. Peridium with a substratum of a very thin and loose, white layer composed of same heteromerous tissue as found in the stipe-columella. *Lactic juice* not observed. *Internal gleba* white in immature specimens, yellowish orange in mature specimens. Gleba cavities flattened, anastomosing, much broader than the septa, empty. Tramal plates 30–70 μm thick, of parallel hyphae and scattered hyphal swellings up to 15 μm thick, no sphaerocysts observed with certainty. *External gleba* exposed near the stipe, at first indistinctly lamellate with gleba cavities scattered between the ridges, exposed gleba cavities in aged specimens mainly irregularly arranged. *Hymenium* about 30 μm thick, consisting of basidia, cystidia and basidia-like pseudoparaphyses; basidia clavate, 30–40 μm long and 12–17 μm broad, hyaline, sterigmata 2–4, up to 6 μm long; cystidia about twice as long as the basidia, variable in shape and length, narrowly acute or gradually tapering into a long, thin apex, with amorphous contents, collapsing with age and hardly visible in aged hymenium; pseudoparaphyses similar to the basidia, non-septate. *Spores* pale yellow under the microscope, dark orange yellow in mass, of variable shape and size, usually subglobose to almost globose, rarely oblong, (6.5–)9–10(–15) μm in diameter when globose–subglobose, up to 16 μm long in oblong spores, echinulate with isolated, narrowly conical spines 0.5–1(–1.5) μm long. Spines about 20–25 in number along the circumference of the spore. Pedicel usually present, (1–)2–3(–6) μm long, hyaline, straight or curved. *Odour* sour, recalling that of wine but very faint.

Intact, fresh gastrocarps were pure white, whereas aged and worm-eaten ones were of a brown colour. No soil was attached to the intact specimens except to the end of the stipe.

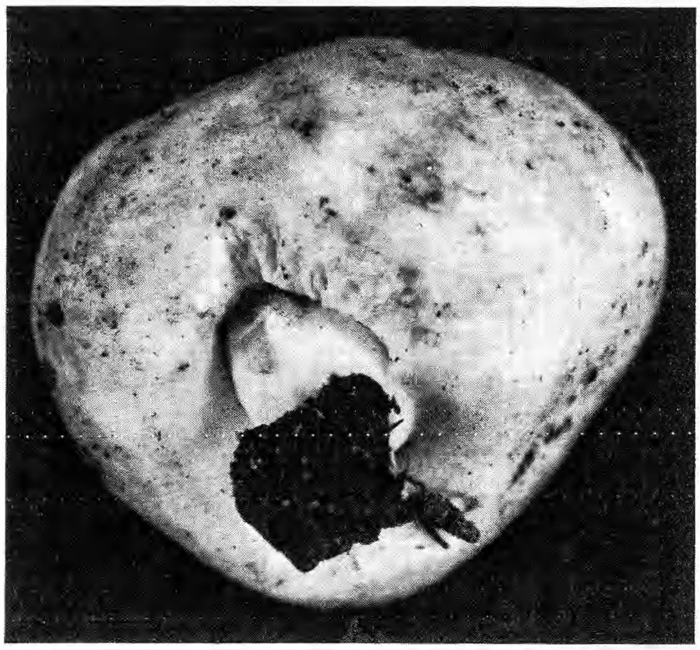

Fig. 2. Fresh gastrocarp of *Elasmomyces krjukowensis* seen from below. A small portion of the lamelled, exposed gleba may be seen near the stipe. – Diameter 1.7 cm – Kers & Plahn 30.VIII.1977 (S). Photo: Bengt Ekberg, SVA. Stockholm.

The genus *Elasmomyces* Cav. is fairly well-known since it is so often mentioned as a link between the Gasteromycetes and Agaricales. Specimens of *Elasmomyces* can actually be mistaken for ‘agaric buttons’. A vertical section through the gastrocarp, however, reveals their gasteromycete nature (cf. Fig. 1 A, B).

The macroscopic characters of *Elasmomyces* (s.str.) are the stipe, the partially exposed and indistinctly lamellate gleba, and the percurrent columella. The most obvious microscopic characters are the more or less spherical spores ornamented with minute spines, the presence of cystidia in the hymenium, and the heteromerous tissue found in the stipe-columella. From the microscopic characters in particular an affinity has been suggested between *Elasmomyces* and the agaricaceous genera *Lactarius* and *Russula* (cf. Bucholtz 1903 p. 160, Malençon 1931 p. 377 ff, Heim 1948 p. 161 ff).

Variation in the Swedish material

Most gastrocarps measured 1–2 cm across when fresh. The smallest specimens were 4–5 mm in diameter, the largest ones 3.5 cm.

The extension of the exposed gleba varies in the material. In many specimens the gleba is exposed only within a narrow sector next to the stipe. Most sections of these specimens, therefore, may give the impression of an angiocarpic

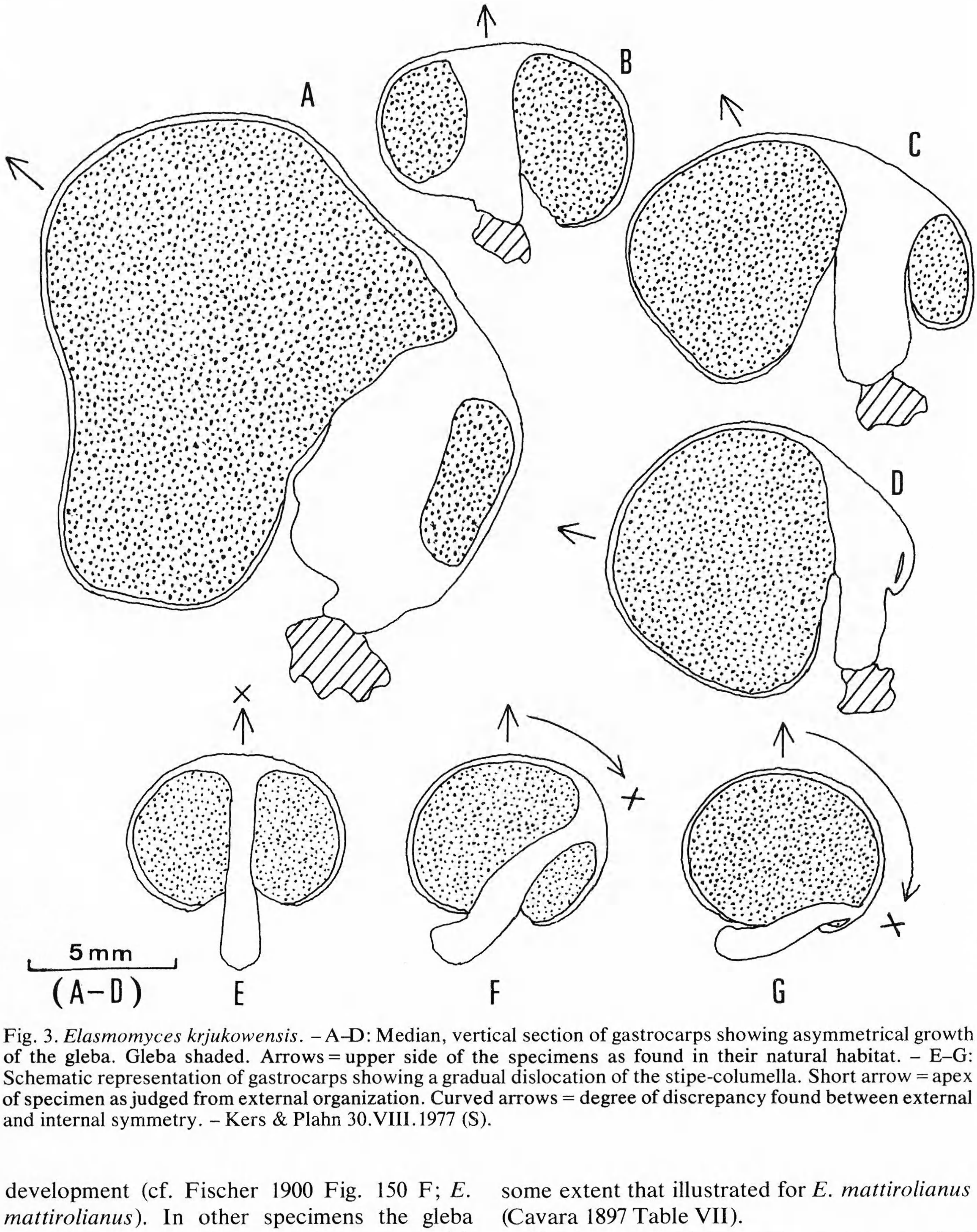

Fig. 3. *Elasmomyces krjukowensis*. – A–D: Median, vertical section of gastrocarps showing asymmetrical growth of the gleba. Gleba shaded. Arrows = upper side of the specimens as found in their natural habitat. – E–G: Schematic representation of gastrocarps showing a gradual dislocation of the stipe-columella. Short arrow = apex of specimen as judged from external organization. Curved arrows = degree of discrepancy found between external and internal symmetry. – Kers & Plahn 30.VIII.1977 (S).

development (cf. Fischer 1900 Fig. 150 F; *E. mattirolianus*). In other specimens the gleba extends all around the (central) stipe. In habit these specimens therefore resemble the pictures of *E. mattirolianus* (cf. Fischer 1900 p. 300, Fig. 150). The variation found in the gross morphology of the Swedish material overlaps to some extent that illustrated for *E. mattirolianus* (Cavara 1897 Table VII).

The exposed gleba undergoes a gradual change during the development of the gastrocarp and therefore differs considerably in various specimens. The following two stages can be recognized.

(A) The primary exposed gleba is radially sculptured by delicate ridges with a few bifurcations and anastomoses. They give the gleba an indistinctly lamellate structure. Openings into the interior gleba are scattered in the furrows between the ridges. This gleba is sterile in its most exterior parts, and is of a pale whitish colour. Its characteristics reflect the gymnocarpy in the species.

(B) The secondary exposed gleba is formed by a disintegration of the very delicate and sometimes arachnoid peridium which is situated around the primary exposed gleba. Simultaneously the exterior parts of the primary exposed gleba also flake off or disintegrate. By this process, the exposed gleba finally consists of parts which were not exposed in the young gastrocarps. This gleba is fertile with the gleba cavities mainly irregularly arranged.

All specimens which I sectioned had a percurrent columella. In a small number of specimens the stipe-columella is S-shaped. The stipe is then laterally intergrown with the exterior wall of the peridium whereas the columella comes more or less close to the inner wall (Fig. 3). In extreme cases the columella is very short and almost intergrown with the inner peridium without a separating fertile gleba (Fig. 3 D). At a casual glance, the columella then appears as if reduced to a small sterile base of the gastrocarp. It is also clear that sections made more or less at right angles to that shown in Fig. 3 can give a false picture of a columella that is *not* percurrent. Atypical specimens in particular might have been confused with *Arcangeliella stephensii* (sensu Fischer 1933 p. 32, Fig. 24, non sensu Hawker 1954 p. 517).

Oleiferous vessels have been observed in the peridium and columella, but not with certainty in the trama. Only a few samples were studied.

Both acute and apiculate cystidia exist in the material, even in the same samples. It is likely that the difference in shape and length depends on the maturity stage of the hymenium; the short, acute cystidia being younger.

The considerable variation in spore size seems characteristic of the species. The variation range is found in single samples and does not reflect a variation between specimens or localities.

The variation shown by the microscopic structures has not been studied in detail.

Habitat

The Gotland finds were made in a wooded meadow in which *Quercus robur* and *Corylus avellana* are the dominant species. No further information about the habitat is available so far. The following observations refer to the Uppland localities and are based on my own field studies there.

The four Swedish mainland localities are situated about 50 km NW of Stockholm and just N of lake Mälaren. Two localities are situated only 550 m apart whereas the other two are at a distance of 4 km and 6 km from the aforementioned ones. The species is, however, not locally frequent in this region.

The fungus grows in deciduous woods with *Quercus robur* and *Corylus avellana* as dominant species and with local stands of *Fraxinus excelsior, Acer platanoides* and *Betula*.

The Uppland localities were grazed by cattle in the past. This could be traced by the scattered occurrence of dead or almost dead specimens of *Juniperus communis* and *Malus sylvestris*, especially frequent in two localities. *Elasmomyces* was found under large, old *Corylus avellana* shrubs and near their stems. In this situation the deep shade of the canopy prevents a grass vegetation from being established, but favours an accumulation of leaf litter. The soil was not densely felted by roots and rhizomes. The finds were made on gentle slopes, which means that the upper soil was well-drained, moderately moist, more porous and contained less clay as compared with the soil in other situations here. The upper soil layer was easily dug by a small hand spade and the soil portions regularly fell apart into a granulated mass of small pieces.

Subepigean specimens are known to occur in this species. No Uppland specimens could be seen unless the covering layer of litter or soil had been scraped off. The specimens occurred from just below the litter to a depth of two--three centimeters below the soil surface.

A comparatively rich flora of other Fungi hypogaei was discovered when we searched for *Elasmomyces* in this region. Species of the genera *Elaphomyces, Tuber, Melanogaster, Hymenogaster, Hysterangium* and *Endogone* were found. They occurred patchwise which seems to reflect the very complicated subter-

Fig. 4. Known distribution of *Elasmomyces* in Europe and Israel.
▼ Type localities for *Elasmomyces krjukowensis* (USSR).
▲ Type locality for *E. mattirolianus* (Italy).
■ Type locality for *Macowanites galileensis* (Israel).
● Material in the literature referred to *E. krjukowensis* or to *E. mattirolianus*.
– The map is based on finds reported in Bucholtz 1902, Cavara 1897, Gross 1968, Hollós 1911, Knapp 1958, Lohwag 1930, Moser et al. 1977, Petri 1909, Soehner 1924, 1949, Sossin 1973, Svrček 1958, Szemere 1965.

ranean conditions which prevail even within a seemingly uniform vegetation type.

Elasmomyces krjukowensis has also been recorded from deciduous woods in Czecho-Slovakia, Germany and the Soviet Union (Svrček 1958 p. 207, Gross 1968, Bucholtz 1901 pp. 314, 315).

Taxonomy

The Swedish material has been identified with *E. krjukowensis*. This species is not, however, well distinguished from *E. mattirolianus* (typus generis). A comparison between the descriptions raises doubts as to the distinctness of these species (cf. Cavara 1897, Saccardo 1899, 1905, Bucholtz 1901, 1902, 1903, Fischer 1900, 1933, Petri 1909, Hollós 1911, Bataille 1923, Zeller & Dodge 1937, Soehner 1949 fide Svrček 1958, Moser 1955, Svrček 1958, Singer & Smith 1960, Szemere 1965, Gross 1968, Sossin 1973).

According to some previous authors the most essential characters distinguishing *E. mattirolianus* from *E. krjukowensis* should be the "lactic ducts" and the "strict angiocarpy" of the former species. There is no strict angiocarpy in the former species, both are gymnocarpic at first. The idea of an angiocarpy in *E. mattirolianus* originates from some authors' interpretation of Fischer's figures of sectioned gastrocarps (Fischer 1900 p. 301). Lohwag found the difference to be fundamental and proposed a new genus for the gymnocarpic species, viz. *Bucholtzia* (Lohwag 1924 pp. 172, 173). The sections reproduced by Fischer (1900) do not necessarily demonstrate an angiocarpy in the species, just an angiocarpic portion of a sectioned gastrocarp. Fischer later declared both species to be gymnocarpic (Fischer 1933 pp. 109, 111).

The difference stated by Fischer (1933) to exist in the degree to which the exposed gleba becomes hidden beneath the expanded 'pileus' is certainly not a significant specific character (Fischer 1933 p. 109). It is true that most gastrocarps illustrated for *E. mattirolianus* have a very agaric-like habit, seldom found in the allied species. An agaric- or "truffle"-like habit may be due to environmental conditions, e.g. an hypogeic or occasional epigeic–subepigeic growth.

Singer & Smith (1960 pp. 60, 77) have recently made a detailed analysis of the types. They found both species to lack lacticiferous vessels but to possess oleiferous ducts (definitions of the terms, see Singer & Smith 1960 p. 79, footnote). These authors kept the species separate essentially by the presence of absence of sphaerocysts in the tramal plates: *E. mattirolianus* lacks these sphaerocysts but shows "occasional hyphal swellings".

The spore size is another character used to distinguish the species. The spores of *E. mattirolianus* are commonly said to be somewhat larger than those of *E. krjukowensis*, viz. (8–)10–15(–16) µm and (8–)9–11.5 µm respectively. New finds of *E. krjukowensis* show a greater spore size than was previously known in this species. From Czecho-Slovakian material Svrček thus gives the spore size as 8.5–14 µm, a variation range that overlaps that of the allied species (Svrček 1958 p. 737). Some spores reach 14 µm in diameter in the Swedish specimens as well. In type material of *E. mattirolianus* (at S) the larger spores are more abundant than in the Swedish specimens. It is possible that a biometrical analysis of the variation range will verify a significant difference as to spore size.

From the list of synonyms, presented in this paper, we have learnt that almost every mycologist who has dealt with *Elasmomyces* has found it necessary to coin a new combination for *E. krjukowensis*. Besides, they have kept the two species discussed here well separated in different genera. The interrelationship of *E. mattirolianus* and *E. krjukowensis* is, however, apparently close. A re-investigation of *E. mattirolianus*, made with new collections from Italy, which better represent the specific variation than merely the type, seems necessary. Because the identity of the two species has not yet been clearly demonstrated I have classified the Swedish material to *E. krjukowensis*. If the two species are shown to be conspecific, the genus *Elasmomyces* Cav. (1897) can no longer be upheld against *Macowanites* Kalchbrenner (1876) (Singer & Smith 1960 p. 78).

Bucholtz described *E. krjukowensis* under *Secotium* because *Elasmomyces* had been reduced to a synonym of *Secotium* (Fischer 1900 p. 300). It is nowadays generally accepted that the two genera have little in common. Nevertheless *Elasmomyces* by tradition is still found listed under Secotiaceae in several flora works.

According to the traditional taxonomy, *Elasmomyces* would be placed in Gasteromycetes and there preferably in Hydnangiaceae. *Elasmomyces, Arcangeliella, Hydnangium* (sensu Fischer) and some other genera show close interrelations. All these genera have been very differently circumscribed by various authors. According to the current taxonomic view these genera form the links of an evolutionary series "the Asterogastraceous Series", to which also the genera *Lactarius* and *Russula* are intimately connected. Within Asterosporales, *Elasmomyces* and allied genera belong to Asterogastraceae whereas *Lactarius* and *Russula* compose the family Russulaceae (Malençon 1931 p. 380 ff, Heim 1948 p. 165).

Definite and natural circumscriptions of the genera within Asterogastraceae are certainly still quite remote. I have found it most appropriate, therefore, not to use any of the recently suggested combinations but to stick to the genus *Elasmomyces* in this presentation.

Geographical distribution

Because the interrelationship of *E. mattirolianus* and *E. krjukowensis* is unclear it is not possible to separate them on a distribution map. A German find presented by Soehner (1949 pp. 14, 15) as *Arcangeliella stephensii* was considered by Svrček to be supposedly identical with *Hydnangium krjukowense* (Svrček 1958 p. 206). Due to the well developed exposed gleba, the illustrated gastrocarps much resemble the original figures of *E. mattirolianus* (Soehner 1949 Fig. 26, 30; Fig. 26 also reproduced in Moser 1955 Abb. XVII, Fig. 13).

All finds of "*Elasmomyces*" known to me from Europe and Israel have been plotted in Fig. 4. Only the Italian material has been treated under *E. mattirolianus*. All records of this species from Central Europe can actually be identified with *E. krjukowensis* as well. The Russian find of *E. mattirolianus* seems questionable and the material needs further studies. The recently described *Macowanites galileensis* from Israel comes close to *E. krjukowensis*, from which it differs in spore ornamentation (Moser et al. 1977 p. 373, Fig. 4).

Elasmomyces mattirolianus and *E. krjukowensis* are known only from Europe. A previous record of *E. mattirolianus* from USA (Oregon) refers to a closely allied but distinct American species (Singer & Smith 1960 pp. 61, 62).

Acknowledgements. Many thanks are due to Mr Evert Plahn, who sent me the material for determination and then invited me to see the localities in which he had found this rare species. I am also much indebted to Miss Sally Brown, Stockholm, who revised my English text and to Dr Nils Lundqvist, Uppsala, for his kindness in reading the manuscript.

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Added in proof

Elasmomyces (*mattirolianus*) has recently been reported from one locality in Belgium, viz. the southern slope of Grande Tinaimont, near Han-sur-Lesse. This locality is included in Fig. 4. Unfortunately the publication was not available when my article was in manuscript (De Vries, G. A. 1977: Contribution à la connaissance des champignons hypogés de la Belgique. *Lejeunia 86:* 1–16).

A single specimen of a fungus, found by Lloyd in 1905 near Stockholm, was tentatively classified by him to *Secotium michailowskianum*. The record still remains doubtful (cf. Arwidsson in *Svensk Bot. Tidskrift 39:* 138–139).

A new species of Phacelophrynium from northern Thailand

Kai Larsen

Larsen, K. 1978 03 31: A new species of Phacelophrynium from northern Thailand. *Bot. Notiser 131:* 83–84. Stockholm. ISSN 0006-8195.

Phacelophrynium exorbitans sp. nov. is described from Northern Thailand. It is related to *P. maximum* (Bl.) K. Schum. The distributional range of *Phacelophrynium* is by this find extended northwards, far beyond its previously known limit.

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Phacelophrynium exorbitans K. Larsen sp. nov. – Fig. 1

Rhizoma horizontale circiter 1 cm crassum, radices numerosas emittens. Surculi erecti 40–50 cm alti, ex omnibus nodis ramigeri, quisque basi duo cataphylla gerens e vaginis solum constituta. Euphylli vagina aperta in parte basali praesertim juxta margines lanata, 13–14 cm longa; petiolus circiter 2 cm longus, parte incrassata circiter 1 cm; lamina glabra, elliptica, basi rotundata, apice acuminata vel breviter caudata ad 17 × 8 cm magna.

Inflorescentiae 2–5 cm longae, singulae vel 2–3 congregatae. Bracteae accurate distichae, carinatae, e basibus circiter 10 mm latis sursum angustatae, apice acutae, 10–15 mm longae, margine scariosae fimbriatae, quaeque inflorescentiam suffulgens e compluribus floribus binatim dispositis formatam. Flores binatim conjuncti non eodem die dehiscentes. Prophyllum 6–7 mm longum, lanceolatum, acutum, in dorso duas alas gerens. Flores subsessiles, ovarium ad apicem versus minute sericeum. Sepala libera, lanceolata, acuta, 4 × 1.5 mm magna. Corollae tubus circiter 1 mm longus, lobi 5 mm longi, elliptici, apice rotundati. Staminodii tubus illo paulum longior. Staminodia exteriora 2 spathulata, alba margine coerulescentia, circiter 5 mm longa; staminodium carnosum 5–6 mm longum, flavidum margine coerulescens; staminodium cucullatum flavidum circiter 5 mm longum. Stamen circiter 6 mm longum, appendice petaloide angusta ornatum. Stylus albus, curvus. Fructus ignotus.

Holotypus die 15 Febr. anni 1977 juxta rivum 400 m supra mare prope pagum Fan ab oppido thailandico Chiam Mai in septentriones situm silvam sempervirentem percurrentem sub numero K.L. 36100 lectus, in caldario Horti Botanici Aarhusiensis ad florendum cultus, siccus in Herbario Jutlandico (AAU) depositus.

In his monograph on Marantaceae, Schumann (1902) erected the genus *Phacelophrynium*, by separating from *Phrynium* all taxa possessing distichous bracts. Schumann's taxonomy of this group has been accepted ever since. Holttum (1951) pointed out that, in any case in some species, the basal bracts of the young subsidiary spikes are not clearly distichous, while the bracts of the main shoot inflorescence always are. In *P. exorbitans* all the bracts are clearly distichous.

The genus *Phacelophrynium* was hitherto only known from the Malay Peninsula, the Nicobares, Java, Sumatra, Borneo and the Philippines. Of the 7 or 8 species known, only one, *P. maximum* (Bl.) K. Schum. was recorded from the Asiatic mainland.

The present new species was collected more than 2000 km N of the previously known distribution area of *P. maximum*. It differs from the latter species in the smaller size of its vegetative and floral parts and by possessing subsessile flowers, 2 outer staminodes and a staminal appendage. Two of the outer and one of the inner staminodes lie close together, thus simulating 3 petals (Fig. 1 E).

The species was found by Mr H. Dixen, Curator of the hothouses of the Botanical Institute at Aarhus, during an expedition to Thailand, led by the author in 1970. When found it was not flowering, but rhizomes sent to Aarhus grew

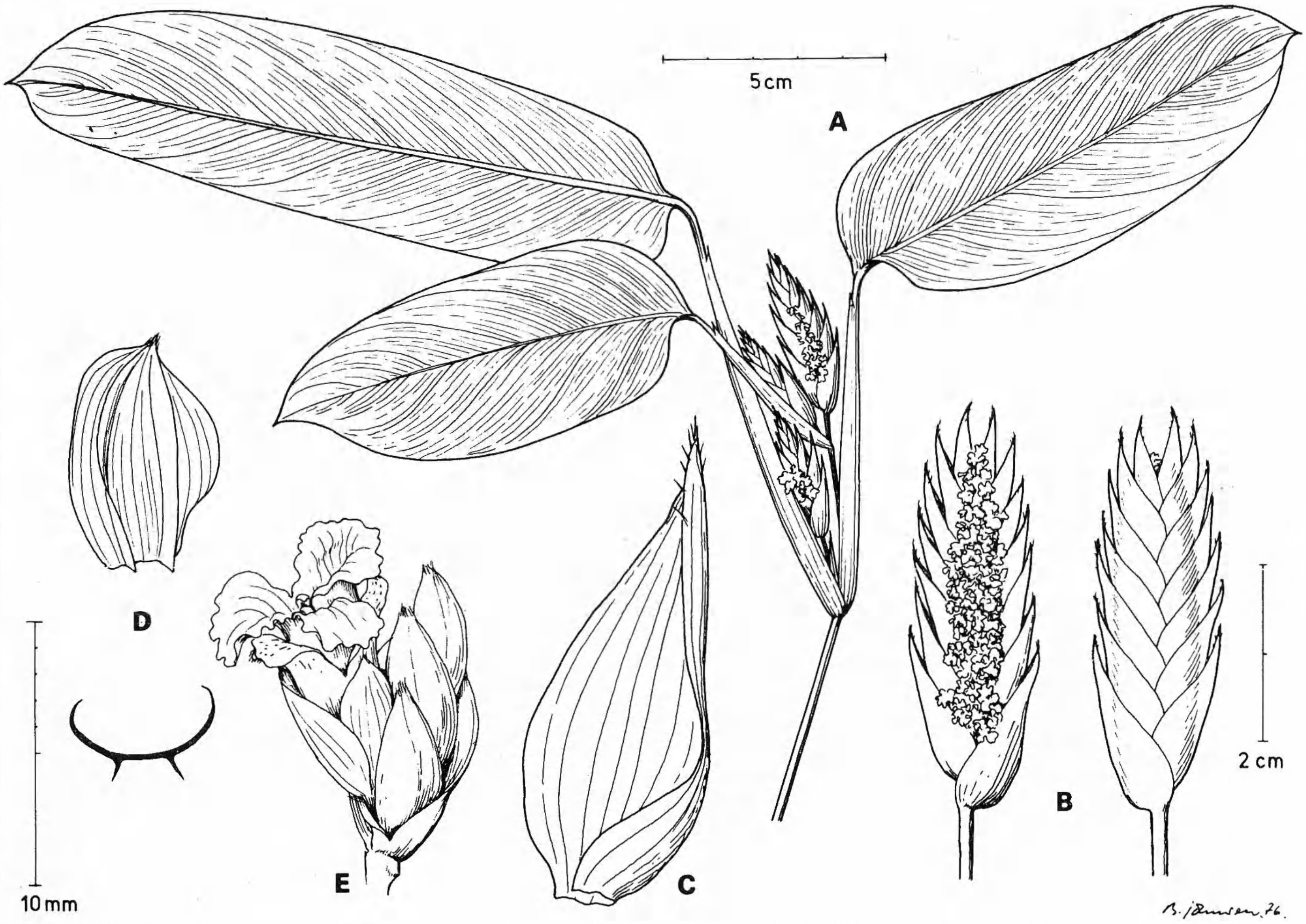

Fig. 1. *Phacelophrynium exorbitans*. – A: Flowering shoot. – B: Inflorescence. – C: Bract. – D: Prophyll. – E: Partial inflorescence.

well, producing large plants with numerous stems, which have flowered during the past 2 years.

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Tropane alkaloids – occurrence and systematic importance in angiosperms

Anneliese Romeike

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A review of the structure and biosynthesis of tropane alkaloids is given. Since the derivatives of the hygrine bases show a similar mode of formation, they have also been included. A list of tropane alkaloids in angiosperms is given. They occur chiefly in the Solanaceae, but there are scattered occurrences in other families as well. No definitive statement on their taxonomic value can be made, but the ability to synthesize this type of alkaloids has probably originated independently within several evolutionary lines.

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In recent times, the role of alkaloids as a tool in the chemotaxonomy of plants has been the subject of many investigations. General considerations about the use of alkaloids in the solution of phytotaxonomic problems are given by Hegnauer 1958, 1963, 1966a, Mothes 1966a, b, 1969, Li & Willaman 1968, Gill & Raszeja 1974, Lazur'evskij & Terent'eva 1974. All these authors emphasize the importance of the biogenetic viewpoint when secondary plant substances are used in chemotaxonomy. To select valuable characters it is not sufficient to compare alkaloids which have a similar structure; there must also be homology in their formation pathways. Thus, the modes of formation in the plants of alkaloids which contain a pyrrolidine ring and which are widely distributed in the vegetable kingdom, do not always coincide.

Structure and biosynthesis

The skeleton of all tropane alkaloids is the bicyclic amine tropane (Fig. 1 I) which represents the combination of a pyrrolidine and a piperidine ring. The stereochemistry of tropane and its derivatives is well investigated (Liebisch 1969 a). A cis-connection between a pyrrolidine and a piperidine ring gives rise to a meso-form and because of this no optical isomers occur. In plant alkaloids the tropane ring in most cases bears one or more hydroxyl groups, positioned on the same side of the cycloheptane ring as the N-bridge (cis- or β-position, Fig. 1 II) or on the opposite side (trans- or α-position, Fig. 1 III). In general, the hydroxyl groups are esterified.

Hitherto, c. 18 amino-alcohols have been found as constituents of tropane alkaloids in plants (Table 1). They can occur free or esterified. 24 different acids have been found (Table 1).

Tropane alkaloid biosynthesis has been very extensively investigated (Liebisch 1969 a). Numerous investigations on solanaceous plants have shown that the pyrrolidine ring of tropane originates from ornithine and that the C-atoms 2, 3 and 4 derive from acetate. The same situation has been shown to hold for the pyrrolidine alkaloids hygrine (O'Donovan & Keogh 1969) and cuscohygrine (O'Donovan & Keogh 1969, Baralle & Gros 1969 a, b, c, Liebisch et al. 1969) and also for the ecgonine alkaloids (Liebisch 1969 a, Liebisch et al. 1972). Hygrine may in vivo become incorporated into hyoscyamine, scopolamine and cuscohygrine (O'Donovan & Keogh 1969, Liebisch et al. 1972). Liebisch et al. (1972) postulated that hygrine-α-carboxylic acid

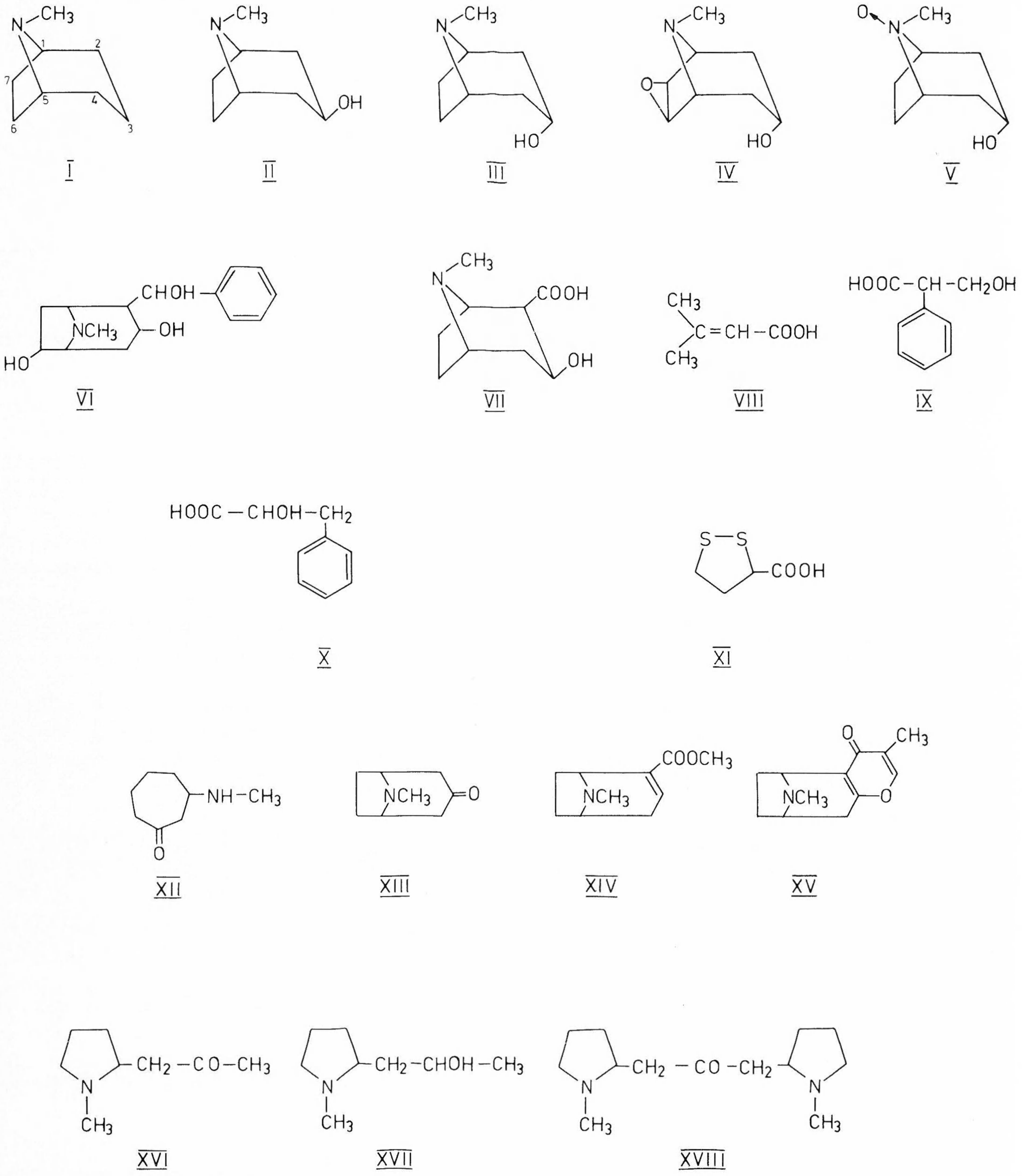

Fig. 1. Structure formulas of some substances mentioned in the text.

is a key metabolite in the biosynthesis of pyrrolidine bases such as the tropane and coca alkaloids.

The pyrrolidine ring of nicotine is also formed from ornithine, but the biosynthetic differences between the pyrrolidine systems of tropine and nicotine are remarkable. Feeding experiments with ornithine ^{14}C-labelled in the α-position, yielded radioactivity in only one of the bridge-C-atoms of the tropane ring, whereas in nicotine the radioactivity was equally located in the C-atoms 2' and 5'; its incorporation must involve a

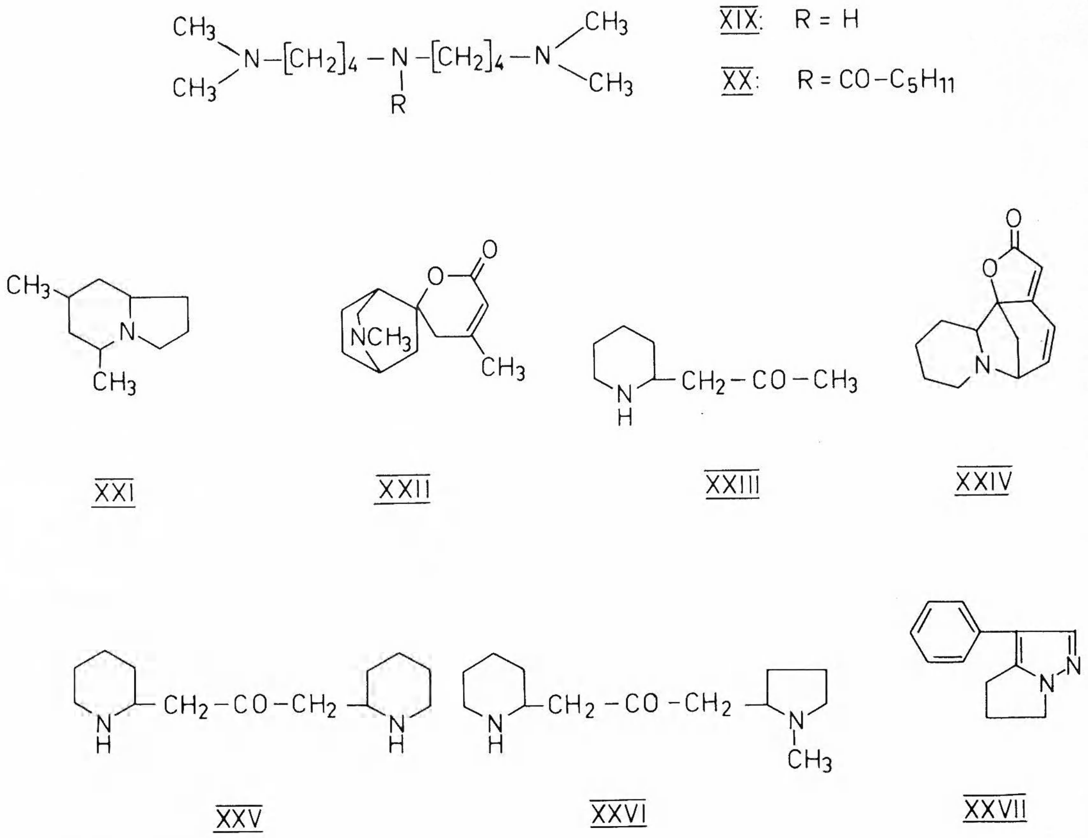

Fig. 2. Structure formulas of some substances mentioned in Table 3.

symmetric intermediate compound, e.g. putrescine (Gross 1969). Contrary to this, ornithine becomes stereospecifically incorporated into the pyrrolidine part of tropane; free putrescine is not involved in this case.

Further pathways leading to the pyrrolidine system are known in plants; for instance, the biosynthesis of stachydrine and similar alkaloids involves proline and the pyrrol skeleton of the porphyrines is formed by condensation of two molecules of δ-aminolevulinic acid (Liebisch 1969 a).

Most of the tropane alkaloids which occur in plants represent esters; the alkamines are esterified with acids of various chemical structure. Most of these acids show a regular distribution in the vegetable kingdom; this is also true for plants which lack tropane alkaloids. Tropic acid is a component found in a large number of tropane alkaloids. It is formed in the plant from phenylalanine and the rearrangement which gives rise to tropic acid involves an intramolecular migration of the carboxyl group (Leete et al. 1975). Phenylalanine is also a precursor of benzoic acid during the biosynthesis of cocaine (Gross & Schütte 1963), 2-hydroxy-3-phenylpropionic acid in the biosynthesis of littorine (Evans & Woolley 1969) and probably also of 2-hydroxytropic acid which occurs esterified with scopine in some solanaceous genera. Tiglic acid is yet another acid frequently found esterified with tropane derivatives. Its precursor in the plant is isoleucine (Evans & Woolley 1965 a) and the pathway involves 2-methylbutyric acid (Basey & Woolley 1973 a, Leete 1973).

Since the derivatives of tropane and the hygrine bases show a common mode of formation, they will be dealt with together in this review, as also physoperuvine (Fig. 1 XII), an alkaloid found very recently in *Physalis peruviana* (Ray et al. 1976). Physoperuvine is isomeric with tropine and hygrine and may be formed in the plant in a shunt of the biosynthetic pathway of the tropane alkaloids.

Table 1. Occurrence of tropane alkaloids and their esters. Roman numbers refer to formulas in Fig. 1. – (1) See references in Boit 1961 – (2) Evans & Treagust 1973 – (3) Pelt et al. 1967 a, b – (4) Loder & Russell 1969 – (5) Coulson & Griffin 1967 – (6) Agar et al. 1974 – (7) Basey & Woolley 1973 b – (8) Evans et al. 1972 a – (9) Evans et al. 1972 b – (10) Khanna et al. 1961 – (11) Evans & Major 1966 – (12) Ghani et al. 1972 – (13) Jackson & Berry 1973 – (14) Yamaguchi & Nishimoto 1965 – (15) Zito & Leary 1966 – (16) Leary et al. 1963 – (17) Platonova & Kusovkov 1963 – (18) Cannon et al. 1969 – (19) Bremner & Cannon 1968 – (20) Hsiao et al. 1973 – (21) Bodendorf & Kummer 1962 – (22) Evans & Major 1968 – (23) Parello et al. 1963 – (24) Johns et al. 1970 – (25) Loder & Russell 1966 – (26) Johns et al. 1971 – (27) Evans & Woolley 1965 b – (28) Pfleger 1964 – (29) Yamaguchi et al. 1974 – (30) Phillipson & Handa 1975 – (30 a) Phillipson & Handa 1973 – (31) Wolfes & Hromotka 1933 – (32) Romeike 1962 – (33) Griffin 1975 – (34) Mirzamatov et al. 1972 – (35) Beresford & Woolley 1974 b – (36) Evans & Griffin 1963 – (37) Evans & Lampard 1972 – (38) Beresford & Woolley 1974 a – (39) Evans & Than 1962 – (40) Mirzamatov et al. 1974 – (41) Agar & Evans 1975 – (42) Johns & Lamberton 1967 – (43) Kan-Fan & Lounasmaa 1973 – (44) Lounasmaa 1975 – (45) Saint-Firmin & Paris 1968 – (46) Agar & Evans 1976 – (47) Griffin 1976 – * Absolute configuration see Fodor & Soti (1964).

Alkamine	Acid	Ester	Genera
Nortropine (nortropan-3α-ol)	Isovaleric acid	Poroidine	*Duboisia* (1)
Do.	(+)-2-methylbutyric acid	Isoporoidine	*Duboisia* (1)
Do.	(−)-tropic acid	Norhyoscyamine	*Anthocercis* (2), *Atropa* (3), *Datura* (1), *Duboisia* (1), *Hyoscyamus* (3), *Mandragora* (1), *Scopolia* (1), *Solandra* (1)
Do.	Veratric acid	Convolvine	*Convolvulus* (1)
Tropine (tropan-3α-ol) (III)	–	–	*Anthocercis* (2), *Atropa* (1), *Bruguiera* (4), *Datura* (1), *Duboisia* (5), *Erythroxylum* (6), *Hyoscyamus* (1), *Physalis* (7), *Salpichroa* (8), *Scopolia* (1), *Solandra* (9), *Withania* (10)
Do.	Acetic acid	3α-acetoxytropane	*Bruguiera* (4), *Datura* (11), *Duboisia* (5), *Solandra* (9)
Do.	Propionic acid	3α-propionyloxytropane	*Bruguiera* (4)
Do.	n-butyric acid	3α-n-butyryloxytropane	*Bruguiera* (4)
Do.	Isobutyric acid	Butropine	*Bruguiera* (4), *Duboisia* (1)
Do.	(+)-2-methylbutyric acid	Valtropine (or isovaleryloxytropane in *Bruguiera*)	*Bruguiera* (4), *Duboisia* (1), *Solandra* (9)
Do.	Tiglic acid	3α-tigloyloxytropane	*Anthocercis* (2), *Datura* (1), *Duboisia* (5), *Hyoscyamus* (12), *Mandragora* (13), *Physalis* (14), *Scopolia* (15), *Solandra* (9), *Withania* (16)
Do.	Senecioic acid (VIII)	3α-senecioyloxytropane	*Dioscorea* (1)
Do.	Benzoic acid	3α-benzoyloxytropane	*Bruguiera* (4), *Erythroxylum* (1)
Do.	m-hydroxybenzoic acid	Cochlearine	*Cochlearia* (17)
Do.	3,4,5-trimethoxybenzoic acid	3α-[3,4,5-trimethoxybenzoyloxy]-tropane	*Erythroxylum* (6)
Do.	Atropic acid	Apoatropine	*Anthocercis* (2), *Atropa* (1), *Datura* (1), *Hyoscyamus* (1), *Physochlaina* (1)
Do.	(0–)-tropic acid (IX)	Hyoscyamine	*Anthocercis* (18), *Anthotroche* (19), *Atropa* (1), *Atropanthe* (20), *Datura* (1), *Duboisia* (1), *Hyoscyamus* (1), *Latua* (21), *Mandragora* (1), *Methysticodendron* (1), *Physochlaina* (1), *Przewalskia* (20), *Salpichroa* (8), *Scopolia* (1), *Solandra* (1)
Do.	(+)-2-hydroxy-3-phenylpropionic acid (X)	Littorine ((−)-3α-[2-hydroxy-3-phenylpropionyloxy]-tropane)	*Anthocercis* (18), *Datura* (22), *Hyoscyamus* (12), *Solandra* (9)
Do.	Vanillic acid	Phyllalbine	*Phyllanthus* (23)

Table 1 (continued).

Alkamine	Acid	Ester	Genera
Do.	Veratric acid	Convolamine	*Convolvulus* (1)
Do.	3,4,5-trimethoxycinnamic acid	3α-[3′,4′,5′-trimethoxycinnamoyloxy]-tropane	*Erythroxylum* (24)
Do.	1,2-dithiolane-3-carbonic acid (XI)	Brugine	*Bruguiera* (25)
Pseudotropine (tropan-3β-ol) (II)	–	–	*Anthocercis* (2), *Datura* (1), *Erythroxylum* (1), *Hyoscyamus* (12), *Physalis* (7), *Salpichroa* (8), *Scopolia* (15), *Solandra* (9), *Withania* (10)
Do.	Tiglic acid	Tigloidine	*Anthocercis* (2), *Datura* (1), *Duboisia* (1), *Hyoscyamus* (12), *Physalis* (7), *Solandra* (9)
Do.	Benzoic acid	Tropacocaine	*Erythroxylum* (1), *Peripentadenia* (26)
2α-hydroxy-norpseudotropine (nortropan-2α,3β-diol)	Benzoic acid	(+)-2α-benzoyloxynortropan-3β-ol	*Peripentadenia* (26)
Norscopine (6β,7β-epoxynortropan-3α-ol)	(±)-tropic acid	(±)-norscopolamine	*Anthocercis* (2), *Datura* (1), *Duboisia* (5), *Hyoscyamus* (3)
Scopine (6β,7β-epoxytropan-3α-ol) (IV)	–	–	*Scopolia* (1), *Hyoscyamus* (45)
Do.	Atropic acid	Aposcopolamine	*Datura* (27), *Duboisia* (5), *Hyoscyamus* (3)
Do.	(−)-tropic acid	(−)-scopolamine	*Anthocercis* (2), *Atropa* (1), *Atropanthe* (20), *Datura* (1), *Duboisia* (1), *Hyoscyamus* (1), *Latua* (21), *Mandragora* (21), *Methysticodendron* (1), *Physochlaina* (1), *Przewalskia* (20), *Scopolia* (1), *Solandra* (9)
Do.	(−)-2-hydroxytropic acid (2,3-dihydroxy-2-phenylpropionic acid)	Daturamine (anisodine)	*Atropanthe* (20), *Datura* (28), *Przewalskia* (20), *Scopolia* (20)
Oscine (scopoline)	–	–	*Datura* (22)
Tropine-N-oxid (V)	Tiglic acid	3α-tigloyloxytropane-N-oxid	*Physalis* (29)
Do.	(−)-tropic acid	Hyoscyamine-N-oxid	*Atropa* (30 a), *Datura* (30), *Hyoscyamus* (30), *Mandragora* (30), *Scopolia* (30)
Scopine-N-oxid	(−)-tropic acid	Scopolamine-N-oxid	*Atropa* (30), *Datura* (30 a), *Hyoscyamus* (30 a), *Scopolia* (30)
(−)-6-hydroxytropine ((−)-tropan-3α,6β-diol, 3S:6S)	Esterified, probably with two molecules of benzoic acid		*Erythroxylum* (31)
Do.	1 mol. isovaleric acid	Valeroidine* ((−)-3α-isovaleryloxytropan-6β-ol)	*Datura* (1), *Duboisia* (1)
Do.	1 mol. (−)-tropic acid	(−)-6β-hydroxyhyoscyamine (absolute configuration see Fodor et al. 1965)	*Datura* (32), *Duboisia* (33), *Mandragora* (20), *Physochlaina* (34), *Przewalskia* (20), *Scopolia* (20)
(+)-6-hydroxytropine ((+)-tropan-3α,6β-diol, 3R:6R)	1 mol. acetic acid	(+)-3α-acetoxytropan-6β-ol	*Peripentadenia* (26)
Do.	1 mol. (+)-2-methylbutyric acid	(+)-6β[2-methylbutyryloxy]-tropan-3α-ol	*Datura* (35)
Do.	1 mol. tiglic acid	(−)-6β-tigloyloxytropan-3α-ol*	*Anthocercis* (2), *Datura* (36)
Do.	Do.	(–)-3α-tigloyloxytropan-6β-ol	*Datura* (37)

Table 1 (continued).

Alkamine	Acid	Ester	Genera
Do.	1 mol. acetic, 1 mol. tiglic acid	(−)-3α-tigloyloxy-6β-acetoxytropane	*Datura* (11)
Do.	1 mol. propionic, 1 mol. tiglic acid	(±)-3α-tigloyloxy-6β-propionyloxytropane	*Datura* (38)
Do.	2 mol. tiglic acid	(−)-3α,6β-ditigloyloxytropane*	*Datura* (1), *Mandragora* (13)
6-hydroxytropine (tropan-3α,6β-diol) no statement about absolute configuration	–	–	*Datura* (39)
Do.	1 mol. p-methoxyphenylacetic acid	Physochlaine (3α-[p-methoxyphenylacetoxy]-tropan-6β-ol)	*Physochlaina* (40)
Do.	1 mol. (+)-2-methylbutyric acid, 1 mol. tiglic acid	6β-[2-methylbutyryloxy]-3α-tigloyloxytropane	*Datura* (37)
Do.	1 mol. benzoic acid, 1 mol. 3,4,5-trimethoxycinnamic acid	6β-benzoyloxy-3α-[3′,4′,5′-trimethoxycinnamoyloxy]-tropane	*Erythroxylum* (41)
Teloidine (tropan-3α,6β,7β-triol)	1 mol. tiglic acid	Meteloidine (3α-tigloyloxytropan-6,7β-diol)	*Anthocercis* (18), *Datura* (1), *Erythroxylum* (42)
Do.	Do.	6β-tigloyloxytropan-3α,7β-diol	*Datura* (37)
Do.	1 mol. 3,4,5-trimethoxybenzoic acid	3α-[3′,4′,5′-trimethoxybenzoyloxy]-tropan-6,7β-diol	*Erythroxylum* (46)
Do.	1 mol. (+)-2-hydroxy-3-phenylpropionic acid	(–)-6,7β-dihydroxylittorine	*Datura* (47)
Do.	2 mol. tiglic acid	3α,6β-ditigloyloxytropan-7β-ol	*Anthocercis* (2), *Datura* (1)
Do.	1 mol. isovaleric acid, 1 mol. tiglic acid	6β-isovaleryloxy-3α-tigloyloxytropan-7β-ol	*Datura* (22)
2-benzyltropine (tentatively 2β-benzyltropan-3α-ol)	Acetic acid	2-benzyl-3-acetoxytropane	*Knightia* (43)
Do.	Benzoic acid	2-benzyl-3-benzoyloxytropane	*Knightia* (43)
2-benzyltropan-3,6-diol (respectively 3,7-diol)	Benzoic acid	2-benzyl-6-benzoyloxytropan-3-ol	*Knightia* (43)
Do.	Cinnamic acid	2-benzyl-3-cinnamoyloxytropan-6-ol	*Knightia* (43)
2-[phenylhydroxymethyl]-tropan-3,6-diol (VI) (respectively 3,7-diol)	Benzoic acid	2-phenylhydroxymethyl-6-benzoyloxytropan-3-ol	*Knightia* (44)
Do.	1 mol. benzoic acid, 1 mol. cinnamic acid	2-phenylhydroxymethyl-3-cinnamoyloxy-6-benzoyloxytropane	*Knightia* (44)
Norecgonine (2β-carboxynortropan-3β-ol)	Formic acid	3β-formyloxynorecgonine	*Erythroxylum* (1)
(−)-ecgonine (2β-carboxytropan-3β-ol) (VII)	Benzoic acid	Benzoylecgonine	*Erythroxylum* (1)
(−)-ecgonine methylester	–	–	*Erythroxylum* (1)
Do.	Benzoic acid	(−)-cocaine	*Erythroxylum* (1)
Do.	Cinnamic acid	Cinnamylcocaine	*Erythroxylum* (1)
Do.	α-truxillic acid	α-truxilline	*Erythroxylum* (1)
Do.	β-truxillic acid	β-truxilline	*Erythroxylum* (1)

Table 2. Occurrence of further tropane derivatives and biogenetically related alkaloids. Roman numbers refer to formulas in Fig. 1. – (1) Evans et al. 1972 c – (2) Romeike 1966 – (3) See references in Boit 1961 – (4) Ray et al. 1976 – (5) Motherwell et al. 1971 – (6) Platonova & Kusovkov 1963 – (7) Lüning & Leander 1965 – (8) Kennedy 1971 – (9) Romeike 1965 – (10) Evans et al. 1972 a – (11) Fitzgerald 1965 – (12) Johns et al. 1967 – (13) Evans & Treagust 1973 – (14) Hsiao et al. 1973 – (15) Evans & Somanabandhu 1974 – (16) See references in Hegnauer 1973 – (17) Evans et al. 1972 b – (18) Leary et al. 1963 – (19) Bick et al. 1975.

Tropinone (XIII): *Cyphomandra* (1), *Nicandra* (2)
(−)-ecgonidine-methylester (XIV): *Erythroxylum* (3)
Physoperuvine (XII): *Physalis* (4)
Bellendine (XV): *Bellendena* (5)
(±)-hygrine (XVI): *Cochlearia* (6), *Convolvulus* (3), *Dendrobium* (7), *Duboisia* (8), *Erythroxylum* (3), *Nicandra* (9), *Salpichroa* (10)
(−)-hygroline (hygroline XVII): *Cochlearia* (6), *Erythroxylum* (3)
(+)-hygroline: *Carallia* (11), *Gynotroches* (12)
Cuscohygrine (XVIII): *Anthocercis* (13), *Atropa* (3), *Atropanthe* (14), *Calystegia* (15), *Convolvulus* (3), *Cyphomandra* (1), *Datura* (3), *Duboisia* (8), *Erythroxylum* (3), *Hyoscyamus* (3), *Mandragora* (3), *Physalis* (16), *Physochlaina* (3), *Przewalskia* (14), *Salpichroa* (10), *Scopolia* (3), *Solandra* (17), *Withania* (18)
Methylbellendine and 2α-benzoyltropane: *Darlingia* (19)

Table 3. Occurrence of alkaloids of other types in tropane-type alkaloid containing species. Roman numbers refer to formulas in Fig. 2. – *Δ_1-N-methylpyrroline is involved in the biogenetic pathway of nicotine in *Nicotiana* (Gross 1969). – (1) Bick et al. 1974 – (2) See references in Boit 1961 – (3) Evans et al. 1972 c – (4) See references in Schreiber 1968 – (5) Lüning & Leander 1965 – (6) Pinder 1964 – (7) Kennedy 1971 – (8) See references in Hegnauer 1973 – (9) See references in Hegnauer 1966 b – (10) Schwarting et al. 1963 – (11) Schröter et al. 1966.

Anthocercis tasmanica: nicotine (1)
Atropa belladonna: N-methylpyrroline* (2), N-methylpyrrolidine (2), nicotine (2), putrescine (2), pyridine (2)
Cyphomandra betacea: solacaproine (3), solamine (3), XIX, XX, tomatidenol- and solasodine-glycosides (4)
Datura stramonium, D. metel, D. meteloides: nicotine (2)
Dendrobium primulinum: 5,7-dimethyl-octahydroindolizine (5), XXI
Dioscorea hispida: dioscorine (6), XXII
Duboisia hopwoodii: anabasine (7), isopelletierine (7), XXIII, nicotine (7), nornicotine (7)
Duboisia myoporoides: anabasine (8), isopelletierine (8), nicotine (8), nornicotine (8), tetramethylputrescine (8)
Erythroxylum coca: anabasine (2), nicotine (9)
Hyoscyamus muticus, H. niger, H. reticulatus: tetramethylputrescine (2)
Phyllanthus discoides: allosecurinine (9), phyllantine (methoxysecurinine) (9), phyllantidine (9), phyllochrisine (diastereoisomeric with securinine) (9), securinine (9), XXIV
Withania somnifera: anaferine (10), XXV, anahygrine (10), XXVI, nicotine (2), isopelletierine (10), withasomnine (11), XXVII

Occurrence

Tropane alkaloids chiefly occur in the Solanaceae, but they are also found in other families which show no taxonomic relationships. However, the classical tropane alkaloids (e.g. hyoscyamine), i.e. esters with tropic acid or related acids of alkamines derived from tropane, are restricted to the Solanaceae. While other acids esterified with tropane alkamines, but outside the alkaloids, are widely distributed in the vegetable kingdom, tropic acid and its derivatives have hitherto only been found in the esterified state in solanaceous plants, with the exception of the occurrence of free tropic acid in *Mandragora* (Staub 1942). In the Solanaceae no tropane derivatives substituted at C-2-position have been found up to now, but such do occur in *Erythroxylum, Peripentadenia, Darlingia* and *Knightia*.

A relationship between the tropane- and hygrine-type alkaloids is evident from their common occurrence in the same species. In members of the Solanaceae which contain tropane alkaloids, cuscohygrine is present in nearly all cases; its occurrence is limited to the roots, the site of synthesis of the tropane alkaloids (with few exceptions, e.g. in *Solandra* spp. it also occurs in the leaves, Evans et al. 1972 b). In *Erythroxylum coca,* cuscohygrine is present in the leaves, together with tropane alkaloids (see references in Hegnauer 1966 b). Cuscohygrine has also been shown to co-occur with tropane alkaloids in *Convolvulus lineatus* (for cuscohygrine see Willaman & Schubert 1961, for convolamine and convolvine see Willaman & Li 1970). In a similar way to cuscohygrine, but in a smaller number of genera, hygrine is distributed in plants which contain tropane alkaloids, e.g. in some genera of the Solanaceae (like cuscohygrine in most cases only in the roots) and in the leaves of *Erythroxylum* species and *Cochlearia arctica*. Hygroline is

Table 4. Genera containing tropane-type alkaloids. Solanaceous genera listed in Table 5.

Convolvulaceae: *Calystegia, Convolvulus*
Cruciferae: *Cochlearia*
Dioscoreaceae: *Dioscorea*
Elaeocarpaceae: *Peripentadenia*
Erythroxylaceae: *Erythroxylum*
Euphorbiaceae: *Phyllanthus*
Orchidaceae: *Dendrobium*
Proteaceae: *Bellendena, Knightia, Darlingia*
Rhizophoraceae: *Bruguiera, Carallia, Gynotroches*

found together with tropane alkaloids only in the leaves of *Erythroxylum coca* and *Cochlearia arctica*. Surprisingly it has hitherto not been detected in the Solanaceae. Its C-atom, which carries the hydroxyl group, corresponds to the C-3-atom of the tropane-ring system which, in nearly all the tropane alkaloids present in plants, also bears a hydroxyl group. Cuscohygrine, a ketonic base, has commonly been found associated with the tropines, whereas tropinone, the only tropane alkaloid to carry a ketogroup at C-3, has only been observed in two species and there in small amounts only.

Table 3 lists all cases so far known of alkaloids which occur together with tropane derivatives and/or hygrine-type bases in one and the same plant species. The biosynthesis of most of these reveals certain relationships with the tropane alkaloids. Thus, ornithine may serve as a precursor of both the nicotine-type alkaloids and of the tropane bases; in feeding experiments with *Withania* it has also been found to be incorporated into withasomnine (O'Donovan & Forde 1970). Parallels between the biosynthesis of the *Punica* alkaloids and of the tropane- and hygrine-bases have been claimed; the piperidine

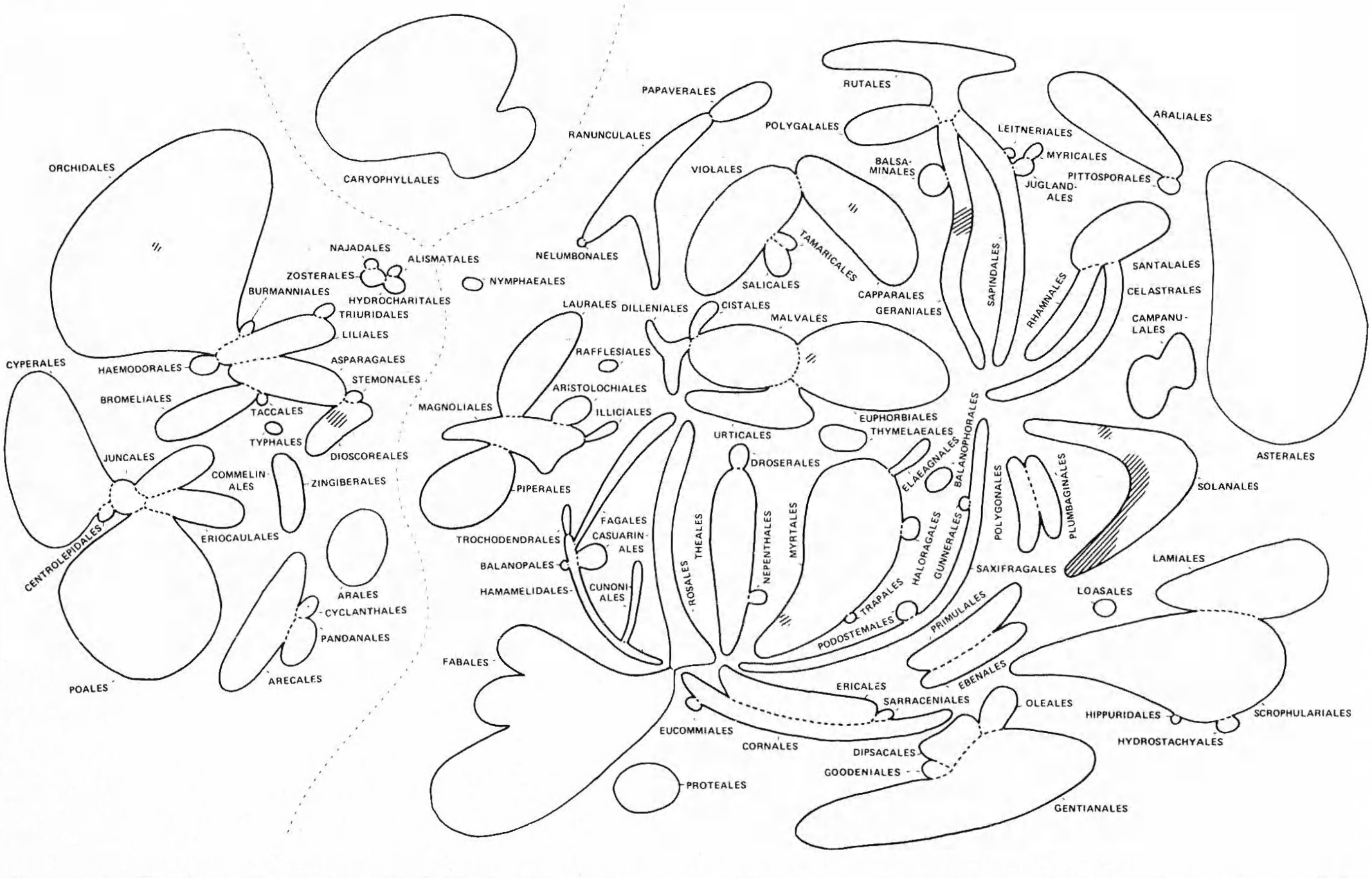

Fig. 3. Distribution of tropane alkaloids in the angiosperms. The presence of these alkaloids cannot be used for drawing far-reaching taxonomic conclusions. According to all current concepts the families in which they are present are too widely scattered. The Solanales form an exception, since tropane alkaloids are found in particular genera of Solanaceae and also in two genera of the undoubtedly closely-allied Convolvulaceae. – The ability to synthesize this type of alkaloids has probably originated within several evolutionary lines. Further finds of tropane alkaloids may be expected. So far, they have not been recorded in groups which contain iridoids, nor for example in groups containing benzylisoquinoline alkaloids, sesquiterpene lactones or polyacetylenes, but this may be mere coincidence. – The basic diagram used here is that by Dahlgren (1975). The present figure was prepared by R. Dahlgren, Botanical Museum, Copenhagen, using the information in the present article, and is inserted by agreement with the author.

Table 5. Distribution of tropane alkaloid containing genera in tribes and subtribes of Solanaceae. – a esters of tropic acid, b tropane esters of other acids, c cuscohygrine, d hygrine, e tropinone, f physoperuvine.

Tribe	Subtribe	Genera
Nicandreae	–	*Nicandra* (e d)
Solaneae	Lyciinae	*Atropa* (a c), *Atropanthe* (a c), *Latua* (a)
	Hyoscyaminae	*Hyoscyamus* (a b c), *Physochlaina* (a b c), *Przewalskia* (a c), *Scopolia* (a b c)
	Solaninae	*Physalis* (b c f), *Withania* (b c)
	Mandragorinae	*Cyphomandra* (e c), *Mandragora* (a b c), *Salpichroa* (a c d)
Datureae	–	*Datura* (a b c), *Methysticodendron* (a), *Solandra* (a b c)
Cestreae	Cestrinae	–
	Goetzeinae	–
	Nicotianinae	*Anthotroche* (a)
Salpiglossideae	–	*Anthocercis* (a b c), *Duboisia* (a b c d)

ring of methylisopelletierine was found to be formed from lysine and its C-3-side chain from acetate (Liebisch 1969 b). Anahygrine forms a connecting link between the hygrines and the isopelletierine-type alkaloids. Its molecule contains both a pyrrolidine and a piperidine ring. Lysine also forms a precursor of the piperidine part of anabasine (Gross 1969) and of securinine (Sankawa et al. 1974). However, feeding experiments with *Dioscorea hispida* revealed no incorporation of lysine into that part of the isoquinuclidine alkaloid dioscorine which corresponds to piperidine (Leete & Pinder 1972). Steroid alkaloids, which are typical components of some solanaceous genera, show no biosynthetic relationships whit the tropane alkaloids; they have been shown to co-occur with tropane bases in *Cyphomandra betacea*.

Although also occurring in other families (Table 4, Fig. 3), the tropane alkaloids are typically components of the Solanaceae, in which they are found in all tribes and in practically all subtribes, except the poorly investigated subtribes Cestrinae and Goetzeinae (Table 5). Esters of tropic acid are not found in the tribe Nicandreae, nor in the subtribe Solaninae of the tribe Solaneae.

New occurrences of hitherto unknown tropane alkaloids in different families are regularly being published, but no definitive statement can yet be made about their taxonomic value, since only a very limited fraction of the vegetable kingdom has so far been analyzed. Even in the Solanaceae, although investigated very extensively, gaps in our knowledge of the chemistry of tropane alkaloids do still exist.

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Some pteridicolous Ascomycetes

Lennart Holm and Kerstin Holm

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In the course of an inventory of the Ascomycetes found on ferns in Sweden a number of morphological and taxonomic problems were encountered. 16 species are commented on and the following new names are published: Discomycetes: *Cryptomycina filicina* (Fr.), *Naevala perexigua* (Rob. ex Desm.), *Nannfeldtia phegopteridis* sp. nov., *Pseudopeltis* gen. nov., *Pseudopeltis filicum* sp. nov. – Pyrenomycetes unitunicati: *Glomerella polypodii* (Rbh.), *Monographos fuckelii* nom. nov., *Monographos minor* sp. nov., *Mycoglaena filicina* sp. nov. – Pyrenomycetes bitunicati: *Schizothyrium speireum* (Fr.), *Scirrhia osmundae* (Peck & Clinton), *Trichothyrina filicum* sp. nov. Lectotypes are proposed for *Cryptomycina filicina* and *Monographos fuckelii.* The genera *Metameris* and *Scirrhodothis* are included in *Scirrhia,* because they possess an ascocarp centrum of *Dothidea*-type.

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Ferns in general harbour a rich and specific mycoflora. This holds true not only for parasitic fungi, such as *Taphrina* and the rust genera *Hyalopsora, Milesia* and *Uredinopsis,* but also for saprophytes, the group which concerns us here. Some ferns, such as *Osmunda* and *Pteridium,* are hosts for very specific fungi only, whereas species of *Athyrium, Dryopteris* and *Matteuccia* seem to harbour much the same mycoflora. These fungi have on the whole been little studied, although the keen-eyed Mme Libert had already paid them some attention. Bubák also deserves mention, for his excellent paper of 1916.

As a part of our investigation of Swedish micro-fungi, especially the Pyrenomycetes, we have included a study of this particular substrate. A previous paper (Holm & Holm 1977) concerned the Leptopeltidaceae. This is a mainly pteridicolous family, which includes some of the most important species of the fungal flora found on ferns. The present paper deals with some new or otherwise noteworthy species within various Ascomycete groups. It is based mainly on material, collected by us (now in UPS). We have also revised the pertinent material in S and UPS; some type specimens were obtained on loan from B, BR, and K. Our sincere thanks are due to the curators of these institutions.

Discomycetes

Cryptomycina filicina (Fr. ex Fr.) L. & K. Holm, comb. nov.

Leptostroma filicinum Fr. ex Fr., Syst. Mycol. 2: 599 (1823) – *Leptostroma filicinum* Fr., Obs. Mycol. 1: 197 (1815) – Lectotype: Fr., Scler. suec. 65 (UPS).

Cryptomycina Osmundae H. Sydow, Ann. Mycol. 21: 174 (1923) – Type: Germany, Silberg in Westphalen, Osmunda regalis, V. 1923, Ludwig (= Syd., Myc. germ. 1928, UPS).

Cryptomycina Osmundae (Schw.) Petrak, Sydowia 10: 298 (1957), nom. illeg. – *Hysterium Osmundae* Schweinitz, Trans. Amer. Phil. Soc. ser. 2, 4: 246 (1834) – Type: USA, Penn., "In stipitibus Osmundae spectabilis, Salem et Bethl." (n.v.).

Fig. 1 D, 2 A, B.

This fungus is apparently confined to the dead stipes of *Osmunda* and is very conspicuous because of its large black stromatic crusts,

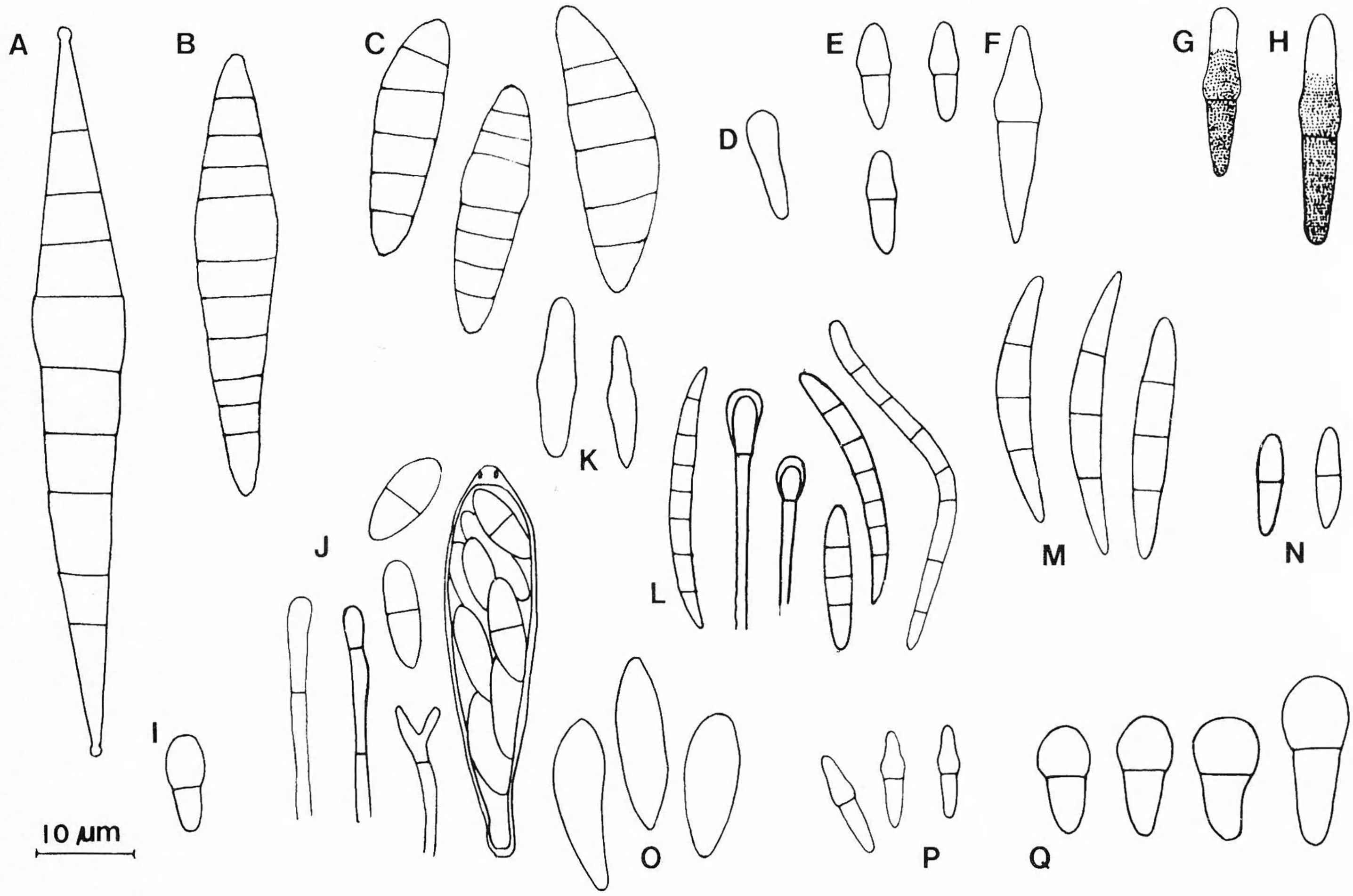

Fig. 1. Spores. – A: *Dangeardiella macrospora*. – B: ?*Dangeardiella fusiforma*, aberrant form. – C: *D. fusiforma*. – D: *Cryptomycina filicina*. – E: *Scirrhia aspidiorum*. – F: Ditto, large-spored form on *Pteridium*. – G: *Scirrhia osmundae*. – H: "*Metameris japonica*". – I: *Morenoina* sp. – J: *Pseudopeltis filicum*, ascus, spores and paraphyses. – K: *Botryosphaeria* sp. – L: *Nannfeldtia phegopteridis*, spores and paraphyses. – M: *Monographos fuckelii*. – N: *M. minor*. – O: *Glomerella polypodii*. – P: *Trichothyrina filicum*. – Q: *Hysteropeltella moravica*. – All × 1000.

which attain 1 cm or more in length. For a full description see Sydow (1923). The asci have an apical ring which is I+.

In spite of its striking appearance this species has so far been little noticed and in fact may be rare. However, it had already been found by Fries, as Bubák (1916), who investigated the original material of *Leptostroma filicinum* Fr., made clear. Bubák concluded that the fungus "keine Leptostromacee ist, sondern ein Askomyzet" (1916 p. 312), although he did not discuss its taxonomy more closely in that article because he intended to treat the pteridicolous ascomycetes in a later paper, which unfortunately never was realized. We can verify his statement that Fries's fungus is an ascomycete, and we identify it with *Cryptomycina osmundae*, described more than a century after Fries by Sydow, who did not, however, refer to Bubák's paper.

We think it is appropriate to lectotypify *Leptostroma filicinum* by Fries's Scler. suec. no. 65, which fixes the name in the sense adopted here. When validly publishing *Leptostroma filicinum* in 1823, Fries apparently included various fungi under this name, since he listed several host plants: "in stipitibus Pteridis, Osmundae regalis, Aspidiorum etc." (p. 599). In the original publication, however, the Royal fern is the only host plant to be mentioned specifically: "In stipitibus Osmundae regalis Etc." (Fries 1815 p. 197), and it seems reasonable to infer that Fries considered *Osmunda* to be the principal host.

We found the fungus in abundance in the only *Osmunda* locality which we visited, viz. Sweden, Gästrikland, Hille par., Brännsågen, at the rivulet Testeboån, 21.V.1975, 562 b.

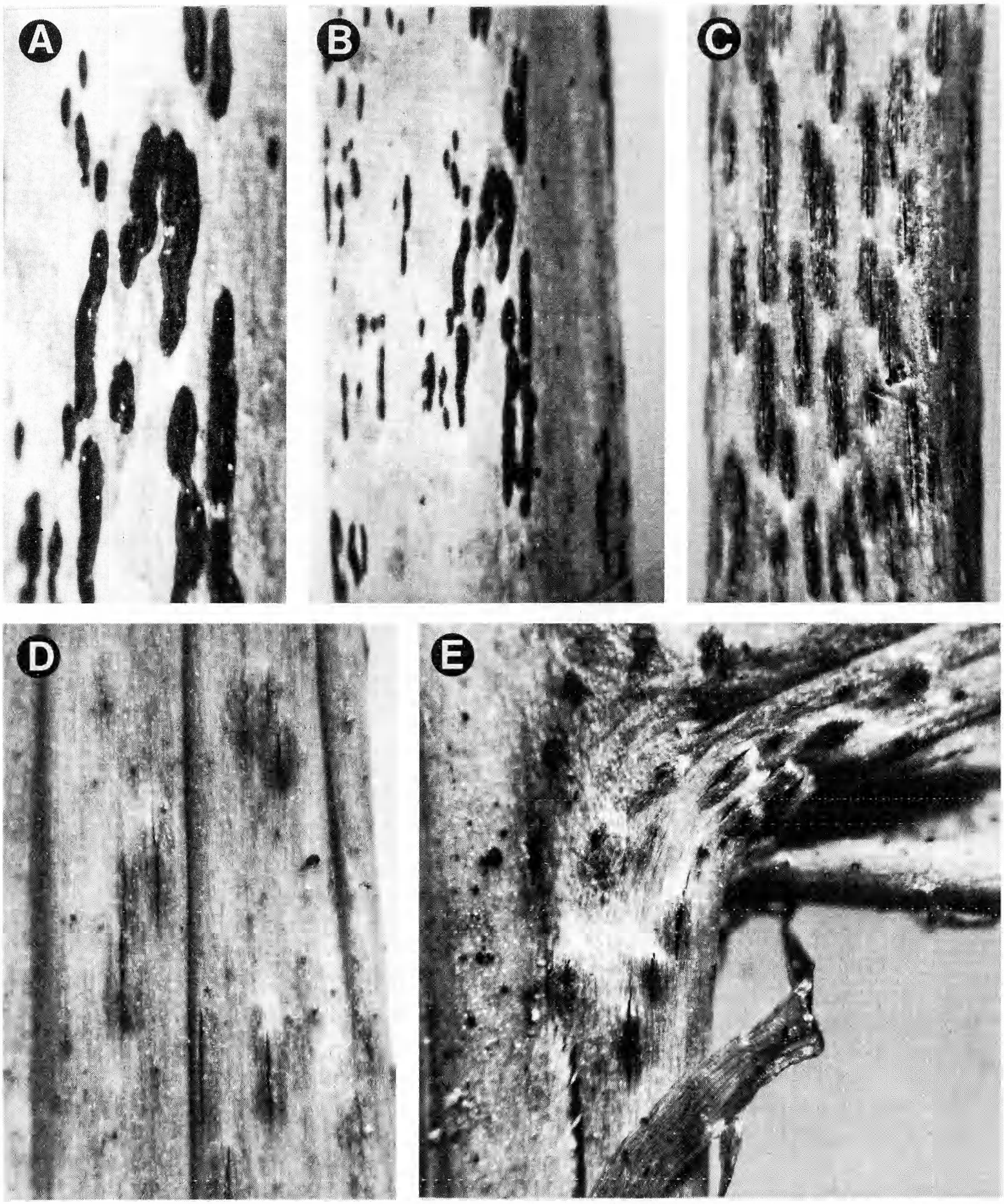

Fig. 2. Ascocarps in surface view. – A: *Cryptomycina filicina*, × 9. – B: Idem, × 4.5. – C: *Scirrhia osmundae*, × 9. – D: *Dangeardiella fusiforma*, × 18. – E: Idem, × 18.

Hysteropeltella moravica Petrak

Petrak, Ann. Mycol. 21: 10 (1923) – Type: Moravia, pr. Podhorn, Dryopteris filix-mas, IV. 1922 (W?).

Fig. 1 Q, 4 C, 8 A.

Ascocarps densely scattered, erumpent, linear, usually 0.2–0.5 mm in length, c. 0.1 mm broad and 50 μm high, opening by a longitudinal slit. *Peridium* c. 20 μm broad, of textura angularis, cells 6–10 μm. *Asci* numerous, subglobose or oblong to clavate, sessile, 30–36 × 12–15 μm, 8-sporous, bitunicate? with truncate apex. Ascus wall strongly thickened at apex, turning blue with iodine. *Spores* irregularly arranged, ± cuneiform, bicellular usually with a somewhat supramedian septum, long hyaline and 11–13 × 5 μm, eventually up to 15 × 5 μm and the thick spore wall turning brownish. *Interthecial threads* 0.

No type material was available but we have no hesitation in identifying our fungus with Petrak's; his detailed description matches our material perfectly, although he did not notice the I reaction, nor did he observe the fully mature, brownish spores. On the other hand, he reported that the asci are surrounded by "spärlichen, undeutlich faserigen Paraphysoiden". We have not seen any interthecial threads.

Petrak established the genus *Hysteropeltella* for this fungus, which certainly merits a genus of its own. He considered it to be a "typische Hypodermiee", which it definitely is not. We think that the ascus characters indicate a kinship with the Lecideaceae, and *Hysteropeltella* may lie not far distant from e.g. *Melaspilea emergens* (Fr.) Rehm.

The fungus is not very conspicuous but it seems quite characteristic and can be recognized even under a hand-lens by its elongate streak-shaped apothecia, which open by a longitudinal slit when wet.

Up to now this species was only known from the type collection, but it seems to be rather common on the petioles of larger ferns. We now have eight collections, in some of which the fungus occurs in abundance.

Sweden: Uppland, Dalby, c. 500 m SW of Högby, in spruce forest, *Athyrium filix-femina,* 27.IV.1975, 477 c. – pr. "Jerusalem", *Dryopteris spinulosa,* 11.VI. & 16.VI.1976, 861a & 873b. – Uppsala-Näs, 700 m W of Högby, *Dryopteris filix-mas,* 27.IV.1975, 479c. – Ekeby, c. 3 km S of the N end of lake Vällen, spruce forest, *Matteuccia struthiopteris,* 9.V.1975, 507 b and 16.VII.1976, 904 a. – *Dalarna.* Vika, pr. Trostbäcken, *Matteuccia struthiopteris,* 20.V.1975, 574c. – *Gästrikland.* Gävle, Lövudden, *M. struthiopteris,* 20.V.1975, J. A. Nannfeldt 23912.

Naevala perexigua (Rob. ex Desm.) L. & K. Holm, comb. nov.

Phacidium perexiguum Roberge ex Desmazières, Ann. Sci. Nat. Bot. ser. 3, 11: 362 (1849).

For comments, see under *Schizothyrium speireum.* (*Naevala perexigua* is *not* pteridicolous!)

Nannfeldtia phegopteridis L. & K. Holm, sp. nov.

Typus: Suecia, Dalecarlia, par. Stora Kopparberg, Finnbo, 27.V.1977. K. & L. Holm no. 1057a (UPS).

Fig. 1 L, 4 D, 7 A.

Apothecia solitaria vel ± gregaria, saepe bina confluentia, superficialia atra, scutata, 150–250 μm diam., maturitate c. 50 μm alta. *Scutellum* centro ± stellatim dehiscens, ex hyphis coalitis radiatim dispositis. *Excipulum* laterale parum evolutum e textura globulosa cellulis minutissimis; excipulum basale 0 sed substrati cellulae subjectae 'hypostromate' repletae. *Asci* cylindrico-clavati, breve stipitati, 65–75 × 10–12 μm, apice rotundati, annulo minuto ope Iodi caerulescenti, octosporae. *Sporae* octonae, parallelae, filiformes, basim versus saepe subattenuatae, (20–)25–35(–40) × 2.5–3.5 μm, numero cellularum valde variabili sed saepe 7-septatae, hyalinae. *Paraphyses* ascos subaequantes, septatae, cellula terminali ad 4 μm inflata, membrana incrassata.

Habitat in petiolis anni praeteriti Lastreae phegopteridis.

This species, like the next one, provides a new example of a superficial Discomycete which externally resembles one of the Microthyriales, cf. Nannfeldt (1976 a). Though similar in many respects, they are probably a heterogeneous assemblage. A characteristic common trait is the presence of a ± superficial shield, which covers the developing apothecium. The shield texture varies a great deal. In the present species it consists of one layer of radiate, coalescent hyphae; in surface view the cells are almost square at the centre of the shield, elongate and often ramified towards the margins (Fig. 7 A).

At maturity the shield cracks centrally, its

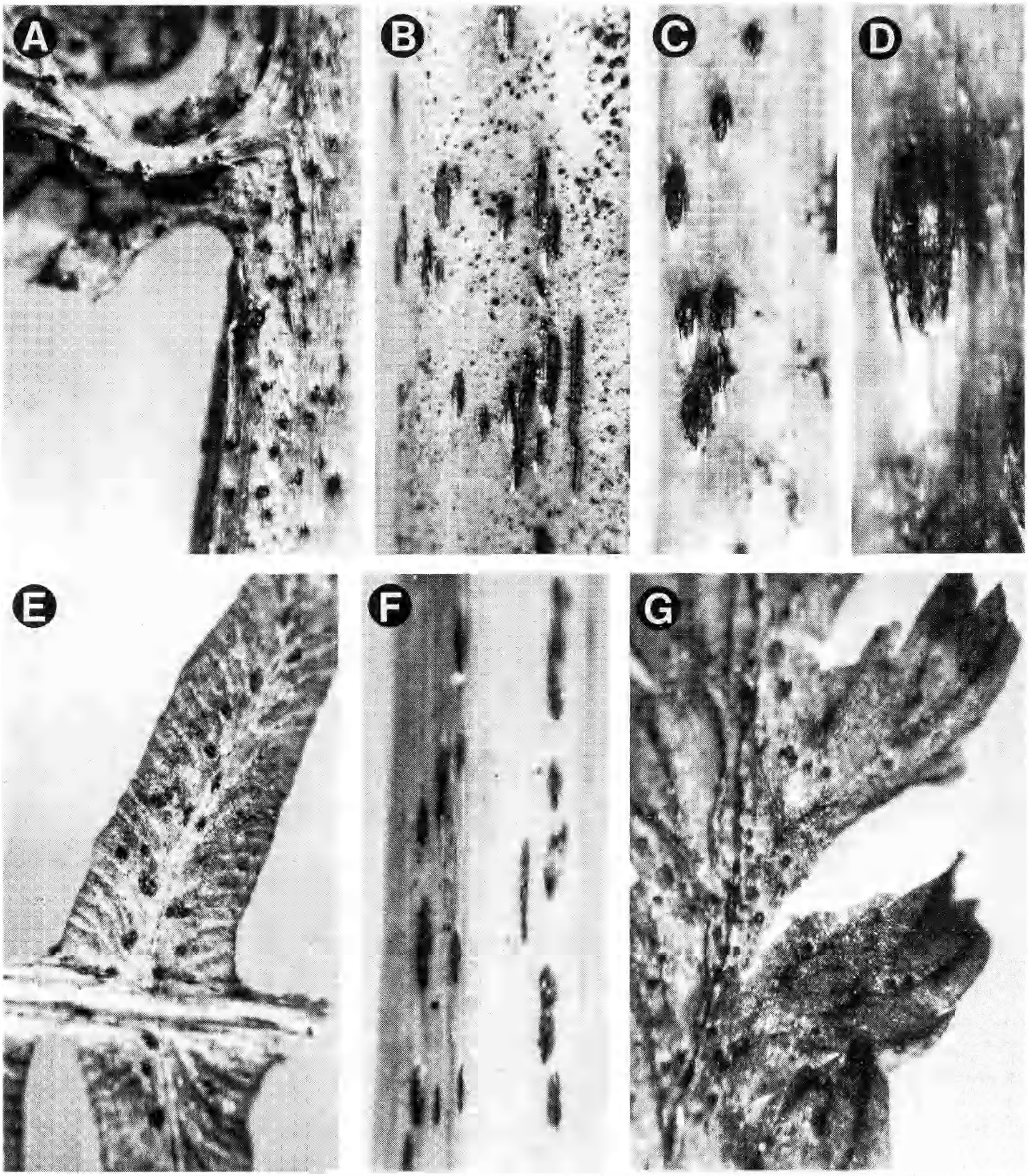

Fig. 3. Ascocarps in surface view. – A: *Scirrhia aspidiorum,* × 18. – B: Idem, × 9. – C: *Dangeardiella macrospora,* × 9. – D: Idem, × 36. – E: *Monographos fuckelii* in leaflets, × 9. – F: Idem in petiole, × 9. – G: *Monographos minor,* × 18.

remnants adhering to the hymenial surface like an epithecium. The peripheral part of the shield is firmly attached to the excipulum, which is poorly developed, especially basally, where it is replaced by an intracellular 'hypostroma'.

N. phegopteridis is easily recognized by its filiform, pluriseptate spores; the number of cells per spore is quite variable, from 4 to 12, but 8 seems to be the most common number.

We suggest, although with some hesitation, that the species be accommodated in *Nannfeldtia,* a genus so far comprising only the type species, *N. atra* Petrak, found on dead leaves of *Carex firma*. There are evident resemblances in the asci, paraphyses and shield structure. It is true, though, that the shield has a distinct, circular margin in *N. atra,* while it grades irregularly into a sparse, superficial mycelium in *N. phegopteridis*. The spores are certainly very dissimilar, but this difference is hardly an essential one: cf. the discomycete genus *Lachnellula* s. lat., whose spores also vary widely, but which, nevertheless, is a very natural genus.

Microthyrium phegopteridis Magnus (in Abh. Nat.-Hist. Ges. Nürnberg 16: 262, 1906) might be a possible synonym, though improbable, since that fungus is said to occur on the leaflets of *Lastrea phegopteris* – we have never found our species on any other substrate than the petioles. *Microthyrium phegopteridis* was described on the basis of immature material (not seen by us), bearing no spores of any kind; we rather think that it belonged to a *Leptothyrium,* which is common on the lamina of this host.

Nannfeldtia phegopteridis is probably common in Scandinavia and is not seldom found in abundance. We have 6 collections from Sweden, Dalarna, and one from Norway, Möre og Romsdal. The petioles of *Lastrea phegopteris* are often heavily infested by *Leptopeltis gregaria* (cf. Holm & Holm 1977) and these two species seem to be ± vicarious.

An apparently related fungus is present in a collection of *Matteuccia struthiopteris* (Sweden, Gävle, Lövudden, 20.V.1975, J. A. Nannfeldt 23912e). Unfortunately the material is scanty and immature.

Pseudopeltis L. & K. Holm, gen. nov.

Typus: *Pseudopeltis filicum.*

Genus novum Discomycetum ex affinitate dubia sed textura scutelli Leptopeltidi persimile: ab illo genere differt i.a. paraphysibus veris.

Pseudopeltis filicum L. & K. Holm, sp. nov.

Typus: Suecia, Uplandia, par. Dalby, in loco c. 200 m ab villa "Jerusalem" inter septentriones et occasum solis spectante, in laminis siccis Dryopteridis filicismaris, 10.VI.1976, K. & L. Holm no. 854b (UPS).

Fig. 1 J, 4 G, 7 B.

Apothecia sparsa, amphigena, subcuticularia, discoidea, 0.1–0.3 mm diam., c. 50 μm alta, scutello radiato stellatim fisso e cellulis serialiter dispositis desuper visis subquadratis, c. 5 μm latis. *Asci* cylindrico-clavati, brevissime stipitati, c. 40 × 10 μm, octospori, annulo apicali ope Iodi et solutione KOH caerulescenti, apice leniter acuti pariete incrassato. *Sporae* anguste ellipsoideae, vulgo 10–12 × 3.5–4 μm, bicellulares, hyalinae, pluriguttulatae. *Paraphyses* univel biseptatae, saepe ramosae, apice incrassatae. Excipulum proprium nullum, hypothecium vix evolutum.

Habitat in lamina foliorum emortuorum filicum.

The scutellate, ± superficial Discomycetes have been much neglected and misunderstood, cf. the preceding species. The present fungus is an extreme representative of that group, in which the excipulum is virtually absent, being replaced by the scutellum. The structure of the latter is strongly reminiscent of *Leptopeltis,* hence the generic name.

This highly-reduced species hardly fits into any genus so far described, but it is possibly related to the Naevioideae. In general appearance the mature, opened apothecia are similar to *Naevala perexigua* (= *N. minutissima*) and the microscopic characters are also compatible with that group. The resemblance with *Leptopeltis* may be more than a mere coincidence, but the centrum structure is different, cf. Holm & Holm (1977 p. 216). A kinship with *Phacidina gracilis,* on *Lycopodium,* although conceivable, would be rather remote.

Of course, *Pseudopeltis filicum* is easily overlooked, but we do not have the impression that it is a common fungus. So far we have only seen it on laminae, never on petioles. Apart from the very rich type collection we only have 3 other packets of rather scanty material:

Sweden: Uppland. Dalby, c. 500 m SE of 'Jerusalem', *Dryopteris filix-mas,* 15.VI.1975, 590b. – *Dalarna.* Garpenberg, Realsbo, *D. spinulosa,* 29.III.1974, 350. – Sundborn, pr. Mjölnarvallen, *Athyrium filix-femina,* 22.VI.1974, 275d.

Pyrenomycetes unitunicati

Glomerella polypodii (Rbh.) L. & K. Holm, comb. nov.

Sphaeria Polypodii Rabenhorst, Herb. Mycol. II: 533 (1857) – *Plectosphaeria polypodii* von Arx & Müller 1954 p. 208 – Type: Germany, Saxony, Polypodium vulgare, 1856, leg. Rbh. (= Herb. Myc. II: 533, B!).

Laestadia Polypodii Sacc. & Magnus ap. Sacc. & Berl., Atti Ist. Ven. Sci. Lett. Arti ser. 6. 3: 737 (1884) – Type: Italy, Albano, leg. Magnus (S!).

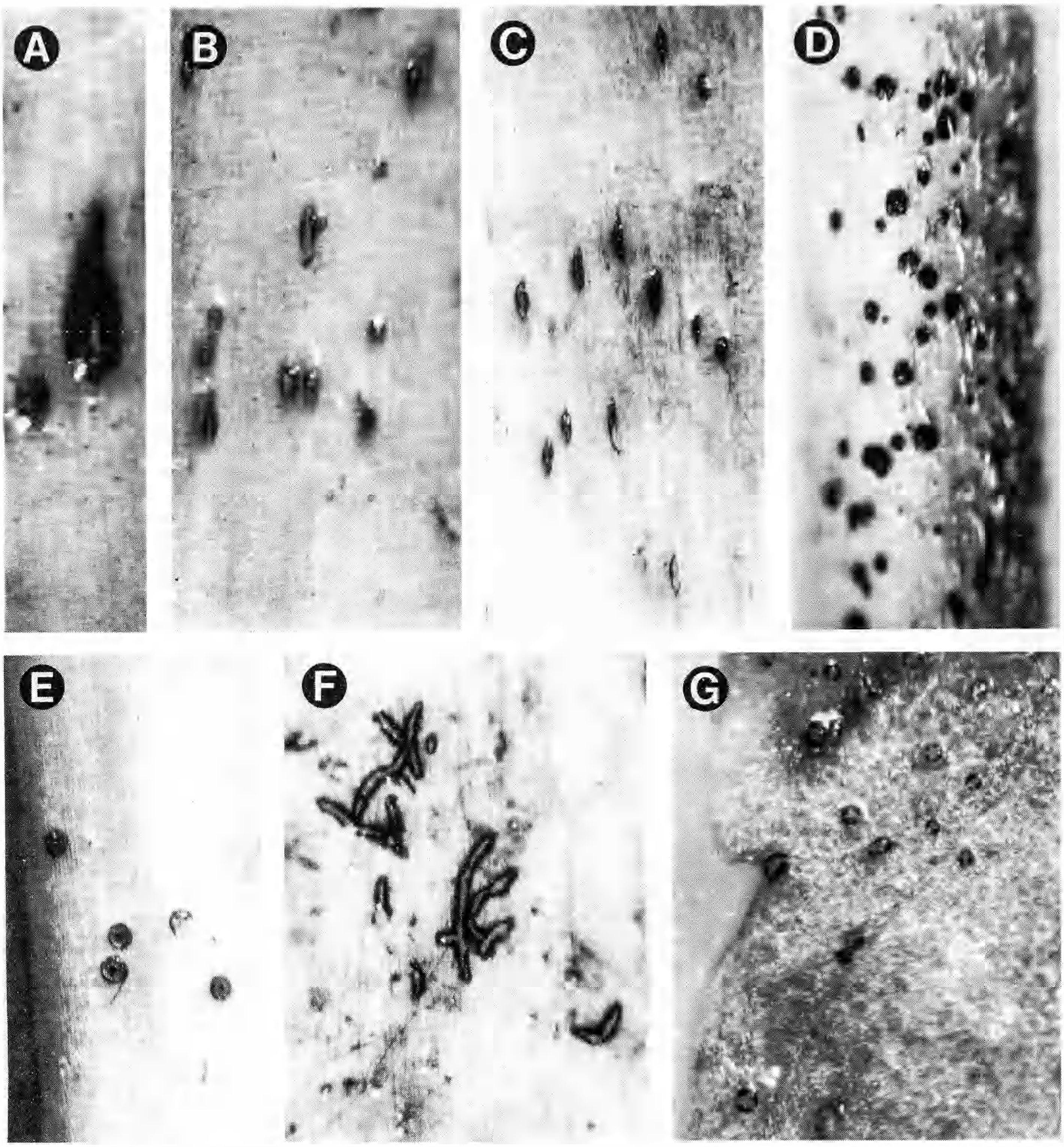

Fig. 4. Ascocarps in surface view. – A: *Mycoglaena filicina,* ×36. – B: Idem, conidial state, ×36. – C: *Hysteropeltella moravica,* × 18. – D: *Nannfeldtia phegopteridis,* × 18. – E: *Trichothyrina filicum,* × 18. – F: *Morenoina* sp., × 36. – G: *Pseudopeltis filicum,* × 36.

Exs.: (Karst. F. fenn. 669 = *Mycosphaerella* sp.) – Rbh., Herb. Myc. II: 533, B – (Roumeg., F. Gall. 2295, immat. in UPS) – D. Sacc., Myc. ital. 845, S – Thüm., F. austr. 1051, verisimiliter, sed spec. vetusta in UPS – Vgr, Micr. 1489 sub nom. *Mycosphaerella tyrolensis,* UPS.

Fig. 1 O, 7 C.

For a full synonymy see von Arx & Müller (1954).

This fungus may occur as a true parasite, forming very distinct, dark spots in living fronds of *Polypodium vulgare*. It can be saprobic, too, in dead fronds, forming barely visible spots. It is possible that infection always takes place in living tissues. The *perithecia* are mainly epiphyllous, rather crowded, c. 150 μm diam., globose when wet, collapsed when dry. *Asci* ± fusiform, c. 50 × 10 μm, with an apical refractive annulus, turning dark, but not blue, with iodine. *Spores* ellipsoid, hyaline, one-celled, generally with two large oil drops and one cyanophilous body (nucleus?), 15–20 × 5–6 μm.

This fungus was formerly regarded as a sphaerellaceous species, until von Höhnel (1918 p. 55) recognized its true affinities. von Arx & Müller (1954) referred it to *Plectosphaera,* with the comment that it was transitional to *Phyllachora,* which must be due to some misunderstanding. The generic limits within the Physosporellaceae are very vague and it seems doubtful whether *Plectosphaera* can be upheld; it is closely related to *Glomerella,* a name which has priority. In any case our fungus closely matches *Glomerella cingulata* and *G. sesleriae,* and seems very well accommodated among them.

Glomerella polypodii has been little collected, despite the fact that the parasitic stage is quite conspicuous. It has also been confused with a parasitic *Mycosphaerella.* As a saprophyte it is easily overlooked, but probably not rare. We have seen 9 collections, from Germany, Austria, Bohemia, Italy and Sweden. The 5 Swedish collections are all from the province of Uppland.

Monographos Fuckel

Fuckel, Jahrb. Nass. Ver. Naturk. 29/30: 24 (1876) – Type: *M. aspidiorum* sensu Fuckel l. c. (≡*M. fuckelii* nom. nov., vide infra).

This genus is one of those which have been founded on a misidentified species. Fuckel considered that the fungus which he studied was *Sphaeria aspidiorum* Libert, which it is not, as first shown by Bubák (1916 p. 324 seq.). According to some nomenclaturalists, *Monographos* should under all circumstances be typified on *Sphaeria aspidiorum:* i.e. it would then represent an obligate younger synonym for *Scirrhia.* However, the name *Monographos* has consistently been used for Fuckel's fungus and we think it wisest to follow established practice.

The taxonomic position of the genus has been a matter of dispute. Fuckel (1876) and Winter (1887 p. 914) referred it to the Dothideaceae, because of the loculate stroma, as did Bubák (1916). Theissen & Sydow (1915 p. 189), however, demonstrated the presence of an iodine positive ring in the ascus apex (cf. below), and considered it to be a sphaeriaceous species, an opinion also held by Obrist (1959 p. 375) and by Müller & von Arx (1973 p. 120). Certainly *Monographos* is unitunicate; we will discuss its affinities more closely in a forthcoming paper.

Monographos fuckelii L. & K. Holm, nom. nov.

Monographos aspidiorum sensu Fuckel, Jahrb. Nass. Ver. Naturk. 29/30: 24 (1876) et auct. rec., non *Sphaeria aspidiorum* Libert, q.e. *Scirrhia aspidiorum* – Lectotype: Fuckel, F. rhen. 2665 (S).

Matrix: Pteridium aquilinum, in the petioles and (rarely?) in the lamina.

Exs.: Fuckel, F. rhen. 2665 (S) – Krieger, F. sax. 288 (S), 730 (S) – Petrak, Fl. Bohem. Mor. II:1:2056 (S); Myc. carp. 461 (S) – Rehm, Asc. 838 (S), 932 (S) – Syd., Myc. germ. 2143 (S) – Except for Krieger, F. sax. 730 ('?*Metasphaeria epipteridea*') all issued as *Monographos aspidiorum.*

Fig. 1 M, 3 E, F, 6 E.

The general appearance of this species depends very much on the substrate. When growing in the *lamina* the ascocarps resemble (always?) epiphyllous spots, but in the stipe they appear as narrow streaks. In the former case they are rather variable in form and size, from circular, c. 0.1 mm diam., to elliptic and 0.5 mm long. They are about 150 μm high, with 1–4 loculi. In the *petioles* the individual ascocarps are about 1 mm long, but only 0.1–0.2 mm broad. They are very flattened, being only 60–75 μm in height, with several loculi. Several ascocarps often unite to form large crusts.

The stroma pseudoparenchyma is mainly composed of a small-celled textura angularis and is hyaline, except the uppermost part. The *loculi,* generally 100–125 μm diam., often seem to be provided with a perithecial wall, which, however, consists of compressed stromal tissue, often of longitudinally elongated cells. The loculi are filled with numerous, multiseptate interascal threads. *Asci* cylindric, very shortly stipitate, c. 70 × 7 μm, 8-spored, with an apically somewhat thickened wall and an annulus which is I+ after treatment with KOH. *Spores* almost cylindrical, often slightly allantoid: 25–28(–30) × 3–4 μm, finally 3-septate, hyaline.

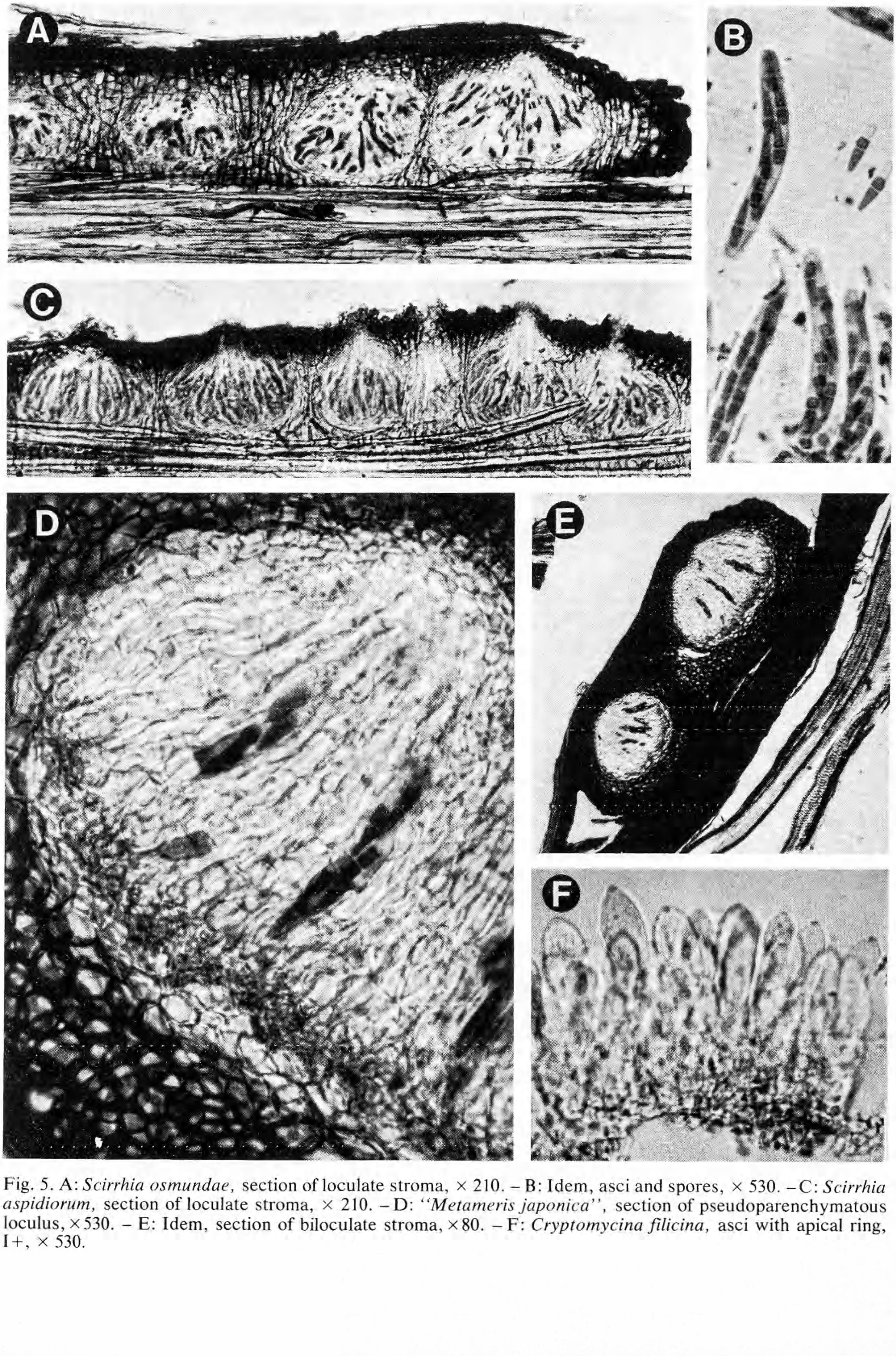

Fig. 5. A: *Scirrhia osmundae,* section of loculate stroma, × 210. – B: Idem, asci and spores, × 530. – C: *Scirrhia aspidiorum,* section of loculate stroma, × 210. – D: *"Metameris japonica",* section of pseudoparenchymatous loculus, ×530. – E: Idem, section of biloculate stroma, ×80. – F: *Cryptomycina filicina,* asci with apical ring, I+, × 530.

A fairly good description was given by Winter (1887 p. 914) though his spore measurements are too low, based as they are on immature type material. There has been some disagreement about the iodine reaction of the asci: a blueing of the ascus 'pore' was first reported by Theissen & Sydow (1915 p. 190) and more recently by Obrist (1959 p. 175). On the other hand Bubák (1916 p. 327) failed to get any reaction. The dissension is apparently explained by a difference in method used: we can confirm that the ascus plug colours strongly with iodine, nota bene after treatment with KOH. This phenomenon was recently reviewed by Nannfeldt (1976 b), and *Monographos* can thus be added to his other examples of this particular response to iodine.

Fuckel identified the fungus with *Sphaeria aspidiorum* Libert, as did Winter. However, as first shown by Bubák (1916 p. 324 seq.), these species are very different. Bubák proposed that Fuckel's taxon should be named '*Monographos aspidiorum* Fuckel', a reasonable idea which has subsequently been accepted by several workers. Of course, that name is nomenclaturally incorrect and we think that *M. fuckelii* would form an appropriate substitute.

A conidial form is said often to be found intermixed; it was fully described by Bubák (1916 p. 297) as *Sphaeriostromella pteridina* (Sacc. & Roum.) Bubák.

M. fuckelii is scarcely a common fungus, and we have not found it in Scandinavia. It is the common host plants which may harbour the rare fungi. Several of the cited exsiccata are duplicates, and we have seen material from only five localities.

Germany: Rheinland, Östrich (Fuckel). – Westphalen, Oechelhausen (Sydow). – Sachsen, Königstein (Krieger). – *Luxemburg:* Baumbusch (Feltgen). – *Czechoslovakia:* Moravia, Wsetin (Petrak).

Monographos minor L. & K. Holm, sp. nov.

Typus: Suecia, Uplandia, par. Dalby, in loco c. 750 m ab villa 'Jerusalem' inter septentriones et occasum solis spectante, in frondibus Athyrii filicis-feminae, 20.VI.1976, K. et L. Holm no. 907a (UPS).

Fig. 1 N, 3 G, 6 A–D.

Species a praecedente imprimis sporis valde minoribus differt.

This species occurs on several of the larger ferns, including bracken, although the sole collection from that host deviates in certain respects and is treated separately below. The 'main form' can be characterized as follows:

Ascocarps scattered, innate–erumpent, usually 100–150 μm diam., collapsed when dry, applanate-globose when wet (or elongate when growing in the stipe), uniloculate. *Peridium* of a textura angularis of small cells (generally c. 5 μm diam.), for the most part c. 10–15 μm broad, but basally often thinner and round, the porus often thicker and heavily pigmented, often with a trace of a clypeus. *Asci* cylindric, subsessile, about 45–50 × 4–5 μm, 8-spored, with a somewhat thickened apex, containing a ring which is I+ after treatment with KOH. *Spores* distichous, with obtuse ends, elliptic-fusiform, 10–12 (–15) × 2.5–3.5 μm, hyaline, uniseptate, guttulate when immature. *Interascal filaments* pluriseptate.

This fungus is generally recognizable even macroscopically, by its collapsed ascocarps which look like a '*Naevia*'. They occur on both sides of the lamina, as well as on the rachis and on the petiole – on the latter substrate the ascocarps become somewhat elongate. As for *Monographos fuckelii,* an iodine reaction is obtained only after treatment with a strong hydroxide solution.

An imperfect form, macroscopically indistinguishable, is often found intermixed and is in all probability connected. It is scolecosporous and apparently very similar to *Sphaeriostromella pteridina,* the imperfect form of *M. fuckelii.*

As mentioned above, a somewhat deviant form has been found in the lamina of bracken. It may be rare on this host, since we have only found it once, intermixed in Rehm, Asc. 270 ('*Hypoderma aquilinum*', i.e. *Leptopeltis pteridis,* cf. Holm & Holm 1977 p. 220), although it was rather abundant, at least in the UPS copy. In this material the ascocarps are considerably larger than those of the 'main form', attaining a diameter of at least 300 μm and possessing up to 3 loculi. The peridium is also stronger. As a matter of fact, in general appearance these ascocarps are strongly reminiscent of the laminicolous ascocarps of *M. fuckelii.* Asci and spores, however, fully agree with those of normal *M. minor,* so we think that the fungus

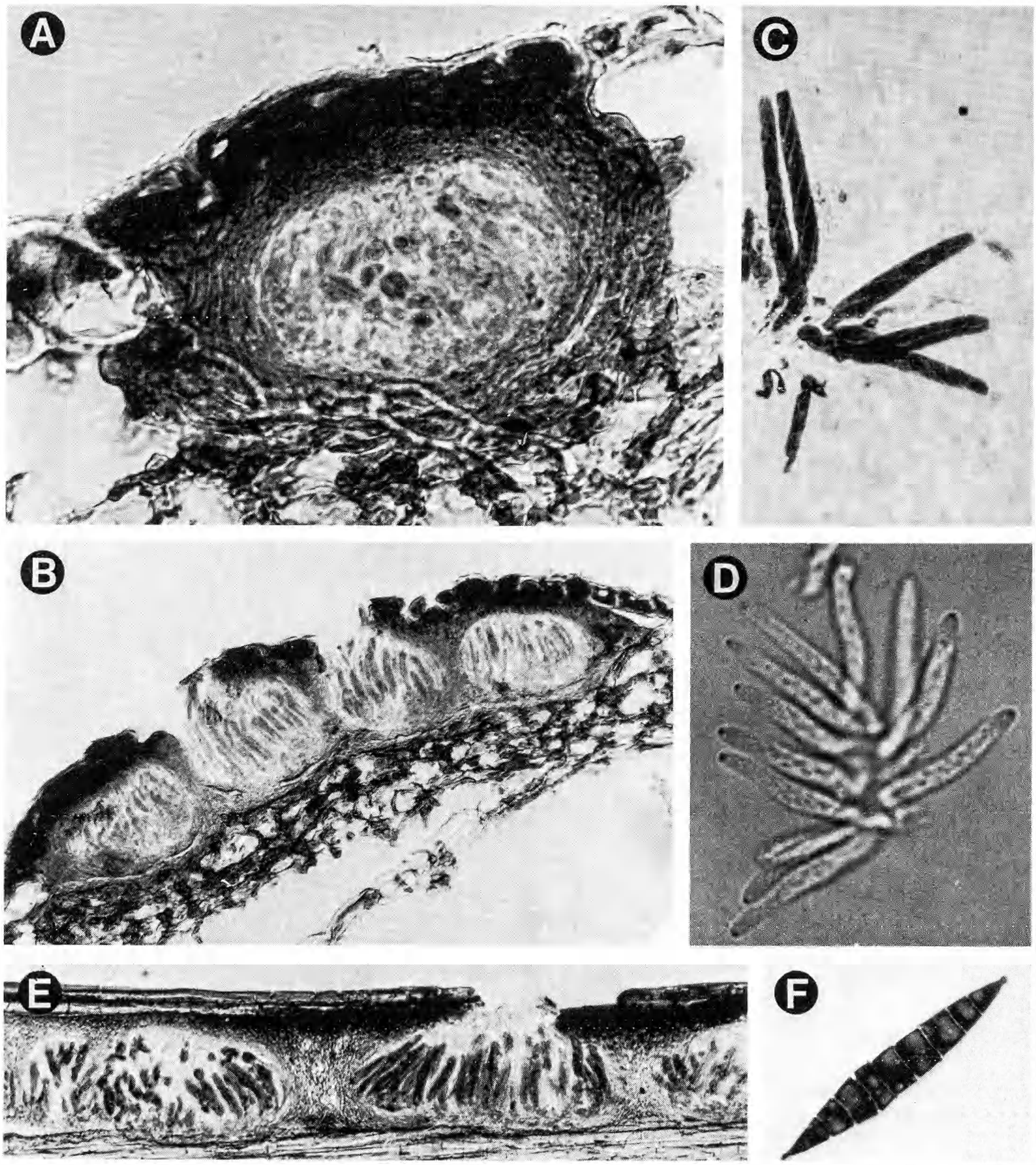

Fig. 6. A: *Monographos minor,* section of uniloculate ascocarp, × 530. – B: Idem, section of pluriloculate ascocarp, × 210. – C: Idem, asci in lactic blue, × 530. – D: Idem, asci in iodine, × 530. – E: *Monographos fuckelii,* section of loculate stroma, × 210. – F: *Dangeardiella macrospora,* spore in lactic blue, with terminal swellings, × 530.

collection on *Pteridium* should be referred to this species.

Monographos minor is scarcely a common species. We have found it in 5 collections only, but it can be quite abundant, as in 855c and 907a. The 'main form' can easily be mistaken for a *Mycosphaerella* at first sight. Besides the type, we have also seen the following material.

Sweden: Uppland. Dalby, c. 200 m NW of 'Jerusalem', 10.VI.1976, *Athyrium filix-femina,* 855c. – Uppsala-Näs, c. 500 m N of S. Focksta, 7.V.1975, *A. filix-femina,* 502c. – *Gästrikland.* Hille, c. 500 m SE of Brännsågen, *Lastrea phegopteris,* 21.V.1975, 560c.

Norway: Möre og Romsdal. c. 4 km NE of Gjöra, near Driva, *Dryopteris filix-mas,* 1.VII.1976, 666b.

Germany: Bavaria. Bayreuth, *Pteridium aquilinum,* IV.1874, leg. Thümen (intermixed in Rehm, Asc. 270).

Mycoglaena filicina L. & K. Holm, sp. nov.

Typus: Suecia, Uplandia, par. Dalby, pr. "Jerusalem", in stipitibus emortuis Athyrii filicis-feminae, 31.V.1976, K. & L. Holm 848a (UPS).

Fig. 4 A, B, 8 B.

Ascocarpia solitaria vel bina aggregata, 150–200 μm diam., 50 μm alta, superne clypeo virido-atro tenuo, 0.3–0.5 mm longo, conjuncta. *Peridium* c. 10 μm latum, e textura pro maxima parte hyalina, apice viridula, cellulis minutissimis (maxime c. 5 μm). *Asci* subcylindracei, ad 75 × 10 μm, unitunicati?, apice leniter incrassati, annulo minuto ope iodi fuscato instructi, octospori. *Sporae* irregulariter biseriatae, ellipsoideae vel paullo cuneatae, 3-septatae, cellula secunda vulgo majore, hyalinae, 12–17 × 4–5 μm. *Filamenta interthecialia* absentia?

This fungus is apparently undescribed, despite being common and characteristic as well. It is even recognizable macroscopically, by its clypeus, which forms a more or less greenish, elongate spot; opening by a pore or a longitudinal slit.

When wet it has a particularly conspicuous colour which reminds one of *Mycoglaena subcaerulescens* (Nyl.) Rehm, and *Winteria lichenoides* (Rehm) Sacc., both of which occur on coniferous wood. All these fungi are certainly closely allied. The spore type recalls "*Odontotrema inclusum*" (Karst.) Karst., a species which ought perhaps to be referred to *Mycoglaena*. The more well-known name *Winteria* Rehm ex Sacc. must unfortunately be abandoned as illegitimate, cf. Holm 1975 p. 486.

An imperfect form is often found intermixed and is without doubt connected. It is similar in appearance (Fig. 4 B), but instead of asci conidia are formed; they are rodlike, 2-celled, hyaline, 10–12 × 1.5–2 μm, produced from a basal layer of pyriform conidiogenous cells. Apart from the clypeus, this form could be ascribed to *Diplodina*.

Mycoglaena filicina is probably widespread, but so far we have only collected it in Sweden, Uppland, where it seems to be common at the base of two-years old petioles of some larger ferns: we have found it on *Athyrium filix-femina* and *Dryopteris filix-mas*.

Pyrenomycetes bitunicati

Botryosphaeria sp.

Fig. 1 K.

Ascocarps rather crowded, immersed-erumpent, c. 100 μm diam., collapsed, almost without papillae. *Asci* subsaccate–cylindric, bitunicate, c. 50 × 10 μm, very shortly pedicellate, 8-spored. *Spores* elliptico-fusiform, terminally obtuse, continuous, hyaline, 13–18 × 5–6 μm. *Interthecial threads* absent.

This fungus is without doubt a member of *Botryosphaeria* s.lat. (including *Guignardia* sensu von Arx & Müller). It is possibly an undescribed pteridicolous species, but it may also be a question of an incidental occurrence on bracken of a species which normally inhabits some unrelated host. We leave this problem to a future monographer of the genus.

We have encountered this fungus once only, but the collection is fairly rich: Sweden, Uppland, Dalby, c. 500 m SSW of 'Jerusalem', in dead fronds of *Pteridium aquilinum,* 8.V.1976, 804 g.

Dangeardiella Sacc. & P. Sydow

Sacc. & P. Sydow, Syll. Fung. 14: 683 (1899) – Type: *D. macrospora.*

The genus was erected with the short diagnosis: "A *Monographo* differt imprimis sporidiis elongatis, pluri (6–8-)cellularibus". However, it is certainly not related to *Monographos,* in whatever sense this genus is conceived, but probably lies closest to certain Lophiostomataceae, as already pointed out by Rostrup (1904). *Dangeardiella* so far comprises two species, both of which were thoroughly dealt with by Obrist (1959); we refer to his paper in the main, merely adding some complementary data.

Dangeardiella fusiforma Obrist

Obrist, Phytopath. Zeitschrift 35: 381 (1959) – Type: Switzerland, Graubünden, Val Tuors, "abgestorbene Blattstiele von Dryopteris filix-mas", E. Müller (ZT).

Fig. 1 C, B, 2 D, E.

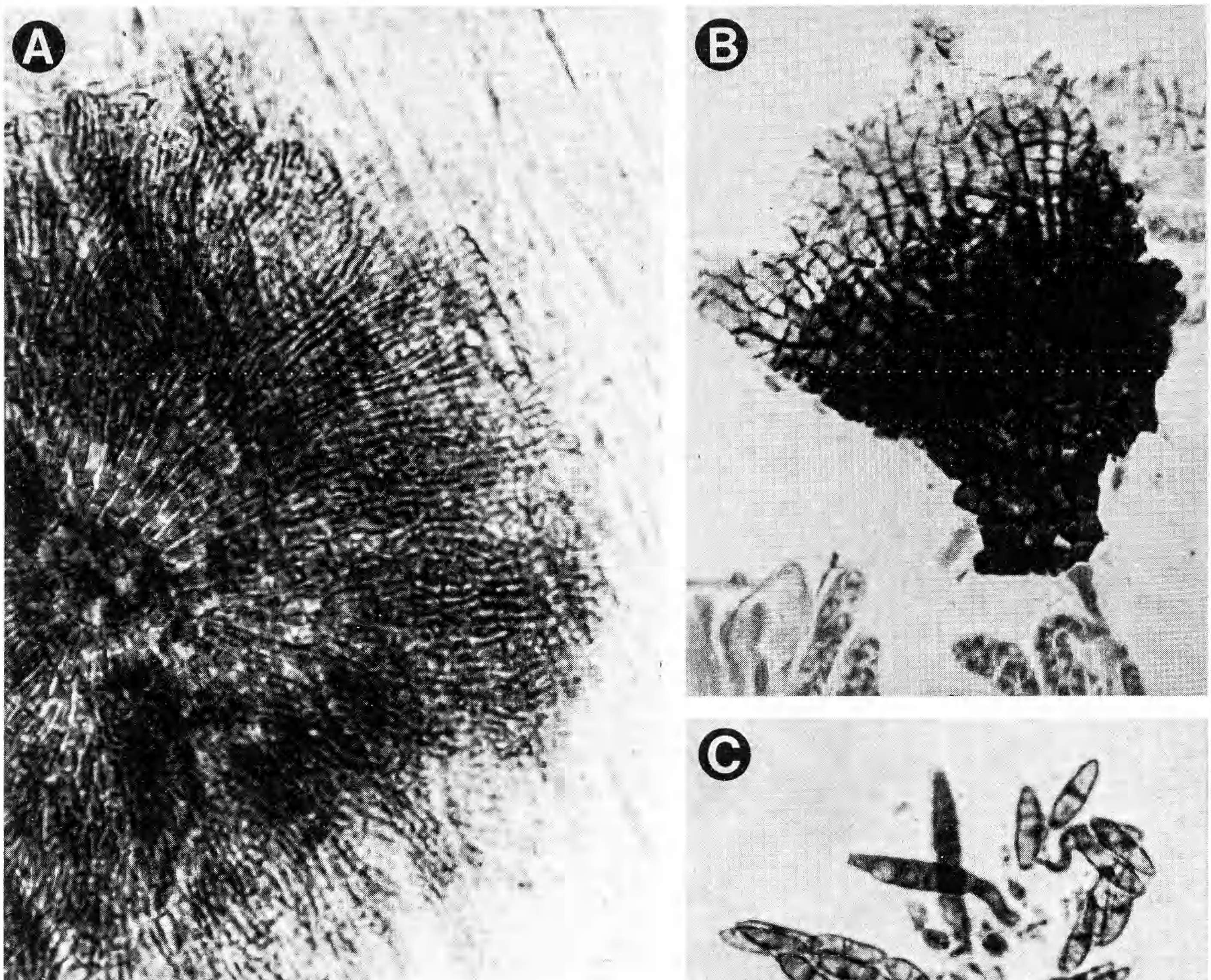

Fig. 7. A: *Nannfeldtia phegopteridis,* ascocarp in surface view. – B: *Pseudopeltis filicum,* part of shield, and asci. – C: *Glomerella polypodii,* asci and spores, in lactic blue. – D: *Trichothyrina filicum,* mature ascocarp in surface view, with asci in lactic blue. – E: Idem, immature ascocarp. – All × 530.

Ascocarps immersed–erumpent, simple or compound. In the former case they consist of a single pseudothecium, c. 250 μm diam., with a distinct, somewhat flattened papilla. The compound ascocarps attain a size of 1 mm, and contain up to at least 3 'loculi' with very reduced partition walls. These ascocarps may fuse to form still larger fruit bodies. The simple ascocarps occur in the nerves of the lamina, the larger ones in the petioles.

The *spores* display a wide variation, and the species is probably heterogeneous. Obrist (1959) reported the spores to be 30–40 × 8–11 μm, 6–8(–10)-celled. We found them to be 25–50 × 6–10 μm, 5–12-celled. Most of our material is rather uniform, with short spores, about 25–30 × 7.5–9 μm, 6–8-celled, elliptico-fusiform, asci almost cylindric, 80–100 × 12–15 μm. Three collections from Norway on *Dryopteris filix-mas,* however, are remarkably different (nos. 639b, 642 and 664b). The spores (Fig. 1 B) are fusiform, 42–50 × 9–10 μm, with 10–12 cells, the asci rather saccate, c. 110–135 × 25 μm. This form recalls *D. macrospora,* but the spores are obtuse and lack the peculiar terminal "balls". It seems rather intermediate. It is noteworthy that Obrist's measurements fall between those of our two forms, and that they refer to material found on *Dryopteris filix-mas. Dangeardiella fusiforma* is so far known only from the type material. We have 10 collections, from 4 different hosts:

Sweden: Skåne. Skäralid, 13.VI.1974, 216a, *Dryopteris dilatata.* – *Uppland.* Ekeby, E of lake Vällen, 9.V.1975, 517b, *Athyrium filix-femina* and 518b, *Dryopteris filix-mas.* – *Dalarna.* Sundborn, Grops, 22.VI.1974, 275b, *Athyrium filix-femina.* – Grops, 18.V.1975, 555a, *Dryopteris dilatata.* – Grops, 23. VII.1975, 707a, *D. dilatata.* – Logärdsdammen, 27. VI.1976, 883b, *D. spinulosa.*

Norway: Sör-Tröndelag. Oppdal, pr. Gjevilsvasshytta, c. 800 m, 29.VI.1975, 639b & 642, *Dryopteris filix-mas.* – *Möre og Romsdal.* Gjöra, 1.VII.1975, 664b, *D. filix-mas.*

Dangeardiella macrospora (Schröt.) Sacc. & P. Sydow

Sacc. & P. Sydow, Syll. Fung. 14: 683 (1899) – *Monographus macrosporus* Schröter, Pilze Schlesiens 2: 477 (1897) – Type: Germany, Silesia, Hirschberg, *Athyrium alpestre.*

Fig. 1 A, 3 C, D, 6 F.

For further synonyms see Obrist 1959 p. 379.

The ascocarps of this species are generally larger and more conspicuous than those of *D. fusiforma.* Simple ascocarps are about 450 μm diam. with a strong papilla and quite similar to those of a *Lophiostoma.* They not only occur in the leaf veins but also on the stipes. The compound fruit-bodies have a long 'crest'. The spores are very characteristic: large, fusiform, 65–75 × 10–11 μm, mostly 10-celled, constricted below the 5th cell, which is inflated. (Obrist's figures represent inverted spores). The terminal, ball-shaped dilatations are a very peculiar feature, first noticed by Obrist, who states that they finally become delimited by a septum forming a separate "Kugelzelle". The asci are almost cylindrical, about 225 × 25 μm diam.

D. macrospora definitely prefers *Athyrium alpestre (=distentifolium)* and has been found on that host in Scandinavia, the Alps and the Riesengebirge. It seems to be rather common in Scandinavia. Rostrup (1904 p. 12) recorded it from Norway on *Dryopteris spinulosa,* and we have found it on *Athyrium filix-femina* in a lowland locality in Norway: Möre og Romsdal, c. 4 km NE of Gjöra, about 200 m.

Scirrhia Nitschke ex Fuckel

Fuckel, Symb. Mycol. 220 (1870) – Lectotype (selected by Clements & Shear 1931 p. 294): *S. rimosa* (Alb. & Schwein. ex Fr.) Nitschke ex Fuckel.

Metameris Theiss. & Sydow, Ann. Mycol. 13: 342 (1915) – Type: *M. japonica* (Syd.) Syd.

Scirrhodothis Theiss. & Sydow, Ann. Mycol. 13: 415 – Lectotype (selected by Clements & Shear 1931 p. 294): *S. confluens* (Starb.) Theiss. & Sydow.

Scirrhophragma Theiss. & Sydow, Ann. Mycol. 13: 423 – Type: *S. regalis* Theiss. & Sydow.

The above synonymy is to some extent controversial. No doubt *Metameris, Scirrhodothis* and *Scirrhophragma* are closely allied, and were united, rightly we think, by von Arx & Müller (1975 p. 80) who used the name *Metameris* for the combined taxon. These authors, however, referred it to the Pleosporaceae, as also did Barr (1972 p. 564), thus separating it far apart from the dothideaceous *Scirrhia.* We cannot follow this classification, because *Metameris,* too, has an ascocarp centrum of *Dothidea* type. This is particularly apparent in *M. japonica,* where the centrum consists of large, broad cells, about 12–15 × 10 μm (cfr. Fig. 5 D). These are not pseudoparaphyses. In *S. aspidiorum* and *S.*

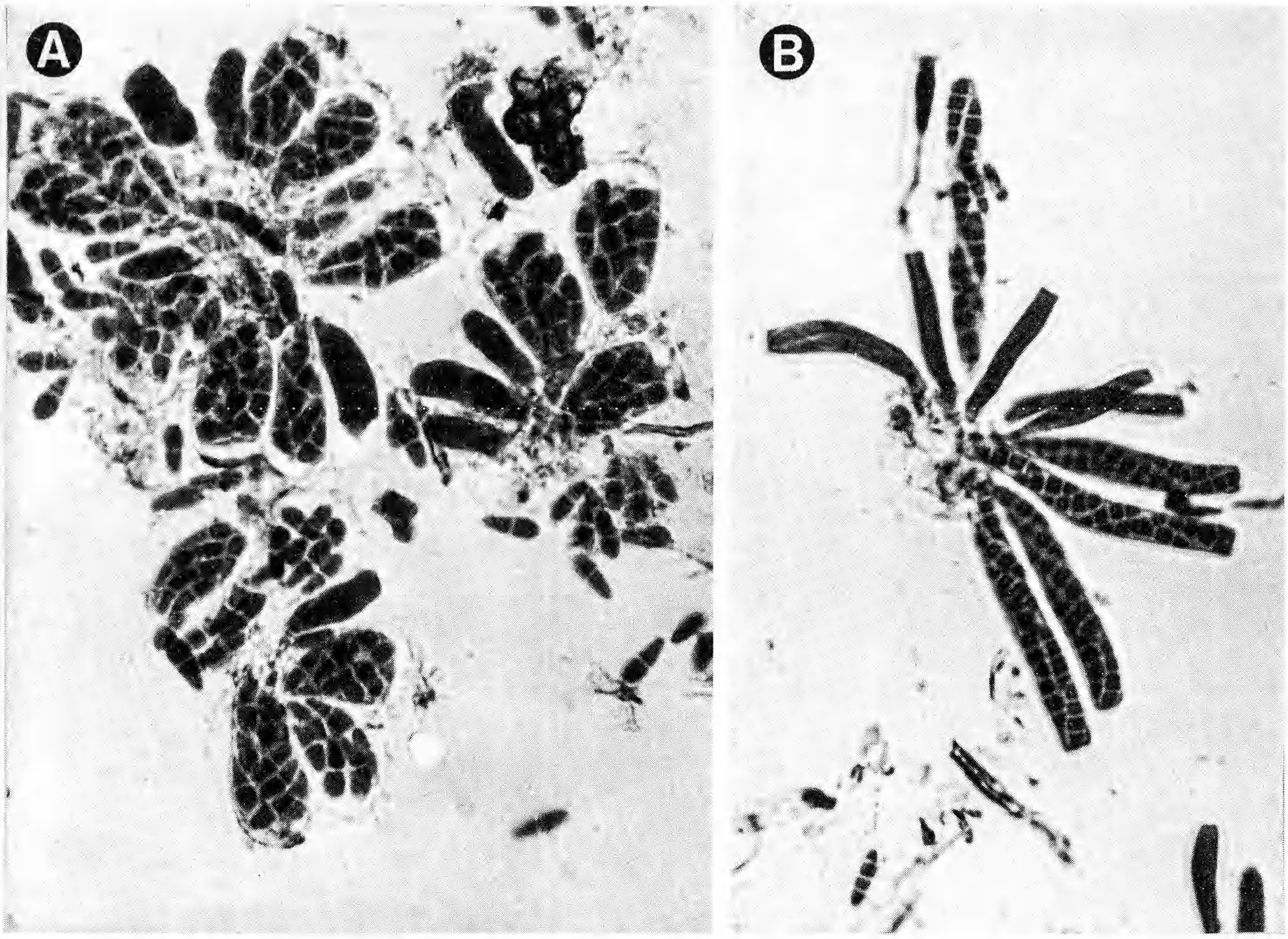

Fig. 8. Asci and spores in lactic blue. – A: *Hysteropeltella moravica*. – B: *Mycoglaena filicina*. – All × 530.

osmundae the centrum is composed of smaller cells, more like the centrum of *S. rimosa*. Accordingly, *Metameris* s.lat. must be referred to the Dothideaceae. It is perhaps questionable whether or not it should be included in *Scirrhia* as done by Müller & von Arx (1962 p. 379). We cannot see any convincing reason why not. Certain differences do exist in stromatic texture, but they are evidently immaterial. In *Scirrhia aspidiorum* the stroma is composed of almost rectangular cells (seen in section), disposed in distinct vertical rows, whereas in the closely related "*Metameris japonica*" the stromatic cells are isodiametric and not serially arranged. We would also cite *S. castagnei* as a further argument for this presumed kinship: morphologically it matches *S. rimosa* very closely, but is biologically more similar to *Metameris*, since it also grows on a pteridophyte viz. *Equisetum*.

Scirrhia aspidiorum (Lib.) Bubák

Bubák, Ber. Deutsch. Bot. Ges. 34: 328 (1916) – *Sphaeria Aspidiorum* Libert, Pl. Crypt. Ard. 342 (1837) – *Scirrhodothis Aspidiorum* von Höhnel, Fragm. Mykol. 1185 (1919) – *Monographos aspidiorum* sensu auct. nonnull., non sensu Fuckel – Type: Belgium, "in stipitibus Aspidiorum. Vere."

Sphaeria pteridicola Berk. & Curtis, Grevillea 4: 145 (1876) ('*pteridicoli*') – *Didymella pteridicola* Sacc., Syll. Fung. 1: 561 (1882) – Type: USA, South Carolina, *Pteridium aquilinum*, Curtis (K! UPS!).

Monographos microsporus Niessl in Krieger, F. sax. 240 (1887) – *Scirrhia microspora* Sacc., Syll. Fung. 9: 1040 (1891) – Type: Germany, Königstein, *Athyrium filix-femina*, Krieger (S!).

Scirrhia confluens Starbäck, Bih. K. Sv. Vet.-Akad. Handl. 15. 3(2): 18 (1889) – *Scirrhodothis confluens* Theissen & Sydow, Ann. Mycol. 13: 415 (1915) – Type: Sweden, Öland, Ottenbylund, *Athyrium filix-femina*, 17.VI.1888, Starbäck (UPS!).

Exs.: Krieger, F. sax. 240 (*'Monographos microsporus'*), 249 (*'M. micr.'*) 775 (*'M. micr.'*) (non 288, q.e. *M. fuckelii*) – Lib., Pl. Crypt. Ar. 342 (S) – Petr., Fl. Bohem. Mor. II:1:2196 (S) (non 2056, q.e. *M. fuckelii*, nec non Myc. carp. 461 idem) – Rbh., F. eur.

3966 (*'M. micr.'*, S) – Rehm, Asc. 931, 1064 (*'M. micr.'*, S) (non 932 q.e. *M. fuckelii*) – Syd., Myc. march. 2066 (S, UPS) (2183? vetustus in S, UPS), non Syd., Myc. germ. 2143, q.e. *M. fuckelii*).

Fig. 1 E, F, 3 A, B, 5 C.

For a detailed description of this well-known species we refer to Obrist (1959 p. 373), who, however, was apparently not fully aware of the great variation which exists in its stroma morphology, which is quite noteworthy. When well-developed, the stromata may attain 5 mm in length and 1 mm in breadth, being composed of vertical series of ± cubic cells and containing numerous separate loculi. This type of stroma may perhaps be considered the basic one, from which the others can be derived along two lines of evolution: (1) the fusion of adjacent loculi through reduction of the intermediate wall; (2) the dismemberment of the stroma into smaller discrete bodies with fewer loculi, ultimately leading to the formation of uniloculate dothithecia. This variability was rightly emphasized by Petrak (1927 p. 365; 1953 p. 306) who pointed out the occurrence of a *Didymella*-like form in the lamina. We have found this form in the larger leaf-veins of *Pteridium aquilinum*. Petrak was inclined to consider *Scirrhia aspidiorum* as "eine, gelegentlich auch in einer stromatischen Form auftretenden *Didymella*" (Petrak 1953 l.c.). This statement seems rather exaggerated, however. The true *Didymellae* have interthecial threads, generally considered to be pseudoparaphyses. Such are not present in *Scirrhia* – also the solitary dothithecia have a pseudoparenchymatous centrum. *Didymella pteridicola* is conspecific; the type material is the normal stipicolous form (for other synonyms, see Bubák 1916 and Petrak 1953.)

Scirrhia aspidiorum seems to be a fairly homogeneous taxon, in spite of occurring on a variety of hosts. The usual form has small obtuse spores, 10–13 × 3 μm. However, we have three collections from *Pteridium aquilinum* (Fig. 1 F), which possess distinctly larger spores (18–23 × 4–5 μm) with somewhat more acute ends (two collections from Sweden, Uppland, 195c & 804d, and one from Norway, Sunndalsöra, 678a). The common small-spored form is also found on *Pteridium*, as exemplified by e.g. Krieger, F. sax. 289, and Petrak, Fl. Bohem. Mor. II:1:2196.

A subspecific taxon has been described, viz. var. *struthiopteris* Krieger ex Rehm, Hedwigia 31: 303 (1892); type: Saxony, *Matteuccia struthiopteris* = Rehm, Asc. 1064 (S!) According to Rehm, the spores are "grösser und breiter als bei der Stammform". This seems very doubtful, but nevertheless *Matteuccia* may possibly have a form of its own: the imperfect state *Sphaeriothyrium filicinum* Bubák does seem to have a marked preference for this host; e.g. we have 4 collections from *Matteuccia*, but only 1 (uncertain) from another host *(Athyrium filix-femina)*.

Scirrhia aspidiorum is common in Sweden, at least in the lowlands, in the leaves of the larger ferns, mainly on the petioles. It is perhaps particularly common on *Athyrium filix-femina*, but we have also found it on *Dryopteris dilatata*, *D. spinulosa*, *D. filix-mas*, *Lastrea dryopteris* (new host?), *L. thelypteris*, *Matteuccia struthiopteris* and *Pteridium aquilinum*.

Scirrhia osmundae (Peck & Clinton) L. & K. Holm, comb. nov.

Dothidea Osmundae Peck & Clinton, Ann. Rep. New York State Mus. 30: 64 (1878) – *Scirrhophragma Osmundae* Obrist 1959 p. 377 – *Metameris Osmundae* von Arx & Müller 1975 p. 80 – Type: USA, N.Y., Buffalo, *Osmunda* sp., leg. Clinton (n.v.).

Scirrhophragma regalis Theissen & Sydow, Ann. Mycol. 13: 423 (1915) – Type: Germany, Sperenberg, *Osmunda regalis*, V. 1912, H. Sydow (S!).

?Monographos japonicus Sydow, Ann. Mycol. 12: 408 (1910) – *Metameris japonica* Theissen & Sydow, Ann. Mycol. 13: 342 (1915) – Type: Japan, Mino, Kawauye-mura, *Osmunda regalis* var. *japonica*, 10. V.1912, K. Hara (S!).

Fig. 1 G (H), 2 C, 5 A, B (D, E).

This species is easily recognized by its characteristic spores. As a matter of fact, the spore type seems to be unique. Its true nature has been misunderstood, however. In our experience the spores are always 2-celled, though appearing to be 3-celled on account of the contraction of the protoplast in the upper cell to leave an air-filled apical space. This peculiar spore type was observed by Theissen & Sydow, but they interpreted the spores as being 3-celled, with the comment that the presumed uppermost cell "nimmt fast keinen Farbstoff an" (Theíssen & Sydow 1915 p. 343). This is obviously a quite constant phenomenon in mature spores – immature ones are plasma-filled in the normal manner.

For a detailed description we refer to Obrist 1959 (though his Fig. 17 a represents inverted spores!). The synonymy given above is also based on his paper. He suggested *Metameris japonica* as a probable synonym, and it is no doubt very closely related, although some minor differences exist. In European material, the stromata are larger, up to 2 mm long and 0.5 mm broad, with numerous loculi, c. 100 μm diam., arranged in up to 3 parallel rows. The spores are 15–18 × 4 μm. The type of *Metameris japonica* (Fig. 1 H, 5 D, E) has smaller stromata, 0.3–0.6 mm, with only 1–3 loculi, which are larger, c. 150 μm diam. The spores are larger, and often broader, up to 26 × 6 μm, but are of the same characteristic type. We leave the question open whether or not the Japanese fungus is conspecific with ours.

Scirrhia osmundae was not known from Europe until 1915, when it was reported from N Germany by Theissen & Sydow. Since then Obrist has published two finds from southernmost Switzerland, Tessin. We can report it from one Swedish locality: Gästrikland, Hille parish, at the rivulet Testeboån, *Osmunda regalis,* 21.V.1975, no. 562a. The fungus occurred in abundance on old petioles. *Osmunda* is rare in Sweden and the above-mentioned locality, in fact a northern outpost, is the only one which we have visited. The fungus is probably more common than the few finds so far would suggest.

Morenoina sp.

Fig. 1 I, 4 F.

A few times we have encountered a fungus similar to *Morenoina epilobii* (Lib.) von Arx, and which is possibly conspecific; however, since we have not yet seen any well developed material of the latter species, the question is still open.

The *ascocarps* are quite superficial, generally rather densely scattered, lirelliform, often ramose, c. 50 μm broad and usually 0.1–0.5 mm long. The *shield* consists of one layer of radiately arranged dark-brown cells, c. 5 × 3 μm, rectangular in surface view, at the margins grading into a sparse, brown mycelium. Basal layer 0, hypostroma 0, interthecial threads 0. *Asci* saccate–subglobose, apparently bitunicate, 18–20 × 12–14 μm, 8-spored. *Spores* irregularly disposed, about ellipsoid, with one median septum, the upper cell somewhat broader, elongate hyaline, lastly faintly brownish, when young with conspicuous oil droplets, 8–10 × 3–4 μm.

At the base of dead petioles of various ferns.

Sweden: Uppland. Uppsala-Näs, c. 700 m W of the farm Högby, *Dryopteris filix-mas,* 27.IV.1975, 479b. – *Härjedalen.* Tännäs, Mt Hamrafjället, SW slope, uppermost part of regio subalpina, 27.VI.1975, *Lastrea dryopteris,* 605c, and *Polystichum lonchitis,* 609c.

Norway: Hedmark. pr. Trysil, 3.VII.1975, *Athyrium filix-femina,* 699b.

Schizothyrium speireum (Fr. ex Fr.) L. & K. Holm, comb. nov.

Sclerotium? speireum Fr. ex Fr., Syst. Mycol. 2: 261 (1822) – *Sphaeria speirea* Fr., Obs. Mycol. 1: 185 (1815) – *Myiocopraloa speirea* Ciferri, Atti Ist. Bot. Lab. Critt. Univ. Pavia ser. 5, 15: 19 (1957) – Type: "In foliis vivis Aegopodii Podagrariae" (Scler. suec. no 206, UPS!).

Schizothyrium perexiguum (Rob. ex Desm.) von Höhnel, sensu auctt., non *Phacidium perexiguum* Rob. ex Desm., q.e. *Naevia minutissima* (Auersw.) Rehm.

Microthyriella Osmundae Booth, Kew Bull. 1957 p. 424 fide Müller & von Arx 1962 p. 200 – Type: England, Norfolk, *Osmunda regalis,* leg. Dennis.

Schizothyrium speireum is one of the common "fly-speck fungi" and is considered to be highly polyphagous, and even pteridicolous, since Müller & von Arx (1962) included *Microthyriella osmundae* in its synonymy. Possibly, however, *Osmunda* has a strain of its own – we have found the fungus in abundance on this host, in the sole *Osmunda* locality which we visited. Otherwise *Schizothyrium* seems rarely to occur on ferns, viz. we found it only once, on the Male Fern, see below. For a description, see Booth 1958 (as '*Microthyriella Osmundae*') and Müller & von Arx 1962 (as '*Schizothyrium perexiguum*').

The nomenclature presents some problems. The name *Schizothyrium perexiguum* is unfortunately untenable, since it is due to a mistake made by von Höhnel (1917 pp. 297, 327). It was based on *Phacidium perexiguum* Rob. ex Desmazières (1849 p. 362). The description is suggestive of *Naevia minutissima* Rehm, a surmise which is confirmed by the authentic material, dead leaves of *Quercus rubra,* distributed in Desmazières, Plantes Crypt. France, éd. 3, no. 793. von Höhnel erroneously identified *Phacidium perexiguum* with *Microsticta vagans*

Desm., a species also present on the same oak leaf material and which is conspecific with our fungus. In consequence, we have to find another epithet for it. We consider that the best solution is to adopt the old name *Sphaeria speirea* Fr., as was done by Ciferri et al. (1957). Authentic material is present in Scler. suec. no. 206; although sterile, at least in the UPS copy, it is otherwise typical.

The following pteridicolous specimens have been seen.

Sweden: Uppland. Västeråker, moist forest with *Daphne,* on dead petioles of *Dryopteris filix-mas,* 20.VI.1976, 889a. –*Gästrikland.* Hille, Brännsågen, at the rivulet Testeboån, on dead petioles of *Osmunda regalis,* 21.V.1975, 562b.

The epithet *perexigua* should be transferred to the discomycete, called *Naevia minutissima* (Awd) Rehm: As *Naevia* is illegitimate when used in this sense, the name was recently replaced by *Naevala* Hein (1976 p. 83); the correct name for the fungus thus becomes *Naevala perexigua* (Rob. ex Desm.) L. & K. Holm, comb. nov. ≡ *Phacidium perexiguum* Roberge ex Desmazières, Ann. Sci. Nat. Bot. ser. 3, 11: 362 (1849).

Trichothyrina filicum L. & K. Holm, sp. nov.

Typus: Suecia, Uplandia, par. Dalby, pr. "Jerusalem", 7.X.1976, *Pteridium aquilinum,* in frondibus anni praeteriti, K. & L. Holm, no. 931a (UPS).

Fig. 1 P, 7 D, E.

Species Trichothyrinae pinophyllae affinis, sed ab ea differt imprimis sporis eguttulatis, cellula superiori basi inflata.

Ascocarps scattered, ≤ 100 μm diam., flattened with a distinct pore. *Asci* rather numerous, c. 25, elongate–pyriform, sessile, 8-spored. *Spores* fusiform, obtuse, 2-celled, distinctly inflated above the median septum, 8–12 × 2.5–3 μm, hyaline, eguttulate. No *interthecial threads* present, and apparently no superficial mycelium.

On dead leaves of various ferns, growing on the petiole as well as on the lamina, particularly on the upper surface.

This minute fungus has evidently not been reported before; nevertheless it seems to be quite common on several ferns. We have found it on *Athyrium filix-femina, Dryopteris dilatata, D. filix-mas, Matteuccia struthiopteris, Polystichum lonchitis* and *Pteridium aquilinum.* It is common in the Uppsala area and certainly has a wide distribution: we have collected it in the subalpine region of Mt Hamrafjället in Härjedalen, Sweden, and have also found it in Norway (Oppdal) and Iceland (Ólafsfjarðarmúli).

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Vegetative anatomy and systematics of Grubbiaceae

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Grubbia nodes are trilacunar. Leaves have recurved margins, upper epidermis with thick cuticle or a cutinized thick wall, a single layer of palisade (including strands of crystal-bearing cells), 3–5 layers of spongy tissue, and a lower epidermis bearing anomocytic stomata and numerous non-glandular unicellular trichomes. Expression of these cell types varies among the three species and their subspecific entities, and shows close correspondence to the taxonomic system. Only a single genus should be recognized. No species or species-group has unique anatomical features. Foliar and nodal anatomy offer only a small amount of information on systematic position of Grubbiaceae, but could be construed as supporting a ''rosoid'' affinity.

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The three species of the South African family Grubbiaceae have what could be termed *Erica*-like leaves. This leaf form is widespread in the various groups of dicotyledons in the fynbos vegetation of Cape Province. Because *Erica*-like leaves have evolved numerous times independently, their anatomy presents a conformation of considerable ecological significance. Although *Erica*-like leaves have received attention on various occasions, each example studied offers potential information on this phenomenon. The parallelisms involved in this leaf form must also be understood in order that true phylogenetic relationships can be discerned.

Wood anatomy of Grubbiaceae has been summarized earlier (Carlquist 1977 a). Do aspects of vegetative anatomy other than wood offer data useful in deciding the phylogenetic position of Grubbiaceae? Van Tieghem's (1897) data are suggestive, but incomplete. Fagerlind (1947) has devoted a paper to the probable affinities of Grubbiaceae, but his conclusion that the family is ericalean does not seem strongly supported. Although data from vegetative anatomy may not be decisive by themselves, they may favor some interpretations more than others.

Leaf anatomy in dicotyledons often shows variations corresponding to the taxonomy of particular groups. That this is true within Grubbiaceae is therefore not surprising. Van Tieghem (1897) demonstrated anatomical differences between the two species of *Grubbia* he studied. There is now a total of three species incorporating six subspecific taxa within the genus (Carlquist 1977 a). All of the data accumulated on leaf anatomy of Grubbiaceae thus far are the work of Solereder (1908) and Van Tieghem (1897). Metcalfe & Chalk (1950) summarize this data.

Material and methods

Liquid-preserved material was available for typical *Grubbia rosmarinifolia* Berg. (Carlquist 4707, 4962), *G. rourkei* Carlquist (Carlquist 5115), and *G. tomentosa* (Thunb.) Harms (Carlquist 5010, 5068). Fixed material was prepared using formalin-acetic-alcohol. Voucher specimens are located in RSA, NBG, and other herbaria. Portions of herbarium specimens of other taxa proved suitable for anatomical study: *G. rosmarinifolia* subsp. *gracilis* (Salter) Carlquist (Lewis 1321, SAM); *G. rosmarinifolia* subsp. *hirsuta* E. Mey. ex A. DC.) Carlquist (Compton 20986, NBG); and *G. rosmarinifolia* subsp. *rosmarinifolia* var. *pinifolia* (Sonder) Carlquist (Stokoe 60060, SAM). I am grateful to Dr John Rourke, Curator of the Compton Herbarium, Kirstenbosch, for this material. Herbarium material portions were expanded in warm 2.5 per cent NaOH, partly clearing the stems, petioles, and leaves. When fully expanded, leaves and stems were subjected to changes of water and stored in 50 per cent ethyl alcohol.

Both fixed material and treated herbarium material were infiltrated with paraffin, sectioned, and stained according to frequently-used techniques in a safranin–fast green series. Transections, longitudinal (parasagittal) and paradermal sections of leaves were prepared. Transections of petioles and serial transections of nodal regions of stems were obtained. Microtechnical tasks were performed by Dr Larry DeBuhr.

The taxonomic concepts developed earlier (Carlquist 1977 a) guided selection of material. The use of liquid-preserved specimens permitted me to judge whether sections of the treated herbarium specimens were both qualitatively and quantitatively comparable to those of liquid-preserved material. In fact, the two kinds of material proved identical except for protoplasts, so that all comparisons are, in fact, quite reliable.

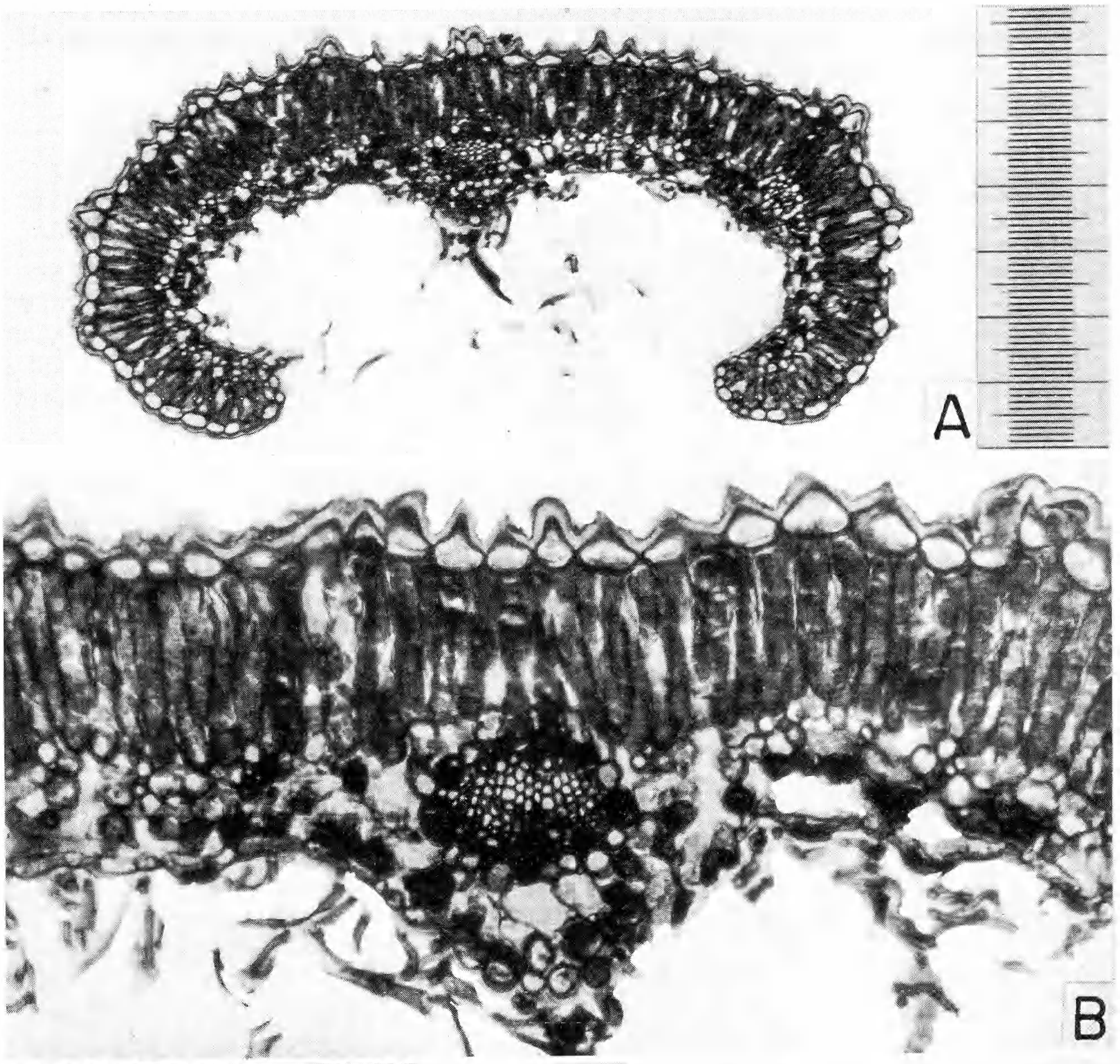
Leaf

In transection, all *Grubbia* leaves can be said to have recurved margins (Figs. 1 A, C, D, 2 A, 4 A, B). Cells of the upper epidermis are much larger than those of the lower epidermis. All trichomes are non-glandular and unicellular. They are borne most abundantly on lower leaf surfaces (Figs. 1 B, C, 2 C, 4 A, B). All stomata occur on abaxial leaf surfaces, intermingled with trichomes. Guard cells have very thick cutinized walls, with the lumen constricted, slit-like as seen in sectional view, parallel to the leaf surface. Subsidiary cells are not present (Fig. 2 B). Subsidiary cells may appear to be present in paradermal sections. However, such cells prove to be outwardly-bent epidermal cells supporting the guard-cell pair (Fig. 3 C, upper left), and these epidermal cells do not differ from other epidermal cells in any way that would distinguish them as subsidiary cells. Cells of both the upper and the lower epidermis are polygonal as seen in face view. A single layer of palisade chlorenchyma cells, often exceptionally long and slender, is present beneath the adaxial epidermis (Figs. 1 B, C, 2 C, 3 A, 4 A, B). Strands of two to four cells, each containing a druse or a rhomboidal crystal, are formed idioblastically in the palisade layer. These crystalliferous cells are much wider than chlorenchymatic palisade cells. Depending on the species, a minimum of two to five layers of spongy tissue occur abaxial to the palisade; more numerous layers occur where veins are present. Seven or more veins (including veinlets) are present in a lamina. Of these, the largest may have fibers near the xylem pole, or both xylem and phloem poles of several veins may be associated with fibers. Tannin deposits are present in large quantities in palisade cells, but to a lesser extent also in other cells, especially those near veins (Fig. 1 B, 2 C, 3 A). Modal variations characterizing particular taxa are given below.

Grubbia rosmarinifolia subsp. *gracilis* (Fig. 1 D). About seven small veins are present in the lamina as seen in transection. The midvein is not associated with an externally prominent midrib. A few fibers were observed near the xylem of the midvein; no fibers were seen in other veins. The leaf margin is not notably recurved; instead, the entire leaf responds to desiccation by curvature of the whole lamina (Fig. 1 D), thereby resembling a single-pocketed type rather than a double-pocketed leaf (e.g., *G. rourkei,* Fig. 2 A). Strands of druse-bearing cells in the palisade consist of two, mostly three cells. Three spongy layers typically present. The leaves studied had laminae about 1.25 mm wide. The outer wall of adaxial epidermal cells was about 10 μm thick, of which about 5 μm was epidermal wall proper and 5 μm was the superposed cuticle. The papillate shape of cells of the adaxial epidermis is related to the presence of very short, sparsely distributed trichomes. Trichomes on the abaxial epidermis slender and thick-walled as in subsp. *rosmarinifolia*.

Grubbia rosmarinifolia subsp. *hirsuta* (Fig. 4 C). Numerous veins present in lamina as seen in transection. Midvein not associated with a pro-

Fig. 1. *Grubbia rosmarinifolia,* leaf sections. – A–C: subsp. *rosmarinifolia,* Carlquist 4707. – A: TS of lamina, showing recurved margins. – B: Portion of lamina including midrib; papillate nature of adaxial epidermis cells is evident. – C: Margin of lamina, adaxial surface to the right; a druse is visible in an enlarged cell in the palisade layer. – D: subsp. *gracilis,* Lewis 1321. TS of lamina. – The photomicrographs have been enlarged at the same scales as applicable photomicrographs of stage micrometer scale. A, D, scale to the right of A (finest division 10 μm). B, C, scale to the right of C (divisions 10 μm).


A
B
C
D

minent midrib. Fibers are associated with xylem of all veins, especially abundant on the adaxial side of the midvein. Leaf margins are recurved as in typical *G. rosmarinifolia*. Strands of druse-bearing cells in the palisade consist of two to four, but mostly three cells. Four layers of spongy chlorenchyma are typically present. The leaves studied had a lamina width of approximately 1.85 mm. Thickness of the outer wall of the adaxial epidermis is about 23 μm, of which 5 μm was the wall proper and 18 μm the superposed cuticle. Trichomes on the adaxial surface related to papillate epidermal cell shape. These trichomes are very thick-walled (Fig. 4 C); the wall does not seem cutinized or lignified in its staining reactions. Trichomes on the adaxial surface much more slender, gradually tapered from the widened base (as in subsp. *rosmarinifolia*); trichome base narrowed appreciably where it is inserted into the epidermis.

Grubbia rosmarinifolia subsp. *rosmarinifolia* var. *rosmarinifolia* (Fig. 1 A–C). Numerous veins present in lamina as seen in transection although only three of these are major veins (Fig. 1 A, C). Fibers adjacent to xylem and phloem poles of the midvein and some other veins. A distinct midrib, with papillate epidermal cells like those of the adaxial epidermis, present abaxial to the midvein. Leaf margins are recurved, forming a pocket subdivided into two channels by the midrib (Fig. 1 A). Strands of druse-bearing cells in the palisade layer composed of one to three, but mostly a pair of cells. Both druses and simple rhomboidal crystals may be observed in these cells; druses are not highly complex, but appear to be formed from the union of a few rhomboidal crystals. An appreciable number of druse-containing cells, not subdivided in any way, occur idioblastically in the spongy tissue as well. Three spongy layers typically occur on the abaxial side of the leaf. Leaves studied were 2.0–2.5 mm wide. The thickness of the outer wall of the adaxial epidermis was about 23 μm, of which about 5 μm was comprised by the wall proper, and about 18 μm by the superposed cuticle. Trichomes on the adaxial epidermis are short and sparse, and are related to the papillate shape of epidermal cells. Trichomes on the abaxial surface are narrow, moderately thin to notably thick-walled; these trichomes are tapered from a widened base. The base abruptly narrows into the peg-like constricted end inserted into the epidermis.

Grubbia rosmarinifolia subsp. *rosmarinifolia* var. *pinifolia*. Leaves of this variety are like those of var. *rosmarinifolia* except in the following respects. Cells of the adaxial epidermis not notably papillate, a fact probably related to the lack of hairs on this epidermis. Thickness of the outer wall of the adaxial epidermis was about 14 μm, of which about 4 μm was comprised by the wall proper, and about 10 μm by the superposed cuticle. The leaf studied was about 2.0 mm wide.

Grubbia rourkei (Fig. 2). Numerous veins, mostly minor, present in the lamina as seen in transection. A few fibers observed adjacent to the xylem and phloem poles of the midvein (Fig. 2 C), but not near other veins. A midrib clearly differentiated on the abaxial side of the leaf (Fig. 2 C), with large epidermal cells like those of the adaxial epidermis. Leaf margins more markedly recurved than in other species, forming two pockets each of which is densely filled with trichomes (Fig. 2 A, C). Strands of crystal-bearing cells in the palisade are composed of one to three, but mostly two cells. Crystals in these cells mostly rhomboidal; a few druses can be said to be present by aggregation of two or three crystals per cell. Four spongy layers typically occur abaxial to this palisade. The leaf studied had a width of 2.2 mm. Thickness of the outer wall of the adaxial epidermal cells was about 14 μm, of which 7 μm was composed of the wall proper and 7 μm of the superposed cuticle. The upper epidermis of this species is highly distinctive (Fig. 2 C). Cells, often in pairs, are elongate as seen in sectional view, forming emergences three-dimensionally. The cuticle is separated from epidermal walls in the valleys formed between pairs of epidermal cells. This separation is undoubtedly related to a subcuticular accumulation of a varnish-like substance which gives leaves a white or sordid-white color when fresh (yellowish in dried specimens). Subcuticular accumulation of such a substance is rather like the subcuticular accumulation of oils and oleoresins in glandular trichomes of various dicotyledons. The epidermis of *G. rourkei* is connected to the palisade by peg-like or arm-like extensions (Fig. 2 C). No epidermal cells are appressed directly to palisade cells. Trichomes

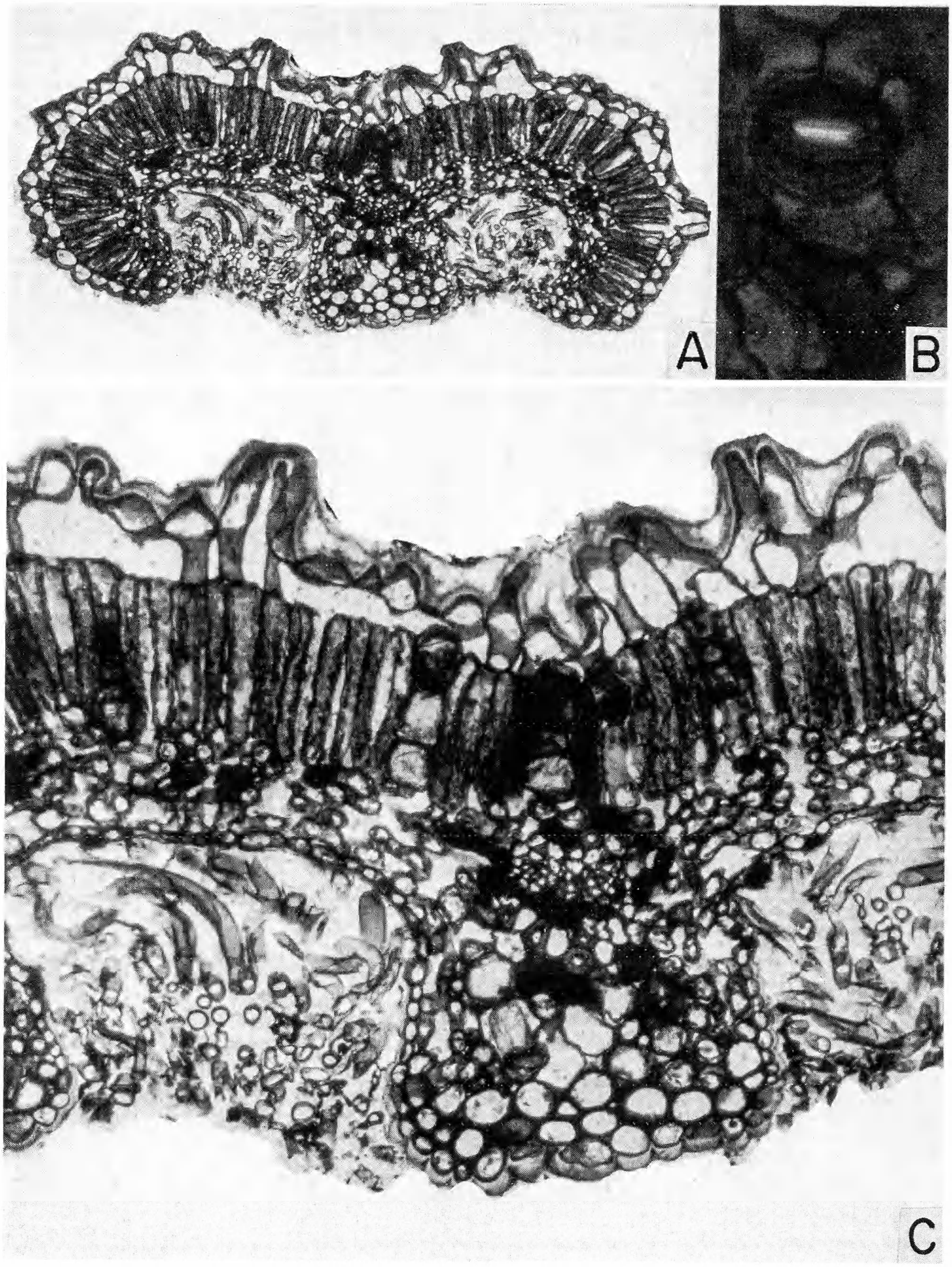


Fig. 2. *Grubbia rourkei,* Carlquist 5115, leaf sections. – A: TS of entire lamina, showing markedly recurved margins. – B: Stoma and adjacent epidermal cells, from paradermal section. – C: TS, central portion of lamina, showing midrib. – A, magnification as in Fig. 1 A. B, magnification as in Fig. 3 C. C, magnification as in Fig. 1 C.

on the abaxial surface are wide, but narrower than those in *G. tomentosa*. They are markedly widened or vesicular from a peg-like base inserted in the epidermis, then gradually tapered to the tip.

Grubbia tomentosa (Figs. 3, 4 A, B). Numerous veins present in the lamina, which is wider than that in other species (Fig. 4 A, B). Midvein much larger than other veins (Fig. 3 A). Midvein, if large, may have two portions (Fig. 3 A). The abaxial collateral bundle of the midvein is normal in orientation. The smaller adaxial bundle, perhaps derived from an adaxial meristem, is inverted in orientation. Fibers are present near xylem and phloem of major veins, and are moderately abundant. The midrib (Fig. 3 A) is well differentiated, and epidermal cells of the abaxial epidermis of the midrib bear thick walls like those of the adaxial epidermis. Leaf margins are recurved (Fig. 4 A, B), but the lamina is too broad for the formation of a distinct pocket or channel. Crystal-bearing cells occur in strands of two to four cells in the palisade (Fig. 4 B). Crystals in these cells are mostly rhomboidal, but a few simple druses, composed of two or several rhomboidal crystals, are present. Four or five spongy layers occur. Leaves studied had widths of 6.5 mm and 3.8 mm, respectively. The outer wall of the adaxial epidermal cells is cutinized, and no discrete cuticle overlying the wall proper is present. This wall is 32 μm and 21 μm thick in the two leaves mentioned, respectively. Trichomes are virtually absent on the adaxial surface. Cells of the adaxial epidermis are, in places, connected with the palisade by limited wall portions, but not by marked arm-like extensions as in *G. rourkei*. The trichomes on the abaxial epidermis are wide, moderately thick-walled, and moderately dense. The trichomes have a narrow peg-like base (Fig. 3 B), inserted into the epidermis, above which the trichome flares, then tapers gradually toward its apex.

Petiole

Petioles of the three species of *Grubbia* conform to the same basic vascular plan. Three traces (a midvein and two laterals) occur almost the length of the petiole. In the upper portion of the petiole, the three fuse just prior to departure of the first secondaries. Ground tissue of petioles contains idioblastic crystal-bearing cells: druses in *G. rosmarinifolia;* less complex druses and solitary rhomboidal crystals in *G. rourkei;* solitary rhomboidal crystals in *G. tomentosa*. The midvein in petioles of *G. rourkei* and *G. tomentosa* is hemiamphicribral. This conformation extends in the midvein where lamina is present, as in *G. tomentosa,* Fig. 3 A. The epidermal cells in all species of *Grubbia* are firmly adherent to the cells of the petiolar ground tissue, which are circular in transection. This contrasts with the adaxial leaf epidermis in *G. tomentosa* and especially *G. rourkei*. Epidermal cells in petioles are, for each species, very like those illustrated for the lamina in these respective species. There are no separations between the cuticle and epidermal cells in petioles, nor is there any chlorenchyma.

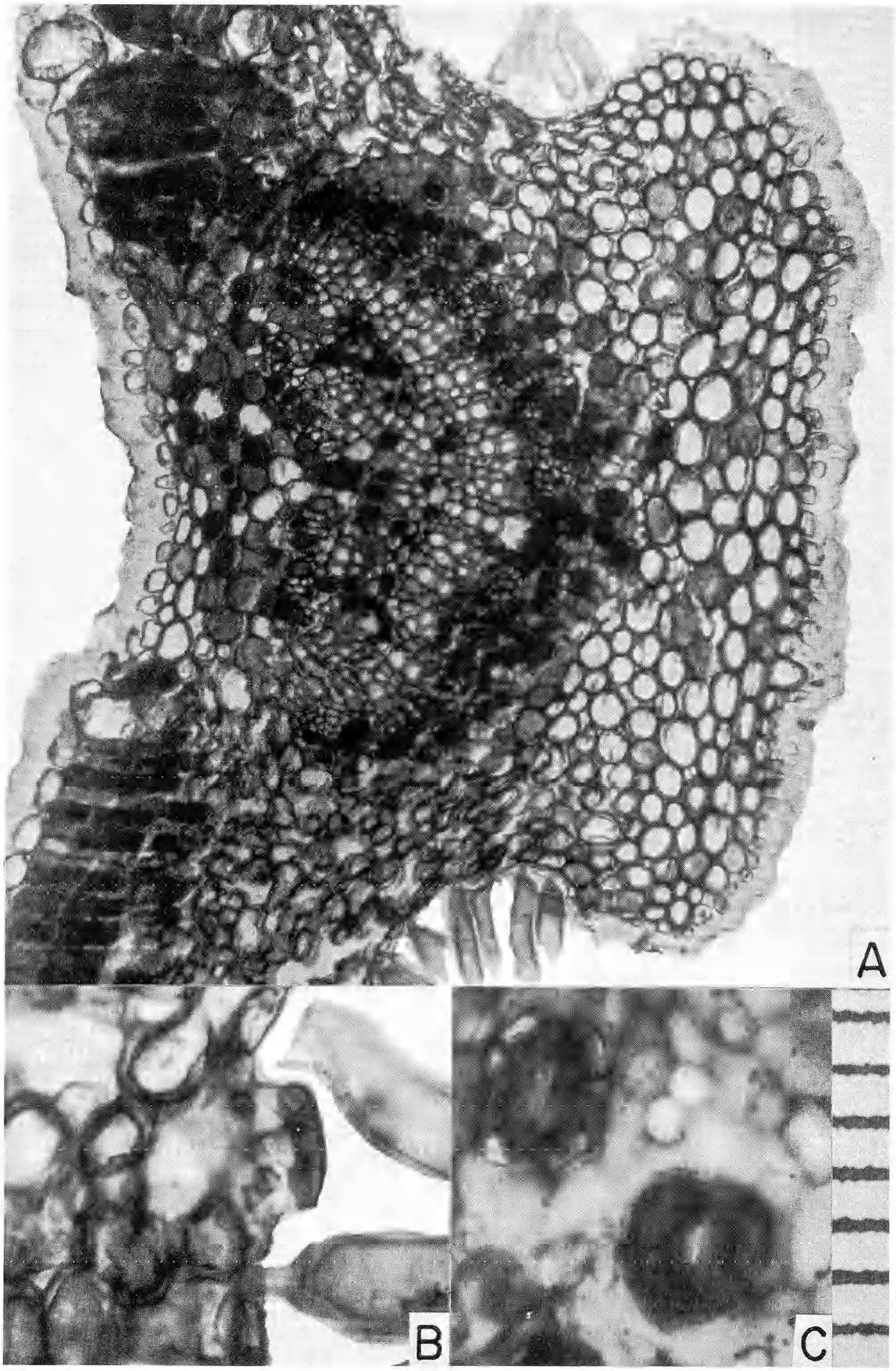
Node

All three species of *Grubbia* have trilacunar nodes. The laterals traverse the sheath formed by the petiolar bases (see Carlquist 1977 a). Leaves are opposite in all species of *Grubbia*. The adjacent laterals join below the node, a familiar pattern in trilacunar nodes with opposite leaves. Thus four vein departures occur at each node: two supplying midveins; two supplying, by branching as one follows them upward, the four lateral veins in the two petioles.

Stem

Solereder (1908) claimed a difference between hypodermis and cortical cells in *G. rosmarinifolia,* but no such cortical differentiation in stems of *G. tomentosa*. My material showed a tannin-filled hypodermis, consisting of relatively

Fig. 3. *Grubbia tomentosa,* Carlquist 5010, leaf sections. – A: TS of midrib region, adaxial face to the left. – B: TS of lamina portion, showing raised guard cells and amphora-shaped bases of trichomes. – C: Stomata and adjacent epidermal cells, from a paradermal section. – A, magnification as in Fig. 1 C. B, C, scale to the right of C (divisions 10 μm).


A
B
C

small, thin-walled cells, in *G. rosmarinifolia* and in *G. rourkei*. Epidermal cells of stems in these species also were filled with tannins. The stems of *G. tomentosa* showed no hypodermal differentiation. Solereder (1908) also claimed presence of separate strands of "pericyclic" fibers in stems of *G. rosmarinifolia*, but presence of a continuous sheath of fibers in stems of *G. tomentosa*. My material showed a discontinuous sheath of fibers in stems of all three species. The alleged contrast could probably be obtained by selection of stems from these three species, however, for some sections show large gaps, some show small gaps in the fiber sheath in any of the species. As noted by Solereder, pith cells have moderately thick lignified walls. The cells are circular in outline, with relatively angular intercellular spaces. Tannins are abundant in some pith cells. Scattered cortical cells contain druses in *G. rosmarinifolia*, solitary rhomboidal crystals in *G. rourkei* and *G. tomentosa*. The cuticle thickness and trichome characteristics described for leaves of the three species apply to the epidermis of stems also (epidermal cells like those of adaxial leaf epidermis, trichomes like those of abaxial leaf epidermis).

Systematic correlations within Grubbiaceae

Foliar anatomy corresponds closely to the system I proposed earlier for Grubbiaceae (Carlquist 1977 a). The division between the two sections is validated. One cannot say that there are any anatomical structures present in *G. rosmarinifolia*, type species of the genus, which are not also present in the two species of section *Strobilocarpus*, *G. rourkei* and *G. tomentosa*. Rather, there are differences in expression of characters (e.g., thick-walled trichomes vs. thin-walled trichomes). This situation does not suggest that two genera should be recognized.

Leaf anatomy of *G. rourkei* places it close to *G. tomentosa*, but with some notable differences. The narrower leaves of *G. rourkei* form pockets on the abaxial surface, corresponding to the *Erica*-like leaf form, much more clearly than do the broader leaves of *G. tomentosa*. These pockets can function in forming zones for attenuating the gradient of humidity from transpiring leaf surfaces to the open air. Attenuation of this gradient is indeed suggested by the dense felt of trichomes, a denser accumulation than in other species of *Grubbia*. The trichomes are thinner walled than those of *G. tomentosa* and not lignified. The adaxial epidermis of *G. rourkei* is connected to the subtending palisade by armlike connections of the epidermal cells. These connections are much more differentiated than in *G. tomentosa*, where the epidermal cells may have limited interfaces with palisade cells, but no attenuations into arms. The outer wall of epidermal cells in *G. rourkei* is differentiated into a cuticle, loose from the epidermal wall it overlies. Spaces between the cuticle and wall accumulate varnish-like materials. In *G. tomentosa*, the epidermal wall is cutinized, but no differentiation into a wall proper and overlying cuticle occurs.

Leaves of *G. rosmarinifolia* differ from those of *G. tomentosa* by possessing the following features: midrib not differentiated; crystals in palisade are druses rather than solitary rhomboidal crystals; cells of the adaxial epidermis with moderately thin cell wall and cuticle, cells papillate; trichomes on abaxial leaf surface slender, thick-walled, not widening out markedly from the narrow base, curved rather than straight; usually three, rather than four or five, spongy layers present.

The three subspecies of *G. rosmarinifolia* may be differentiated by virtue of foliar anatomy. Leaves of *G. rosmarinifolia* subsp. *gracilis* lack marked recurvature of margins and have only about seven veins, as seen in transection. Leaves of *G. rosmarinifolia* subsp. *hirsuta* have numerous straight hairs, which have thick non-lignified walls, on the adaxial surface. Leaves of *G. rosmarinifolia* subsp. *rosmarinifolia* have recurved margins, numerous veins as seen in transection, and, on the adaxial surface of the leaf, very sparse, short, straight, non-glandular trichomes. Papillate shape of adaxial epidermal cells is related to the fact that these cells may bear hairs in *G. rosmarinifolia* subsp. *rosmarinifolia*. Within this subspecies, var. *pinifolia* tends to have fewer trichomes on the adaxial surface and accordingly few papillate epidermal cells.

Systematic position of Grubbiaceae

Solereder (1908) has refuted, on anatomical bases, the classical idea that Grubbiaceae should be allied to Santalaceae. Nevertheless, that idea

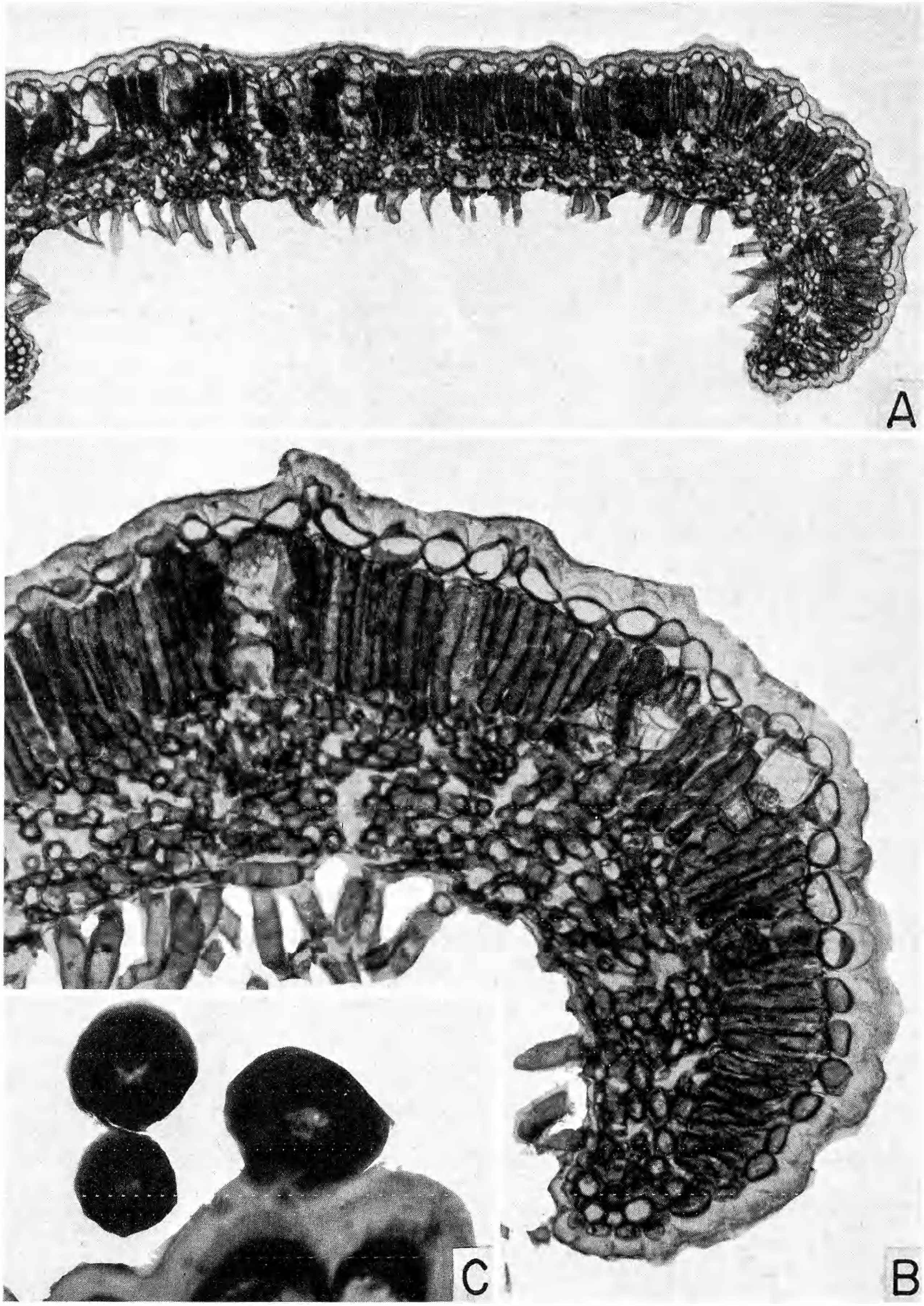


Fig. 4. *Grubbia,* leaf sections. – A, B: *G. tomentosa,* Carlquist 5010. – A: Lamina, margin at right, midrib portion at extreme left. – B: Margin region enlarged; rhomboidal crystals visible in large cells of palisade region. – C: *G. rosmarinifolia* subsp. *hirsuta,* Compton 20986. Portion of adaxial epidermis from TS of leaf. Hispid trichomes show as dark circles. – A, magnification as in Fig. 1 A. B, magnification as in Fig. 1 C. C, magnification as in Fig. 3 C.

still persists (see Carlquist 1977 b for a resumé). The idea that Grubbiaceae have affinities with Ericaceae, offered by Fagerlind (1948), does not seem strongly supported at present. For example, Ericaceae have unilacunar nodes, whereas those of Grubbiaceae are trilacunar. One characteristic does not decide the relationship of a family of dicotyledons, however. The most viable proposition appears to be the rosoid position suggested in a general way by Van Tieghem (1897), and in more specific ways by such recent authors as Thorne (1968, 1976). Such "rosoid" families as Pittosporaceae, Escalloniaceae, and Grossulariaceae agree with Grubbiaceae in such vegetative features as trilacunar nodes, the occurrence of crystals in leaves, and the presence of non-glandular trichomes on leaves. The literature on phylogenetic placement of Grubbiaceae has been reviewed earlier (Carlquist 1977 b). Before more secure concepts can be presented, data from floral anatomy, ovule morphology, embryology, seed anatomy, and pollen structure must be studied.

Ecological implications of leaf anatomy

The *Erica*-like leaf in *Grubbia* is an adaptation to xeromorphy according to Marloth (1913). Marloth mentions that relative humidity can fall as low as 25% in *Grubbia* localities, thereby providing a reason for foliar xeromorphy in plants which grow in wet soils, as does *Grubbia rosmarinifolia* typically. A drop in relative humidity is probably less important per se than the winds which occur so markedly in montane Cape Province. In the above account, the term "ericoid" is deliberately avoided. A mystique has developed concerning the definition of "ericoid" leaves. These definitions may be regarded as a mystique because particular morphological criteria are used as a source of definition, not the function of the ericoid leaves. Thus, leaves with somewhat different morphology but essentially the same general shape and function may be regarded as "ericoid" or "non-ericoid" under that scheme. The term "*Erica*-like" is used above to denote a foliar structure which has the effect of (1) condensation in size and shape to achieve lowered transpiration; (2) comparatively dense chlorenchyma appropriate to sunny localities with low soil moisture, low humidity, or both, for periods of various duration; (3) attenuation of a moisture gradient from the stomatal-bearing surface of leaf to the exterior, through pockets, hairs, or other devices. *Erica*-like may be used to connote one morphological feature, a tendency toward a linear shape. Wider leaves might be expected, if they grow in the same type of environment, to have some compensatory features. Within the genus *Grubbia,* there is a very rough correlation, subject to exceptions. The leaves of *G. tomentosa* are wider than those of other species, but their epidermal walls are very thick; there is no cuticle, but the entire thickness of the wall is cutinized.

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Embryology of Cyrilla and Cliftonia (Cyrillaceae)

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In both *Cyrilla racemiflora* L. and *Cliftonia monophylla* (Lam.) Britton ex Sarg. the anthers are tetrasporangiate. In *C. racemiflora* ontogeny of the anther wall conforms to the Dicotyledonous type. The anther wall of *C. racemiflora* is 4-layered and that of *C. monophylla* 4- or 5-layered. Tapetum is secretory, with initially uninucleate cells, which later become binucleate. The microspore tetrads are tetrahedral. The pollen grains are shed at the 2-celled stage. The ovules are anatropous, unitegmic and tenuinucellate. The inner epidermis of the integument differentiates into an endothelium. Embryo sac development is of the Polygonum type. In *C. racemiflora* the organised embryo sac possesses a broad micropylar and a narrow chalazal end, whereas in *C. monophylla* it is long and narrow. Functionless, aposporic embryo sacs are present in *C. monophylla*. The endosperm is cellular. Its first two divisions are transverse, forming a row of 4 cells. Both micropylar and chalazal endosperm haustoria are present. These are one-celled and binucleate. The zygote elongates considerably before undergoing division. The seed lacks a seed coat at maturity. On the basis of these embryological characters Cyrillaceae should be placed in Ericales and not in Celastrales.

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In Cyrillaceae there are 3 genera and 14 species (Melchior 1964), all of which are deciduous or evergreen small trees, distributed along the coastal plain of the SE United States, Central America and N South America (Thomas 1961).

Perusal of the literature suggests that no detailed embryological work has been carried out on this family (see Davis 1966). Copeland (1953) briefly dealt with the structure of the seed of Cyrillaceae. Vijayaraghavan (1969) described the male and female gametophytes of *Cliftonia monophylla*. No information exists about the development of the anther wall, endosperm, seed coat or pericarp.

The taxonomic position of this family is in dispute. Gundersen (1950), Hutchinson (1959) and Melchior (1964) placed Cyrillaceae in the order Celastrales, whereas Cronquist (1968) and Takhtajan (1969) included it in the order Ericales (see also Willis 1973).

The present investigation was therefore undertaken to study the embryology of *Cyrilla racemiflora* L. and *Cliftonia monophylla* (Lam.) Britton ex Sarg. Both genera are monotypic. The systematic position of the family Cyrillaceae is discussed on the basis of embryological characters.

Material and methods

Buds, flowers and fruits of *Cyrilla racemiflora* and *Cliftonia monophylla* were obtained through the courtesy of Dr R. M. Jefferson, Dept. of Agriculture, Washington, D.C., USA and Dr K. L. Webb, Marine Institute, University of Georgia, Georgia, USA. Formalin-acetic acid-alcohol (1:1:19) was used as fixative and the material was stored in 70 % ethanol. The material was dehydrated and cleared in alcohol-xylene or tertiary butyl alcohol series and embedded in paraffin wax (melting point 58–60°C). To facilitate dehydration and infiltration, the sides of fruits were trimmed beforehand. The embedded fruits were partially exposed, by trimming the blocks, and then soaked, either in water for 2 days or in modified Gifford's (1950) solution for 3 or 4 days. Sections (8–16 μm)

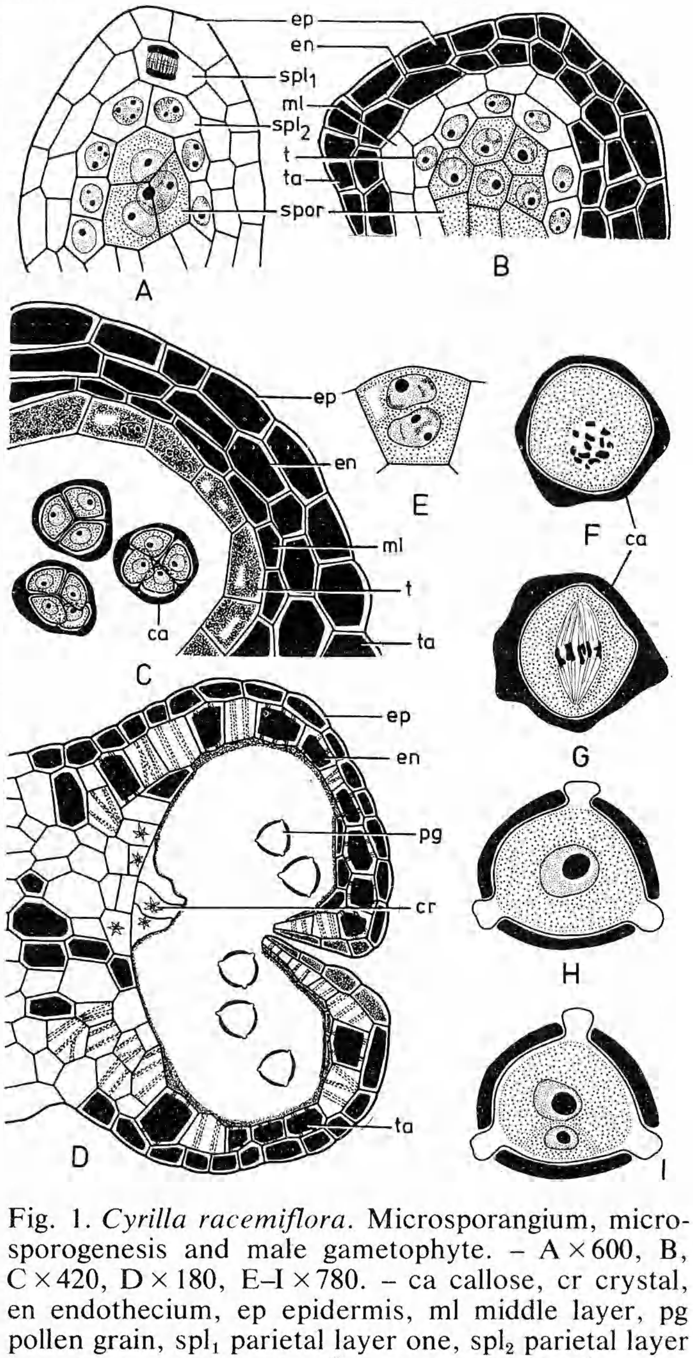

Fig. 1. *Cyrilla racemiflora.* Microsporangium, microsporogenesis and male gametophyte. – A × 600, B, C × 420, D × 180, E–I × 780. – ca callose, cr crystal, en endothecium, ep epidermis, ml middle layer, pg pollen grain, spl$_1$ parietal layer one, spl$_2$ parietal layer two, spor sporogenous cell, t tapetum, ta tannin.

were cut and stained with safranin and fast green. Callose and tannins were localised by the methods of Eschrich & Currier (1964) and Reeve (1951), respectively.

Cyrilla racemiflora

Microsporangium, microsporogenesis and male gametophyte

The anthers are tetrasporangiate. A TS of the youngest anther available shows a mass of sporogenous cells surrounded by an epidermal and two secondary parietal layers, spl$_1$ and spl$_2$ (Fig. 1 A). The outer parietal layer (spl$_1$) divides periclinally (Fig. 1 A) to form two further layers, of which the outer develops into the endothecium and the inner forms the middle layer. The inner parietal layer (spl$_2$) matures directly into the tapetum. The number of wall layers increases no further (Fig. 1 B). Anther wall development thus conforms to the Dicotyledonous type (Davis 1966).

The epidermal and endothecial cells are full of tannin (Fig. 1 B, C). The tapetal cells are initially uninucleate, becoming binucleate (Fig. 1 E) at the microspore mother cell stage. At the microspore tetrad stage, the tanniniferous middle layer becomes compressed and the tapetum starts to degenerate (Fig. 1 C). Prior to dehiscence, the endothecial cells develop fibrous thickenings. A few cells of the connective also possess thickenings, tannin and druses (Fig. 1 D).

In the microspore mother cells cytokinesis is of the simultaneous type, resulting in the formation of tetrahedral tetrads (Fig. 1 C). Thick callose surrounds the meiocytes (Fig. 1 F, G) and persists up to the tetrad stage (Fig. 1 C). The pollen grains are tricolporate with a thick, smooth exine and thin intine (Fig. 1 H). Asymmetrical division of the microspore nucleus results in a small, lenticular generative cell and a large vegetative cell (Fig. 1 I). The pollen grains are shed at the 2-celled stage.

Megasporangium, megasporogensis and female gametophyte

Ovular primordia arise from the placenta as small protuberances. The integumentary initials appear at the archesporial cell stage. The mature ovule is anatropous, unitegmic and tenuinucellate, with a long and narrow micropyle. Druses, tannin-filled cells and stomata are visible in the funiculus. At about the megaspore tetrad stage, the cells of the inner epidermis of the integument become radially elongated and form the endothelium.

One of the hypodermal cells enlarges, becomes more conspicuous than the surrounding cells due to its denser cytoplasm and more prominent nucleus, and acts as the archesporial cell (Fig. 2 A). In one preparation two archesporial cells were observed (Fig. 2 B). The archesporial cell functions directly as the megaspore mother cell

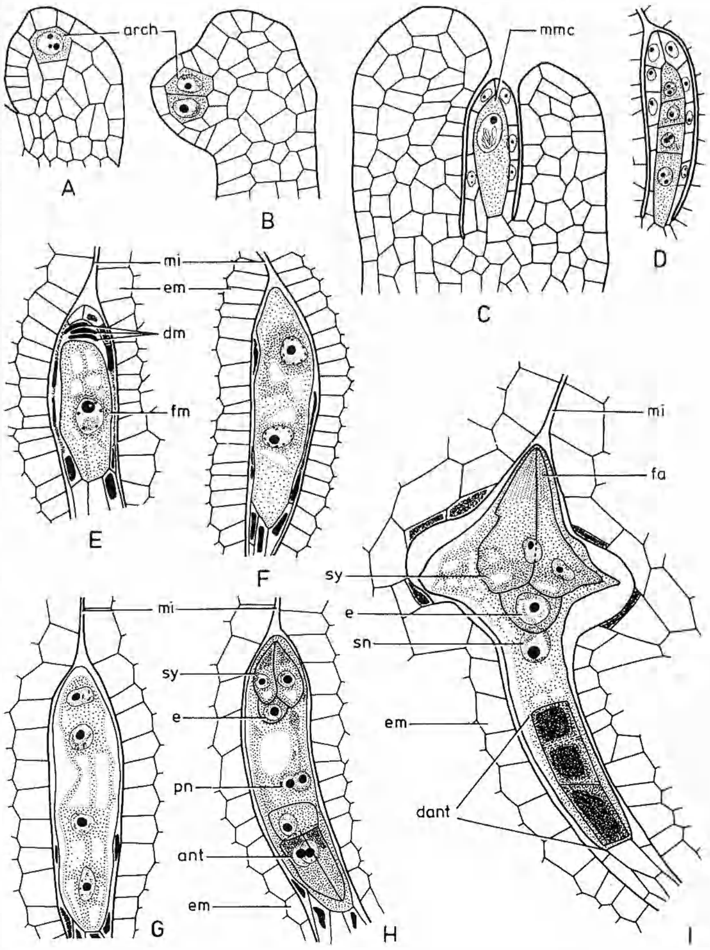

Fig. 2. *Cyrilla racemiflora*. Megasporogenesis and female gametophyte. – All × 360. – ant antipodal cell, arch archesporial cell, dant degenerated antipodal cell, dm degenerated megaspore, e egg, em endothelium, fa filiform apparatus, fm functional megaspore, mi micropyle, mmc megaspore mother cell, pn polar nucleus, sn secondary nucleus, sy synergid.

(Fig. 2 C), which enlarges and undergoes meiosis, resulting in the formation of a linear tetrad of megaspores (Fig. 2 D). In a tetrad, the chalazal megaspore is functional, while the nonfunctional megaspores degenerate (Fig. 2 E). The functional megaspore elongates, its cytoplasm becomes vacuolate and its nucleus undergoes three successive divisions to form an 8-nucleate gametophyte of the Polygonum type (Fig. 2 F–H).

In an organised embryo sac there are one egg, 2 synergids, 2 polar nuclei and 3 antipodal cells (Fig. 2 H). The mature embryo sac has a broad micropylar end and a narrow chalazal end (Fig. 2 I). The synergids show hooks and a prominent filiform apparatus (Fig. 2 I). Degeneration of the egg apparatus is very common. The polar nuclei are equal in size. They fuse to form the secondary nucleus, which lies close to the egg (Fig. 2 I).

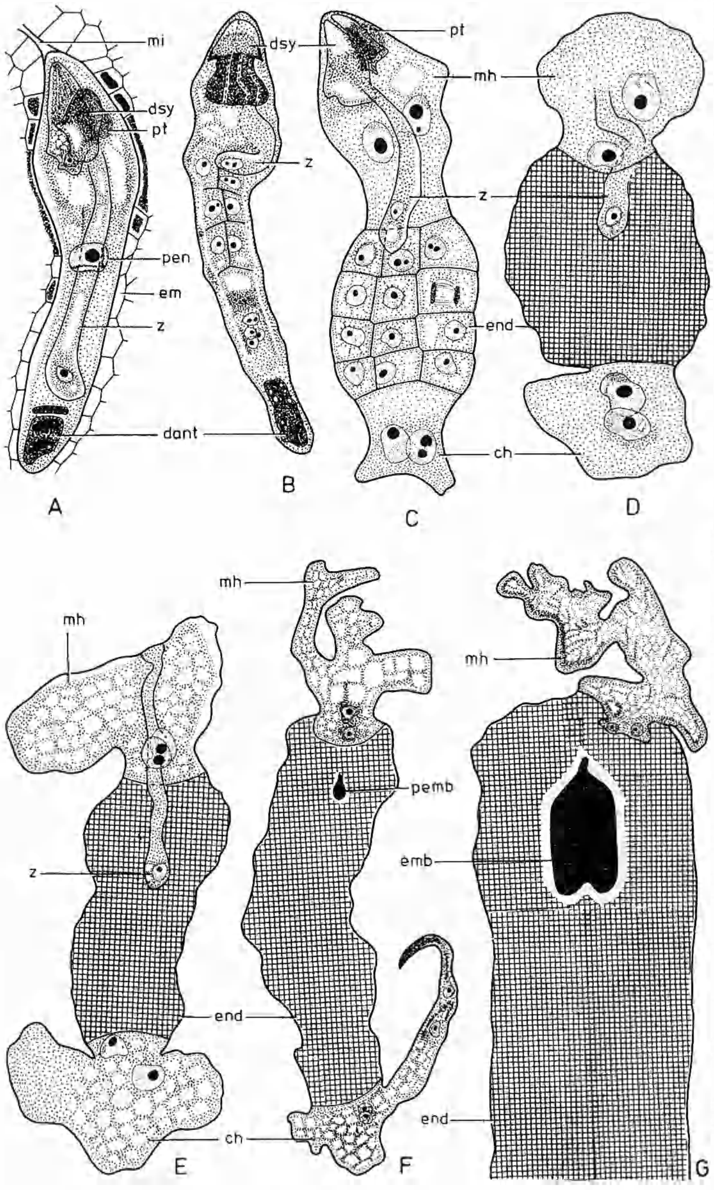

Fig. 3. *Cyrilla racemiflora*. Endosperm development. – A–C × 225, D–G × 190. – ch chalazal haustorium, dant degenerated antipodal cell, dsy degenerated synergid, em endothelium, emb embryo, end endosperm, mh micropylar haustorium, mi micropyle, pemb proembryo, pen primary endosperm nucleus, pt pollen tube, z zygote.

The large, uninucleate antipodal cells are arranged in either a linear or a T-shaped manner and degenerate after fertilization.

Endosperm and embryo development

The primary endosperm nucleus lies in the narrow central part of the embryo sac (Fig. 3 A). In one preparation a 7-celled endosperm was observed, with a pair of cells at the micropylar end, 2 tiers of small cells in the middle and a large cell towards the chalazal end (Fig. 3 B).

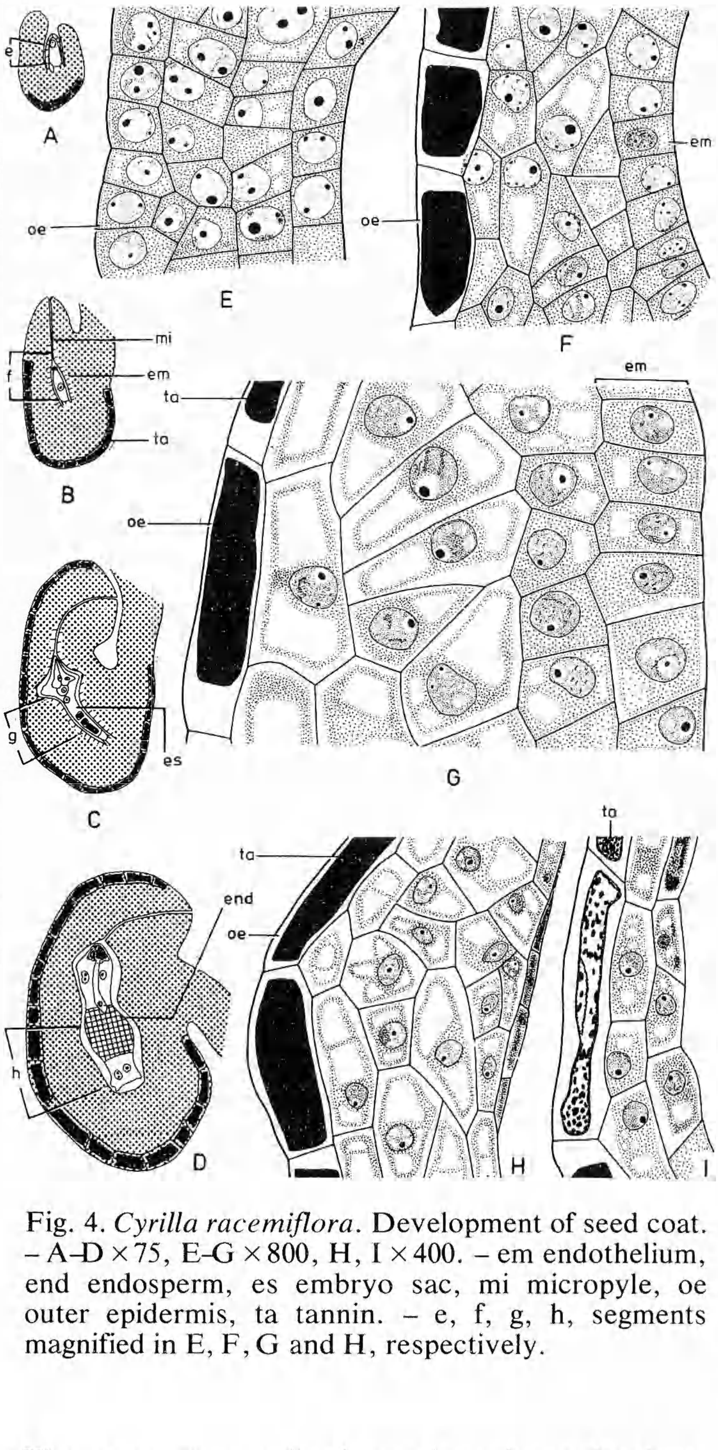

Fig. 4. *Cyrilla racemiflora*. Development of seed coat. – A–D ×75, E–G ×800, H, I ×400. – em endothelium, end endosperm, es embryo sac, mi micropyle, oe outer epidermis, ta tannin. – e, f, g, h, segments magnified in E, F, G and H, respectively.

The upper two cells form the micropylar haustorium, the cells of the central tiers form the endosperm proper and the lowermost large cell develops into the chalazal haustorium. The endosperm is cellular. The micropylar haustorium is one-celled with 2, rarely 3 or 4, large nuclei (Fig. 3 C, D), and subsequently becomes vacuolated (Fig. 3 E, F). It is aggressive, branches profusely (Fig. 3 F, G) and penetrates into the funicular cells. It persists up to the dicotyledonous embryo stage (Fig. 3 G). The chalazal haustorium is also one-celled and usually binucleate (Fig. 3 C–E), rarely with 4 (Fig. 3 B, F) or 6 nuclei, and degenerates by the dicotyledonous embryo stage. In one preparation a tubular process of the haustorium was seen (Fig. 3 F).

The zygote elongates considerably before undergoing division. In one preparation it extended as far as the antipodal cells (Fig. 3 A). As degeneration of both eggs and zygotes was very common, embryogenesis could not be studied in detail. Two-celled globular and dicotyledonous embryos have been observed.

Seed coat

At the megaspore mother cell stage (Fig. 4 A) the integument consists of 4 layers of small, densely cytoplasmic parenchymatous cells (Fig. 4 E). A few of the outer epidermal cells lining the chalazal part of the ovule are tanniniferous (Fig. 4 A). At about the megaspore tetrad stage the integument becomes 5-layered. The inner epidermal cells elongate radially to form the endothelium (Fig. 4 F). The number of tanniniferous cells in the outer epidermis increases (Fig. 4 B). At the mature embryo sac stage (Fig. 4 C) the integument consists of 5 or 6 layers of cells. The endothelial cells increase in size; those lining the micropylar canal becoming larger than others. Most of the integumentary cells become vacuolated (Fig. 4G). In section of a young seed (Fig. 4 D) all the epidermal cells, except a few near the micropyle, were filled with tannin. The endothelium later degenerates (Fig. 4 H) and the adjacent cells become crushed (Fig. 4 I). At about the globular stage of the proembryo, only the tanniniferous outer epidermis is present and even this layer disintegrates finally. Mature seeds have no seed coat.

Pericarp

Prior to fertilization the ovary wall consists of a papillate outer epidermis, followed by 2 layers of small parenchymatous cells, 2 or 3 layers of large cells, a few of which are tanniniferous, 2 layers of small, crystal-containing, parenchymatous cells and the inner epidermis. Stomata are present in the septum. After fertilization the pericarp increases in thickness by 2 or 3 layers. Most of the cells become tanniniferous. The cells of the inner epidermis and of 1 or 2 of the adjacent layers become thick-walled and pitted.

At the dicotyledonous embryo stage pits were also observed in other cells of the pericarp.

Cliftonia monophylla

Microsporangium, microsporogenesis and male gametophyte

The anthers are tetrasporangiate. The young anther possesses a 4-layered wall, comprising epidermis, endothecium, middle layer and tapetum (Fig. 5 A). Sometimes the anther wall becomes 5-layered, due to periclinal division of the middle layer (Fig. 5 B). Initially the tapetal cells are uninucleate, but become binucleate at the microspore mother cell stage. The cells of the epidermis, endothecium and middle layers are tanniniferous (Fig. 5 B). At about the microspore tetrad stage the middle layers become compressed, while the endothecial and tapetal cells increase in size (Fig. 5 C). At the one-celled pollen grain stage the tapetum starts to degenerate (Fig. 5 D). Prior to dehiscence, the endothecium develops fibrous thickenings (Fig. 5 D). A few cells of the connective also possess such thickenings, tannin and druses.

In the microspore mother cells cytokinesis is of the simultaneous type, resulting in tetrahedral tetrads (Fig. 5 C). A thick callose layer surrounds the meiocytes (Fig. 5 E–H) and persists up to the tetrad stage. The pollen grains are densely cytoplasmic, tricolporate, with a thick, smooth exine and a thin intine (Fig. 5 I). Asymmetrical division of the microspore nucleus results in a small, lenticular generative cell and a large vegetative cell (Fig. 5 J). The pollen grains are shed at the 2-celled stage.

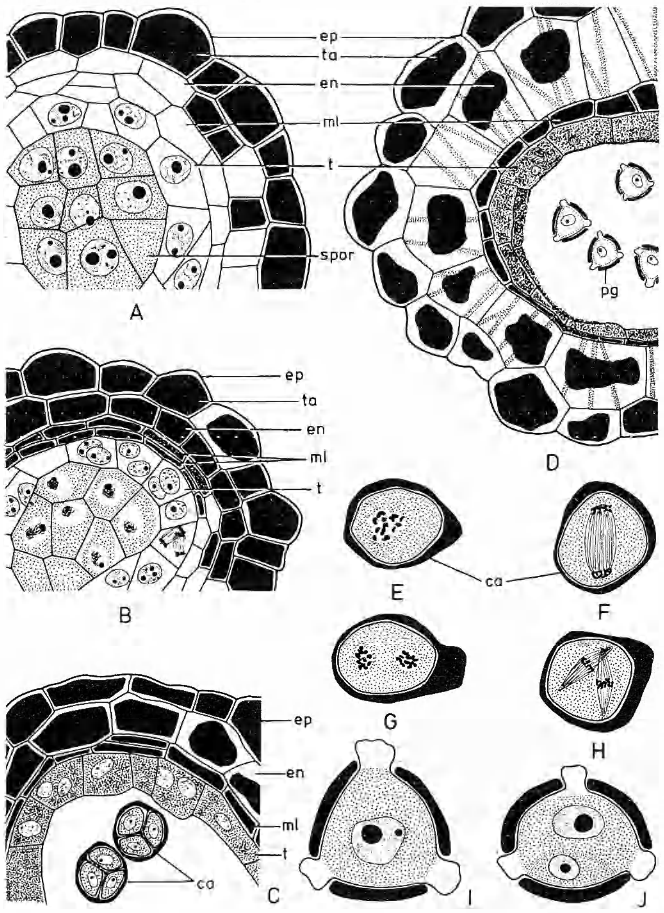

Fig. 5. *Cliftonia monophylla*. Microsporangium, microsporogenesis and male gametophyte. – A × 525, B, C × 360, D × 200, E–J × 720. – Abbreviations as in Fig. 1.

Megasporangium, megasporogenesis and female gametophyte

The ovule is anatropous, unitegmic and tenuinucellate, with a long micropyle. At the megaspore tetrad stage, the densely cytoplasmic cells of the inner epidermis of the integument elongate radially and form the endothelium. The endothelium consists of cells of various sizes.

The hypodermal archesporial cell functions directly as the megaspore mother cell (Fig. 6 A). It enlarges and undergoes meiotic division to form first a dyad (Fig. 6 B) and later a linear tetrad of megaspores (Fig. 6 C). The chalazal megaspore is functional, while the remaining non-functional megaspores degenerate (Fig. 6 D). The functional megaspore enlarges and its nucleus undergoes three successive divisions to form an 8-nucleate embryo sac of the Polygonum type (Fig. 6 E–G). Remnants of such degenerate megaspores were visible up to 4-nucleate stage of the embryo sac (Fig. 6 E). The mature embryo sac is long and narrow, containing an egg, 2 synergids, 2 polar nuclei and 3 antipodal cells (Fig. 6 G). The synergids possess hooks and a filiform apparatus (Fig. 6 H). The polar nuclei are equal-sized. The secondary nucleus lies in the central part of the embryo sac (Fig. 6 H). The uninucleate antipodal cells are arranged in either a T-shaped or ⊥-shaped manner and degenerate after fertilization.

Aposporous embryo sacs

At about the megaspore mother cell stage (Fig. 7 A), a few of the cells in the chalazal region of the

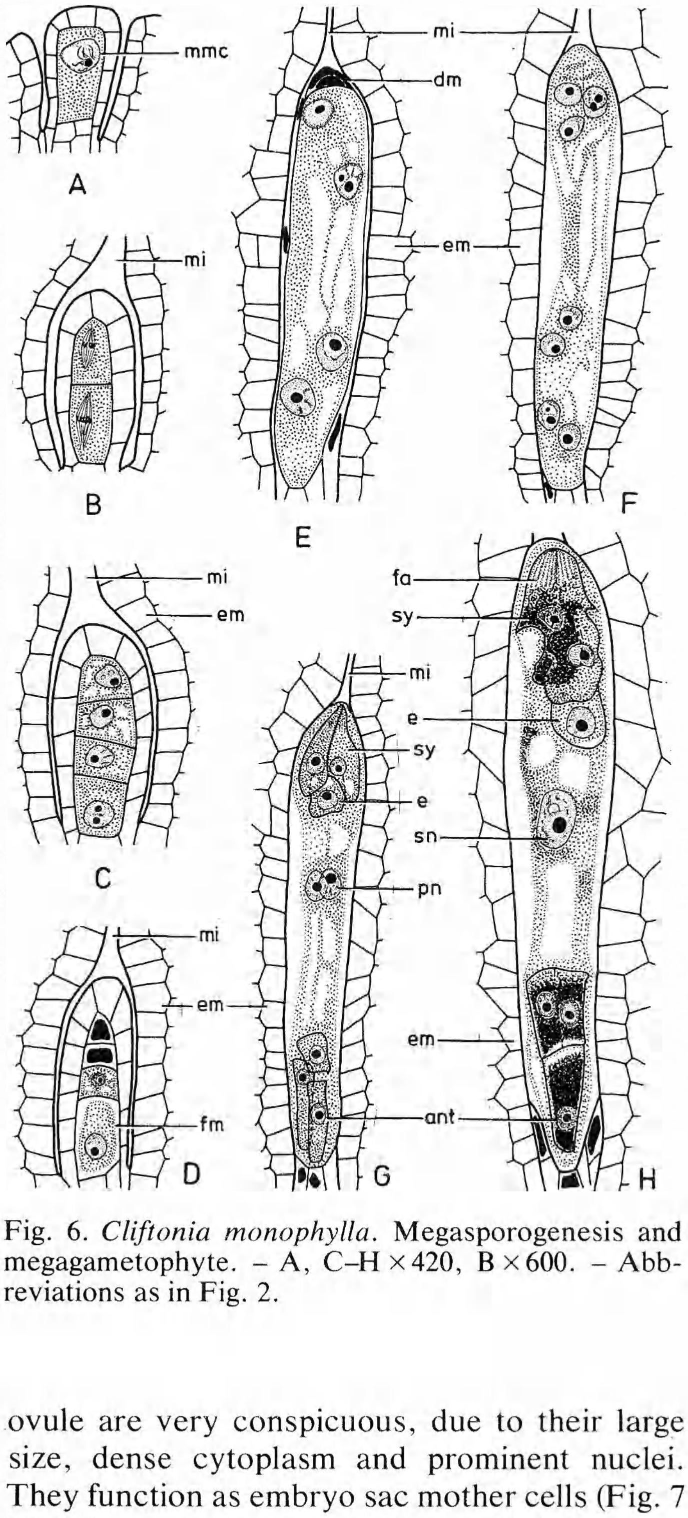

Fig. 6. *Cliftonia monophylla.* Megasporogenesis and megagametophyte. – A, C–H ×420, B ×600. – Abbreviations as in Fig. 2.

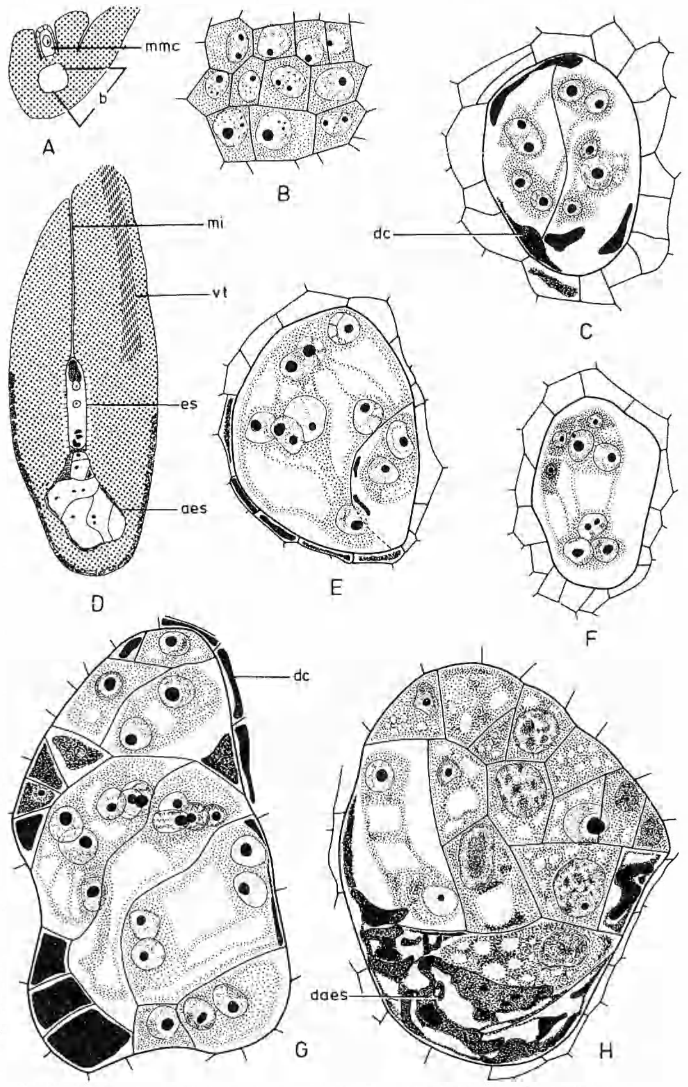

Fig. 7. *Cliftonia monophylla.* Aposporous embryo sacs. – A, D ×100, B, C, E–H ×460. – aes aposporous embryo sac, b segment enlarged in B, daes degenerated aposporous embryo sac, dc degenerated cell, es embryo sac, mi micropyle, mmc megaspore mother cell, vt vascular trace.

ovule are very conspicuous, due to their large size, dense cytoplasm and prominent nuclei. They function as embryo sac mother cells (Fig. 7 B). Subsequently, these cells may (1) degenerate in situ, without undergoing any changes (Fig. 7 H); (2) persist, without undergoing any change; (3) enlarge and become vacuolate, but their nuclei fail to divide and the cells finally degenerate; (4) enlarge, become vacuolate and form 2-, 4-, 6-, (Fig. 7 C, G) or 8-nucleate embryo sacs (Fig. 7 E).

The number of cells which divide to form aposporous embryo sacs varies. In some instances only one cell is functional, whereas in other cases 2 to 8 cells form embryo sacs (Fig. 7 G). Mitotic division is asynchronous in those cells which are destined to form aposporous embryo sacs. Co-existence of an 8-nucleate gametophyte with a 2- (Fig. 7 E) or 4-nucleate embryo sac in the same ovule was often observed. In a mature ovule a considerable part of the chalaza is occupied by these aposporous embryo sacs (Fig. 7 D). In one preparation an 8-nucleate gametophyte, with 3 nuclei at either pole (Fig. 7 F), was observed. The usual arrangement of the nuclei resembled that found in a normal embryo sac, although no walls were observed surrounding the nuclei. The aposporous embryo sacs degenerate during the course of endosperm development.

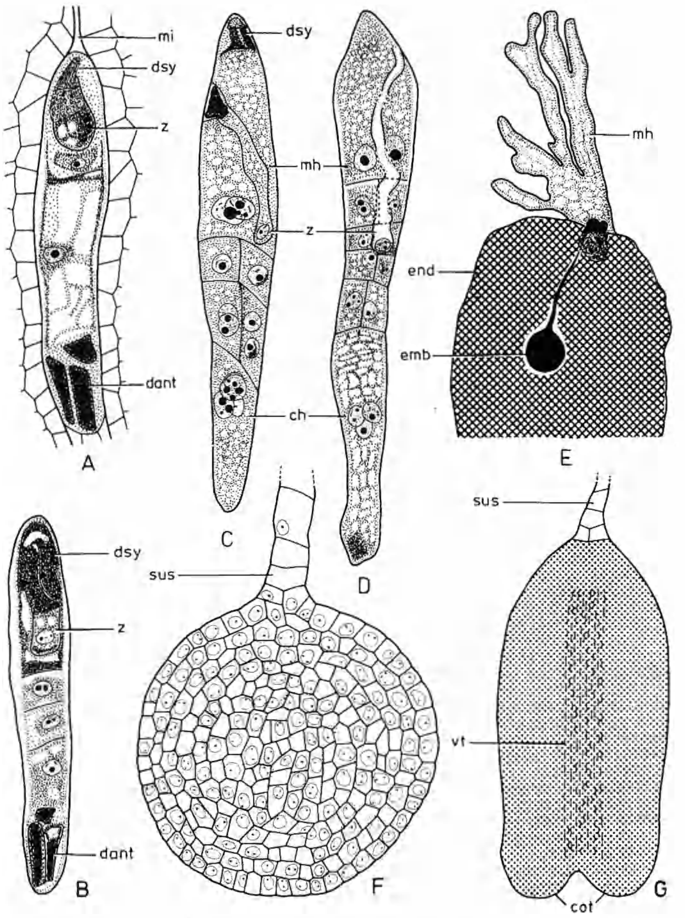

Fig. 8. *Cliftonia monophylla*. Endosperm and embryo development. – A × 360, B, C, F × 240, D × 190, E × 40, G × 100. – ch chalazal haustorium, cot cotyledons, dant degenerated antipodal cell, dsy degenerated synergid, emb embryo, end endosperm, mh micropylar haustorium, mi micropyle, sus suspensor, vt vascular trace, z zygote.

Endosperm and embryo development

The primary endosperm nucleus divides before that of the zygote. Nuclear division is transverse, resulting in the formation of a micropylar and a chalazal chamber (Fig. 8 A). In each chamber, the next division is transverse, yielding a row of 4 cells (Fig. 8 B). The two central cells then divide vertically and the endosperm becomes 6-celled (Fig. 8 C). The micropylar and chalazal cells enlarge, become binucleate and organised into the micropylar and chalazal haustoria, respectively. The cells of the two central tiers form the endosperm proper. The endosperm is cellular. Degenerate synergids were visible up to the 8-celled endosperm stage. The micropylar haustorium remains binucleate (Fig. 8 C–E), whereas the chalazal haustorium rarely becomes 3- (Fig. 8 D) or 4-nucleate (Fig. 8 C). The micropylar haustorium is aggressive, branches (Fig. 8 E) and penetrates into the funicular cells. At the dicotyledonous embryo stage, a strongly-vacuolated micropylar haustorium and the remnants of a chalazal haustorium were observed, although the nuclei of the former were degenerate.

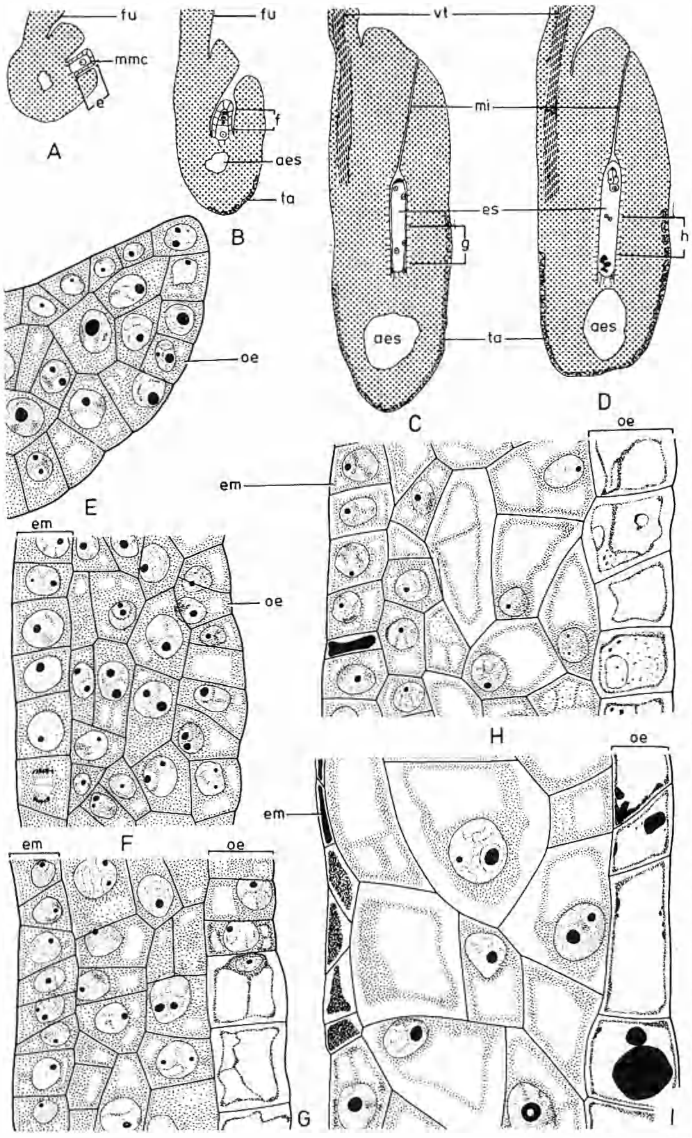

Fig. 9. *Cliftonia monophylla*. Development of seed coat. – A–D × 100, E–I × 740. – aes aposporous embryo sac, em endothelium, es embryo sac, fu funiculus, mi micropyle, mmc megaspore mother cell, oe outer epidermis, ta tannin, vt vascular trace. – e, f, g, h, segments magnified in E, F, G and H, respectively.

The zygote elongates considerably before undergoing division (Fig. 8 D). Degeneration of both egg and zygote was common and hence embryogenesis could not be studied in detail. Both globular (Fig. 8 F) and dicotyledonous (Fig. 8 G) embryos were observed.

Table 1. A comparison of embryological characteristics in Cyrillaceae and families of the orders Ericales and Celastrales. – Data obtained from Adatia & Gavde 1962, Ahluwalia 1962, Chou 1952, Copeland 1933, 1943, 1947, 1954, 1963, Creech 1955, Crété 1951, David 1938, Davis 1966, Doyel 1942, Ganapathy 1970, Ganapathy & Palser 1964, Herr 1959, 1961, Kavaljian 1952, Maheshwari 1950, Mauritzon 1936a, Narang 1953, Pacini 1969, Padmanabhan 1961, Palser 1952, Paterson 1961, Pyykkö 1968, Safijowska 1960, Samuelsson 1913, Stevens 1911, 1919, Veillet-Bartoszewska 1959, Yamazaki 1975.

Character	Cyrillaceae	Clethraceae	Epacridaceae	Ericaceae	Pyrolaceae
Endothecium	Fibrous	Fibrous	Not known	Not known	Not known
Tapetum	Secretory, binucleate	Secretory, binucleate	Not known	Secretory, binucleate	Secretory, binucleate
Druses in connective	Present	Present	Not known	Present	Not known
Microspore tetrads	Tetrahedral	Tetrahedral	Not known	Not known	Not known
Shedding stage of pollen	2-celled	2-celled	3-celled	2-celled	2-celled
Ovule	Unitegmic, tenuinucellate	Unitegmic, tenuinucellate	Unitegmic, tenuinucellate	Unitegmic, tenuinucellate	Unitegmic, tenuinucellate
Endothelium	Present	Present	Present	Present	Present
Embryo sac	Polygonum type with broad micropylar and narrow chalazal end	Polygonum type with broad micropylar and narrow chalazal end	Polygonum type with broad micropylar and narrow chalazal end	Polygonum type with broad micropylar and narrow chalazal end	Polygonum type with broad micropylar and narrow chalazal end
Antipodal cells	Uninucleate, persist after fertilization	Not known	Not known	Uninucleate, persist after fertilization	Uninucleate, persist after fertilization
Endosperm development	Cellular; first 2 divisions transverse, resulting in a linear, 4-celled endosperm	Cellular; first 2 divisions transverse, resulting in a linear, 4-celled endosperm	Cellular; first 2 divisions transverse, resulting in a linear, 4-celled endosperm	Cellular; first 2 divisions transverse, resulting in a linear, 4-celled endosperm	Cellular; first 2 divisions transverse, resulting in a linear, 4-celled endosperm
Endosperm haustoria	Both micropylar and chalazal	Both micropylar and chalazal	Both micropylar and chalazal	Both micropylar and chalazal	Both micropylar and chalazal
Seed coat	Absent	Only outer epidermis persists	Only outer epidermis persists	Only outer epidermis persists	Only outer epidermis persists

Seed coat

At the megaspore mother cell stage (Fig. 9 A), the integument consists of 3 or 4 layers of small, densely cytoplasmic, parenchymatous cells (Fig. 9 E). At the functional megaspore stage (Fig. 9 B) the integument becomes 5-layered (Fig. 9 F) and tannin accumulates in a few of the epidermal cells in the chalazal region of the ovule. The cells of the outer epidermis become vacuolated and the cells of the inner epidermis differentiate to form the endothelium (Fig. 9 F). At about the 4-nucleate (Fig. 9 C, G) and mature embryo sac stages (Fig. 9 H), tannin accumulation, in the form of granules, was further observed in cells of the outer epidermis. At the 10-celled stage of the endosperm, the endothelium degenerates (Fig. 9 I) and the epidermal cells situated towards the chalazal part of the ovule become completely tannin-filled. The other cells of the integument

Aquifoliaceae	Celastraceae	Hippocrateaceae	Icacinaceae	Salvadoraceae	Stackhousiaceae
Fibrous	Fibrous	Fibrous	Fibrous	Fibrous	Fibrous
Not known	Secretory, multinucleate	Secretory, multinucleate	Secretory, multinucleate	Not known	Secretory, binucleate
Not known	Not known	Not known	Not known	Not known	Not known
Not known	Tetrahedral and decussate	Tetrahedral and decussate	Tetrahedral	Tetrahedral and decussate	Tetrahedral, decussate and isobilateral
2-celled	2-celled	2-celled	2-celled	Not known	3-celled
Unitegmic, crassinucellate	Bitegmic, tenuinucellate or crassinucellate	Bitegmic, crassinucellate	Unitegmic, crassinucellate	Bitegmic, crassinucellate	Bitegmic, tenuinucellate
Present	Present	Present	Absent	Absent	Absent
Polygonum type	Polygonum type	Polygonum type	Polygonum type	Polygonum type	Polygonum type
Uninucleate, persist after fertilization	Uninucleate, ephemeral	Uninucleate, ephemeral	Uninucleate, ephemeral	Not known	Become 6–8-nucleate
Cellular; linear, 4-celled endosperm not formed	Nuclear	Nuclear	Nuclear	Nuclear	Nuclear
Absent	Absent	Absent	Absent	Absent	Absent
Massive	Massive	Massive	Massive	Massive	Massive

become strongly vacuolated and subsequently crushed. At the dicotyledonous stage of the embryo, no seed coat was observed.

Pericarp

Before fertilization, the ovary wall consists of a papillate outer epidermis, 4 or 5 layers of tannin-filled cells, 2 or 3 layers of small parenchymatous cells and lastly an inner epidermis. After fertilization, the pericarp becomes 13–15-layered. The outer epidermis is succeeded by 4 or 5 layers of narrowly elongate cells, which constitute the fruit wing; 4 or 5 layers of large and 2 or 3 layers of small parenchymatous cells and lastly an inner epidermis. Most of the cells are tanniniferous. Druses were also seen in a few cells.

Discussion

In *Cyrilla racemiflora* anther wall development conforms to the Dicotyledonous type (Davis 1966), the first reported instance for the family Cyrillaceae. Similarly, presence of druses in the connective in *Cyrilla racemiflora* and *Cliftonia monophylla* and of stomata on funiculus in *Cyrilla racemiflora* had not been previously observed. The embryo sac development of the two investigated taxa was of the Polygonum type (see also Vijayaraghavan 1969). Aposporous embryo sacs were observed in *Cliftonia monophylla,* thus confirming the earlier report of Vijayaraghavan (1969). In *Cliftonia monophylla* the formation of a linear, 4-celled endosperm, a characteristic of Ericales (Maheshwari 1950), is noteworthy. The micropylar and chalazal endospermal haustoria are one-celled and 2-nucleate in both taxa. Copeland (1953) reported 3 nuclei in the micropylar haustorium of *C. racemiflora.* In the present observations, *C. racemiflora* rarely exhibited a 3-nucleate micropylar haustorium. The structure of the seed coat and the pericarp has here been described for the first time in this family.

Systematic considerations

The family Cyrillaceae has been placed in either the orders Celastrales (Gundersen 1950, Hutchinson 1959, Melchior 1964) or Ericales (Cronquist 1968, Takhtajan 1969). The number of families that have formerly been included in these two orders has varied. Families usually included in the order Ericales are Clethraceae, Epacridaceae, Ericaceae and Pyrolaceae; those included in Celastrales are Aquifoliaceae, Celastraceae, Hippocrateaceae, Icacinaceae, Salvadoraceae and Stackhousiaceae. In Table 1, the embryological features shown by *Cyrilla racemiflora* and *Cliftonia monophylla* are compared with those shown by members of the above families. *Cyrilla racemiflora* and *Cliftonia monophylla* share the following characters with members of Clethraceae, Epacridaceae, Ericaceae and Pyrolaceae: (1) Secretory tapetum; (2) unitegmic, tenuinucellate ovules; (3) integumentary tapetum; (4) Polygonum type of embryo sac development; (5) mature embryo sac with a broad micropylar end and a narrow chalazal end; (6) Cellular endosperm – the first two divisions of which are transverse, resulting in a row of 4 cells; (7) formation of micropylar and chalazal endosperm haustoria and (8) elongation of the zygote.

Cyrillaceae further resemble Clethraceae in the following embryological features: (1) fibrous endothecium; (2) druses present in the cells of the connective; and (3) pollen grains not shed in tetrads.

Maheshwari (1950) listed 12 embryological features which he considered to be characteristic of Ericales: (1) absence of a fibrous layer in the anthers; (2) anther tapetum of glandular type, with multinucleate cells; (3) microspores remaining together in tetrads; (4) pollen grains two-celled; (5) unitegmic ovules with a thin nucellus, which soon disappears so that the embryo sac comes in direct contact with the integumentary tapetum; (6) absence of parietal cells in the ovule; (7) embryo sac monosporic and eight-nucleate, broad at the micropylar end and narrow at the chalazal end; (8) a fluted, hollow style, which connects the lumen of the ovary with the exterior and along which the pollen tubes make their way into the ovary; (9) endosperm cellular; the first two divisions transverse, giving rise to a row of four superposed cells; (10) formation of endosperm haustoria at both ends of the embryo sac, micropylar as well as chalazal; (11) a single-layered seed coat formed from the outermost layer of the integument, the remaining layers of which become re-absorbed during the growth of the endosperm and embryo; (12) seeds albuminous, with a fleshy endosperm and a straight embryo. Palser (1961) added a few further features, of which the more important were the presence of a single archesporial cell and considerable elongation of the zygote. Cyrillaceae show most of these characters except those relating to the microsporangium and the microspores. These latter differences, however, appear to be of minor importance, since Palser (1961) stated "that the embryology of the group is not quite as homogeneous as it was formerly thought to be."

Characters such as multinucleate tapetal cells, crassinucellate ovules, nuclear endosperm and a massive seed coat, all present in members of Celastrales, have never been observed in Cyrillaceae (present work, Copeland 1953, Vijayaraghavan 1969). Mauritzon (1936 b) believed the embryological features of Cyrillaceae to resemble those of Aquifoliaceae. This view was not confirmed by the present work. Cyrillaceae differ from Aquifoliaceae in quite a number of characters: (1) tenuinucellate ovules; (2) absence of a hypostase; (3) formation of a linear, 4-celled endosperm; (4) presence of endosperm haustoria and (5) lack of a seed coat.

Dahlgren (1975) also included Cyrillaceae in the Ericales, on the basis of morphological, anatomical, embryological, palynological, cytological and chemical characters. Erdtman (1952) remarked, "Pollen morphology does not, as it seems, speak against a relationship between Cyrillaceae and Ericales." Walker & Doyle (1975) also found that the pollen grains of Cyrillaceae are similar to those of some families in Ericales. The family Cyrillaceae should thus be placed near Clethraceae in the order Ericales.

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Zur Kenntnis der Gattung Rubus L. Sect. Rubus in Dänemark

Anfred Pedersen und Heinrich E. Weber

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A historical survey of the exploration of the Danish *Rubus* flora is given. Three new varieties are published: *R. atrichantherus* Krause var. *vestitior* Weber, *R. drejeri* G. Jens. var. *microphyllus* Pedersen & Weber and *R. insularis* Aresch. var. *parvifolius* O. Gel. ex Pedersen & Weber. Two new combinations are made: *R. ammobius* Focke var. *pseudoplicatus* (Frid. & Gel.) Weber and *R. sciocharis* Sudre var. *microphyllus* (Frid. & Gel.) Weber. Five native species, new to Denmark, are reported: *R. chlorothyrsos* Focke, *hypomalacus* Focke, *incurvatus* Bab. (previously known from the British Isles only), *integribasis* P. J. Muell. and *septentrionalis* Watson. What was previously called *R. rhombifolius* Weihe in Denmark belongs to an undescribed species of the *R. villicaulis* group. *R. bertramii* G. Br., *mucronulatus* Bor., *phyllothyrsus* K. Frid., *silvaticus* Weihe & Nees and *scheutzii* Lindeb. are also present in Denmark, although listed as doubtful or omitted from various floras and handbooks. Since 1922 the following species have been erroneously reported from Denmark: *R. amplificatus* Lees, *arduennensis* Lib. ex Lej., *atrocaulis* P. J. Muell., *babingtonii* Bell Salt., *bloxamii* Lees, *candicans* Weihe, *chaerophyllus* Sag. & Sch., *cruentatus* P. J. Muell., *fissus* Lindl., *flensburgensis* K. Frid., *foliosus* Weihe, *hartmanii* Gand., *hedycarpus* Focke, *leucostachys* Schl. ex Sm., *macrophyllus* Weihe & Nees, *nemoralis* P. J. Muell., *rhodanthus* Watson, *rhombifolius* Weihe, *schlechtendalii* Weihe ex Link and *serpens* Weihe. A list of the Danish *Rubus* sect. *Rubus* is given; 55 species in all, of which 5 are more or less naturalized garden escapes.

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Historischer Überblick

Johan Lange und seine Zeit (1851–1884)

Die Erforschung der Gattung *Rubus* in Dänemark begann mit Johan Lange im Jahre 1851. Damals erschien die 1. Auflage seines ,,Haandbog i den danske Flora'', in dem statt des üblichen ,,*Rubus fruticosus* L.'' bereits 12 verschiedene *Rubus*-Taxa der Sect. *Rubus* für Dänemark aufgeführt sind. Das war etwa ein Vierteljahrhundert nach der Veröffentlichung der umfangreichen Monographie der ,,Rubi Germanici'' (1822–27) von A. Weihe und C. G. Nees, in der mit 50 detailliert beschriebenen *Rubus*-Arten (nach heutiger Rangstufe) der Grundstein der europäischen *Rubus*-Forschung gelegt worden war. Die Batologie (*Rubus*-Forschung) war danach auch schon in einigen anderen Ländern in Gang gekommen, so in Schweden durch J. Arrhenius (1839), in Frankreich durch A. Godron (1843, 1848), in England durch C. Babington (1846).

In Dänemark identifizierte Lange (1851) 5 der hier vorkommenden Brombeeren korrekt mit den von Weihe & Nees behandelten Arten: *Rubus plicatus* Weihe & Nees, *R. vestitus* Weihe, *R. radula* Weihe, *R. sprengelii* Weihe und *R. bellardii* Weihe & Nees (≡*R. glandulosus* Bell.). Als neues Taxon veröffentlichte er zunächst nur provisorisch *Rubus sprengelii * arrhenii,* den er im August 1846 in der Marienhölzung bei Flensburg entdeckt hatte und den er dann als Art in der 2. Auflage seines Handbuches gültig publizierte (Lange 1859). Lange besass einen sicheren Blick für die Polymorphie der Brombeeren und beschrieb in der Folgezeit vor allem als Herausgeber der ,,Flora Danica'' eine Reihe weiterer *Rubi,* die später als zum Teil weitverbreitete europäische Arten auch in anderen Ländern entdeckt wurden. Dazu gehören *R. macrothyrsus* (1870, t. 2832; loc. typ. Viehburger Holz bei Kiel, leg. Lange, August 1845) und *R. sciaphilus* (1883, t. 3026), den Lange bereits 1867 im Teglværksskoven bei Nyborg auf Fünen entdeckte, aber zunächst (1879) aufgrund einer Bestimmung von W. O. Focke als Schattenform von *R. gratus* Focke angesehen hatte. Ausserdem nahm Lange in dieses Werk die ihm vom Autor zugesandte Originalbeschreibung des *Rubus drejeri* G. Jens. auf, eine Art, die der Apotheker G. Jensen (1818–86) bei seinem Heimatort Quern in Angeln 1867 gefunden hatte. Erwähnenswert ist ausserdem Vaupell (1863: 53–55), der in seinem Werke über die dänischen Wälder auch ausführlich auf die Rolle der dort vorkommenden Brombeeren einging. Allerdings beschränkte er sich auf die Mitteilung, dass an der Ostküste Süd-Jütlands und Schleswigs mehr als 20 verschiedene *Rubi* zu beobachten seien, ohne deren taxonomische Klärung weiter zu verfolgen.

Lange (1869) hatte zwar 1868 versucht, auf einer Sitzung der Dansk Botanisk Forening die Mitglieder für die Brombeerforschung zu interessieren, hatte damit jedoch keinen dauerhaften Erfolg. So blieb denn die Erkundung der *Rubus*-Flora Dänemarks zunächst im wesentlichen das Werk Langes. Diese erste Phase endete 1884 mit einer Übersicht in Botanisk Tidsskrift (Lange & Mortensen 1884). Hierin sind 21 Brombeerarten (Sect. *Rubus*) behandelt und bis auf einige Ausnahmen wie beispielsweise ,,*Rubus hirtus*'' (=*R. pallidus* Weihe), ,,*Rubus discolor*'' (=*R. lindebergii* P. J. Muell. und *R. insularis* Aresch.) und ,,*Rubus macrophyllus*'' (=*R. insularis*) durchwegs richtig erkannt.

K. Friderichsen und O. Gelert (1884–1899)

Im Jahre 1883 begannen als cand. pharm. K. Friderichsen (1853–1932) und O. Gelert (1862–1899) ihre Zusammenarbeit, der wir den wesentlichsten Beitrag zur Kenntnis der dänischen *Rubus*-Flora verdanken. Ihr Interesse war teils von J. Lange, teils von W. O. Focke, Bremen, angeregt worden. Focke hatte 1877 seine ,,Synopsis Ruborum Germaniae'' veröffentlicht und damit einen bedeutenden Anstoss zur Neubelebung der Batologie gegeben; er war auch die Autorität, dessen Entscheidung bei kritischen Bestimmungen den Ausschlag gab. Zur Dokumentation ihrer Artauffassungen und um neue Arten allgemein bekannt zu machen, gaben Friderichsen und Gelert unter der Bezeichnung ,,Rubi exsiccati Daniae et Slesvigiae'' von 1885 bis 1888 in drei Lieferungen ein insgesamt 101 Nummern umfassendes Exsikkatenwerk heraus. Als erste neue Art und gleichzeitig als Ausdruck der Freundschaft dieser beiden Batologen wurde *Rubus gelertii* von Friderichsen (1886) veröffentlicht. Ein Jahr später erschien dann ihr Hauptwerk ,,Danmarks og Slesvigs Rubi'', das bis heute die grundlegende Bearbeitung der dänischen Brombeerflora geblieben ist. Neben den *Rubi Corylifolii,* die Friderichsen allein bearbeitete, und die er zu einer Sammelart *R. milliformis* Frid. & Gel. zusammenzog, sind in dieser Arbeit 43 der sogenannten ,,guten *Rubus*-Arten'' (nach heutiger Rangstufe; Sect. *Rubus*) für das Gebiet aufgeführt, 30 davon für den Raum des heutigen Dänemark einschliesslich des hier verwilderten *R. laciniatus.* Es zeugt für die gründliche Arbeit, dass nur 5 Arten hierin falsch aufgefasst wurden, weil die Autoren den Typus der betreffenden Taxa nicht kannten, sondern sich vielmehr meist der allgemeinen Tradition der Benennung dieser Arten anschlossen. Das gilt für *Rubus ,,fissus''* (=*R. scissus*), *R. ,,dumosus''* (=*R. cardiophyllus*), *R. ,,rhombifolius''* (=*R. rhombiferus*), *R. ,,mucronulatus''* (=*R. atrichantherus*) und *R. ,,serpens''* (=*R. pallidifolius*). *Rubus ,,piletostachys''* (=*R. vestitus* var. *magnifolius* G. Jens. in sched. =*R. flexuosus*) wurde als zweifelhaft aufgeführt. *Rubus anglosaxonicus* O. Gel. (ein jüngeres Synonym zu *R. micans* Godron) und zwei von G. Jensen benannte Arten, *R. langei* und *R. monachus* (letzterer nur eine unbedeutende Lokal-Ausbildung aus Angeln), sind neu. Im Jahre 1888 lieferten Friderichsen & Gelert ein französisches Resumée ihrer Arbeit, dem *R. propexus* K. Frid. als neue Art (bei Kiel) beigefügt wurde. Ausserdem übernahmen die beiden Autoren die Bearbeitung der Gattung in der 4. Auflage des Handbuches von Lange (1888).

Trotz dieser hervorragenden Arbeiten fand die

Batologie in Dänemark kein breiteres Interesse. Vermutlich publizierten Friderichsen und Gelert auch deswegen alle ihre Ergebnisse zwischen 1890 und 1900 in deutschen Zeitschriften. Ausserdem lieferten sie 1889–1893 insgesamt 110 Nummern (1450 Bögen) für die Exsikkate der ,,Association rubologique'', die der französische Batologe N. Boulay herausgab, sowie 1894–1901 eine Reihe von Beiträgen für die ,,Rubi praesertim gallici exsiccati'' von Boulay & Bouly de Lesdain. Einige schleswigsche Arten und *R. phyllothyrsus* K. Frid., der später auch in Dänemark gefunden wurde, sind in diesen Sammlungen erstmals gültig publiziert. Vor allem das brombeerreiche Gebiet um Husum, das Anklänge an die britische *Rubus*-Flora hat, lieferte neue Entdeckungen.

K. Friderichsen in der Zeit von 1899–1932

Im Jahre 1899 starb Gelert im Alter von nur 37 Jahren. Er war einer der genauesten und zuverlässigsten *Rubus*-Kenner seiner Zeit. Friderichsen war danach in Dänemark allein mit seinem Wissen über die *Rubus*-Flora und war nun als Apotheker in den brombeerarmen Gegenden Nordjütlands tätig (Gudumholm, Kjellerup). Aus dieser Zeit stammen die Bearbeitungen der Gattung *Rubus* für die 3. und 4. Auflage der Flora von Dänemark von Raunkiær (1914, 1922). Der Schlüssel von 1922 ist der umfangreichste. Aber wenn man die Versuche anderer, damit Brombeeren zu bestimmen, betrachtet, scheint es so, als wäre er der einzige gewesen, der ihn verwenden konnte.

In der 4. Auflage der Flora von Raunkiær werden gegen Ende der zunächst von Friderichsen und Gelert, später von Friderichsen allein bestimmten Phase der dänischen *Rubus*-Forschung insgesamt 52 Arten (heutige Rangstufe) der Sect. *Rubus* als im heutigen Dänemark vorkommend angegeben (darunter 2 als verwilderte Kulturpflanzen). Davon sind 10 falsch gedeutet. Diese zahlreichen Irrtümer hatten vor allem zwei Gründe: Unbedeutende Lokalbildungen (meist ,,Individualarten'', vermutlich spontane Hybriden) wurden mit guten Arten identifiziert, die in ganz anderen Gebieten aufgestellt waren. Beispiele dafür sind etwa *R. ,,cruentatus''* und *R. ,,bloxamii''*. Mehr noch wirkte sich Friderichsens Tendenz aus, gut charakterisiert und bereits korrekt beschriebene Taxa mit älteren, angeblich synonymen Arten zusammenzuwerfen. So ersetzte er beispielsweise den Namen *R. langei* irrtümlich durch *R. atrocaulis* P. J. Muell., *R. marianus* findet sich unter der falschen Bezeichnung *R. chaerophyllus* Sag. & Sch., *R. vestitus* wird als *R. leucostachys* Schleicher geführt. Wenig glücklich fasste Friderichsen ausserdem völlig verschiedene Pflanzen als Subtaxa bestimmter Arten zusammen, ein Verfahren, das auch von anderen Batologen angewandt wurde und das bis heute viel Verwirrung gestiftet hat. So werden etwa *R. thyrsanthus* und *R. candicans* als Subtaxa von *R. arduennensis* geführt, *R. phyllothyrsus* und *R. flensburgensis* sind *R. babingtonii* zugeordnet und *R. dasyphyllus* erscheint als Varietät des tatsächlich völlig andersartigen *R. adornatus*.

Gegenüber dem Werk von 1887 sind in der Arbeit von Friderichsen (1922) noch die folgenden 14 Arten als in Dänemark vorkommend nachgewiesen: *R. affinis* Weihe & Nees, *R. bertramii* G. Br. (=*R. biformis* Boulay), *R. dasyphyllus* (Rogers) Marsh. (als *R. adornatus* P. J. Muell. var.), *R. flexuosus* P. J. Muell. (als *R. foliosus* Weihe), *R. fuscus* Weihe, *R. infestus* Weihe, *R. leptothyrsos* G. Br. (=*R. danicus* Focke), *R. macrothyrsus* Lange, *R. marianus* (Krause) Weber (als *R. chaerophyllus* Sag. & Sch.), *R. mucronulatus* Bor. (als *R. mucronatus* Blox. var.), *R. pallidifolius* Krause (als *R. serpens* Weihe), *R. phyllothyrsus* K. Frid. (als *R. babingtonii* Bell Salt. var.), *R. polyanthemus* Lindeb. und *R. silvaticus* Weihe & Nees.

Friderichsens umfangreiches *Rubus*-Herbarium befindet sich heute im Botanischen Museum in København (C) und ist von unschätzbarem Wert für das *Rubus*-Studium in Dänemark. Da Friderichsen sich von allen Batologen bislang auch am intensivsten mit den kritischen *Rubi Corylifolii* beschäftigt hat, ist es auch international von grossem Interesse. Bedeutend aus dieser Zeit sind auch die Sammlungen von N. Sørensen und A. Edmondt Andersen (C).

Die Zeit nach K. Friderichsen (seit 1932)

Nach dem Tode Friderichsens im Jahre 1932 kam das *Rubus*-Studium in Dänemark völlig zum Erliegen. In der 5. bis 7. Auflage der Flora von Raunkiær (1934, 1942, 1950) wird der Stand von 1922 nicht überschritten. Friderichsens detaillierte Behandlung der *Corylifolii* ist vielmehr aus Platzgründen gestrichen. Es war niemand in Dänemark vorhanden, der weitere Daten geliefert hätte. Allerdings wurden von J. Lindhard (AAU) und Valdemar Christensen (C) weiterhin in dieser Zeit Brombeeren gesammelt. Vor allem hat jedoch M. P. Christiansen, der ein guter *Rubus*-Kenner war, über fast 50 Jahre allmählich eine umfangreiche Sammlung zusammengetragen, die sich heute im C befindet.

Die *Rubus*-Flora Dänemarks wurde in dieser Zeit nur in einigen ausländischen Arbeiten mit berücksichtigt. So mit kritischer Revision von C. E. Gustafsson (1938) in seiner Arbeit über die skandinavischen *Rubi*. Derselbe Autor hatte bereits 1935 *Rubus kollundicola* als neue Art von Kollund in SO-Jütland beschrieben. Kanér (1941) berichtete über die Entdeckung von *Rubus scheutzii* Lindeb. in NO-Seeland. Hultén (1950) berücksichtigte bei seinen Verbreitungskarten auch Dänemark. Hylander (1955) nahm in seine Artenliste einige Korrekturen auf, die von Gustafsson (1938) herrühren, Oredsson (1969–70) wertete bei seinen Dänemark betreffenden Verbreitungsangaben lediglich die Daten aus Raunkiærs Flora und die Karten von Hultén aus. Vor allem durch Watson (1958) wurden die irrtümlichen Angaben von Friderichsen wieder im Umlauf gebracht und um weitere vermehrt. Diese Daten sind unter anderen später durch Huber (1961) in Hegi und durch Heslop-Harrison (1968) in die Flora Europaea übernommen worden und liefern ein nicht ganz zutreffendes Bild des tatsächlichen Artenbestandes in Dänemark.

In neuerer Zeit hat A. Hansen (1964) auf einige verwilderte *Rubi* in Dänemark hingewiesen. Hansen & Pedersen (1968) behandeln das Vorkommen von *Rubus laciniatus* Willd. in Dänemark, Weber (1971) publizierte einige Notizen zur *Rubus*-Flora Bornholms. Bei Weber (1972) sind alle bis dahin aus Dänemark bekannten *Rubus*-Arten ausführlich verschlüsselt und beschrieben sowie bis auf wenige Ausnahmen abgebildet.

Bemerkungen zu einzelnen Taxa

Im Gegensatz zu anderen Ländern ist die dänische *Rubus*-Flora nach den Arbeiten von Lange, Friderichsen und Gelert im wesentlichen richtig erfasst. Dennoch gibt es einige falsche Daten, die von der 4. Auflage von 1922 bis in die 7. Auflage von 1950 der Flora von Raunkiær tradiert wurden oder aufgrund einzelner Fehlinterpretationen von Focke (z.B. 1902–3, 1914) und von Watson (1958) zustandekamen. Die korrekte Zuordnung von *Rubus*-Vorkommen zwischen Nord- und Südschleswig wurde wohl auch zusätzlich wegen der 1920 erfolgten Grenzverschiebung zwischen Dänemark und Deutschland für Ausländer erschwert.

Die hier mitgeteilten Berichtigungen beziehen sich hauptsächlich auf taxonomische Umgrenzungen. Fehler, die durch falsche Synonymie-Auffassungen zustandegekommen sind, gehen ebenso wie das gültige Autorzitat aus der korrigierten Liste der dänischen *Rubus* Sect. *Rubus* im letzten Abschnitt hervor.

Hinsichtlich ihrer Gesamtverbreitung werden die einheimischen Arten (nach Weber 1977) in folgende Kategorien eingeteilt:

A. *Weitverbreitete Arten*. (Arealdurchmesser 500 km bis über 1000 km).
B. *Regionalarten*. (Arealdurchmesser 50–250 km).
C. *Lokalarten*. (Arealdurchmesser maximal 20 km).
D. *,,Individualarten''*. (Morphologisch isolierte, fertile Einzelsträucher oder vegetativ daraus entstandene Individualpopulationen, die z.B. eine Hecke oder ein Waldstück erfüllen können. Oft als ,,Arten'' beschrieben. Vermutlich hybridogenen Ursprungs).

Die hier behandelten Arten gehören bis auf die Lokalarten *R. contiguus* und *R. kollundicola* ausschliesslich zu den Kategorien A und B. ,,Individualarten'' sind nur dann diskutiert, wenn sie bereits als ,,species'' beschrieben sind (wie *R. flensburgensis*) oder in der Literatur mit anderen Arten identifiziert wurden. In Mittel- und Westeuropa gibt es Tausende solcher ,,Individualarten'', die sogar in einzelnen Gebieten einen grossen Teil der *Rubus*-Flora stellen können, und es wäre sinnlos, derartige Einzelbildungen (ebenso wie kleinräumig verbreitete Lokalarten) taxonomisch würdigen zu wollen. Sie spielen nur insofern eine Rolle, als dass sie häufig mit bereits beschriebenen anderen Arten verwechselt werden.

Rubus allegheniensis Porter

Belege: 11, davon 6 in Jütland, 5 auf Seeland (C et Herb. auct.).

Nordamerikanische Art, die in Dänemark gelegentlich gebaut wird und an einigen Stellen verwildert auftritt.

Rubus ammobius Focke var. **pseudoplicatus** (Frid. & Gel.) Weber comb. nov.

R. sulcatus Vest var. *pseudo-plicata* Friderichsen & Gelert, Bot. Tidsskrift 16: 58 (1887).

Differt a var. *ammobio* foliis supra laetius viridibus, subtus viridibus vix tomentosis, turione minus fusco. Crescit in Dania.

Lectotypus: Dänemark, Jylland, ,,in silva ad Haderslev'', 28.6. + 3.8.1886 K. Friderichsen Rubi Dan. et Slesv. exs. 31, als *R. sulcatus* Vest var. *pseudoplicata* Frid. & Gel. (C).

Belege: 12, alle in SO-Jütland (C et Herb. auct.).

Rubus ammobius, eine im nordwestlichen Mitteleuropa (West-Niedersachsen, Westfalen, Niederlande, Nord-Belgien) verbreitete und stellenweise häufige Art, hat ein disjunktes Areal im südlichen Jütland. Von hier wurde die Pflanze von Friderichsen & Gelert (1887) als *Rubus sulcatus* var. *pseudoplicatus* neu beschrieben. Später (in Raunkiær 1922) erkannte Friderichsen die Synonymie mit *R. ammobius* Focke.

Zweifellos handelt es sich um dieselbe Art. Doch zeigt sich bei näherer Untersuchung, dass die dänischen Pflanzen in einigen Merkmalen von dem typischen *Rubus ammobius* abweichen. Während *R. ammobius* s.str. dicht grauweissfilzige Blattunterseiten hat, sind diese bei der dänischen Sippe grün. Die schwache Filzbehaarung ist normalerweise nur an den jüngsten Blättern oder mit der Lupe zu erkennen. Die Farbe der Blätter ist frisch grün, nicht dunkelgrün wie beim typischen *R. ammobius,* auch fehlt die matt dunkelrotbraune Farbe des Schösslings, der bei der dänischen Pflanze wie bie den übrigen *Suberecti* gefärbt ist. Dadurch weicht der dänische *R. ammobius* vor allem im Habitus stark vom Bild der typischen Pflanze ab und nähert sich mehr *Rubus plicatus,* wie das ja auch in dem von Friderichsen & Gelert gewählten Namen zum Ausdruck kommt.

Aufgrund dieser Verschiedenheiten erscheint es angemessen, die dänischen Pflanzen als eine Varietät von *Rubus ammobius* aufzufassen.

Rubus amplificatus Lees

Diese Art ist nicht in Dänemark gefunden. Die Angaben von Friderichsen (1924; Soesmarke) und Watson (1958; Haderslev) beruhen auf Fehlbestimmungen von *R. insularis.*

Rubus arduennensis Lib. ex Lej.

Unter diesem Namen vereinigte Friderichsen eine ganze Reihe von Taxa (cf. Friderichsen 1899). In der 3. und 4. Auflage der Flora von Raunkiær führte er hierunter als Unterarten *R. grabowskii* Weihe mit f. *thyrsanthus* (Focke) und *R. candicans* Weihe auf, welches in der 5. und 6. Auflage wiederholt wurde. In Raunkiær (1950) ist *R. arduennensis* fälschlich als Synonym von *R. thyrsoideus* Wimm. gebraucht. *R. candicans* wird nicht mehr erwähnt, obwohl die Verbreitungsangaben des ,,*R. arduennensis''* sich auf *R. candicans* sensu K. Frid. non Weihe ex Rchb. beziehen. Tatsächlich jedoch kommen weder *R. montanus* Lib. ex Lej. (=*R. candicans* Weihe ex Rchb.) noch *R. arduennensis* Lib. ex Lej. in Dänemark vor. Die Gruppe wird hier allein von *R. thyrsanthus* Focke vertreten.

Rubus armeniacus Focke

Belege: 282, über das ganze Land verbreitet (C et Herb. auct.).

Rubus armeniacus wurde von Friderichsen in den früheren Auflagen der Flora von Raunkiær (unter *R. hedycarpus*) mit aufgeführt. In der letzten Auflage (1950) fehlt die Art jedoch, obwohl sie in Dänemark (wie auch in anderen Ländern) sehr häufig verwildert und stellenweise gut eingebürgert ist. Das Taxon ist unter *R. hedycarpus* näher behandelt.

Rubus atrichantherus Krause

Diese in SO-Jütland nicht seltene Pflanze wurde von Friderichsen & Gelert zunächst als *R. mucronulatus* Bor. s.str. angesehen. Später betrachtete Friderichsen (1914, 1922) sie als Unterart von *R. mucronatus* Blox. *Rubus atrichantherus* und *R. mucronulatus* Bor. (≡*R. mucronatus* Blox. non Ser.) sind nach heutiger Auffassung als gute Arten anzusehen.

Rubus atrichantherus Krause var. **vestitior** Weber var. nov.

Differt a var. *atrichanthero* turione multo magis glanduloso (glandulis stipitatis multis ut in *R. drejeri* G. Jens.) et vulgo magis piloso. Inflorescentia densius glandulosa. Crescit in Dania et Germania.

Holotypus: Deutschland, Schleswig-Holstein, Mölln, „Am Blöcken", 21.8.1976 Weber Nr. 76.821.4 (C; isotypi in HBG et in Herb. auct.).

Belege: Dänemark: 24 Fundorte (fast die Hälfte der *R. atrichantherus*-Nachweise) (C et Herb. auct.). – DDR, Mecklenburg: nördlich Sülten, Kreis Wismar, 14.6.1975 H. E. Weber (Herb. Weber), Kiefernforst östlich vom Göldenitzer Hochmoor, 21.8.1975 J. Duty (Herb. Weber). – Bundesrepublik, Schleswig-Holstein, Mölln "Am Blöcken", 4.9.1967 H. E. Weber (Herb. Weber) und 21.8.1976 (Typus-Coll.).

R. atrichantherus tritt normalerweise mit nur sehr schwach drüsigem und kaum behaarten Schössling auf. Daneben gibt es jedoch eine Abänderung, die bereits 1898 von Erichsen bei Mölln in Holstein gefunden und bei Ranke (1900: 18) erwähnt wurde. Weil bis dahin nur dieser eine Standort bekannt war, wurde diese Varietät auch bei Weber (1972: 261) nicht taxonomisch validiert. Inzwischen hat sich jedoch gezeigt, dass sie in Mecklenburg sehr verbreitet ist und dort den typischen *R. atrichantherus* so gut wie ganz ersetzt. Auch in Dänemark ist sie inzwischen von verschiedenen Fundorten bekannt geworden. Durch den Drüsenreichtum (ca. 10 Stieldrüsen pro cm der Schösslingsseiten) besitzt diese Varietät ein fremdartiges, an *R. drejeri* G. Jens. erinnerndes Aussehen. Auch der Blütenstand ist wesentlich dichter stieldrüsig als bei der var. *atrichantherus*. Blattform und Bestachelung entsprechen aber ganz dem typischen *R. atrichantherus,* so dass die stark stieldrüsige Varietät – auch wegen der kahlen Antheren – eindeutig von *R. drejeri* unterschieden bleibt. Wegen ihrer weiten Verbreitung ist die drüsenreiche Abänderung, die anscheinend keine fliessenden Übergänge zum typischen *R. atrichantherus* besitzt, hier als besondere Varietät beschrieben.

Rubus babingtonii Bell Salt.

Siehe unter *R. flensburgensis* K. Frid. und *R. phyllothyrsus* K. Frid.

Rubus bertramii G. Br.

Belege: 7, alle aus SW-Jütland (C et Herb. auct.).

Diese Art, die bei Weber (1972: 123) als zweifelhaft für Dänemark angegeben wurde, ist durch neuere Sammlungen und durch das Studium weiterer älterer Belege inzwischen bestätigt worden.

Rubus bloxamii Lees

Siehe unter *R. kollundicola* C. E. Gust.

Rubus chlorothyrsos Focke

Belege: Møn, Ulfshale Skov, 24.9.1961, 26.7.1962 und 31.7.1971 M. P. Christiansen; 2.9.1971 A. Hansen; Ulfshale Hede, Aug. 1975 A. Pedersen; Ulfshale Skov und Hede, Aug. 1976 und Aug. 1977 A. Pedersen. (C et Herb. auct.).

Diese Art wurde zwar früher von Dänemark angegeben (seit Focke 1902 von Watson 1958, Huber 1961 und Heslop-Harrison 1968), doch beruhen alle diese Angaben auf Verwechslungen oder unterschiedlichen Artauffassungen, indem teils *R. axillaris,* teils auch *R. phyllothyrsus* als synonym zu *R. chlorothyrsos* betrachtet wurden. Der echte *R. chlorothyrsos,* der bislang nördlich bis Bergenhusen (Südschleswig) bekannt war, wurde erstmals 1961 von M. P. Christiansen auf Ulfshale (Insel Møn) gesammelt, jedoch erst 1975 richtig erkannt. Die Art wächst hier auf Waldlichtungen und zusammen mit *Juniperus communis* in den angrenzenden Heidebereichen.

Rubus cruentatus P. J. Muell.

Diese mitteleuropäische Art kommt in Dänemark nicht vor. Der angebliche Fund in Oles Kobbel auf der Insel Als (Friderichsen 1922, Raunkiær 1950) bezieht sich auf eine mit *Rubus vestitus* verwandte „Individualart", die man auch heute noch häufig in diesem Walde finden kann.

Rubus drejeri G. Jens. var. **microphyllus** Pedersen & Weber var. nov.

Differt a var. *drejeri* foliis perparvis. Crescit in Dania.

Holotypus: Dänemark, Als, Wallhecke bei Mommark, 28.9.1962 M. P. Christiansen (C).

Belege: Nur der Holotypus.

Rubus flensburgensis K. Frid.

Hierbei handelt es sich um eine inzwischen verschollene Individualart, die früher bei Flensburg-Kielseng gefunden wurde. Später (ab 1922) fasste Friderichsen sie als Varietät des ganz verschiedenartigen *R. babingtonii* Bell Salt. auf und glaubte, diese Pflanze auch in Dänemark gefunden zu haben. Wie die Herbarbelege zeigen, beruhen jedoch sämtliche Angaben für *R. flensburgensis* aus Dänemark auf Fehlbestimmungen, so dass dieses Taxon von der dänischen Liste zu streichen ist.

Rubus hartmanii Gandoger

Gandoger 1884; Gandoger ex Sudre 1905; ≡*R. horridus* Hartman 1832 non C. F. Schultz 1819.

Diese in Schweden und England vorkommende Art wurde zweimal auch für Dänemark angegeben. Friderichsen & Gelert (1887: 90) erwähnen ein jetzt verschollenes Exemplar unsicherer Herkunft (vermutlich Seeland) aus dem Herbarium T. Holm. Watson (1958: 194) führt ohne Angabe einer Quelle Bornholm als Fundort auf. Bislang hat sich weder in den Herbarien noch durch neuere Geländeuntersuchungen ein sicherer Nachweis für das Vorkommen von *R. hartmanii* in Dänemark erbringen lassen.

Rubus hedycarpus Focke

Die Angaben für diese Art bei Friderichsen (1922) beziehen sich vorwiegend auf den nahe verwandten *Rubus armeniacus* Focke. Das angebliche Vorkommen der ,,ssp. *godronii* Lecq. & Lam.'' bei Esbjerg beruht dagegen auf einer Fehlbestimmung von *R. ulmifolius*. Auch *R. incurvatus* Bab. wurde in sched. von Friderichsen als *R. hedycarpus* ssp. *godronii* bestimmt. Der von Friderichsen (als Unterart von *R. hedycarpus*) angegebene französische *R. gillotii* Boulay kommt in Dänemark ebenfalls nicht vor.

Rubus hypomalacus Focke

Beleg: SO-Jütland, Kollund, 19.7.1926 C. E. Gustafsson (C).

Rubus hypomalacus wurde 1926 von C. E. Gustafsson bei Kollund in SO-Jütland gefunden. Der Herbarbeleg ist bereits von Friderichsen richtig bestimmt. Der Fund wurde jedoch nach dessen Tod in die nächsten Auflagen der Flora von Raunkiær nicht aufgenommen. Die Art tritt unmittelbar in Nähe der Grenze auf. Jenseits davon ist sie seit 1826 beim Kupfermühlenholz nachgewiesen, von wo sie durch ganz Schleswig-Holstein durch Mitteleuropa bis in die ČSSR verbreitet ist (vgl. Weber 1972).

Rubus incurvatus Bab. – Fig. 1–2

Belege: N-Jütland, Vendsyssel, Slotved Skov bei Sindal, 8.8.1912 Mathiesen jun. Nov. 1975 F. Thorning-Lund (C); in der Nähe der Gl. Sindal Kirche und Kiesgrube nördl. Slotved Skov 8.10.1977 F. Thorning-Lund (C et Herb. auct.).

Diese britische Art wurde bereits 1912 von dem Sohn des Waldhüters im Slotved Wald bei Sindal in Vendsyssel (N-Jütland) gesammelt und von Friderichsen als *R. hedycarpus* ssp. *godronii* bestimmt. 1975 wurde sie von F. Thorning-Lund in demselben Gebiet wieder aufgefunden. Die Identität mit *R. incurvatus*, die inzwischen auch der britische Batologe A. Newton bestätigte, wurde jedoch erst jetzt aufgeklärt. Damit ist überhaupt der erste Nachweis für diese Art für den Kontinent erbracht. (Die von Beek 1974 mitgeteilten Vorkommen in den Niederlanden beziehen sich auf eine andere Pflanze). Die Übereinstimmungen der jütischen, vor allem der nordjütischen *Rubus*-Flora zu derjenigen Englands werden auch durch Arten wie *R. dasyphyllus*, *R. septentrionalis*, *R. polyanthemus*, *R. lindebergii*, *R. bertramii* und *R. mucronulatus* unterstrichen.

Rubus insularis Aresch. var. **parvifolius** O. Gel. ex Pedersen & Weber var. nov.

Differt a var. *insulari* foliis nanis. Planta manifeste gracilior. Crescit in Dania.

Holotypus: Dänemark, Lolland, Langet Skov, 3.8. 1897 Carl Christensen (C).

Belege: Falster, Pandebjerg, 1854 H. Mortensen (C); am Weg östlich Pandebjerg, Sept. 1977 A. Pedersen (Herb. auct.). O-Jütland, Ludvigseje Skov bei Hovedgaard, 21.7.1890 C. Raunkiær (C). Bogø bei Møn, in einer Wallhecke, 1917 M. P. Christiansen (C). S-Seeland, Rosenfeldt, in einer Wallhecke, 25.8. 1918 M. P. Christiansen (C); Nørrehave bei Langebæk, Sept. 1977 A. Pedersen (Herb. auct.).

Parallel zu anderen Arten bildet auch *R. in-*

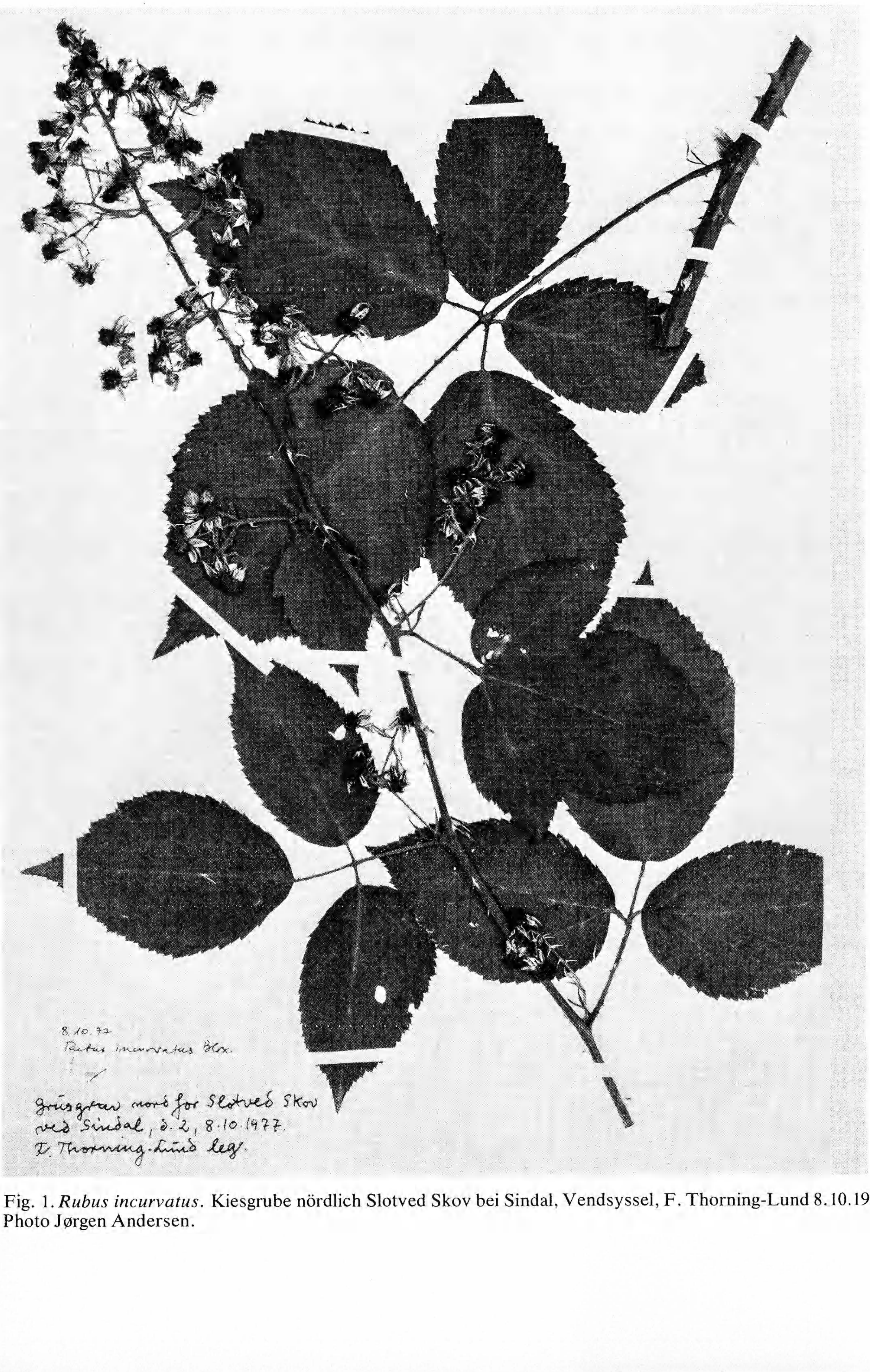

Fig. 1. *Rubus incurvatus*. Kiesgrube nördlich Slotved Skov bei Sindal, Vendsyssel, F. Thorning-Lund 8.10.1977. Photo Jørgen Andersen.

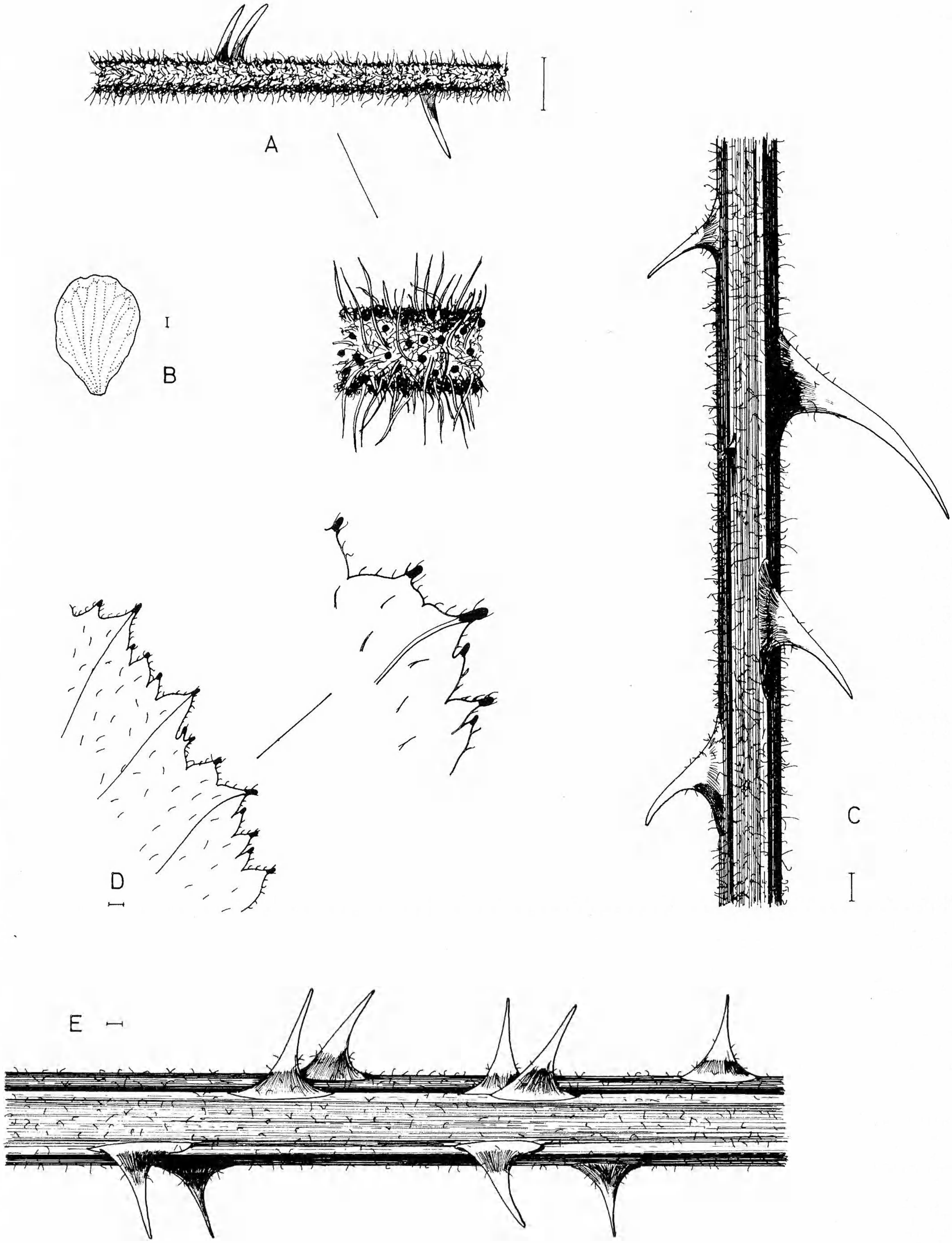

Fig. 2. *Rubus incurvatus*. A: Blütenstiel (*peduncle*). – B: Kronblatt (*petal*). – C: Teil der Blütenstandsachse (*part of the rachis*). – D: Serratur des Endblättchens (*serration of the terminal leaflet*). – E: Schösslingsabschnitt (part of primocane). – Alle Mass-striche (*all scale units*) = 1 mm. – England, Flint, Dobs hill. Herb. Weber 76.719.2.

sularis eine Zwergform aus, die zuerst von O. Gelert (in sched.) erkannt und als var. *parvifolius* benannt und inzwischen an mehreren Orten in Dänemark nachgewiesen wurde.

Rubus integribasis P. J. Muell.

Belege: N-Jütland, Insel Mors, Legind, 15.7.1936 J. Lindhard (AAU); am Fusse der Legind Bjerge, Juli 1976 A. Pedersen (C et Herb. auct.); Thy, am Wege nördlich Ydby Kirche, Juli 1976 (C et Herb. auct.). O-Jütland, Mørkholt südöstlich Vejle, in einer Wallhecke, Juli 1976 A. Pedersen (Herb. auct.).

Rubus integribasis wurde erstmals 1936 von J. Lindhard am Rande der Legind Bjerge auf der Insel Mors (N-Jütland) aufgesammelt. 1976 wurde er dort wiedergefunden und auch in Thy (N-Jütland) und in der Nähe von Vejle entdeckt. Die erst jetzt in Dänemark richtig identifizierte Art war bislang nicht weiter nördlich als bei Kiel bekannt. Die Verbreitung ist damit etwa 280 km weiter nach Norden verschoben. Südwärts reicht das Areal dieser mit *R. divaricatus* verwandten Pflanze bis nach Nordfrankreich.

Rubus kollundicola C. E. Gust.

Belege: SO-Jütland, Kollund, in den Feldhecken nördlich Hotel Kollund, auch im Tal bei der Waldschlucht westlich Kollund, 18.8.1921 K. Friderichsen; Kollund 4.8.1922 K. Friderichsen; 7.8.1926 C. E. Gustafsson; 9.7.1927 K. Friderichsen. Kollund Skov, Waldrand im Grenztal gegenüber dem Kupfermühlenwald, 9.8.1927 K. Friderichsen. Kollund, 27.9.1962 und 1965 M. P. Christiansen (Alle C). Wallhecken nördlich Kollund Skov, Juli 1975 A. Pedersen (Herb. auct.)

Hierbei handelt es sich um eine von Gustafsson (1935) beschriebene Lokalart, die ein beschränktes Areal bei Kollund (SO-Jütland) besiedelt und deshalb eigentlich keine taxonomische Behandlung verdient. Sie war vorher auch schon Friderichsen in die Hände gefallen, der sie (in sched.) teils als *R. densinotus* K. Frid ined. und *R. kollundensis* K. Frid. ined., teils als *R. cruentatus* P. J. Muell. und *R. propexus* K. Frid. deutete.

In Raunkiær (1922–50) ist diese Sippe fälschlich als *R. bloxamii* Lees aufgeführt. Diese Deutung dürfte auf Sudre (1908–13) zurückgehen, der *R. propexus* als synonym zu *R. bloxamii* betrachtete, obwohl diese beiden Taxa deutlich voneinander abweichen. Die Herbarbögen Friderichsens zeigen, dass er die Pflanze von Kollund für eine Form von *R. propexus* hielt. Da er den echten *R. bloxamii* nicht kannte, andererseits aber auf Sudre vertraute, führte er die Sippe folgerichtig als *R. bloxamii* auf, ohne jedoch auch das angebliche Synonym *R. propexus* zu zitieren.

Auch Weber (1972) zog *R. kollundicola* zu *R. propexus*. Tatsächlich sind beide Sippen äusserst ähnlich. Ein späterer Vergleich zahlreicher Herbarbelege zeigte jedoch, dass *R. propexus* durch eine etwas andere Blattform (Endblättchen mit aufgesetzter, längerer Spitze) und Serratur (gleichmässig, ohne auswärtsgerichtete Hauptzähne wie bei *R. kollundicola*) von der Kollunder Pflanze abweicht. Beide Taxa sind damit als ganz unbedeutende Sippen einzustufen, von denen die eine, *Rubus propexus* (wohl „Individualart''), nach Überbauung ihres Originalstandorts bei Kiel heute verschollen ist.

Rubus leucostachys Schl. ex Sm.

Diese Art wurde von Friderichsen 1922 und später (in Raunkiærs Flora) irrtümlich als synonym mit *R. vestitus* Weihe angesehen und von Heslop-Harrison (1968) neben *R. vestitus* für Dänemark angegeben, wo *R. leucostachys* jedoch fehlt.

Rubus macrophyllus Weihe

Siehe unter *Rubus schlechtendalii* Weihe.

Rubus mucronulatus Bor.

≡*R. mucronatus* Blox.

Belege: 12, alle von Djursland, O-Jütland (C et Herb. auct.).

Diese Art wurde erstmals 1913 von Poul Larsen in Mejlgaard Overskov auf Djursland gesammelt und von Friderichsen richtig (als *R. mucronatus* var. *drejeriformis*) bestimmt. Unter diesem Synonym wird sie auch von Friderichsen (1922) angegeben, doch fehlt die Angabe in den späteren Ausgaben der Flora von Raunkiær. Auch Erichsen (1923: 259) beobachtete die Art in Dänemark (um Løgumkloster im SW-Jütland). Wenn er auch keinen Herbarbeleg einsammelte (jedenfalls in HBG nicht auffindbar), so ist jedoch an der Angabe Erichsens, der dieses Taxon gut kannte, nicht zu zweifeln. Neuerdings ist eine bedeutende

Verbreitung des *Rubus mucronulatus* in den Wäldern von Djursland nachgewiesen. Die Art ist vorwiegend britisch; auf dem Kontinent hat sie ihre Hauptverbreitung im westlichen Schleswig-Holstein (nördlich bis Husum) und tritt ausserdem in den nördlichen Niederlanden auf (vgl. Karte 71 Weber 1972).

Rubus nemoralis P. J. Muell.

=*R. selmeri* Lindeb.

Das angebliche Vorkommen dieser Art wird in der Literatur seit Focke (1902: 484) immer wieder zitiert, ohne dass dieses Taxon hier bislang tatsächlich nachgewiesen werden konnte. Zwar ist es nicht unwahrscheinlich, dass die Art doch noch irgendwo in Dänemark wächst, da ihr Areal auf dem Kontinent von Nordfrankreich bis Norwegen reicht und sie auch im benachbarten Schleswig-Holstein nicht selten ist (der nächste Fundort liegt nur wenige Kilometer von Dänemark entfernt auf Sylt). Friderichsen und Gelert haben daher wiederholt auf *R. nemoralis* als eine vielleicht auch in Dänemark zu erwartende Art aufmerksam gemacht.

Rubus pergratus Blanch.

Belege: NO-Seeland, Charlottenlund Skov, 16.9.1932 Knud Jessen (C); Juli 1976 A. Pedersen (C et Herb. auct.). O-Seeland, Wäldchen am Vallensbæk Strand an der Mündung der St. Vejle Au, 25.8.1968 A. Hansen (C).

Diese in Nordamerika heimische Art wird in Dänemark selten kultiviert, ist jetzt aber in NO-Seeland verwildert, vor allem in grosser Menge im Charlottenlund Skov.

Rubus phyllothyrsus K. Frid.

Belege: O-Jütland, Hannerup Skov bei Fredericia, an einem Bahndamm, Aug. 1896 O. Gelert; 2.8.1962, 25.9.1962 und 12.8.1963 M. P. Christiansen (alle C); Juli 1976 A. Pedersen (Herb. auct.).

Rubus phyllothyrsus wurde von Friderichsen (1914, 1922) als *R. babingtonii* Bell Salt. var. *phyllothyrsus* (K. Frid.) Rogers betrachtet. In den späteren Auflagen der Flora von Raunkiær (1934–50) fehlt das Taxon. Der einzige Fundort des *R. phyllothyrsus* in Dänemark, Fredericia (Hannerup Skov, leg. O. Gelert 1896 und später), wird jedoch noch erwähnt, aber irrtümlich *R. flensburgensis* K. Frid. (als *R. babingtonii* var. *flensburgensis*) zugeschrieben, eine Pflanze, die in Dänemark bislang nicht nachgewiesen ist.

Rubus radula Weihe var. **exilis** Lange

Lange 1885; =*R. exilis* Lange 1883 prov.

Belege: Fünen, Falsled bei Faaborg, Knickwall an der Strasse beim Hof Petersminde, 8.8.1879 J. Lange; 26.7.1884, 24.7.1893 O. Gelert; 22.8.1893 A. Edm. Andersen; 18.7.1904 Eug. Warming; Juli 1917 N. Sørensen; 6.8.1965 M. P. Christiansen; in der Umgebung von Odense, 17.7.1956 H. Eilstrup (alle C); am Bøgebjerg-Strand nordöstlich Kerteminde, Aug. 1975 A. Pedersen (Herb. auct.). S-Seeland, Præstø Hestehave, 1965 M. P. Christiansen (C). Brandsø im Lillebælt, 1884 J. Lind (C).

Offenbar handelt es sich nicht um eine Varietät von *R. radula,* sondern um eine sterile Hybride, an der allerdings vermutlich *R. radula* beteiligt ist.

Rubus rhodanthus Watson

≡*R. carpinifolius* var. *roseus* Weihe & Nees

Rubus rhodanthus wurde von Watson (1958: 82, von dort auch übernommen von Huber 1961) als in Dänemark vorkommende Art angegeben. Vermutlich bezog Watson die alten irrtümlichen Angaben für *R. rhombifolius* Weihe auf diese Art, weil er zu Unrecht glaubte, dass sein *R. rhodanthus* mit dem *R. rhombifolius* der meisten Autoren identisch wäre. Tatsächlich handelt es sich jedoch bei *R. rhodanthus* um eine nur bei Mennighüffen (Westfalen) von Weihe gefundene Lokalart, die *R. adspersus* Weihe ex Weber nahesteht, doch weder mit diesem noch mit *R. rhombifolius* auct. zu vereinigen ist.

Rubus rhombifolius sensu Frid. & Gel. non Weihe

Belege: SO-Jütland, Errigsted nördlich Haderslev, 13.7.1882, 17.7.1884, 28.8.1884 und 26.7.1885 K. Friderichsen (C); Wallhecken südlich Errigsted, Juli 1977 A. Pedersen (Herb. auct.).

Hierbei handelt es sich um eine Weitverbreitete Art, die von den meisten Autoren (auch von Focke) als *R. rhombifolius* gedeutet wurde, aber von dem echten *R. rhombifolius* stark abweicht. Weber (1972) betrachtete sie vorbehaltlich als eine besondere Ausbildung von

R. schlechtendalii Weihe ex Link, mit dem grössere Ähnlichkeiten vorliegen. Die Art, die von Polen bis ins mittlere Mitteleuropa weit verbreitet ist und bislang meist als *R. rhombifolius,* aber auch als Varietät von *R. villicaulis* oder *R. gratus* betrachtet wurde, soll im Rahmen einer Revision der *Rubus villicaulis*-Gruppe neu beschrieben werden. Das von Friderichsen in 1882 entdeckte, noch 1977 bestätigte Vorkommen bei Errigsted nahe Haderslev liegt etwas isoliert und findet Anschluss an das Hauptareal dieser Art erst im südlichen Holstein und in Mecklenburg.

Rubus scheutzii Lindeb.

Beleg: NO-Seeland, zwischen Aalsgaarde und Hellebæk, 1917 R. Kanér als *Rubus floribundus* Kanér ined. (C).

Der bislang einzige Nachweis für Dänemark gelang bei dieser Art R. Kanér 1917. Er entdeckte sie zwischen Aalsgaarde und Hellebæk bei Helsingør, konnte sie aber bei einer erneuten Nachsuche 1930 dort nicht wiederfinden (Kanér 1941). Auch 1977 war die Art dort nicht mehr nachzuweisen. Dennoch ist *R. scheutzii* nach seinen heutigen Vorkommen nicht lediglich als eine auf Südschweden beschränkte Regionalart, sondern als Weitverbreitete Art einzustufen, da er inzwischen auch in Mitteleuropa (Bundesrepublik Deutschland: Westfalen) gefunden worden ist (Wittig & Weber 1978).

Rubus schlechtendalii Weihe ex Link

Diese Art wurde von Friderichsen (1922, als *R. macrophyllus* ssp.) für Haderslev angegeben, weil er eine Schattenform von *R. insularis* irrtümlich so gedeutet hatte.

Rubus sciocharis Sudre var. **microphyllus** (Frid. & Gel.) Weber comb. nov.

≡*R. sciaphilus* Lange *β microphyllus* (Frid. & Gel.) O. Gel. in Lange, Haandbog i den danske flora, ed. 4, p. 782 (1888); ≡*R. sciaphilus* Lange f. *microphylla* Frid. & Gel. in Bot. Tidsskr. 16: 73 (1887).

Holotypus: Dänemark, Jylland, ,,Anslet nahe Haderslev'', 1886 K. Friderichsen (C).

Belege: SO-Jütland, Anslet bei Haderslev, Okt. 1886 K. Friderichsen; Hølsgaarde nahe Fredericia, 17.7. 1887 O. Gelert. Brandsø im Lillebælt, 17.7.1892 O. Gelert. Als, Wallhecke nördlich Pøl, 2.8.1922 M. P. Christiansen. (Alle C).

Wegen zwei älterer Homonyme ist der illegitime Name *R. sciaphilus* Lange durch den korrekten Namen *R. sciocharis* Sudre (Bat. eur. 68, 1907) zu ersetzen. Damit ergibt sich die Notwendigkeit der Neukombination der Zwergvarietät var. *microphyllus.* Sie wurde zwar schon von Watson (1958: 63) gebraucht, allerdings ohne bibliographischen Hinweis auf das Basionym und war somit bislang noch nicht gültig veröffentlicht.

Rubus septentrionalis Watson – Fig. 3

≡*R. confinis* Lindeb. non P. J. Muell.

Belege: N-Jütland, Thy, Sindrup, auf einer Halde bei Draget, Juli 1976 A. Pedersen (C et Herb. auct.); südlich Sindrup, Juli 1976 F. Thorning-Lund (Herb. auct.).

Diese Art ist erst 1976 in Dänemark entdeckt worden. Der nordjütische Fundort fügt sich gut in das Gesamtareal dieser nordischen Brombeere ein, die von Bohuslän in Schweden über SO-Norwegen bis nach Schottland verbreitet ist. Die Pflanze steht *R. insularis* nahe, unterscheidet sich davon jedoch vor allem durch gefurchte, dichter und gerader bestachelte Schösslinge, zierlichere, langgestielte Blätter und Blättchen, die vor allem im Blütenstand oft grob gesägt sind, und kleinere, meist weisse Blüten.

Rubus silvaticus Weihe & Nees

Beleg: NO-Seeland, Geel Skov bei Holte, Aug. 1885 O. Gelert (C).

Diese Art ist bislang nur an einer Stelle im Geel Skov (NO-Seeland) von Gelert gefunden worden. Der schon von Gelert richtig bestimmte Beleg enthält zwar keinen Blütenstand und wurde daher von Gustafsson (1938), der mit dem in Schweden fehlenden *R. silvaticus* wenig vertraut gewesen sein dürfte, in Zweifel gezogen. Vermutlich ist deshalb die Art bei Hylander (1955) nicht mit aufgenommen. Trotz des fehlenden Blütenstands ist der Beleg jedoch eindeutig als *R. silvaticus* gesichert, weil der Schössling und die Blätter sehr typisch entwickelt sind und nicht etwa mit Formen von *R. sprengelii* Weihe verwechselt werden können.

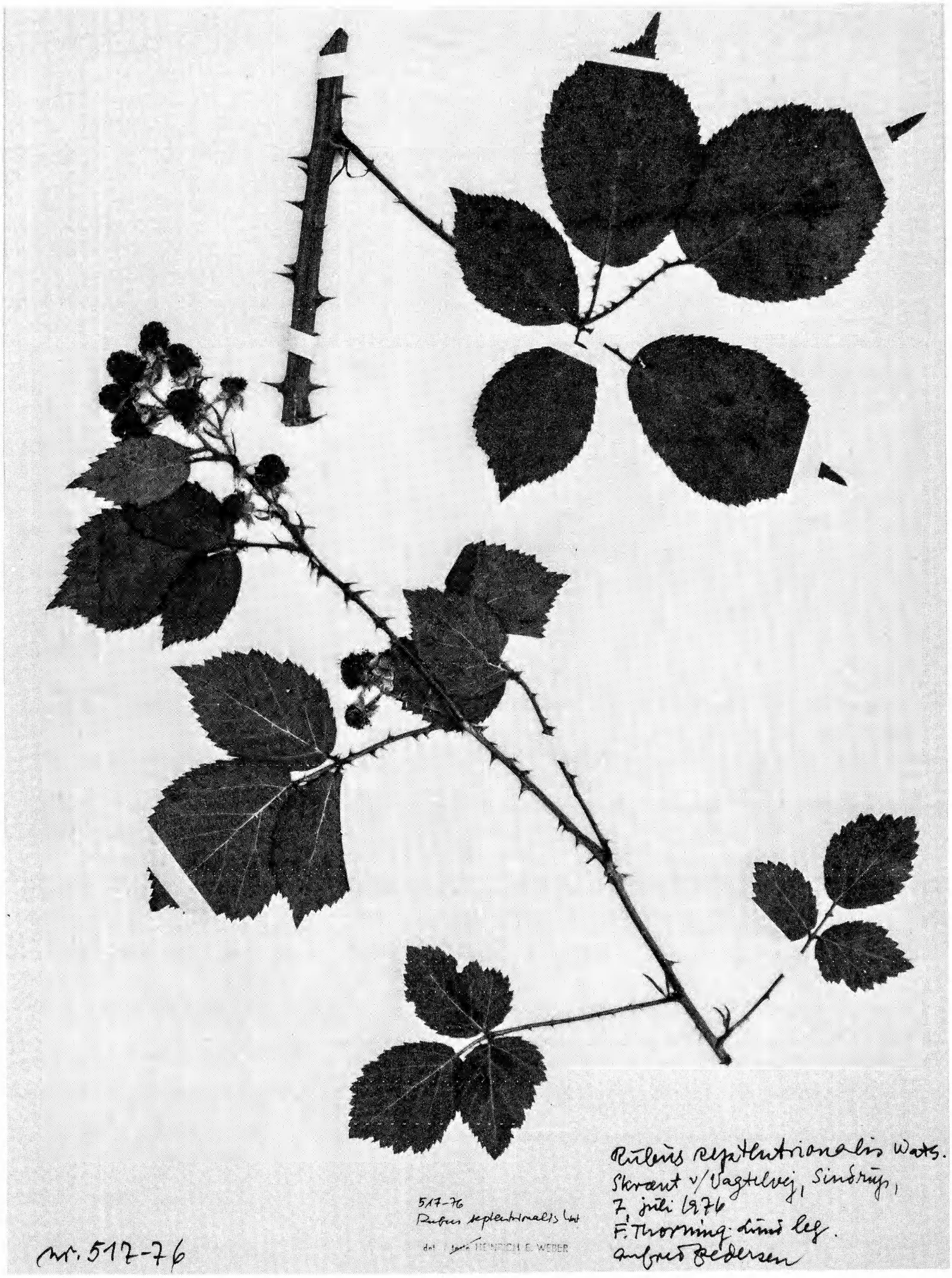

Fig. 3. *Rubus septentrionalis*. Südlich von Sindrup, Thy, F. Thorning-Lund leg. Juli 1976. Photo Jørgen Andersen.

Rubus taeniarum Lindeb.

Rubus taeniarum ist seit Watson (1958) mehrfach in der Literatur als getrenntes Taxon neben *R. infestus* Weihe für Dänemark angegeben worden. Tatsächlich kommt *R. infestus* in Dänemark vor. *R. taeniarum* ist lediglich ein jüngeres Synonym dazu. Bei *R. infestus* sensu Watson 1958 handelt es sich dagegen um eine andere Sippe, die inzwischen als *R. infestior* Edees beschrieben wurde.

Rubus ulmifolius Schott fil.

Belege: W-Jütland, *Pinus mugo*-Pflanzung auf einem Hünengrab zwischen Esbjerg und Jerne, 1910 und 31.7.1961 N. Sørensen, Aug. 1914 P. M. Pedersen (C). O-Jütland, Djursland, auf einem Hügel im Ostteil der Emmedsbo-Plantage, Aug. 1977 E. Wessberg (Herb. auct.). O-Seeland, Skovhusvænget bei Lellinge westlich Køge, südlicher Waldrand, Dez. 1974 und Aug. 1975 A. Pedersen (C et Herb. auct.).

Rubus ulmifolius, eine west- und südeuropäische Art, ist in Dänemark nur selten angepflanzt und wurde bislang an wenigen Stellen verwildert gefunden.

Liste der Arten der Sect. Rubus in Dänemark

Bislang sind insgesamt 55 *Rubus*-Arten der Sect. *Rubus* (neben vielen anderen aus der hier nicht behandelten Sect. *Corylifolii*) in Dänemark nachgewiesen. Davon sind 50 einheimisch. Ausserdem gibt es 5 (* in der Liste) verwilderte und zum Teil eingebürgerte Arten. Bei den einheimischen Species ist der Anteil der Weitverbreiteten Arten (Arealkategorie A) mit 43 Arten (=86 %) beachtlich gross, ausser 2 Lokalarten (Kategorie C: *R. contiguus* und *R. kollundicola*) kommen nur 5 Regionalarten (Kategorie B) vor, die zum Teil auch Übergänge zu weiterer Verbreitung zeigen: *R. atrichantherus, R. marianus, R. pallidifolius, R. phyllothyrsus* und *R. pseudothyrsanthus*. Darüber hinaus sind bis jetzt 16 taxonomisch zu vernachlässigende ,,Individualarten'' (Kategorie D) in Dänemark gefunden worden und machen somit nur einen verschwindend geringen Anteil an der Gesamtflora aus.

Von den Subtaxa sind nur die wichtigsten hier aufgenommen. Eine Beschreibung der zahlreichen, meist standörtlich bedingten Abänderungen bei diesen allgemein stark modifizierbaren Pflanzen erscheint taxonomisch irrelevant. Typisch für die nordischen Arealbereiche ist das Auftreten von deutlich vom Typus abweichenden Zwergformen (z.B. als ,,var. *microphyllus*'' benannt). Sie sind nicht als Modifikation zu betrachten, sondern behalten unter verschiedenen Standortsbedingungen diesen Merkmalskomplex bei, so dass man sie als genetisch fixierte Varietäten einstufen kann. Trotz der modifikatorischen Plastizität sind die *Rubus*-Arten der Sect. *Rubus* in Dänemark klar voneinander getrennte Species, die keine Übergänge bilden und nur sehr selten hybridisieren.

Rubus affinis Weihe & Nees var. *subsenticosus* K. Frid.
R. allegheniensis Porter
R. ammobius Focke var. *pseudoplicatus* (Frid. & Gel.) Weber
R. armeniacus Focke (=*R. hedycarpus* sensu K. Frid. p.p. non Focke, nom. illeg.)
R. arrhenii (Lange) Lange
R. atrichantherus Krause
  var. *atrichantherus*
  var. *vestitior* Weber
  var. *microphyllus* (Frid. & Gel.) Krause
R. axillaris Lej. (=*R. scanicus* Aresch.)
R. bellardii Weihe & Nees (≡*R. glandulosus* Bellardi nom. ambig.)
R. bertramii G. Br. (=*R. biformis* Boulay)
R. cardiophyllus P. J. Muell. & Lef. (=*R. rhamnifolius* sensu auct. plur. p.p. non Weihe & Nees)
R. chlorothyrsos Focke
R. cimbricus Focke
R. contiguus (O. Gel.) Krause
R. dasyphyllus (Rogers) Marsh.
R. divaricatus P. J. Muell. (=*R. nitidus* Weihe & Nees p.p. non Rafin.)
R. drejeri G. Jens. ex Lange
  var. *drejeri*
  var. *microphyllus* Peders. & Weber
R. egregius Focke
R. flexuosus P. J. Muell. (=*R. foliosus* sensu K. Frid. non Weihe)
R. fuscus Weihe
R. gelertii K. Frid.
R. gratus Focke
R. hypomalacus Focke
R. incurvatus Bab.
R. infestus Weihe (=*R. taeniarum* Lindeb.)
R. insularis Aresch.
  var. *insularis*
  var. *parvifolius* O. Gel. ex Peders. & Weber
R. integribasis P. J. Muell. (=*R. holsaticus* Erichs.)
R. kollundicola C. E. Gust. (=*R. bloxamii* sensu K. Frid. non Lees)
R. laciniatus Willd.
R. langei G. Jens. ex Frid. & Gel. (=*R. atrocaulis* sensu K. Frid. non P. J. Muell.)
R. leptothyrsos G.Br. (=*R. danicus* Focke)
R. lindebergii P. J. Muell.

var. *lindebergii*
var. *parvifolius* Neum.
R. macrothyrsus Lange
R. marianus (Krause) Weber (=*R. chaerophyllus* sensu K. Frid. non Sag. & Schultze)
R. mucronulatus Bor. (≡*R. mucronatus* Blox. non Ser.; =*R. drejeriformis* (K. Frid.) Weber ≡*R. mucronulatus* var. *drejeriformis* K. Frid.)
R. nessensis W. Hall (≡*R. suberectus* Anders.)
R. pallidifolius Krause (=*R. serpens* sensu Frid. & Gel. et auct. plur. p.p. non Weihe)
R. pallidus Weihe
**R. pergratus* Blanch.
R. phyllothyrsus K. Frid. (=*R. babingtonii* sensu K. Frid. p.p. non Bell Salt.)
R. plicatus Weihe & Nees (=*R. fruticosus* L. s.str. nom.ambig.)
var. *plicatus*
var. *micranthus* Lange
R. polyanthemus Lindeb.
R. pseudothyrsanthus (Frid. & Gel.) K. Frid.
R. pyramidalis Kaltenb.
var. *pyramidalis*
var. *parvifolius* Frid. & Gel.
R. radula Weihe
var. *radula*
var. *microphyllus* Lindeb.
R. rhombiferus Weber ined. (=*R. rhombifolius* sensu Frid. & Gel. et auct. plur. non Weihe)
R. scheutzii Lindeb.
R. sciocharis Sudre (≡*R. sciaphilus* Lange non *R. sciophilus* P. J. Muell. & Lef.)
var. *sciocharis*
var. *microphyllus* (Frid. & Gel.) Weber
R. scissus Watson (=*R. fissus* sensu K. Frid. & Gel. et auct. mult. non Lindley)
R. septentrionalis Watson (≡*R. confinis* Lindeb. non P. J. Muell.)
R. silvaticus Weihe & Nees
R. sprengelii Weihe
R. sulcatus Vest
R. thyrsanthus Focke (=*R. arduennensis* sensu K. Frid. p.p. non Lib. ex Lej.)
**R. ulmifolius* Schott fil.
R. vestitus Weihe (=*R. leucostachys* sensu K. Frid. non Schl.)
var. *vestitus* (= var. *chloroscarythros* Krause)
var. *diversifolius* Lindley (= var. *albiflorus* Boulay)
var. *parvifolius* O. Gel.

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Vascular plants from the McCarthy area, Wrangell Mountains, Alaska

Olle Nordell and Alf Schmitt

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Some vascular plants new to the McCarthy area of the Wrangell Mountains, Alaska, are reported, including: *Aphragmus eschscholtzianus* Andrz., *Aquilegia formosa* Fisch., *Epilobium lactiflorum* Hausskn., *Papaver alboroseum* Hult., *Potentilla flabellifolia* Hook. and *Saxifraga spicata* D. Don. *Potentilla flabellifolia* is new to Alaska.

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During the first two weeks of July 1976 the authors collected vascular plants in the McCarthy area of the Wrangell Mountains, Alaska. According to Hultén (1940) only a few botanists have been previously active in this area. Hultén made a collection from Nabesna, in the northern part of the mountain chain; Murray (1968) collected in 1966 and 1967 in the Skolai Pass and the Chitistone Pass areas, 50 km E of McCarthy; and Scott (1974) made a more thorough investigation of the Chitistone Pass flora.

Our main collection was done W of Bonanza Peak, 5 km N of McCarthy (61°30'N, 142°51'W, US Geol. Surv. Top. Ser.), at 1000–1700 m. Some interesting species were also found along the McCarthy Creek and near the Nicolai Mine (61°26'N, 142°46'W).

Bonanza Ridge consists mainly of greenstone (Nicolai Greenstone) with lesser outcrops of limestone rock (Chitistone Limestone) (US Geol. Surv. Top. Ser.).

The habitats visited were as follows:

Alpine meadow. A southfacing meadow, steeply-inclined with a rich vegetation of tall herbs such as: *Aconitum delphinifolium, Aquilegia formosa, Delphinium glaucum* and *Zygadenus elegans.* Other typical species were *Artemisia arctica, Epilobium angustifolium* and *Festuca altaica.*

Dwarf-shrub heaths. The greater part of the hillsides were covered by heaths, typically including the following species: *Anemone narcissiflora, A. parviflora, Arctostaphylos alpina, Cassiope tetragona, Dryas* spp., *Empetrum hermaphroditum, Festuca altaica, Juniperus horizontalis, Lupinus arcticus* and *Vaccinium vitis-idaea.* Another locality, a NW-facing hillside sloping down to a stream (Jumbo Creek) was dominated by willow shrubs. The field layer typically comprised: *Dodecatheon frigidum, Empetrum hermaphroditum, Festuca altaica, Juniperus horizontalis, Potentilla fruticosa, Salix reticulata, Trientalis europaea* and *Vaccinium* spp. The bottom layer, composed of mosses and lichens, was well developed.

Rock faces, boulder fields and screes. A large part of the area consisted of rock faces, boulder fields and gravel screes almost devoid of vegetation. A few scattered vascular plants, mosses and lichens were found. Typical species included: *Antennaria* spp., *Epilobium latifolium, Dryas* spp., *Oxyria digyna, Salix polaris, Saxifraga bronchialis, S. cernua, S. tricuspidata* and *Silene acaulis.*

Streambanks (Jumbo Creek). In the leeds of a stream the snow lay until late in summer, but on the margin such species were present as: *Artemisia arctica, Epilobium latifolium, Potentilla* *fruticosa, Ranunculus pygmaeus,* low-growing *Salix* spp. and *Silene acaulis.*

Scrub–woodland. A S-facing hillslope, subject to solifluction, with a scrubby cover of *Populus balsamifera* and *Alnus crispa.* The field layer was similar to that of an alpine meadow.

Ruderal habitats. The following typical species were found along the narrow gravel-surfaced road which formerly lead to the Bonanza Mine (1700 m), now disused and heavily eroded: *Agropyron violaceum, Carex atrosquamea, C. podocarpa, Equisetum arvense, E. pratense, Minuartia stricta, Phleum commutatum, Polemonium acutiflorum, Rorippa hispida* and *Sagina intermedia.*

Recent moraine. Close to McCarthy was an area of frontal moraine recently laid bare by the Root Glacier. Only *Dryas drummondii* had managed to cover any larger patches. Other species present included: *Agropyron violaceum, Crepis elegans, Descurainia richardsonii, Festuca brachyphylla, Oxytropis campestris, Polemonium pulcherrimum* and *Trisetum spicatum.*

List of species

Only those species are listed which are not recorded in Hultén's (1968), Murray's (1968) and Scott's (1974) maps and species lists for the area W of the Canadian border, S and E of the Copper River and N of the Chitina River. For a complete list of species see Nordell & Schmitt (1977; stencilled report available from the Department of Plant Taxonomy, Lund). Collection numbers are given immediately after the names of taxa. The greater part of our collections are deposited at LD. Duplicates will be sent to ALA.

Lycopodium alpinum L. – 425. Solitary specimens on heaths, 1500–1700 m.

Cryptogramma crispa (L.) R. Br. var. *acrostichoides* (R. Br.) Clarke – 419. Rare in rock crevices, 1700 m.

Cystopteris fragilis (L.) Bernh. ssp. *dickieana* (Sim.) Hyl. – 525. Solitary specimens in rock crevices, 1700 m.

Cystopteris montana (Lam.) Bernh. – 580. Solitary specimens in *Populus* scrub.

Dryopteris fragrans (L.) Schott – 420, 430. Common on rocky slopes up to 1500 m.

Phleum commutatum Gandoger var. *americanum* (Fourn.) Hult. – 139, 484. Rather common on heaths and along the old road.

Agrostis mertensii Trin. (*A. borealis* Hartm.) – 490. Scattered tussocks in an alpine meadow alongside the Bonanza Creek.

Festuca vivipara (L.) Sm. – 301, 431, 433, 600. Common up to 1700 m.

Agropyron violaceum (Hornem.) Lange ssp. *andinum* (Scribn. & Sm.) Melderis – 609. Common along the old road up to 1100 m.

Carex brunnescens (Pers.) Poir. – 137, 548.

Two subspecies occur in Alaska, ssp. *alaskana* Kalela and ssp. *pacifica* Kalela. Our specimens do not exceed 24 cm in height but the shape of the perigynia resembles that of ssp. *pacifica.*

Carex dioica L. ssp. *gynocrates* (Wormsk.) Hult. – 613. Common on peatbogs (800 m), in the vicinity of Nicolai Mine.

Carex misandra R. Br. – 617. Solitary specimens in rocky areas, in the vicinity of Nicolai Mine.

Carex vaginata Tausch – Not collected. Rather common on the peatbogs and in the damp woodland alongside the McCarthy Creek, 800 m.

Carex sp. – 544. Very common along the old road, up to about 1200 m, forming dense tussocks up to 40 cm in height.

We hesitate to state whether this collection belongs to *C. preslii* Steud. or to *C. macloviana* d'Urv. ssp. *pachystachya* (Cham.) Hult. The morphology of the perigynia and scales is as follows: Perigynium 4 × 2 mm, ovate, with broad wings and a beak 1 mm long. Body of the perigynium marginally serrulate, with obscure nerves ventrally. Beak with some small teeth in upper half, reddish brown. Body of the perigynium greenish, tinged light yellowish-brown in the centre; wings brown. Scales acute, yellow-brown with a green midvein and a narrow, hyaline margin, shorter than the perigynium.

Juncus drummondii E. Mey. – 545. Common along the old road, up to 1100 m.

Juncus bufonius L. – 619. Sporadic along an old road along the McCarthy Creek.

Veratrum viride Ait. ssp. *eschscholtzii* (Gray) Löve & Löve – Not collected. Some specimens found in a wet meadow alongside the Bonanza Creek, 1200 m.

Coeloglossum viride (L.) Hartm. ssp. *bracteatum* (Muhl.) Hult. – 641. Solitary specimens in the alpine meadow.

Stellaria calycantha (Ledeb.) Bong. var. *isophylla* (Fern.) Fern. – 142. Solitary specimens in the alpine meadow.

Cerastium fontanum Baumg. ssp. *triviale* (Link) Jalas – 136. Some specimens found along the old road, 1400 m.

Aquilegia formosa Fisch. – 204, 505. Common in the wetter parts of the alpine meadow, 1200 m.

Papaver alboroseum Hult. – 1, 101, 160, 166, 171, 303, 464.

These collections come from sandy and gravelly soils, with very sparse vegetation, at altitudes from 1100–1500 m, and consist mostly of dense clusters with several decumbent scapes. The petals are pink, with a bright yellow spot at the base. Some specimens have 6–7 stigma rays.

This species is known from its type locality in E Asia (Hultén 1968, Komarov 1970). In Alaska it has been reported from the Kenai Peninsula and in the vicinity of the Portage Glacier, and is also reported from the northern slopes of the Brooks Range (Wiggins & Thomas 1962), though this latter record has been disputed. It was reported by Murray (1971) from the St Elias Mts in Yukon.

According to Komarov (1970) it is a critical species, closely related to *P. microcarpum* DC. Porsild (1955) considers that it may be more closely related to *P. pygmaeus* Rydb. than to the Asiatic type. *P. pygmaeus* grows in the southern Canadian Rocky Mts and the adjacent parts of Montana.

Papaver nudicaule L. – 445, 446. Solitary specimens along the unsurfaced road running through Kennicott.

Aphragmus eschscholtzianus Andrz. – 137. One specimen found on solifluction soil alongside the Bonanza Creek, 1500 m. It has previously been found at Chitistone Pass (Murray 1968).

Rorippa hispida (Desv.) Britt. var. *hispida* – 482. Solitary specimens along the old road, 1500 m.

Draba stenoloba Ledeb. – 62, 238, 483. On boulder fields and gravel screes, up to 1400 m.

Arabis lyrata L. ssp. *kamchatica* (Fisch.) Hult. – 217, 481. Solitary specimens on heaths and along the old road, up to 1400 m.

Saxifraga flagellaris Willd. ssp. *setigera* (Pursh) Tolm. – 513, 529, (531). Solitary specimens on boulder fields and gravel screes, at 1500 m.

One specimen (531) has at least one flower with a turbinate calyx tube, which is characteristic for ssp. *platysepala* (Trautv.) Pors. Transitions between the two subspecies probably occur in this area (Hultén 1968).

Saxifraga nelsoniana D. Don – 229, 263; 510. Common in the alpine meadow, up to 1500 m.

Our plants have 2–5 capsules about 3 mm in length. The largest leaves have 7–12 teeth. These specimens probably form intermediates between ssp. *pacifica* (Hult.) Hult. and ssp. *charlottae* Calder & Savile.

Saxifraga spicata D. Don – 626. Rather common in the damp woodland alongside the McCarthy Creek, 800 m.

Potentilla flabellifolia Hook. – 237. In the sloping S-exposed meadow, 1200 m.

We can find no published records of this species from Alaska or Yukon. It is mentioned as occurring from Sierra Nevada in California to the Rocky Mountains in British Columbia, in wet meadows, on stream banks, on alpine or subalpine ridges and talus slopes (Hitchcock et al. 1961). The present find extends the distribution limit of the species nearly 1000 km further NW.

The morphology of our plants is as follows: Stems 18 cm, nearly glabrous, from a brown rootstock. Basal leaves numerous, trifoliate with 7 teeth on the leaflets, glabrous except on the nerves of the lower surface, 10–15 mm long, borne on petioles up to 7 cm. Leaflets cuneate-obovate. Petioles with a few, long, straight hairs. Cauline leaves 2. Stipules 8–10 mm, ovate and somewhat pubescent, especially on the margins. Cymes 2–4-flowered. Disc red-brown. Sepals 4–5 mm, acute, not much longer than the entire, obtuse bractlets. Sepals and bractlets pubescent with long hairs. Petals bright yellow, obcordate, longer than the sepals.

Epilobium hornemannii Reichenb. – 233, 274, 503. Scattered in the alpine meadow, 1200 m.

Epilobium lactiflorum Hausskn. – 245. One specimen found along the Jumbo Creek.

Few earlier Alaskan records for this species: the Anchorage area, Juneau and Sitka (Hultén 1968).

Oxycoccus microcarpus Turcz. – 627. Very common on peatbogs alongside McCarthy Creek, 800 m.

Trientalis europaea L. ssp. *arctica* (Fisch.) Hult. – 452, 533. Rather common in meadows and heaths, up to 1400 m.

Antennaria monocephala DC. – 58, 411, 462, 479. Common in heaths and on boulder fields, 1400–1500 m.

Number 58 differs from the rest in having larger flowerheads and leaves which are more pubescent above. These are characters typical of ssp. *angustata* (Greene) Hult.

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The Madeiran lizard–flower connection observed in a natural habitat

Ivar Elvers

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On Madeira, lizards *(Lacerta muralis dugesii)* not only visit the flowers of introduced species, growing in front of man-made stone walls, but also those of the endemic species *Muschia aurea* (Campanulaceae), which grows on dry, sunny natural rockfaces. This observation may indicate a possible ecologic background to the origin of lizard–flower connections on this island.

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Previously (Elvers 1977) I reported that on the island of Madeira the small lizard *Lacerta muralis dugesii* sometimes visits flowers, in a manner much resembling that of ordinary animal pollinators. However, such visits were mainly observed on introduced garden plants, and only on specimens growing in front of a sunny house or terrace wall, such walls being favourite habitats for the lizards. It might therefore be thought that the lizards' discovery of the flowers is a recently acquired habit, analogous, e.g., to the habit of tits to open bottles left on doorsteps.

The plant species visited by the lizards were all sturdy perennial herbs or small shrubs, with showy, robust flowers with ample nectar production. Since the publication of my previous paper, I have made a search for lizards visiting some native plant possessing similar features, and growing in less unnatural surroundings.

Muschia aurea (Campanulaceae) was chosen as a test case. It is an endemic perennial herb with a very short basal stem, bearing 20–30 cm long annual shoots with terminal panicles of cup-shaped flowers 2–3 cm across, with a firm, campanulaceous receptacle and yellow sepals and petals.

M. aurea grows in the coastal regions of southern Madeira, typically on dry, sunny rock-faces (Fig. 1 A). These habitats form natural counterparts to the man-made habitats mentioned above, and are also inhabited by lizards.

The pollination biology of a related species, *M. wollastonii,* also an endemic of Madeira, is known to show some peculiar and enigmatic features (Vogel 1954 p. 328), suggesting that further interesting observations could be made on this genus.

My studies were made in August 1977, towards the end of the flowering period. The plants were often visited by the lizards, which poked their heads right into the flowers (Fig. 1 B) just as they had been seen to do in the flowers of cultivated plants. Their posture on the flowers often resembled that adopted by bumblebees *(Bombus terrestris),* which also visited these flowers (Fig. 1 C), although more rarely than did the lizards. No other flower visitors were observed. The purpose of the flower visits was obviously to drink nectar. Even though the smooth, slippery body surface of the lizards renders them poor pollen vectors, they no doubt achieve some pollination.

The flowering season of *Muschia aurea* falls in the rainless summer period, when most of the associated plant species have already withered (Fig. 1 A). However, *M. aurea* is very drought resistant and its roots penetrate deep into the water conducting rock fissures (Lowe 1868).

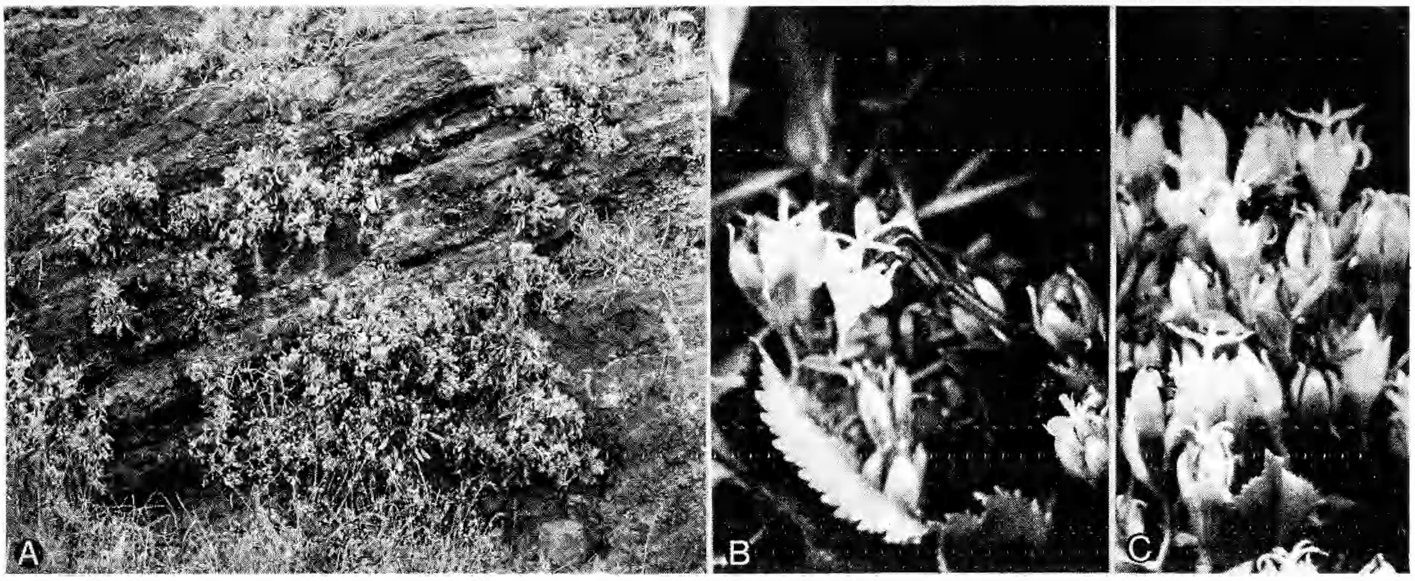

Fig. 1. *Muschia aurea* in the Garajau region on southern Madeira, August 1977. – A: Habitat. – B: Flower visited by *Lacerta muralis dugesii*. – C: Flower visited by *Bombus terrestris*. – Photo Ivar Elvers.

The lizards may have been helped to adapt to living in these dry surroundings by developing the habit of licking up nectar from the flowers. The nectar thus may be of greater importance for them as a source of water than as a source of nourishment.

I should like to thank Professor K. Faegri, Bergen, Norway, for helpful comments on the manuscript.

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Asterionella thomassonii, eine neue Kieselalge aus Afrika

Arnold Nauwerck

Nauwerck, A. 1978 03 31: Asterionella thomassonii, eine neue Kieselalge aus Afrika. [Asterionella thomassonii, a new diatom species from Africa.] *Bot. Notiser 131:* 161–165. Stockholm. ISSN 0006-8195.

Asterionella thomassonii sp. nov. is described from Lake Shinweweshiba in NE Zambia. The new species, which seems to be closely related to *A. candelabrum* Bourrelly & Manguin from Madagascar, shows relationships to *A. ralfsii* W. Smith sensu Körner, but also to *Eunotia zazuminensis* (Cabejszekowna, Lundh-Almestrand) Körner and calls into question whether a separation of the latter from *Asterionella* is justified.

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Anlässlich limnologischer Untersuchungen in Zentralafrika 1966 besuchte ich u.a. den Bangweolusee. Bei dieser Gelegenheit konnte ich in dem nahe bei Samfya gelegenen kleinen See Shinweweshiba eine Massenvegetation einer eigentümlichen, *Asterionella*-ähnlichen Diatomee beobachten. Es ergab sich, dass die Alge mit keiner bisher beschriebenen Art identisch war. Der Fund kann also so interessant angesehen werden, dass eine gesonderte Beschreibung berechtigt erscheint.

Asterionella thomassonii Nauwerck sp. nov.

Typus: Fig. 2.

Cellulae oblongae, valde heteropolae, longitudine 25–62 μm, coloniis paucarum cellularum in stellae figuram redactis coniunctae. Capitipolus 1,5–1,7 μm latus, oblonge rotundatus, pedipolus 3–4 μm latus valde dilatatus, plus minusve triangularis, centrali inflexione transverse abscissus. Pars cellulae media, interdum leviter foras flexa, 1,3–1,5 μm lata. In latere valvari pseudorhaphe ex axe longo cellulae leviter eiecta sine area media. Striae transapicales utrimque, longitudinis inaequalis atque interdum paulum alternantes. Striis alterius lateris pseudorhaphes 4–7, alterius lateris plerumque 3–5 pori. In 10 μm numerantur 22–28 striae. In parte cellulae media numerus striarum plerumque est circiter 24 in 10 μm. Inter strias sunt tori in extrema valva in denticulos non tenues exacuti. Apud pedipolum ordines pororum longiores densioresque fiunt et denique in extremam partem cellulae colliduntur radiorum modo trans polum procurrentes. Etiam apud capitipolum ordines pororum radiorum modo currunt. In capitipolo ipso valva duos ordines spinarum crassarum fert, ordinem superiorem 8 spinas habentem, inferiorem atque minus regularem plerumque una vel duabus spinis minus habentem. Etiam a latere pleurali cellulae plus minusve heteropolae sunt. Latitudo variat secundum statum divisionis inter circiter 3–6 μm in pedipolo, circiter 2,5–4 μm in capitipolo et circiter 1,5–3 μm in media cellula. Pleurae uno vel duobus ordinibus horizontalibus pororum tenuium praeditae sunt atque ad extremas partes cellularum latiores fiunt. Nonnumquam etiam plura tenuiora cingula silicea ad extremas partes cellularum insertae sunt.

Ökologie

Der See Shinweweshiba ist nur wenige Hektar gross und dürfte kaum mehr als 10 m Tiefe erreichen. Genauere Angaben über seine Morphologie liegen nicht vor. Die geschützte Lage des Sees in einer Senke in lichtem Buschwald macht zumindest zeitweise Temperaturschichtung wahrscheinlich. Die Strandvegetation an den sandigen und verhältnismässig steil abfallenden Ufern ist gering. Zur Zeit der Probenentnahme am 6. Juli 1966, war die Oberflächentemperatur des Wassers 20,5°C. Die Wasserfarbe war gelbbraun, die Sichttiefe 1,5 m und der pH-Wert 7,2. Der Sauerstoffgehalt von 7,50 mg/l entsprach einem Sättigungsgrad von 94 %. Andere chemische Analysen liegen nicht vor.

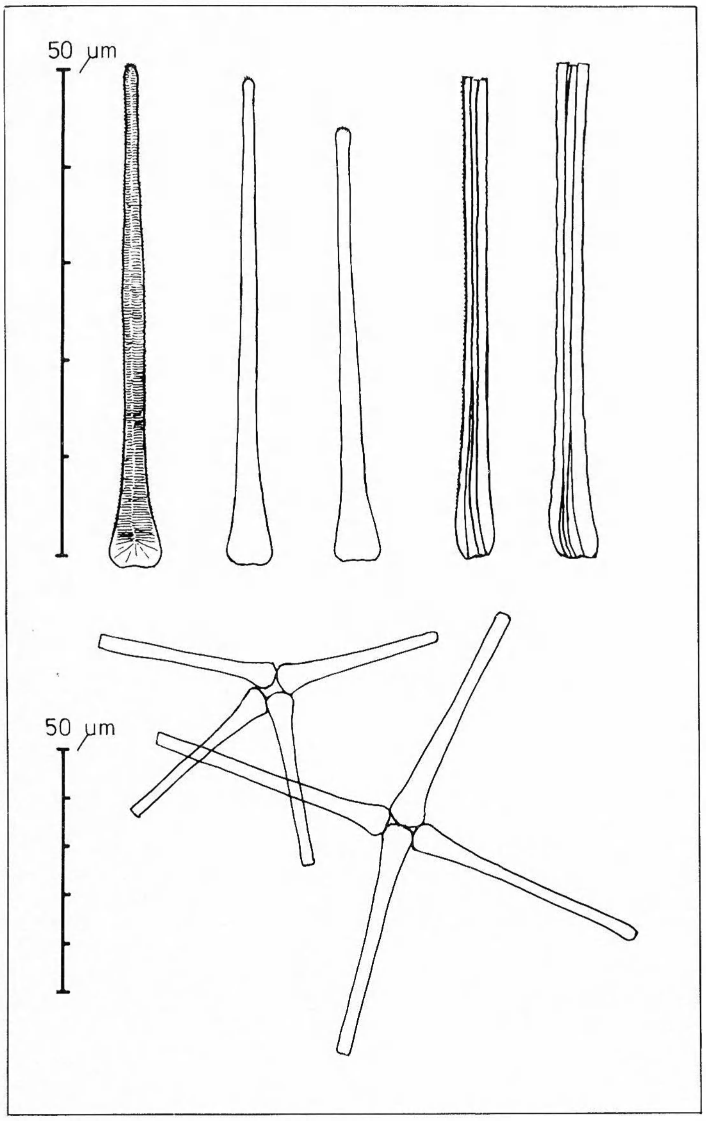

Fig. 1. *Asterionella thomassonii,* Zeichnung nach lichtmikroskopischem Bild.

Die Wasserqualität lässt sich indessen mit der des Bangweolusees vergleichen. Am gleichen Datum betrug dort der pH-Wert 7,6, die Leitfähigkeit war 21,5 µS/cm, der Karbonatgehalt 0,080 mäqu./l, der Sulfatgehalt 0,195 mäqu./l, der Silikatgehalt 3,07 mg/l. Der Totalstickstoffgehalt betrug 1,015 mg/l, davon 15 µg/l Nitratstickstoff, der Totalphosphorgehalt betrug 33 µg/l. Allerdings war das Phytoplankton des Bangweolusees bei der selben Gelegenheit ganz von chroococcalen Blaualgen beherrscht und die Biomasse pro Liter war um ein mehrfaches grösser als im Shinweweshiba. Es muss auch bemerkt werden, dass die Wasserchemie des Bangweolusees innerhalb des Strandvegetationsgürtels erheblich von der des freien Wassers abwich. Es war brauner, der pH-Wert war 6,4 (vgl. auch Symoens 1968), und das spärliche Plankton bestand fast nur aus Desmidiaceen. Labormessungen ergaben auch für das offene Wasser etwa einen halben Grad niederere pH-Werte als die Feldmessungen. Man darf also annehmen, dass der relativ hohe pH-Wert des Shinweweshiba ebenso wie der des Bangweolusees zum Teil durch die Massenvegetation der Algen selbst bedingt war.

Die neue Art machte mit ca. 6 Millionen Zellen pro Liter etwa 80% der Biomasse des Phytoplanktons im Oberflächenwasser des Sees aus. Wichtigste Begleitformen waren *Melosira*-Arten, *Rhizosolenia, Lyngbya circumcreta, Ceratium brachyceros,* verschiedene *Staurastrum*-Arten und vor allem eine Reihe von sehr kleinen (4–8 µm) *Cosmarium*-Arten. Heterokonten waren relativ zahlreich. Chrysomonadinen und Cryptomonadinen fehlten ganz.

Morphologie

Unsere Alge zeigt folgende Eigenarten. In frischem Zustand waren die Zellen zu sternförmigen Kolonien vereinigt und zwar mehr als 80% der Population in Viererverbänden. Die nächsthäufige Zellzahl war 5 pro Kolonie. Kleinere Verbände oder Einzelzellen ebenso wie grössere Verbände mit bis zu höchstens 8 Zellen kamen nur vereinzelt vor. Auffällig war, dass die Zellen oft mit der ganzen Breite des Fusspols aneinander aufsassen (Fig. 1). Auf den ersten Blick scheint dies, wie auch die begrenzte Zellzahl der Kolonien, mit Breite und Form der Fusspole zusammenzuhängen.

Die Zellform ist asterionella-artig, von der Valvarseite betrachtet stark heteropol mit einem breiten Fusspol und einem kleinen Kopfpol. Auch in der Gürtelbandansicht sind die Zellen deutlich heteropol. Die Länge der Zellen variiert zwischen etwa 30 µm und etwa 60 µm. Noch kleinere bzw. noch grössere Zellen sind anzutreffen. Die gemessenen Extremwerte waren 25 µm und 62 µm. Die Grössenzusammensetzung der Population zeigt eine Normalverteilung um einen Mittelwert = Medianwert von ca. 38 µm, also keine schiefe Verteilung oder Häufung um bestimmte Grössenklassen wie man sie bei Diatomeenpopulationen oft findet.

Die Zellbreite misst in Valvaransicht etwa 1,5 µm im Mittelteil der Zelle. Die schmalste Stelle, eine leichte Einschnürung unterhalb des Kopfpols, misst etwa 1,2–1,3 µm. Eine Auftreibung

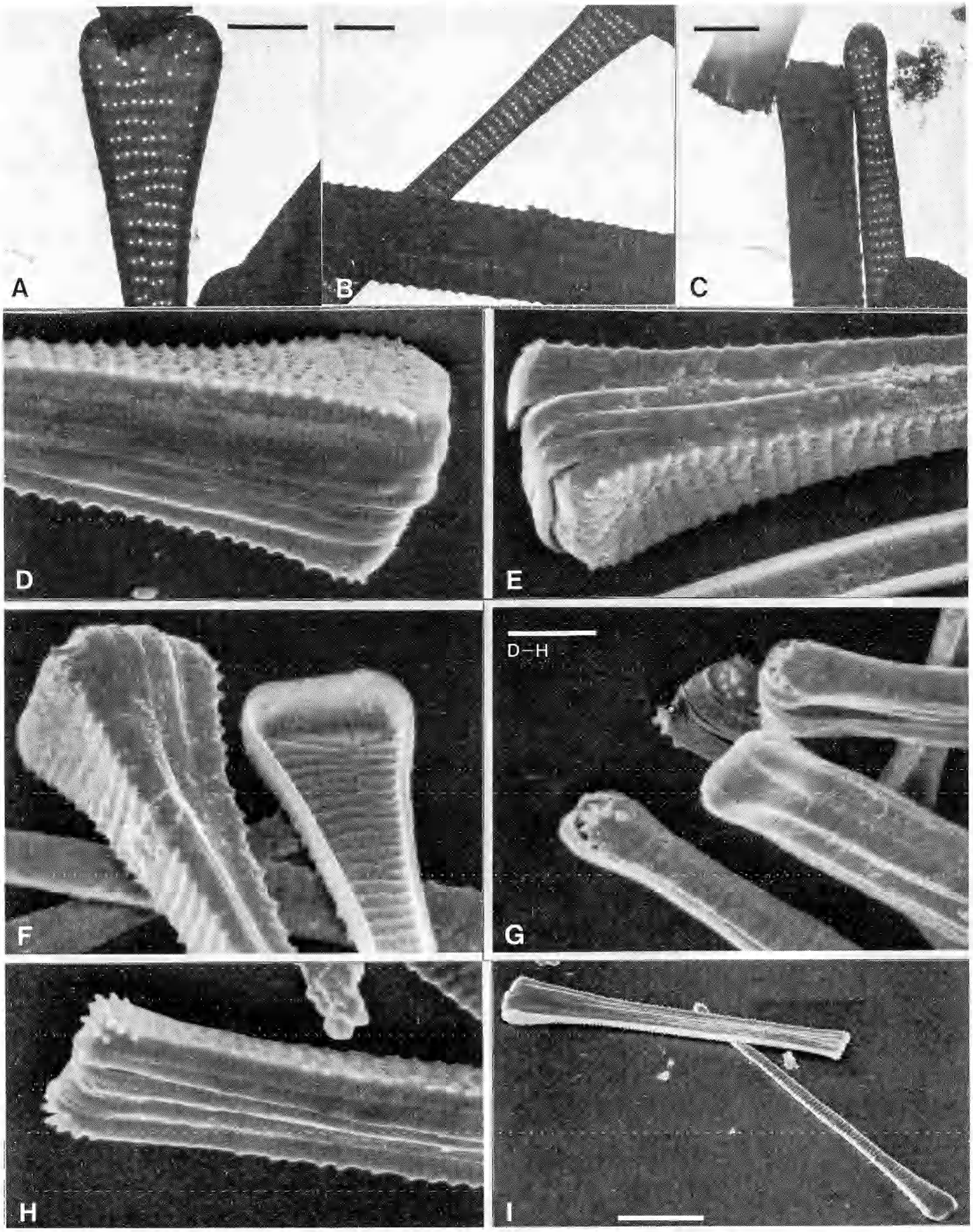

Fig. 2. *Asterionella thomassonii*. A–C: Elektronenmikroskopisches Durchsichtsbild (Foto: G. Cronberg). – D–I: Elektronenmikroskopisches Aufsichtsbild (Foto: J. Ellervik). – Schale 2 μm (A–H), 10 μm (I).

des mittleren Zellabschnitts findet sich nur andeutungsweise bei manchen Zellen, im allgemeinen laufen die Zellseiten von der Einbuchtung des Fusspols ab ziemlich gleichmässig und nur wenig mehr sich verschmälernd dem Kopfende zu.

Der Kopfpol ist länglich abgerundet, sein Durchmesser etwa 1,2–1,5 μm, also kaum viel mehr als die Halseinschnürung unterhalb desselben. Der Fusspol ist 3,5–4,5 μm breit, quer abgeschnitten und an der Basis deutlich eingedellt, mit gerundeten oder abgestumpften Ecken. In Gürtelbandansicht variiert die Breite des Fusspols zwischen 2,5 μm und 6 μm, die des Kopfpols zwischen 1,5 μm und 4 μm, je nach Teilungszustand der Zelle. Gewöhnlich ist der Fusspol mindestens um ein Drittel breiter als der Kopfpol. Die schmalste Stelle der Zelle, in Valvaransicht etwa in der Mitte der Zelle gelegen, ist am häufigsten 2,5–3 μm breit.

Die Streifung der Valvarfläche ist sehr fein. Je nach Zellabschnitt und Zelle kann man 22–26, gelegentlich auch mehr striae pro 10 μm zählen. Im mittleren Zellabschnitt ist die gewöhnliche Zahl etwa 24 pro 10 μm. Eine Pseudoraphe existiert eigentlich nicht, jedenfalls lassen die Streifen kein Mittelfeld frei, jedoch wird durch Unterbrechung der Porenreihen und eine gewisse Versetzung der Poren eine assymetrisch verlaufende Mittellinie angedeutet.

Wie das elektronenmikroskopische Bild (Fig. 2) zeigt, bestehen die Porenreihen auf der einen Seite der Valva aus 2–5, auf der anderen aus 3–7 Poren. Im Mittelteil der Zelle stehen sich gewöhnlich Reihen von 3 und 5 Poren mehr oder weniger gegeneinander versetzt gegenüber. Am Fusspol, wo die Porenreihen am längsten sind, schlagen dieselben nach der Mitte zusammen und laufen strahlen- oder fächerförmig über den Fusspol hinaus. Auch am Kopfpol ziehen sich die Porenreihen von seitwärts nach der Mitte zusammen.

Das elektronenmikroskopische Bild zeigt weiter die im lichtoptischen Mikroskop kaum wahrzunehmende Bezahnung der Schalen. Die zwischen den Porenreihen sich erhebenden Kieselrippen oder Wülste laufen quer über die Valva und seitlich ein Stück über diese hinunter. An der Zellkante entlang ist ihr Scheitel zu Zähnchen zugespitzt. Die Zahl der Zähnchen pro 10 μm korrespondiert etwa mit der Zahl der Porenreihen, jedoch fehlen die Zähnchen auch öfters, wie auch Poren bisweilen verschmolzen sind und viele Zellen überhaupt Alters- oder Abnutzungserscheinungen der Schalenstruktur zeigen. So war die Zeichnung der Gürtelbänder nur ausnahmsweise zu erkennen, und es ist nicht sicher, ob eine einzelne Reihe feiner Poren, etwa 40–42 pro 10 μm, die einzige Feinstruktur ausmacht.

Die auffälligste Skulptur der Schale überhaupt, allerdings auch sie nicht immer erhalten, findet man am Kopfpol in Form eines doppelten Kranzes von kräftigen Dörnchen oder Zähnchen, davon in einer oberen Reihe 6–8, in einer unteren, manchmal weniger regelmässigen Reihe etwas weniger.

Taxonomie

Ohne Zweifel erfüllt die vorliegende Art im wesentlichen die Kriterien des Genus *Asterionella* nach der jüngsten Neuumschreibung von Körner (1970). Zellform, Transapikalstreifung, Koloniebildung fallen durchaus in den Rahmen der Gattung. Habitusmässig erinnert die Art sehr stark an *A. ralfsii* v. *americana* Körner. Die wenigzelligen Kolonien und die schuhlöffelförmig gebogenen Fusspole hat sie gemeinsam mit *A. candelabrum* Bourrelly & Manguin (Bourrelly & Manguin 1949). Wie *A. candelabrum* zeigt sie auch nur eine sehr schmale Pseudoraphe. Allerdings ist die Pseudoraphe im Gegensatz zu der von *A. candelabrum* leicht seitwärts aus der Mittelachse verschoben und hat auch kein gegen den Fusspol erweitertes freies Feld.

Unsere Alge steht also offensichtlich zwischen *Asterionella formosa* und *A. ralfsii* einerseits und *Eunotia (Asterionella) zazuminensis* andererseits und stellt somit eine neue Art dar. Trotz einer wichtigen Abweichung vom bisherigen Signalement der Gattung hat sie doch so viele unverkennbare Gemeinsamkeiten mit dieser, dass sie zu *Asterionella* gestellt werden muss. Tatsächlich habe ich Eigentümlichkeiten wie leichte Assymmetrie der Transapikalstreifung und Andeutung von Kieselzähnchen am Kopfpol anhand von elektronenmikroskopischen Bildern, die mir Gertrud Cronberg (Lund) freundlicherweise zur Verfügung stellte, auch bei *A. formosa* feststellen können.

Körner hat bei seiner Überstellung von *Asterionella zazuminensis* zu *Eunotia* strikte

Mass-stäbe für das Genus *Asterionella* und weite Mass-stäbe für das Genus *Eunotia* walten lassen. Es bleibt natürlich eine Ermessenssache, wo man die Grenze zwischen den beiden Genera ziehen will. Jedenfalls scheint ziemlich sicher, dass das Genus *Asterionella* über die neue Art und über *Eunotia (Asterionella) zazuminensis* mit dem Genus *Eunotia* s.l. verbunden ist.

Zu diskutieren wäre noch die Verwandtschaft der neuen Art mit *Asterionella candelabrum*, die von Madagaskar, also geographisch nicht allzu weit vom Fundort der neuen Art beschrieben und seither nicht mehr vermerkt worden ist. Bezüglich Grösse der Zellen und Zahl der Transapikalstreifen pro 10 μm sowie in der Ausbildung der Pseudoraphe bestehen hier gewisse Unterschiede, denen jedoch im Hinblick auf die Variabilität von anderen *Asterionella*-Arten wie auch der neuen Art kaum besondere Signifikanz beigemessen werden kann. Wie schon Körner (1970) hervorhebt, ist es umgekehrt eher wahrscheinlich, dass die von Manguin und Bourrelly unterschiedene *f. baculatum* der *A. candelabrum* noch innerhalb der Variabilität dieser Art liegt. Die zentrale und deutliche Pseudoraphe bei *A. candelabrum* in der Zeichnung Manguins könnte zwar einen wesentlichen Unterschied darstellen, jedoch darf hier die nur nach Lichtmikroskop angefertigte Zeichnung nicht allzu streng gewertet werden. Vieles spricht also für eine nahe Verwandtschaft wenn nicht gar Identität der beiden Arten. Solange indessen das entscheidende Charaktermerkmal, das Porenmuster der Zellpole, bei *A. candelabrum* nicht aufgeklärt ist, kann die vorliegende Art nicht mit ihr identifiziert werden.

Körner (1970) vermutet, das es sich bei *Asterionella candelabrum* um eine Form von *A. ralfsii* handelt. Zwar nennt er in seiner Revision nur europäische und nordamerikanische Fundorte der letzteren, notiert aber auf einer Verbreitungskarte auch Fundorte aus West-, Zentral- und Südafrika sowie aus Madagaskar. Die Quellen dieser Angaben sind nicht eindeutig auszumachen. Die von ihm zitierten Autoren gebrauchen den Artnamen nicht oder nicht im Sinne Körners. Falls nicht einfach eine Verwechslung vorliegt, handelt es sich dabei möglicherweise um Funde von *Asterionella gracillima* (Hantzsch) Heib., die Körner mit *A. ralfsii* identifiziert. Thomasson (1966) erwähnt *A. gracillima* und *A. zazuminensis* aus dem See Shiwa Ngandu in Ost-Zambia. Er gibt zwar keine Abbildungen der betreffenden Algen, verweist aber auf Ähnlichkeit mit den Arten Bourrellys und Manguins aus Madagaskar. In eigenem Planktonmaterial aus diesem See habe ich keine *Asterionella* feststellen können, dagegen fand ich die neue Art auch in Buchten des Bangweolu und es erscheint wahrscheinlich, dass sie in dem seenreichen Gebiet um den Bangweolu weiter verbreitet ist. Es ist möglich, dass sie sich auch hinter manchen älteren Angaben von *A. gracillima* aus afrikanischen Gewässern verbirgt.

Ich möchte die neue *Asterionella* meinem Freunde Kuno Thomasson widmen, dessen algologische Arbeiten viel zur Kenntnis des Planktons der afrikanischen Seen beigetragen haben. Für Hilfe mit den elektronmikroskopischen Aufnahmen danke ich Gertrud Cronberg, Lund, und Jan Ellervik, Umeå.

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Three species of Christiansenia (Corticiaceae) and the teratological galls on Collybia dryophila

James Ginns and Stellan Sunhede

Ginns, J. & Sunhede, S. 1978 03 31: Three species of Christiansenia (Corticiaceae) and the teratological galls on Collybia dryophila. *Bot. Notiser 131:* 167–173. Stockholm. ISSN 0006-8195.

Collybia dryophila (Fr.) Kummer has for many years been known to bear tumours or galls, but the cause of these galls has been interpreted in different ways. In this study 12 collections of such galls have been investigated. Three closely related species of resupinate fungi grow on the surface of the galls and we believe that they also cause the formation of the galls. One of the species was described earlier, the other two are here proposed as new. Similarities in the shape of basidia and the production of conidia indicate that they are species of *Christiansenia* Hauerslev. The three species are *C. mycetophila* comb. nov. (*Tremella mycetophila* Peck), *C. effibulata* sp. nov. and *C. tumefaciens* sp. nov.

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Over 60 years ago Burt (1915 p. 656) declared that *Tremella mycetophila* Peck (1879) was no more than "a teratological production of *Collybia dryophila*". This was a surprising conclusion as he (Burt 1901) and Hone (1909) had illustrated basidia and basidiospores, found on the galls on *C. dryophila* (Fr.) Kummer, which had little resemblance to the basidia and spores of *C. dryophila*. Ramsbottom's (1933) inability to find any evidence of a parasite on British collections of *T. mycetophila* supported Burt's (1915) statement. However, by his own admission Ramsbottom had studied poorly prepared material. Subsequent reports, including the most recent discussions by Donk (1966 p. 322) and Michael & Hennig (1970 p. 33) accept the interpretation that the tremelloid galls are simply a proliferation of the tissues of *C. dryophila* in response to excessively wet growing conditions.

We first saw these extraordinary growths on fresh fruitbodies of *Collybia dryophila* from Sweden (Fig. 1 A, B, D) and were led to critically examine additional collections from Canada, Denmark and the U.S.A., including Peck's type specimen of *Tremella mycetophila*. Three species of *Christiansenia* Hauerslev were found growing on these galls and we present below descriptions of *C. mycetophila*, *C. effibulata*, *C. tumefaciens* and a revision of some features which have been used to characterize the genus.

Christiansenia Hauerslev

Hauerslev, Friesia 9: 43 (1969). – Generic type: *C. pallida* Hauerslev.

Basidiocarps gelatinous and hyaline when fresh and wet, drying to a subinvisible, glossy film; hyphae sparse, narrow (up to 4 μm in diameter), branched, with clamp connections or (one species) with simple septa only; basidia suburniform or narrowly cone-shaped, initially a rounded to broadly clavate vesicle which extends to form a cylinder or cone of variable length, with 2–6 sterigmata depending upon the species; spores hyaline, smooth, thin-walled, nonamyloid; conidia often present. Growing on basidiocarps of *Collybia*, *Leucogyrophana* and *Phanerochaete*.

Christiansenia mycetophila (Peck) Ginns & Sunhede comb. nov.

Basionym: *Tremella mycetophila* Peck, Rep. New York State Museum 28: 53, 1879. – *Exobasidium mycetophilum* (Peck) Burt, Bull. Torrey Bot. Club 28: 285–287, 1901. – Lectotype: U.S.A., New York, Essex County, North Elba, Peck (NYS).

Basidiocarps a thin, glossy film on the surface of the *Collybia*-galls; subiculum of a layer of hyphae which are hyaline, thin-walled, contorted, branched, 2–3μm wide with clamp connections; conidiophores arboriform, simple-septate, erect (Fig. 2 A: b, E); conidia of two types, the most common are subglobose to broadly ellipsoid blastospores 2–4 × 1.5–2.5 μm, which arise by budding from the apical cells of the conidiophores or from basidiospores (Fig. 2 C, E), the second type are apparently arthrospores often 7–13 × 2 μm (Fig. 2 D); basidia cylindrical, long, generally tapering gradually (Fig. 2 A) but in some cases rather abruptly narrowed to a stem-like base about 15 μm long, always with a clamp connection at the base, (40–)50–80 × 6–8 μm; sterigmata 4, rarely 3, up to 5(–6) μm long, sometimes stuck together, the tips with refractive, oily contents (Fig. 2 A); basidiospores narrowly ellipsoid, in profile cylindrical, the adaxial side occasionally slightly concave 6–7(–9) × 1.5–2(–2.3) μm (Fig. 2 B, C), broadly attached (cf. Fig. 3 A: b), often stuck together in pairs (Fig. 2 B). Growing on galls on the lamellae, surface of pilei and stems of *Collybia dryophila*.

The collection here designated as lectotype for *C. mycetophila* contains the specimen illustrated by Peck and was the basis for his field notes (John Haines, pers. comm.) from which he prepared his description.

Other collections. Canada: Ontario, Merivale 31.VIII.1949 Hoare & Groves (DAOM 22042) – Ottawa, C.E.F., Forest Belt 19.VII.1937 Groves (DAOM 7447) – Ottawa 11.VII.1976 Grainger (DAOM 157068) – *Québec,* Gatineau County, Mt. Burnet 23.VII.1935 Drayton (DAOM F 5592) – Wakefield 23.VII.1952 Gibson (DAOM 35297) – Pointe Gatineau 5.IX.1977 Riel (DAOM 165360).

U.S.A.: New York, Madison County, Oneida, Warne (NYS).

Christiansenia effibulata Ginns & Sunhede sp. nov.

Holotype: Sweden, Bohuslän, Ucklum par., Presstorp 7.VIII.1977 Sonja Hansson (GB).

Christianseniae mycetophilae similis, sed hyphis effibulatis, angustis (2–4 μm), basidiis cylindricis, brevibus (35–55 μm), sterigmatibus 2, raro 3, sporis cylindricis vel anguste obovatis, 6–8 × 1.8–2.5 μm.

Basidiocarps a thin film on the surface of *Collybia*-galls; hyphae hyaline, thin-walled, simple-septate, 2–4 μm wide; basidia cylindrical, (25–)35–55 × 5–7 μm, with 2, rarely 3 sterigmata, each up to 5(–7) μm long with the tips containing a refractive, oily deposit (Figs. 1 F; 3 A: b, c); basidiospores cylindrical to narrowly obovate, in profile cylindrical, rarely suballantoid, the adaxial side rather abruptly tapered to the point of attachment, (5.5–)6–8(–10) × 1.8–2.5 μm, broadly attached (Fig. 3 A: a, b); blastospores subglobose to broadly ellipsoid, 2–3.5 × 1.5–2 μm, formed by budding from basidiospores or, more commonly, from the apices of conidiophores (Figs. 1 E; 3 A: a); arthrospores rather few, up to 13 × 2 μm, arising by fragmentation of conidiophore branches. Substrate as in *C. mycetophila* (Fig. 1 A, B, D).

Other collections. Sweden: Småland, Dörarp parish, Färjansö 27.VI.1977 Sunhede 7402 (pers. herb.) – *Södermanland,* Botkyrka parish, Alby 19.IX.1977 K. Eriksson (GB).

Christiansenia tumefaciens Ginns & Sunhede sp. nov.

Holotype: Denmark, Sjaelland, Vemmetofte skov 23.IX.1977 Karin Toft (GB).

Christianseniae mycetophilae similis, hyphis fibulatis, angustis (ad 3 μm), basidiis anguste infundibuliformibus 40–70 μm longis, sterigmatibus 4, interdum 2–3; sporis oblique lacrymoideis 6–8 × 3–4 μm.

Basidiocarps a thin film on the surface of *Collybia*-galls; hyphae thin-walled, with clamp connections up to 3 μm wide (Fig. 3 B: d); basidia narrowly cone-shaped, 40–70 × (6–)8–13 μm; sterigmata 4, rarely 2 or 3, each up to 8 μm long with the tips generally without a refractive oily deposit (Fig. 3 B: d, h); basidiospores obliquely lacrymoid with a broad, blunt base, 6–8(–9) × 3–4 μm and obliquely attached to the sterigmata, often with oily drops (Fig. 3 B: a–c); conidiophores arboriform, simple-septate; blas-

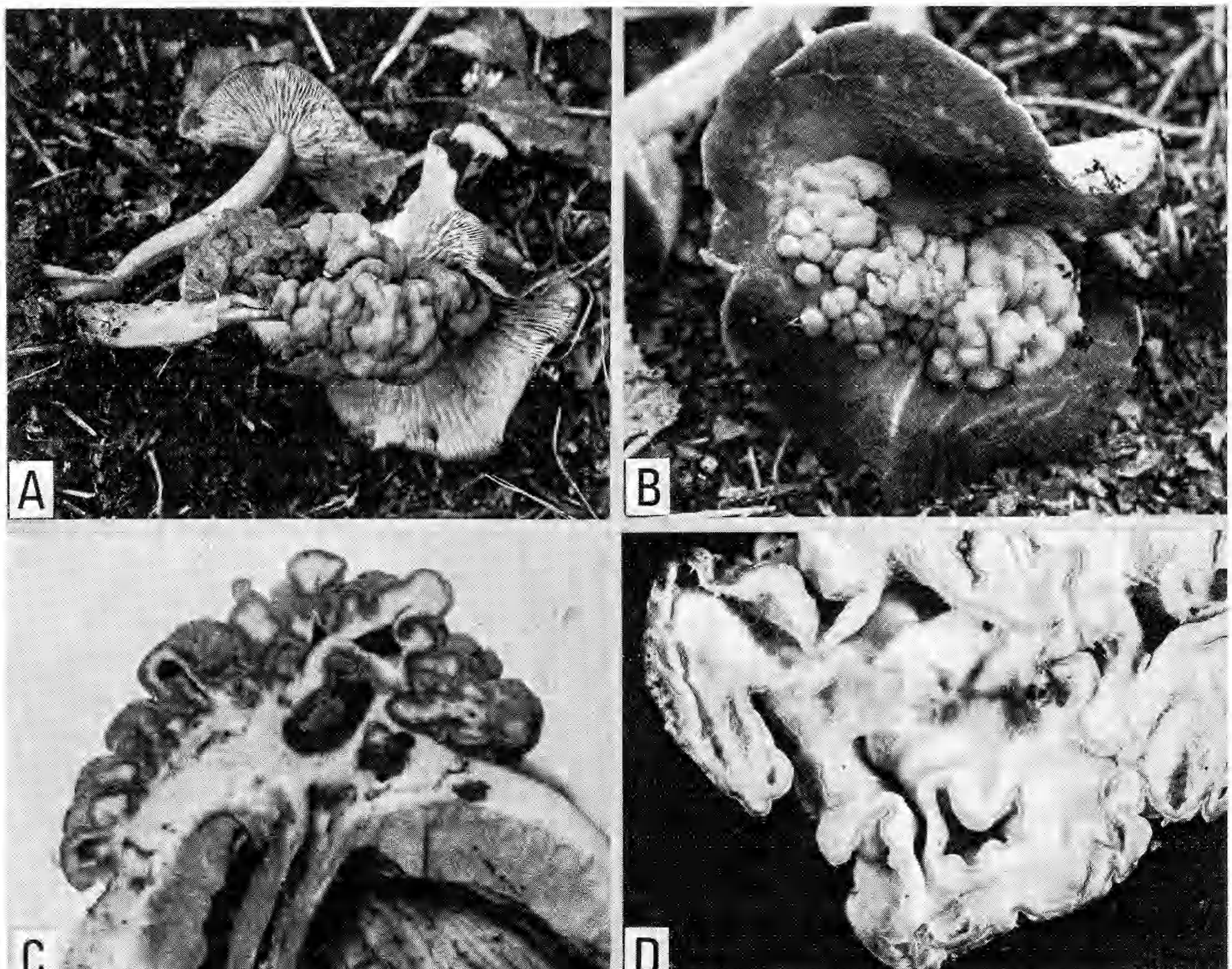

Fig. 1. *Christiansenia effibulata* (A, B, D–F) and *C. tumefaciens* (C). – A, B: Galls on stem and pileus surface of *Collybia dryophila*. – C: Section through gall showing the broad attachment to the pileus of *C. dryophila*. – D: Section through a gall. The darker thin layer on the gall surface is the locus of the parasite. – E: Conidiophore. – F: Basidia. Note the refractive oily deposit inside the apex of the sterigmata. – A, B: Sunhede 7402. – C: Toft (holotype). – D–F: Hansson (holotype).

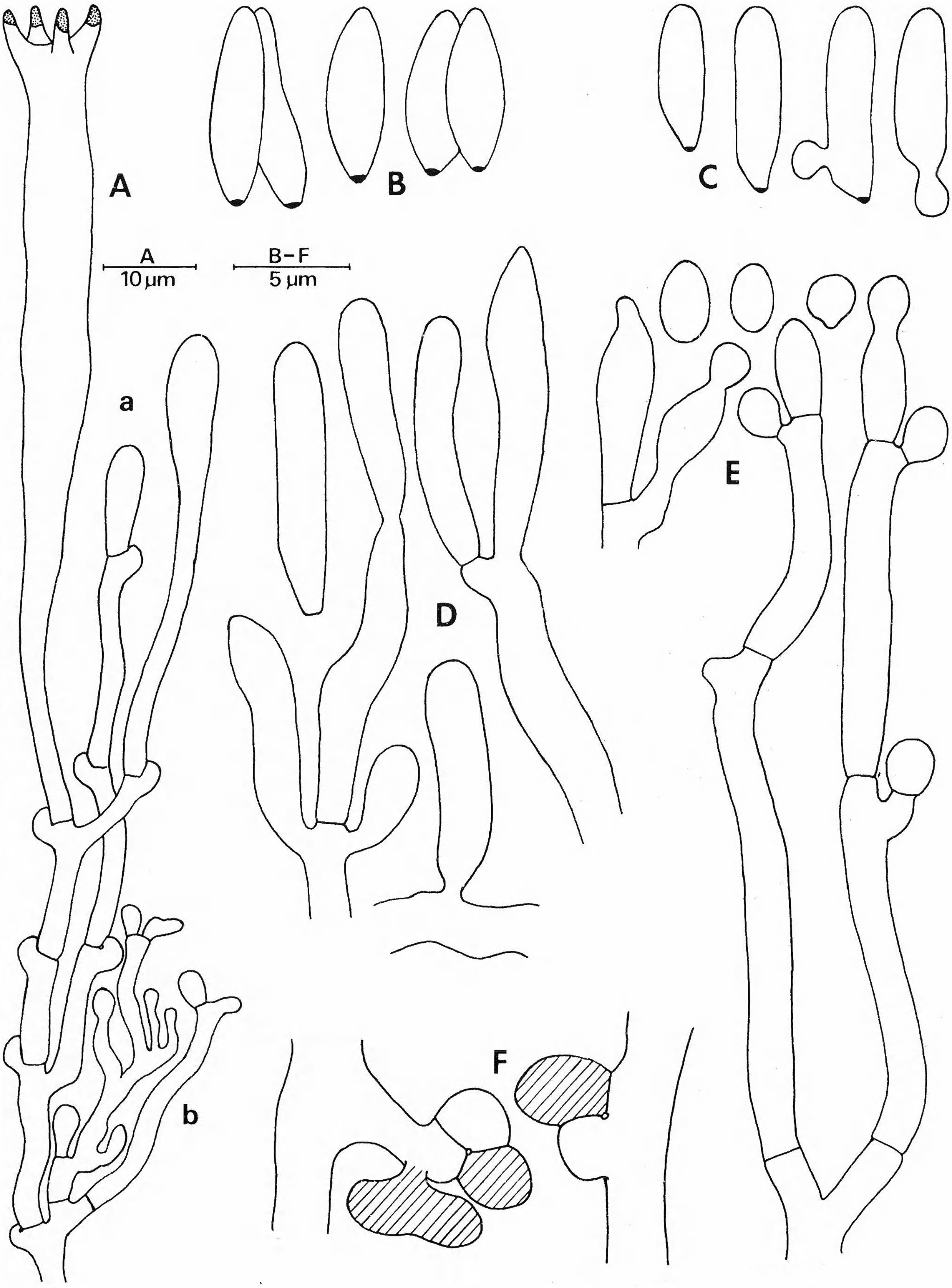

Fig. 2. *Christiansenia mycetophila*. – A: (a) mature and young basidia, (b) conidiophores. – B: Basidiospores in face view. – C: Basidiospores in profile, with two producing blastospores. – D: Arthrospore production. – E: Blastospore production. – F: Small, inflated hyphal cells (obliquely lined). – A–C, E DAOM 7447. – D, F: DAOM 157068.

Fig. 3. A: *Christiansenia effibulata*. (a) four basidiospores in face view (upper right) and three in profile, with two producing blastospores (left margin), (b) basidium with attached spores and a developing conidiophore at the base, (c) young and mature basidia. – B: *C. tumefaciens*. (a) two basidiospores with small pimple indicating former point of attachment, (b) one spore producing blastospore, (c) two developing basidiospores attached to sterigmata, (d, e, g, h) mature and young basidia, (f) small, inflated hyphal cells. – A: Hansson (holotype). – B: Toft (holotype).

tospores and arthrospores as in *C. effibulata*. Substrate as in *C. mycetophila* (Fig. 1 C).

The species is only known from the type collection.

Discussion

Christiansenia mycetophila, *C. effibulata* and *C. tumefaciens* are congeneric with *C. pallida*, the type species for the genus. However, including these three species in *Christiansenia* necessitated minor revisions in the generic description. The revised generic description given above is based on the description in Eriksson & Ryvarden (1973 p. 239).

The three species of *Christiansenia* are macroscopically inseparable. The tremelloid galls (Fig. 1 A–D) occur on the lamellae, the surface of the pilei, and the stipes of the fruitbodies of *Collybia dryophila*. When small (several mm in diameter) they are tuberculate to hemispherical with the apex flattened or slightly depressed. Fully developed galls are several cm in diameter and can nearly envelope the mushroom. The presence of numerous (over 35 on one mushroom) tubercles on the pileus of *C. dryophila* suggests that the large galls arise when small ones coalesce (cf. Fig. 1 B). The galls are composed principally of hyphae of *C. dryophila*. The *Christiansenia* occurs only in the superficial gelatinous layer about 0.1–0.5 mm thick (Fig. 1 C, D).

The collections studied, sometimes consisting of galls on several fruitbodies of the mushrooms, were entirely of only one species of *Christiansenia*.

Two of the three species, *C. mycetophila* and *C. effibulata*, have similar basidia and in both of these species the basidiospores are relatively broadly attached and placed directly over the sterigmata. The usual condition in the Holobasidiomycetidae is that the basidiospores are narrowly attached and develop offset from the longitudinal axis of the sterigmata (see, for example, Eriksson & Ryvarden 1973 Fig. 94 d). The mode of attachment in *C. mycetophila* and *C. effibulata* may make it difficult for these fungi to forcibly discharge their basidiospores and perhaps the mechanism has been lost. In *C. tumefaciens* the spores are borne on the sterigmata in the stance typical for Holobasidiomycetidae. The point of attachment is distinct in being located a short distance from the spore base (Fig. 3 B: c).

Another unusual, characteristic feature of the first two species is the refractive oily deposit inside apex of the sterigmata (Figs. 1 F, 2 A, 3 A: b, c). It can be seen in sterigmata with the basidiospore still attached as well as in sterigmata of old, otherwise empty and partially collapsed basidia. Most basidiospores of mature size have a layer or a lump of this oily deposit at the point where the spore had been attached (Figs. 2 B, C; 3 A: a). This conspicuous oily deposit in the tips of the sterigmata occurs only rarely in the sterigmata of *C. tumefaciens*.

We were astonished to find three closely related fungi on the *Collybia*-galls differing in such important characteristics as clamp connections, spore shape and spore attachment to sterigmata. Rather few collections were studied and it is possible that more types will exist in nature. *Christiansenia tumefaciens* may be more primitive than the other two species because it has clamps and obliquely attached spores. However, cytological studies may help to explain how these three species developed. It thus remains to be shown whether the basidiospores of *C. mycetophila* and *C. effibulata* are true basidiospores or simply a kind of conidia produced from a basidium.

Microscopically the hyphae of *C. dryophila* in the galls appear normal except they are excessively branched. There is no evidence that the parasites penetrate the host cells. No parasite hyphae were seen growing inside the host cells. The actual attachment of the parasite to the host seems to be superficial. The three species of *Christiansenia* produce on the hyphae small, inflated cells (Figs. 2 F, 3 B: f) which are rich in protoplasma, i.e. they strongly color in protoplasmic stains. These cells are likely appressed to the host and probably function in obtaining nourishment for the parasite.

We have not studied the *Christiansenia* species in culture but Bandoni (pers. comm.) and Weresub (pers. comm.) have provided us with their observations. Both found that cultures from spore drops from gall surfaces gave only *Collybia dryophila*. However the four of us agree that this does not definitely indicate that only this fungus is present. Many parasites are very difficult to grow under laboratory conditions. Furthermore, we did not find *C. dryophila* basidia on the galls but yet some free basidiospores of it were present, presumably fallen by chance upon the galls. If some such spores also fell from the galls, it would explain that *C. dryophila* could grow out from spore drops using gall surfaces.

Our investigation has convinced us that the galls consist of two elements, one inner part formed of the hyphae of *Collybia dryophila* and an outer layer of *Christiansenia*-hyphae and hymenium. We have not seen any galls without *Christiansenia* and we therefore believe that these species are parasites on *Collybia dryophila* and also cause the galls. We reject the idea that the *Christiansenia*-basidia, hyphae and spores are produced by the *Collybia*.

Several Basidiomycetes are, like *Christiansenia* species, parasitic on species of the Holobasidiomycetidae. Perhaps the best known are some species of *Tremella* Fr. For example, *T. encephala* Pers. (Bandoni 1961) causes the formation of a cerebriform gall on *Stereum sanguinolentum* (Fr.) Fr. The basidiocarp of *T. encephala* is relatively thick (several mm when fresh) and the host, *S. sanguinolentum,* is confined to the small, white, irregularly shaped core of the gall. The attachment of the host to the parasite is apparently the same as that in the species of *Christiansenia.*

T. mycophaga Martin and *T. simplex* Jacks. & Martin constitute an interesting parallel to *Christiansenia mycetophila* and *C. effibulata* in so far as one of them is fibulate *(T. mycophaga)* and the other *(T. simplex)* effibulate and as both may occur as parasites on the same host, *Aleurodiscus amorphus* (Fr.) Schroet. (Christiansen 1954).

Acknowledgements. We are most grateful to Dr John Eriksson who encouraged this study and actively participated in its development. K. Hjortstam checked some of our morphological observations. Drs R. J. Bandoni, Vancouver and Luella K. Weresub, Ottawa shared their observations and notes on cultural studies. We are also indebted to the curators of DAOM and NYS for loan of specimens and to Professor Å. Fridh, Göteborg, for correcting the Latin diagnoses.

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Studies in African Cyperaceae XVII

Kyllingiella R. Haines & K. Lye, gen. nov.

Richard Wheeler Haines and Kåre Arnstein Lye

Haines, R. W. & Lye, K. A. 1978 03 31: Studies in African Cyperaceae XVII. Kyllingiella R. Haines & K. Lye, gen. nov. *Bot. Notiser 131:* 175–177. Stockholm. ISSN 0006-8195.

A new genus, *Kyllingiella,* based on *Kyllingia microcephala* Steud., is described and illustrated. This plant has usually been included in Scirpeae as *Scirpus microcephalus* (Steud.) Dandy or *Scirpus kyllingioides* (A. Rich.) Boeck. *Kyllingiella* is, however, a typical representative of Cypereae and possibly most closely related to *Isolepis* R. Br. A new species, *Kyllingiella ugandensis* R. Haines & K. Lye, is described from N Uganda.

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Steudel (1842) described a new plant from Ethiopia which he named *Kyllingia microcephala*. This plant was a typical *Kyllinga* in several respects. It had the white capitate inflorescence and the general habit of a *Kyllinga*. However, it differed in having spirally arranged glumes, which a *Kyllinga* never has, and A. Richard (1851 p. 502) gave the species the name *Isolepis kyllingioides*. Böckeler (1870) transferred this plant to *Scirpus* under the name *Scirpus kyllingioides*.

Recent authors (with the exception of Haines & Lye (1971) and Raynal (1976), who name this plant *Isolepis microcephala*) regard this plant as a *Scirpus,* for which the name *Scirpus microcephalus* (Steud.) Dandy is used, cf. Napper (1963), Hooper (1972), Lowe & Stanfield (1974). In our opinion it is almost unbelievable that botanists can associate this white *Kyllinga*-like plant with the temperate *Scirpus sylvaticus,* the type species of *Scirpus*. At least with Van der Veken's (1965) classical embryological paper in mind one would expect that such associations should be entirely eliminated. It appears that the only character in common between *Scirpus sylvaticus* and *Isolepis microcephala* is their spirally arranged glumes. Druyts-Voets (1970) reports that *Scirpus microcephalus* has a eucyperoid stem and leaf anatomy.

In a previous paper (Haines & Lye 1971) we tried to show that the genus *Isolepis* could have been evolved from *Cyperus* through the genera *Lipocarpha* and *Hemicarpha*. This development and taxonomic position was accepted by Raynal (1973), but only for species with a chlorocyperoid culm anatomy, and he established a new genus, *Rikliella* J. Rayn., for these species.

Even with the exclusion of *Rikliella* the genus *Isolepis* remains heterogeneous. It is not unlikely that some species have evolved from a *Cyperus*-like ancestor by a mere change of glume position, while others have developed from eucyperoid plants by reduction of spikelet structure in a similar way as *Rikliella*.

While it was possible to find intermediate plants between the genera *Isolepis* R. Br. and *Eleogiton* Link (cf. Lye & Haines 1974), *Isolepis microcephala* has a rather unique position within the genus. We have therefore come to the conclusion that a new genus should be established for this and a few related undescribed species. We have given this genus the name *Kyllingiella,* since it looks like a small *Kyllinga* in general habit.

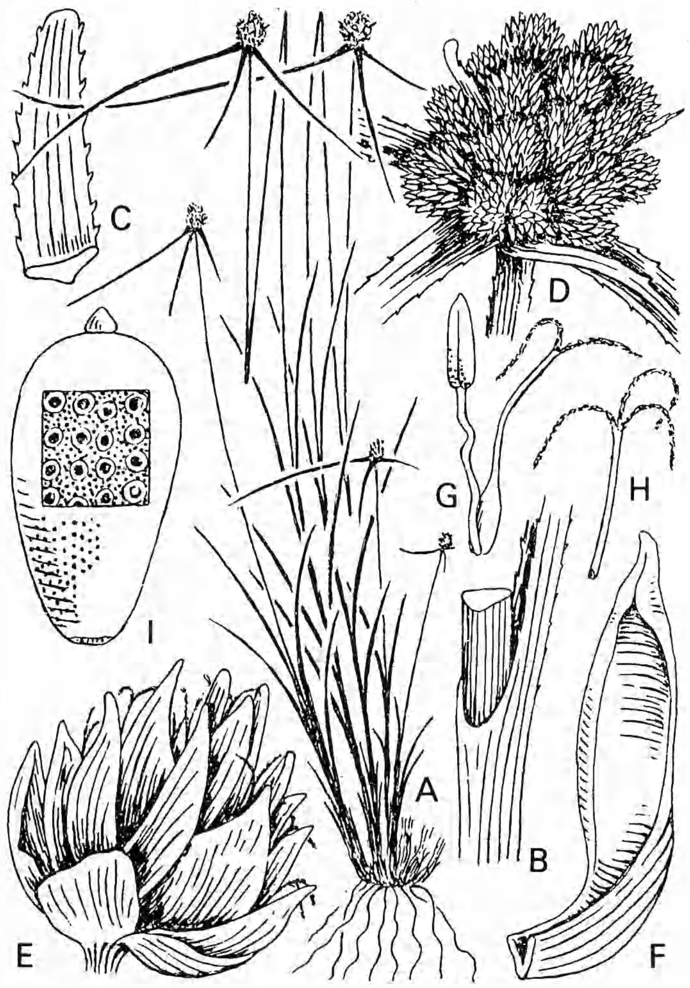

Fig. 1. *Kyllingiella microcephala*. – A: Habit, reduced. – B: Detail from culm showing throat of leaf-sheath. – C: Leaf-tip. – D: Capitate inflorescence. – E: Part of inflorescence. – F: Prophyll. – G: Flower with one stamen and gynoecium with a 2-branched style. – H: Style with 3 branches. – I: Nutlet. – Drawn from Haines 4218 (Lokapel, Karamoja, Uganda) by Richard Wheeler Haines.

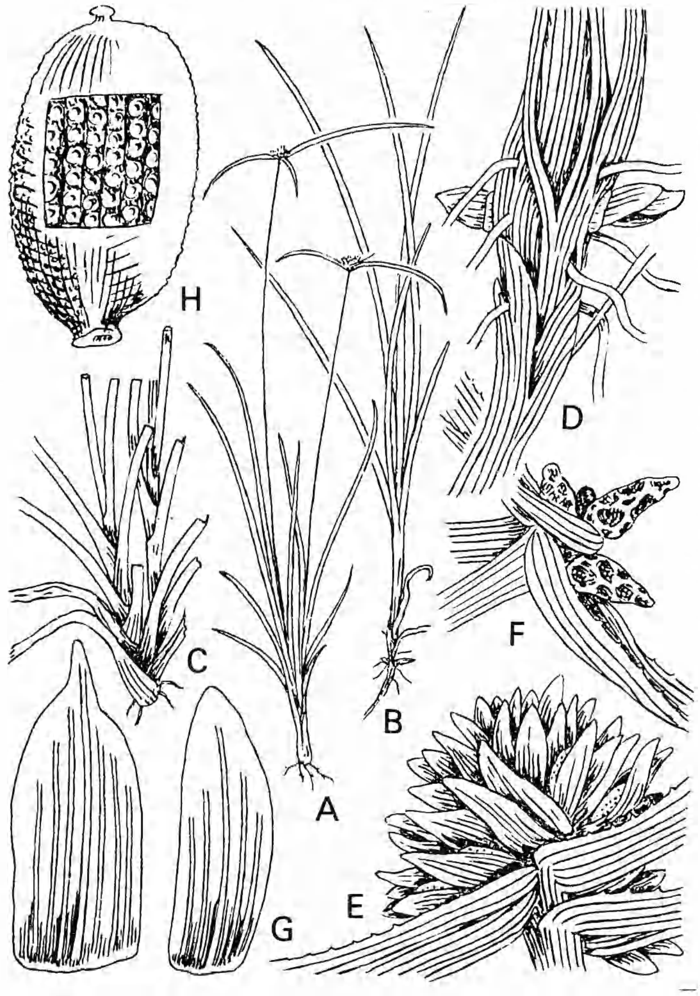

Fig. 2. *Kyllingiella ugandensis*. – A, B: Habit, reduced. – C: Plant base. – D: Base of culm. – E: Inflorescence. – F: Old inflorescence with all spikelets gone. – G: Pseudoglumes. – H: Nutlet. – Drawn from the holotype by Richard Wheeler Haines.

Kyllingiella R. Haines & K. Lye, gen. nov.

Typus generis: *Kyllingiella microcephala* (Steud.) R. Haines & K. Lye.

Rhizoma abbreviatum. *Culmi* plures caespitosi, 5–40 cm alti et 0.2–0.5 mm lati. *Folia* 1–7, 3–15 cm longa et 1–2 mm lata; *vaginae* longae, brunneae vel canescentes. *Inflorescentia* congesta 2–8 mm diam. perdensa. *Spiculae* numerosae, ovato-oblongae, 1-florae. *Squamae* 1.2–2.4 mm longae, ovato-lanceolatae, obtusae, stramineo-albidae, obsolete nervosae. *Stylus* bifidus vel trifidus. *Nux* 0.5–0.8 mm longa et 0.3–0.6 mm lata, elliptica vel obovata, minute punctata.

The genus *Kyllingiella* R. Haines & K. Lye is very similar to *Isolepis* R. Br. in spikelet structure, but this does not necessarily mean that these two genera are very closely related. The almost nerveless, white glumes of *Kyllingiella* are very different from the glumes of *Isolepis setacea* (L.) R. Br., the type species of *Isolepis*. Also the very different nutlets indicate that these plants may have evolved from very different ancestors. As regards *Kyllingiella* these ancestors are almost certainly *Cyperus*-like, but this is not necessarily so as regards *Isolepis*.

Kyllingiella microcephala (Steud.) R. Haines & K. Lye, comb. nov. – Fig. 1

Basionym: *Kyllingia microcephala* Steud. in Flora 25: 597 (1842). – *Scirpus microcephalus* (Steud.) Dandy in F. W. Andrews, Fl. Pl. Sudan III: 366 (1956). – *Isolepis kyllingioides* A. Rich. in Tent. Fl. Abyss. II: 502 (1851). – *Scirpus kyllingioides* (A. Rich.) Boeck. in Linnaea 36: 733 (1870). – Holotypus: Schimper 650, prope Gon Amba, Ethiopia (P).

Kyllingiella ugandensis R. Haines & K. Lye, sp. nov. – Fig. 2

Holotypus: M. P. Kertland 111, 6. 1963, Uganda, Acholi, Lotuturi (MHU).

Herbae perennes. *Rhizoma* abbreviatum. *Culmus* 8–15 cm longus et 0.2–0.5 mm latus. *Folia* 3–7, 4–15 cm longa et 1.0–1.5 mm lata, scabrida; *vaginae* longae, brunneae vel viridae. *Inflorescentia* congesta 2–4 mm diam. perdensa. *Spiculae* numerosae, 1-florae. *Squamae* 1.8–2.4 mm longae, lanceolatae, obtusae, albidae. *Stylus* trifidus. *Nux* 0.7–0.8 mm longa et 0.4–0.6 mm lata, elliptica, brunnea, minute punctata.

A very slender perennial with a short, erect, slender rhizome. *Stems* 8–15 cm, 0.2–0.5 mm thick, triangular in transection at least above, the base slightly swollen and covered by old dark leaf-sheaths. On each stem 3–7 well developed *leaves,* usually 4–15 cm long and 1.0–1.5 mm wide, flat, but margins frequently enrolled when dry; upper surface with large rectangular cells; margins and midrib with short spine-like teeth; leaf-sheath green or pale brown below; ligule absent. *Inflorescence* a dwarf terminal head (2–3 mm long and 3–4 mm wide) of many small ovate pseudospikelets, remaining whitish when dry. Inflorescence-bracts usually 2–3, spreading, the longest 1.5–4.0 cm long, ieafy; margins and midrib with densely set, short, spine-like hairs. *Pseudospikelets* about 2 mm long, consisting of a strongly notched central axis (as in *Lipocarpha* and *Ascolepis*) and about 6–10 pseudoglumes, all the lower ones fertile, subtending a naked flower representing a reduced spikelet. *Pseudoglumes* 1.8–2.4 mm long, whitish, lanceolate with slightly incurved margin; apex obtuse, not bent or cucullate; midrib usually distinct. *Perianth* segments absent. Stamens not seen. *Style* branches 3. *Nutlet* 0.7–0.8 mm long and 0.4–0.6 mm wide, obovate to elliptic, dark grey to brownish; surface with a metallic shine and minute tubercles in longitudinal rows; the base of the style persisting as a minute knob.

Probably in dry grassland, 1200 m (4000 ft). Very rare. Uganda, Acholi (only recorded from near Lotuturu).

This species is closely related to *Kyllingiella microcephala* but differs in the much smaller inflorescence-heads, the much smaller and ovate (not globose) pseudospikelets, the larger glumes without cucullate and bent apex, and the slightly larger nutlet.

In addition to *K. microcephala* and *K. ugandensis* there are one or two undescribed species of the genus from S Tanzania and Zambia.

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Botanical literature

Moberg, R. 1977: *The lichen genus Physcia and allied genera in Fennoscandia.* Symbolae Botanicae Upsalienses 22(1). Uppsala. 6 + 108 pp., 42 figures in text, 2 plates (illustrating type material in herb. Acharius, Helsinki) and 26 distribution maps. ISBN 91-554-0648-3. ISSN 0082-0644. Price SKr 50:– (wrappers).

Physcia was formerly considered to be a fairly well-known genus, at least so far the European and North American species were concerned. The classic studies by Lynge and Du Rietz in the 1910's and 20's led to an apparently stable species concept and nomenclature. Magnusson (Lichen Fora, 1929) at first recognized 21 species in Scandinavia and later (Check-list, 1936, following Lynge's account in Rabenhorst's Kryptogamen-Flora) 23 species from the same area.

In 1965 Poelt segregated the species known as *P. grisea, muscigena* and *pulverulenta* as a new genus, *Physconia,* mainly founded on characters of spore morphology. He also pointed out that the sorediate–isidiate species *P. grisea* is a complex which can be subdivided into four separate species, which differ in cortex morphology and to some extent phytochemically. Poelt's concepts have gradually become accepted by most lichenologists.

This monograph was presented as Moberg's Ph. D. thesis at the Institute of Systematic Botany, University of Uppsala, on June 2nd, 1977. Moberg follows the general trend in modern lichenology, to divide the traditional lichen genera into smaller units of generic rank. Hence *Physcia* s.lat. now appears as four separate genera, viz. *Physcia* s.str., *Physconia, Physciopsis* and *Phaeophyscia. Physcia* s.str. now comprises 10 species: *P. adscendens, semipinnata* (formerly known as *leptalea*), *tenella, aipolia, caesia, phaea* (=*melops*), *magnussonii, dimidiata, dubia* and *stellaris. Physconia* comprises 6 species: *detersa, enteroxantha, muscigena, perisidiosa* (=*farrea* auct.), *pulverulenta* and *grisea.* The minute species previously generally known as *Physcia adglutinata* now represents the sole Scandinavian species in the genus *Physciopsis.* It is widely distributed over other parts of Europe but is rare in our area (2 localities each in Sweden and Norway). *Phaeophyscia* is described here as a new genus, primarily differing from *Physcia* s.str. by its brownish thallus and lack of atranorin. It comprises 8 species: *P. ciliata, constipata, endococcina, endophoenicea, kairamoi, nigricans, orbicularis* and *sciastra.*

According to the species concept accepted by Moberg, *Physcia* s.lat. thus comprises 25 species in Sweden, Norway, Finland and Denmark (not 23 as stated in the abstract!). Three of these, *P. endophoenicea, kairamoi* and *magnussonii,* have first been reported from our area during the past ten years.

Brief introductory chapters on Morphology, Chemistry, Distribution and Habitat, and Primary and Secondary Species precede the main part, devoted to Taxonomy. The author has paid much attention to nomenclature and typification. Each species is described in detail, with remarks on its chemistry, variability and affinities. Distribution data and habitat are also discussed. Some SEM and TEM micrographs illustrate important details of the ultrastructure of spores and other tissues. However, some other photographs in the text showing the habit of certain species are less instructive. As a matter of fact greyish lichens are notoriously difficult subjects for black-and-white photography.

Moberg's revision is both thorough and critical and contributes very much to our knowledge of this genus. Some comments and questions may nevertheless be justified.

As mentioned above, the species usually called *P. leptalea* (Ach.) DC. is here presented as *P. semipinnata* (Gmelin) Moberg. It is evident that *Lichen leptaleus* Ach. (sec. the original description in 1798) is a sorediate saxicolous species. It is not identical with the non-sorediate corticolous species later known as *P. leptalea*. Moberg rejects *L. leptaleus* for another reason. It is supposed to be a superfluous name, since Acharius wrote "Forsan huc referendus: *Lichen semipinnatus* Leers herb. Gmel." "Forsan" means "perhaps" and the quoted phrase does not indicate that Acharius published his name in synonymy. From Gmelin's brief description and his reference to Leers it is not clear whether *L. semipinnatus* is *P. leptalea* auct., non Ach. Instead of selecting a neotype, as Moberg has done, the reviewer would have first investigated whether or not Gmelin's name could be lectotypified on the basis of his citation of Dillenius, Historia muscorum (1741). According to Crombie (1880) at least a part of the relevant material preserved in Dillenius' Herbarium refers to *"P. leptalea"*.

The lichen usually known as *P. marina* or *P. subobscura* is treated by Moberg as *P. tenella* var. *marina*. It grows exclusively on maritime rocks, whereas the main type (var. *tenella*) is generally corticolous. If Moberg's statement that "the differences between the taxa probably are induced by the different habitat" is correct, then he should have considered them simply as modifications lacking taxonomic rank.

The distributions of most species have been summarized in maps based on the Universal Transverse Mercator grid-system used in the Atlas Florae Europaeae. Only exceptionally (some rare species) are exact localities published. Instead, complete lists of all the known localities have been deposited in the Stockholm and Uppsala Herbaria.

No mention is made of the fact that some species may have become rare or even have disappeared during the past few decades because of air pollution. Recent studies from the British Isles have reported the rapid disappearance of several corticolous macrolichens in industrial areas. In Denmark Søchting (*Urt* 1977 p. 70) included *P. pulverulenta* in his group of "very sensitive species". This agrees with the reviewer's own experience of this species in highly polluted areas in southern Sweden. The use of different symbols on the maps for this and other species for localities recorded before and after 1960 would have been of considerable interest.

Some other maps show notable generalized types of distribution areas (e.g. of southern, northern or alpine species) which are analogous with those also known among species of bryophytes and vascular plants. A few species of *Physcia* seem to be so far unknown from large areas in Småland and Östergötland, although these gaps can probably be filled in by making further field studies.

Moberg's thesis will hopefully be followed by similar monographs of other lichen genera, not the least of crustose lichens. There are several groups among these, for instance in the Pyrenocarpeae and in the "Gloeolichenes", where hardly any research has been done, at least not in Scandinavia, for more than one hundred years. The latest flora with an aim to cover the whole field of lichens, though it was never completed, was Th. M. Fries, *Lichenographia Scandinavica*, 1–2, (1871–1874). This fact should be a challenge to Scandinavian lichenologists to produce a complete Scandinavian Lichen Flora in the not too distant future.

Ove Almborn

Haslam, S. M., Sell, P. D. & Wolsely, P. A. 1977: *A flora of the Maltese Islands*. LXXII + 560 pp., 70 plates with c. 450 line drawings. Malta University Press. Price (paper) £ M 3.50.

This is the first complete flora of the Maltese Islands since J. Borg's *Descriptive flora of the Maltese Islands* (1927), recently reprinted by O. Koeltz.

The opening chapters include information on geography, topography, climate, soils, vegetation, and other physical aspects. A good proportion of the information given here is original. There is also a useful section on the history of the study of the Maltese flora, but although the information here is essentially accurate, it leaves the reader with the impression that hardly any work was done in this field in the period between the two floras.

The flora includes descriptions of about 1130 species (of which some 160 are commonly cultivated plants). Apart from the authors' own observations, the records have been based mostly on the work of Grech-Delicata (1853), Sommier & Caruana-Gatto (1915), Borg (1927), G. Lanfranco (1955, 1969) and Kramer & Westra (1972). The way in which they quote the records is inconsistent since they fail to acknowledge a number of records given by the above and other authors. Thus they fail to quote Sommier & Caruana-Gatto for 200 records, G. Lanfranco for about 70, Kramer & Westra for 14. Only about a dozen of Borg's records have been overlooked but the authors seem to ignore completely the existence of his *Third supplement* (1935) with the result that some half-dozen newly recorded species are left out of the flora.

The authors also ignore the existence of a number of important papers published in *The Maltese Naturalist*. Considering that the most recent insertion in their bibliography is dated 1975 it works out that 9 of the relevant papers appearing between 1970 and 1974 have been disregarded. It is evident that the authors had access to this periodical since they cite two papers from it. This resulted in the omission from the flora of more than 40 species and in the failure to correct old records in the light of new information (e.g. *Centaurea pullata* and *Gaudiniopsis macra* which should be replaced).

The status given to the plants included in the flora also shows a number of inconsistencies. Thus a number of cultivars and hybrids of *Narcissus* which very occasionally escape from cultivation are given a full treatment. Conversely such important taxa as *Enarthrocarpus pterocarpus*, *Polygonum equisetiforme* and *Nicotiana longiflora* are relegated to a brief mention. Various doubtful records appearing in the old floras have been included here without comment while many validly recorded and confirmed species in the recent papers of Kramer & Westra, E. Lanfranco and Silverwood (all cited in the bibliography) have been left out of the flora completely and arbitrarily. Among victims of such treatment are *Polygonum patulum, Chenopodium ficifolium, Ononis alopecuroides* (a frequent plant), *Cephalaria syriaca, Rumex obtusifolius* (common) and *Rumex sanguineus*.

Some of the genera receive a poor treatment. Thus only four out of at least eight species of *Rumex* and only five out of nine species of *Amaranthus* are recorded. *Andropogon distachyus* must have been omitted by oversight since this is common and well known. The authors also failed to take into consideration a number of recent revisions of genera such as those of Runemark *(Parapholis)*, Pignatti *(Phagnalon)* and Steinberg *(Adonis)*, all of which bear on the Maltese plants. They misquote Sommier & Caruana-Gatto claiming that according to these authors, *Cerastium brachypetalum* is more frequent than *C. glomeratum*, whereas Sommier & Caruana-Gatto actually claim the reverse.

On the credit side I should mention the inclusion of four new records: *Carex spicata, Origanum onites, Myriophyllum verticillatum* and *Paspalum dilatatum*. Some of the misidentifications appearing in the older floras have been put right. These include *Fraxinus angustifolia, Carex otrubae, Onopordum argolicum* and *Aster squamatus*, replacing *F. excelsior, C. vulpina, C. sibthorpianum* and *A. subulatus* respectively. Other positive features include the incorporation of a very useful glossary and the very low price which brings this relatively vast work within reach of everybody's pockets.

The illustrations are generally very well executed and accurately display the character of the plants they portray. It is a pity that as a result of the quality of printing and reduction, some of the diagrams have lost clarity. It is also unfortunate that some of the diagrams represent plants other than those which they are meant to portray. Thus *"Galium aparine"* is *Rubia peregrina* (which features twice in the same plate), *"Vicia tetrasperma"* is *V. leucantha, "Frankenia levis"* is *F. pulverulenta, "Chenopodium album"* is *C. opulifolium*. The names of *Ferula communis* and *Foeniculum vulgare* have been switched (printer's error?).

The authors have given new Maltese and English names to some of the species. I do not personally agree with inventing new vernacular names where they do not exist but if it has to be done, this should be the responsibility of a board of botanists and linguists and not arbitrarily. Some of the new names are impractical, e.g. Widen il Ġurdien Idellek *(Cerastium glomeratum)*, Kittien tal-Imħarbat *(Linum strictum)* and Xnejn inħaxlet (sic; *Trifolium campestre* and *scabrum*). Calling *Scilla autumnalis* Għansal tax-Xitwa (transl. Winter Squill) is misleading. Silla Qatranija for *Psoralea bituminosa* is superfluous since this plant already enjoys at least two vernacular names. Some of the new English names are not much better, e.g. Bloody Broomrape *(Orobanche sanguinea)*. It is strange then that some well-established Maltese names have been omitted e.g. Tuffieħ is-Serp *(Solanum luteum)* and Għallis *(Notobasis syriaca)*.

In spite of the numerous technical faults outlined, this book is still valuable when considered simply as an identification guide. The incorporation of keys and the diagrams, especially the details given on the legumes of the many *Medicago* species and the flowers of *Ophrys* would make this book much easier to use than Borg's flora. I urge anybody interested in identifying Maltese plants to get the book. I cannot help mentioning that had the authors taken the trouble to consult people actively working on the Maltese flora, all the technical faults mentioned could very easily have been averted.

Edwin Lanfranco

Kokwaro, J. O. 1976: *Medicinal plants of East Africa*. 384 pp., 2 maps and 36 figs. East African literature bureau, Nairobi. Price K. Sh. 65:80 (soft cover) or 96:50 (hard cover).

Apart from introductory chapters, indices to vernacular and Latin names, and a glossary of medicinal terms the book is arranged in two main parts. The first one gives a survey of the about 1200 species treated, conveniently arranged with families and genera of angiosperms in alphabetical order. Under each species details are given about which parts of the plants have been used, how they should be treated, and against which diseases they have been found helpful. A number of species are illustrated by line-drawings or photographs. Some species have been applied only against one disease, as *Juniperus procera* against intestinal worms, whereas others, like *Bridelia micrantha,* have a variety of uses. The second part attempts a survey of diseases in East Africa and enumerates the plant species used against each of them. The number of plant species employed against each disease varies very much. Thus no less than 111 were used as antidotes against snake bites, while 3 are reported of use against cancer and none against sleeping sickness.

The wealth of information on medicinal uses of East African plants given in this book will doubtless be invaluable for future research on plant medicines. Its usefulness is, however, somewhat reduced by weaknesses in documentation. That the authors of Latin names are omitted would hardly cause any trouble, since they can easily be found from relevant floras. A more serious drawback is that no voucher specimens are quoted for the records of medicinal use. Any pharmacologist embarking on research on these matters should have the possibility to check the determination of those species for which information is utilized; but that seems to be impossible here. All pieces of information concerning medicinal use of a species are integrated into a common description, and the only reference given to sources of information appears in the tribal names of the plant, the distribution of the main tribes being shown in one of the maps. Presumably voucher specimens for many records do in fact exist in the East African Herbarium or in the Herbarium of the Botany Department, University of Nairobi, but this is nowhere mentioned.

It is also unfortunate that no distinction is made between information gathered by the author in the field, supplied by his students, or gleaned by himself and/or collaborators from collector's labels in the East African Herbarium. The last-mentioned source will probably have been the most important one, but this is not mentioned in the book. An ideal type of reference system might have been to quote one voucher specimen for each area from which a certain medicinal use of a plant species has been recorded. It would also have been interesting to have indicated on a map from which areas information on medicinal use of plants have been recorded by the author, by his students, and by (other) collectors represented in the East African Herbarium; and, not least, from which areas no information at all is available.

In spite of this criticism of some details I find it quite obvious that Dr Kokwaro's book represents a very important contribution towards the salvage of knowledge concerning traditional medicinal plants in East Africa. As emphasized by the author, much of the knowledge about traditional plant medicines possessed by the present generation of East African herbalists is likely to follow them in the grave, unless saved by careful exploration in the way exemplified by him. There is also little doubt that very much more remains to be found out. The urgency of this task is enhanced by the fact that many of the plant species concerned are themselves threatened by extinction. It is therefore imperative to intensify the exploration of tropical floras not only with respect to medicinal plants but equally much considering threatened plant species and ecosystems in general. Dr Kokwaro must be congratulated on a good start concerning East African medicinal plants. Let us hope that his work will be followed by further and more detailed botanical-pharmacognostic studies so that as much as possible of existing knowledge on traditional plant medicines can be adequately documented and utilized in modern pharmacology.

Olov Hedberg

Ružička, J. 1977: *Die Desmidiaceen Mitteleuropas*. Band 1, 1. Lieferung. 292 pp., 44 plates. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart. Price DM 138.–.

This book is the result of many years of intensive research and dedication to a single subject, desmids. The author deserves every credit for his prodigious industry.

Desmids form one of the largest groups of freshwater algae. Many genera teem with species, e.g. *Cosmarium* has more than 2000, and *Staurastrum* has more than 1000 taxa. Most desmids are beautiful in form and have always attracted the attention of phycologists. This has resulted in an immense number of publications dealing with desmids, 6000–7000 at least. Of course, a great many are of little taxonomic or ecological use, simply because the taxonomic treatment of material is inadequate.

At the beginning of this century West & West started the publication of a large, five-volume monograph of British desmids. The fifth volume was compiled after their deaths. That monograph is still of great use to phycologists and has already been reprinted. In 1935 Krieger started to publish a comprehensive flora of desmids, which remains unfinished due to the death of the author. That flora has also been reprinted and is widely used for desmid identification. Gerloff has made an effort to continue Krieger's work, by producing a monograph on *Cosmarium*. However, its publication has been interrupted for many years. A Russian equivalent to Krieger's flora was started in 1952 by Kossinskaja, due to her death it is incomplete, extending only to *Micrasterias*. [N.b. the author transcribes her name Kossinskaja, not Kosinskaja.] An exhaustive North American desmid flora was initiated in 1972 by Prescott, Croasdale and Vinyard; three parts of that monumental treatise have hitherto been published.

Now a Central European desmid flora has been launched by the eminent Czechoslovakian desmidiologist Dr Jiři Ružička. The first part, which extends to the genus *Triplastrum*, is a very handsome volume.

The many preparatory studies published by Dr Ružička provide some idea of the character of his flora. It is quite evident that the author has a juridical background, not only from the very instructive chapter on nomenclature, but also because he has carefully brought all taxa into compliance with the Code. As a result, for example, our old friend *Closterium ulna* Focke should now be called *C. directum* Arch., and the legal name of *C. libellula* Focke is *C. closteroides* (Ralfs) Louis & Peters. Most phycologists prefer to apply commonly used names; therefore we should be grateful to the author for sparing us from many troubles with the problems of nomenclatural legality.

The author has re-established *Pleurotaenium rectum* Delp. and *P. maximum* (Reinsch) Lund., which were formerly considered as varieties of *P. trabecula* (Ehr.) ex Näg., and likewise *P. crenulatum* (Ehr.) ex Ralfs in Rabenh., which seems to be more related to *P. nodulosum* (Bréb.) De Bary than to *P. ehrenbergii* (Bréb.) De Bary. *P. nodulosum* has been picked out from amongst the varieties grouped with *P. coronatum* (Bréb.) Rabenh. The distinction often lies in very subtle and variable details in cell shape, and is therefore often almost a matter of taste. Practical application in the future will pass the ultimate verdict.

The arrangement of the flora is exemplary. Every taxon has been clearly described and the synonyms are listed. Moreover, there are extremely useful paragraphs on distinguishing characters, taxonomy and variation. The alpha and omega for any phycological work are the illustrations: when making an identification one's own figures should be carefully compared with the published ones. Accordingly, the author has provided no fewer than 44 plates. The figures have been skilfully chosen from amongst those already published, although many are excellent originals made by the author. As a rule every taxon is exemplified by several illustrations and, where necessary, there are also close-ups of the proximal ends and the membrane structure of the cells. The careful arrangement of the figures on the plates is instructive, often making direct comparisons between allied taxa practicable.

Finally, the proper name for the last taxon treated in this book should be *Triplastrum spinulosum* (Kisselev) Gauthier-Lièvre, according to the Code, Art. 11.

Kuno Thomasson

Drouet, F. 1977: *Revision of the Nostocaceae with constricted trichomes*. Beiheft zur Nova Hedwigia 54. 258 pp., 42 figs. J. Cramer Verlag, Vaduz. Price DM 100.–.

This supposedly exhaustive revision is the fourth in a series published by the author since 1956. The first one was reviewed by Skuja in *Svensk Bot. Tidskr. 50:* 550–556 (1956), and the comments then made also apply to the subsequent revisions. There is no denying that a great need exists for reliable treatments of many groups of the blue-green algae. However, any knowledgeable reader will find it hard to make use of the present taxonomic results. The results of his revisions represent a kind of 'phycology without tears': the Nostocaceae are simply divided according to the shape of the trichome into two groups, those with a cylindrical trichome and those with a constricted one. Those with cylindrical trichomes consist of three genera, characterized by the shape of the terminal vegetative cells: *Scytonema* (1 taxon), *Calothrix* (2) and *Raphidiopsis* (1). Likewise, those with constricted trichomes are grouped according to the shape of the terminal vegetative cells into the genera *Nostoc* (2) and *Anabaina* (2). No more trouble with bothersome taxonomic details such as the shape of heterocysts, spores, etc.! Naturally enough, every one of his taxa has hundreds of synonyms.

Dr Drouet has fixed ideas and a theory which he is determined to communicate. He expects the facts to accommodate themselves to his grand design. A serious phycologist has hardly any use for his taxonomy, because it would involve loss of much information, often of a potentially ecological kind. Nevertheless, some documentary value does attach to this book, because the author has undertaken a lot of independent research, as well as a total revision and countercheck of all the available material, both published and in collections. The book accordingly forms a valuable source of information about hitherto-described taxa, distribution, collections, publications, etc.

Although it has been found necessary to point out that the work has only a restricted value from the taxonomic point of view, this is not meant to denigrate Dr Drouet's work. The long hours of unremitting and unglamorous toil which he has put in over a number of years on a monotonous task which few phycologists would not have found daunting, and the usefulness of the information thereby gathered together deserve very great praise.

Kuno Thomasson