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New species of Homothecium and Ramalodium from S America

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Four new taxa of the Collemataceae are described: *Ramalodium austroamericanum* and *Homothecium intermedium* from Argentina, *H. sorediosum* from Chile, and *H. opulentum* var. *redonii* from Chile and Argentina. The formation of isidia and soredia in species of *Homothecium* is compared to corresponding processes in other cyanophilic lichens. The developmental morphology of the ascocarp in *Homothecium* and *Ramalodium* is analysed in detail. An emendation of the generic diagnosis of *Homothecium* and *Ramalodium* is given.

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The species of *Homothecium* and *Ramalodium,* genera of the Collemataceae possessing simple spores, are rare lichens. The genus *Homothecium* is endemic in S America. Hitherto, two of the species recognized, *H. chilense* (Räs.) Henss. and *H. patagonicum* (Räs.) Henss., were only known from the type locality, while the type species, *H. opulentum* (Mont.) Massal., has been collected several times (Henssen 1965). In the course of field studies in S America in 1973–74, we specifically searched for *Homothecium* species and discovered, besides *H. opulentum* and *H. patagonicum,* two undescribed *Homothecium* species, here named *H. sorediosum* and *H. intermedium. H. sorediosum* produces soredia, a unique feature in the Collemataceae. A new variety of *H. opulentum* has been communicated by Professor J. Redon (Valparaiso) and is named in his honour as var. *redonii.* Collections made in Juan Fernandez by Dr Imshaug (East Lansing) included another specimen of the new *H. sorediosum* and interesting material of *H. opulentum.*

The three *Ramalodium* species previously known (Henssen 1965) are endemic: *R. succulentum* Nyl. in Cromb. to Australia (Tasmania was previously erroneously cited as the country of origin; according to Dr G. C. Bratt the type locality, "Grose River" is in Victoria, Australia), *R. neocaledonicum* (Räs.) Henss. to New Caledonia, and *R. japonicum* (Asah.) Henss. to Japan. A further species of *Ramalodium,* here described as *R. austroamericanum,* was discovered. The occurrence of a new *Ramalodium* species in S America considerably extends the distributional range of the genus.

As a result of the new taxa described here, an emendation of the generic diagnosis of the genera *Homothecium* and *Ramalodium* has been necessary.

Methods. The freezing microtome sections were mounted in lactophenol cotton-blue. The measurements given of spores, sections and other anatomical structures concern permanent preparations mounted in lactophenol. The photomicrographs were taken with a M 20 Wild microscope and a M 7 Wild stereomicroscope. The camera lucida drawings were prepared by means of a Wild drawing tube.

Delimitation of Homothecium and Ramalodium

The developmental morphology of the ascocarp was used to separate *Homothecium* and *Ramalodium:* in mature apothecia, the excipulum

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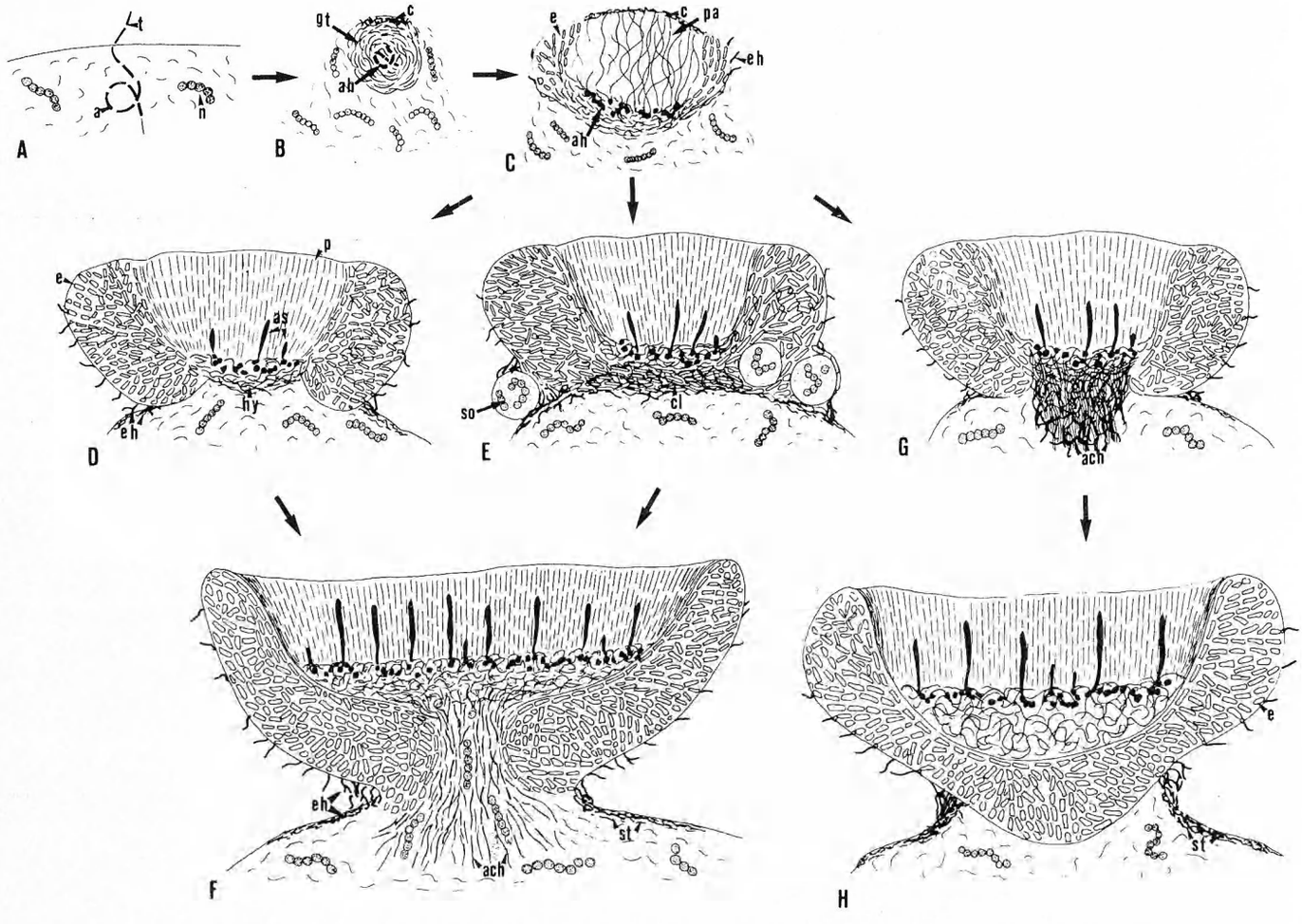
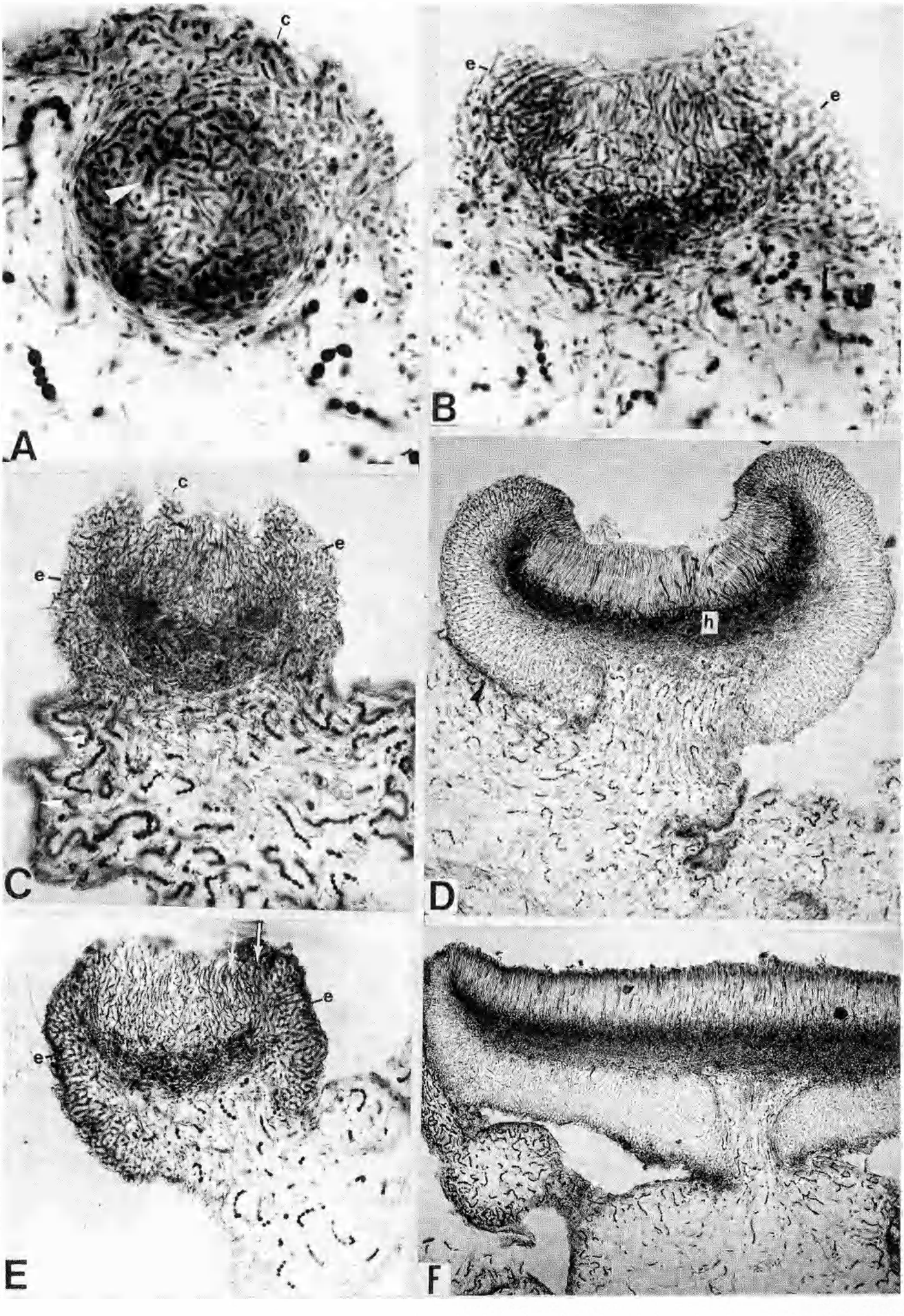


Fig. 1. Ascocarp development in *Homothecium* and *Ramalodium* (schematically). – A–C: Initial stages common to both genera. – A: Ascogonium immersed in the thallus. – B: Elevated primordium with the generative tissue enclosing the ascogonial cells, and forming a covering layer below the thallus surface. – C: Young stage with paraphysoids, ascogenous hyphae and some rows of excipulum proprium cells. – D: Young apothecium of *Homothecium* spp. (exclusive *H. sorediosum*) with an annular excipulum. – E: Young apothecium of *H. sorediosum* with soredia partly enclosed by excipular hyphae, and a connecting structure between the inner edges of the annular excipulum. – F: Mature apothecium of *Homothecium,* a strand of anchoring hyphae bypassing the inner edges of the annular excipulum. – G: Young apothecium of *R. austroamericanum,* the anchoring hyphae intertwining to form a plectenchyma which connects the inner margins of the excipulum ring. – H: Mature apothecium of *Ramalodium* with uniform cupular excipulum. – a ascogonium, ach anchoring hyphae, ah ascogenous hyphae, as asci, c covering layer, cl connecting layer, e excipulum, eh hyphae developing from the marginal excipulum cells, gt generative tissue, hy hypothecium, n *Nostoc,* p paraphyses, pa paraphysoids, so soredia, t trichogyne.

Fig. 2. Ascocarp development in *Homothecium* (microtome sections). – A: *H. opulentum* var. *redonii* (holotype), immersed primordium (side cut, × 500; c covering layer, arrow indicating part of ascogonium). – B: *H. opulentum* var. *opulentum* (Santesson 3208, UPS), primordium with paraphysoids and asymmetrical excipulum (e; ×400). – C: *H. opulentum* var. *redonii* (holotype), elevated primordium with symmetrical excipulum (e), rest of covering layer (c) and precortical structure (indicated by arrows; ×200). – D–F: *H. opulentum* var. *opulentum* (D Henssen 24596a, E, F Santesson 3459, UPS). – D: Apothecium with excipulum partly in contact with adjacent thallus (h hypothecium; × 100). – E: Young apothecium with central paraphysoids and true paraphyses at the margin, the latter indicated by arrows (× 175). – F: Part of a mature apothecium with annular excipulum (× 60).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proprium is cupular in *Ramalodium* in contrast to *Homothecium* where it is annular (Henssen 1965). Another feature of value in the delimitation of the two genera is the ascus structure; in *Homothecium,* the ascus contains an amyloid ring within the apical pore, while in *Ramalodium* only the outer gelatinous part of the ascus wall stains blue in iodine (Fig. 13 A–C).

The well developed and richly fertile material of the new *Ramalodium* species available enabled the sequence of development of the apothecia to be followed in detail within this genus. *Homothecium sorediosum* revealed some interesting evolutionary trends not seen in other species.

Ascocarp development

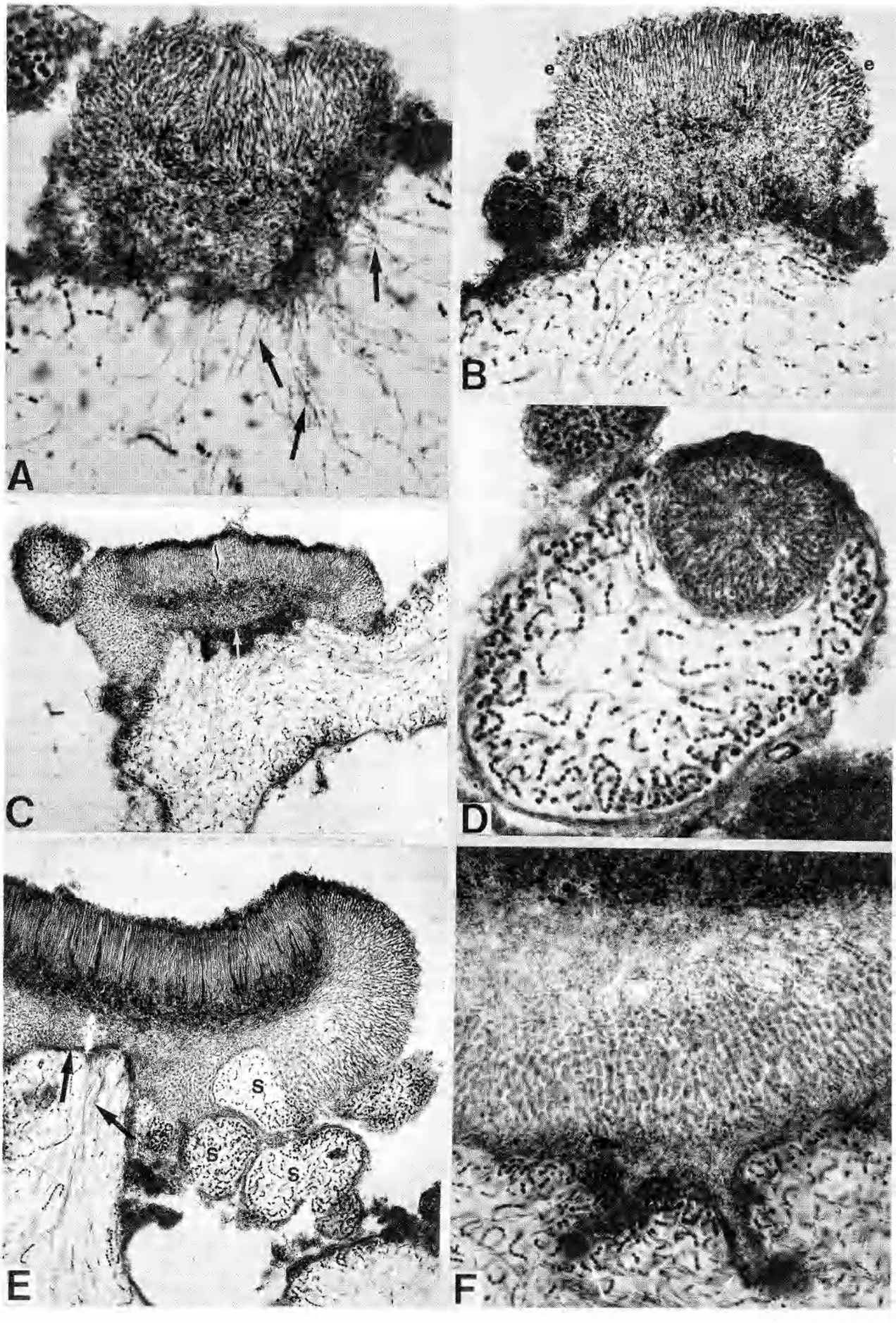
Both *Homothecium* and *Ramalodium* have lecideine apothecia. The thick excipulum proprium is composed of radiating and reticulately interconnecting hyphae (Fig. 1, 2 D, F, 4, 5 D–F). So far as has been observed in *H. opulentum, H. patagonicum* and *R. austroamericanum,* the ascocarps derive from a single ascogonium and its stalk cells, the usual pattern in the Collemataceae (Henssen 1965, 1976, Henssen & Jahns 1973). The primordia are immersed in the thallus (Fig. 2 A, 5 A–B), the young ascocarp subsequently becoming gradually elevated above the thallus surface. The first paraphyses formed are paraphysoids (the terminology used follows Henssen 1976) which are covered by a layer of generative tissue of variable thickness (Fig. 1 B, 2 A, 3 A, 5 A–B). The covering layer sooner or later ruptures to reveal the disc (Fig. 2 B–C, 5 C, 6 E, 14 B). The paraphysoids stretch and eventually develop free tips, their walls becoming markedly gelatinized. During further development the paraphyses grow, especially in the marginal part of the hymenium where they arise from branched hyphae (Fig. 2 E, 4 E).

Homothecium (Fig. 1 A–F). As mentioned above, the differentiation of the excipulum proprium differs in the two genera. In *Homothecium* the excipulum is confined to the marginal part, the central part of the subhymenium remaining in permanent contact with the adjacent thallus. A strand of anchoring hyphae extends from this part of the subhymenium far into the thallus, so doing by passing the inner edges of the excipulum (Fig. 1 F, 2 D–F, 3 E, 4 F, 11 H, 12 C). The different stages of such a development in *H. opulentum* and *H. intermedium* are depicted on Fig. 2. Hyphae grow out from the marginal cells of the excipulum, especially towards the basal part, these extensions often making contact with the underlying thallus and producing a firm connection between the excipulum and thallus surface (Fig. 2 D).

In *H. sorediosum* a distinct zone of plectenchymatic tissue connects the inner edges of the excipulum in young apothecia (Fig. 1 E, 3 C, E) corresponding to the development in *Ramalodium* (see below). Furthermore, the tendency to unite the apothecium with the adjacent thallus is more pronounced in this species: connecting mats of hyphae (Fig. 4 B) or root-like strands which invade the thallus (Fig. 3 F) may be developed; soredia sited at the base of the excipulum are enveloped by the outgrowing hyphae and become more or less incorporated (Fig. 1 E, 3 E, 4 A, 8 G). The inner edge of the annular excipulum is more irregularly formed than in other species (Fig. 4 F).

Ramalodium (Fig. 1 A–C, G–H). In *Ramalodium* the differentiation of the excipulum starts, as in *Homothecium,* with the formation of an annular ring (Fig. 1 G, 5 C) but soon a connecting plectenchyma is formed by the outgrowing anchoring hyphae (Fig. 5 D). Gradually, this tissue simulates the structure of the marginal excipulum (Fig. 5 F, 6 B). In older apothecia the exact limits of the two parts of the excipulum are more or less indistinct (Fig. 5 E, 6 C, 13 H). The secondarily produced part

Fig. 3. Ascocarp development in *Homothecium sorediosum* (microtome sections of the holotype). – A: Young ascocarp fastened by anchoring hyphae (× 200). – B: Later stage with better developed excipulum (e) and the first asci (indicated by arrows; × 200). – C: Young apothecium with a plectenchyma connecting the inner edges of the annular excipulum (× 100). – D: Immersed pycnidium (× 260). – E: Part of apothecium with incorporated soredia (s), arrows indicating the connecting plectenchyma and a strand of anchoring hyphae arising from this layer (× 100). – F: Basal part of mature apothecium with foot-like strand of excipulary hyphae invaginating the thallus surface (× 200).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of the cupular excipulum is frequently enlarged into an irregularly shaped stipe which may function as a foot-like anchor, serving to fasten the ascocarp in the strongly gelatinous thallus (Fig. 13 H).

In general, the mature apothecia are raised above the thallus surface; rarely, they remain immersed when the surrounding tissue also develops upwards together with the expanding ascocarp (Fig. 6 C). Hyphae originating from the border cells of the excipulum establish contact with the adjacent thallus as in *Homothecium* (Fig. 5 E, 13 H). In *R. austroamericanum* a lax plectenchyma may be formed by the excipulary hairs (Fig. 6 B, D, F). The hyphal tips may either invade the thallus and elongate into anchoring hyphae, or form a primitive cortex (Fig. 6 F).

The gradual development of the cupular excipulum in *Ramalodium* is a particular feature of the genus. A plectenchyma connecting the inner edges of the annular excipulum occurs also in *Homothecium sorediosum,* as mentioned above. However, this tissue remains rather restricted and has only been observed in young stages of the ascocarp. Other genera of the Collemataceae have a uniform excipular cup originating from a single hyphal source simultaneously around the young hymenium (Henssen 1976).

A corresponding successional development of a cupular excipulum is also known in the Umbilicariaceae in certain *Umbilicaria* species (Henssen 1970). A plectenchyma differentiating below the subhymenium of an apothecium with an annular excipulum also occurs in the Pannariaceae, for example in the *Parmeliella pycnophora* group and in species of *Erioderma* (Keuck 1977), but this plectenchyma is a supporting tissue formed by medullary hyphae of the thallus.

Homothecium Massal. emend. Henss.

Homothecium Massal., *Alcuni generi di lichini nuovamente limitati e descritti* p. 7 (1855) – Type species: *H. opulentum* (Mont.) Massal.

Thallus orbicular-membranaceous, lobate or granulose, bearing isidia or (in one species) soredia, cartilaginous when dry, gelatinous when moist. Simple or tufts of rhizoidal hyphae attaching the thallus to the substrate as well as adjacent lobes to each other. Hyphae thin, forming a loose network throughout the thallus or partly horizontally aligned in the thallus centre. Thallus either ecorticate or partly corticate or with a continuous primitive cortex.

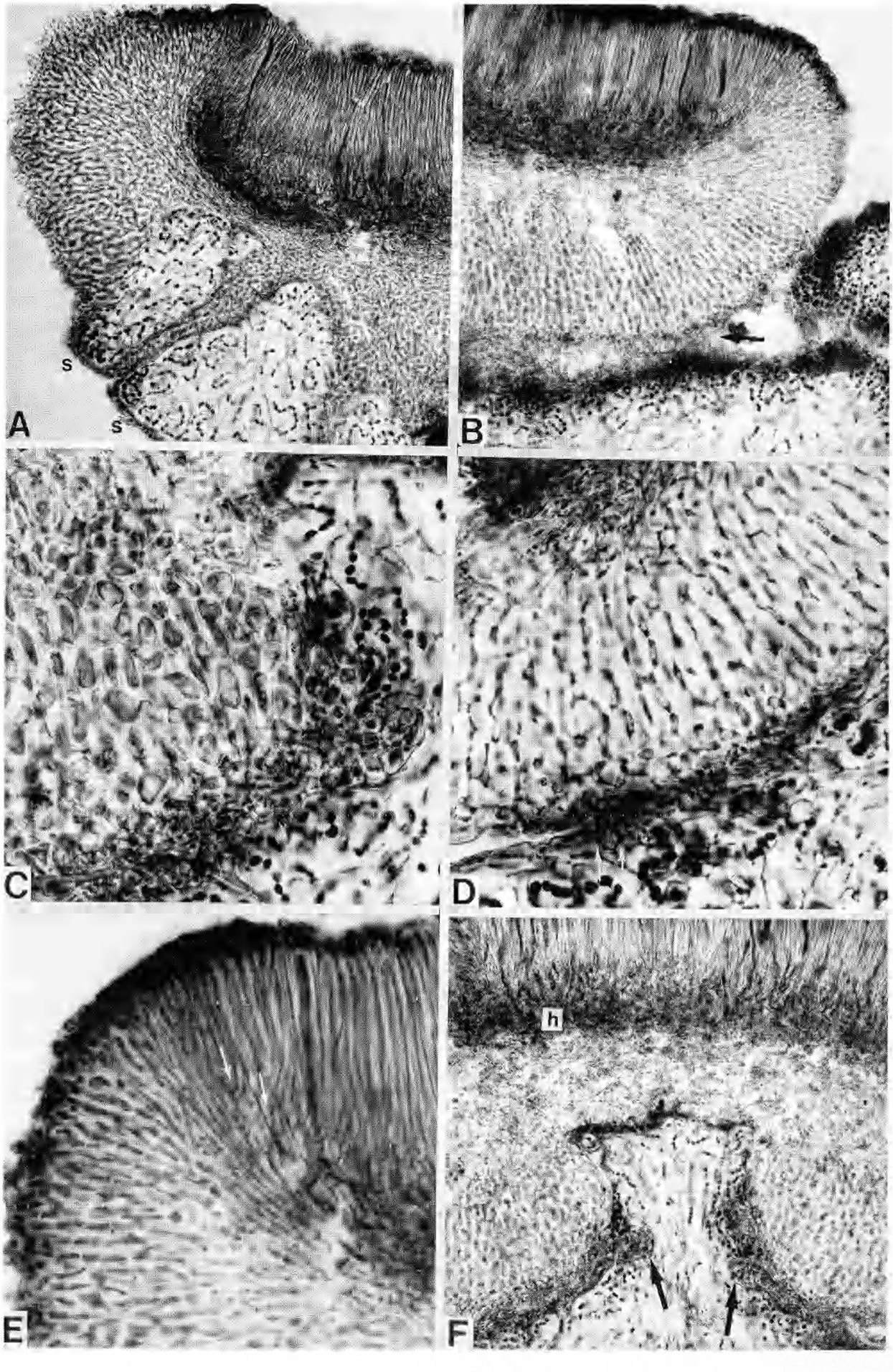
Apothecia laminal, sessile, disc yellow-orange, red- or dark-brown, urceolate when young, without a thalline margin, proper margin distinct or disappearing. Excipulum proprium annular, composed of reticulately connected hyphae with gelatinous walls. Asci cylindrical or obclavate, apex thickened, incorporating an amyloid ring structure. Spores 8 per ascus, simple, colourless, ellipsoid, the walls thick and uneven. Paraphyses partly anastomosing and branched, the apices thickened or not. Pycnidia with short-celled, branched conidiophores producing conidia both terminally and laterally.

Phycobiont: *Nostoc,* cells bluish-violet or green.

Morphology of the thallus

The thallus is bluish- to violet-grey in *H. chilense, H. intermedium* and *H. opulentum* var. *redonii,* dark brown and almost transparent in *H. patagonicum* and blackish in *H. sorediosum*. In *H. opulentum* var. *opulentum* the colour varies in the different specimens, being olive, greenish or rarely having a tinge of bluish- or violet-grey. The basic thallus form in *Homothecium* is a fenestrated membrane with intersecting raised ridges. The thallus becomes strongly gelatinized when moist. The basic structure is best seen in *H. opulentum* where the thallus is partly a membrane with many holes and veins, and partly composed of radiate-anastomosing lobes (Fig. 7 A–D). In *H. chilense* the thallus is covered by terete lobes (Fig. 7 E, 10 C). *H. intermedium* is transitional having

Fig. 4. Anatomy of the *Homothecium* ascocarp (microtome sections). – A–C: *H. sorediosum* (holotype). – A: Part of young apothecium, excipulum forming root-like structures between enclosed soredia (s; × 170). – B: Margin of an old apothecium with hyphal mat between excipulum and adjacent thallus (× 80). – C: Inner edge of the annular excipulum, the cells relatively broad and short (× 420). – D: *H. opulentum* var. *opulentum* (Henssen 24596a), basal part of excipulum fastened to the underlying thallus (× 420). – E, F: *H. sorediosum* (holotype). – E: Upper edge of apothecium with true paraphyses arising from branched hyphae (× 420). – F: Central lower part of an old apothecium, irregular edges of the annular excipulum indicated by arrows, hypothecium (h) darker staining.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membranaceous areas as well as thin lobes (Fig. 7 F–G). *H. patagonicum* is the species with the most distinct, flattened lobes (Fig. 10 E–F). *H. sorediosum* is characterized by a very polymorphic thallus varying from more or less the substrate covering granules, minutely anastomosing membranes to small, thick lobes (Fig. 10 A–B, D, G). The thallus surface might be smooth, slightly rugose or strongly wrinkled (Fig. 7 C–J).

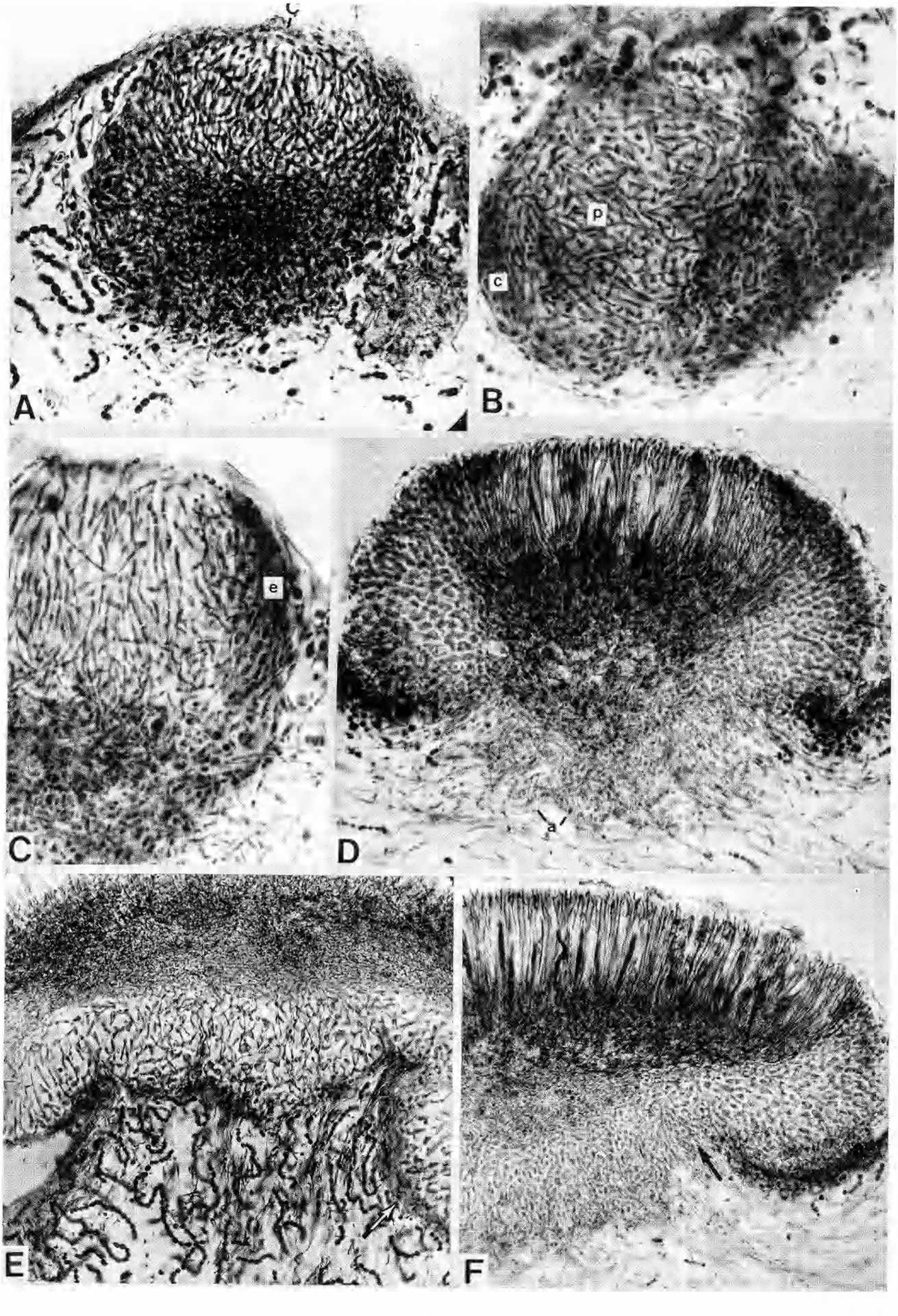
Isidia. With the exception of *H. sorediosum* all species produce isidia. Isidia are fairly frequent in the Collemataceae, accepting the interpretation of the term adopted by Degelius (1954 p. 41), and including both corticate and ecorticate outgrowths of the thallus. In *Homothecium* species the isidia are easily severed when the thallus is dry and thus appear to function as diaspores. In *H. intermedium* the isidia are laminal (Fig. 7 F–G) and tend to enlarge giving rise to ridges and lobes. In *H. opulentum* the lobes and ridges are mainly formed first and the isidia arise secondarily from the margins or surface of the ridges of the lobes (Fig. 7 A–D). In *H. patagonicum* the isidia are produced predominantly along the margins of the lobes (Fig. 7 H, 10 E), in the newly collected specimen from Neuquén in Argentina the central part is composed of terete isidiate lobes (Fig. 10 F).

Soredia. The occurrence of soredia in *H. sorediosum* is remarkable. Their presence is unique within the Collemataceae sensu stricto (Henssen 1965). The soredia may be formed on any part of the thallus, even on the underside, and sometimes occur so abundantly that the lobes become more or less entirely dissolved (Fig. 8 E, F). In as far as the production of soredia in this new species is limited to certain areas of the thallus, these sites might be defined as soralia; it should, however, be stressed that no soralia of a distinct and constant shape occur. The sites of soredial production are often obscured by the fact that the soredia tend to develop in situ or on adjacent lobes resulting in a dense cover of pustules (Fig. 10 D, G). It is difficult to decide if a particular nodule seen under the dissecting microscope is a true soredium or one which has subsequently proliferated secondarily. Frequently soredia are distributed onto the disc of the apothecia where they may become attached (Fig. 10 B). The frequent incorporation of soredia into the developing excipulum has been mentioned above.

The soredia develop in the following way: chains of algal cells are surrounded by actively growing hyphal branches, a process which induces an increase in the division and replication of the enclosed algal cells. As the first soredia produced are gradually released, new ones arise from below (Fig. 8 E, F). The development of the soredia is exogenous and corresponds to the "type of development II" of Beltman (1978) described in the Parmeliaceae apart from the initial stage: in the Parmeliaceae according to Beltman, it is not the multiplication of the fungal hyphae but the division of the algal cells that initiates the formation of the soredia.

The external hyphal cover which surrounds the algal cells varies considerably from a thick enveloping sheath to a few, randomly adjacent hyphae (Fig. 8 A, C, D, F, 9 B). In some cases the external hyphae are entirely lacking, such soredia incorporate fungal cells within the gelatinous sheath of the *Nostoc* colony only (Fig. 8 B, 9 C). Such "naked" soredia resemble the lichenized hormocysts of certain *Lempholemma* species (Degelius 1945, Henssen 1968, 1969). Similar soredia with the fungal hyphae more or less restricted to the gelatinous matrix have been recently described in detail by Wetmore (1974) as the characteristic type of soredia in *Peltula*. The cells of the phycobiont in *Peltula* are penetrated by haustoria. Haustoria also occur in the lichenized hormocysts of *Lempholemma* but are

Fig. 5. Ascocarp development in *Ramalodium* (microtome sections). – A: *R. succulentum* (holotype, H), immersed primordium with paraphysoids and covering layer (c; × 350). – B–C: *R. austroamericanum* (holotype). – B: Transversely inserted primordium with differentiating paraphysoids (p) and covering layer (c; × 420). – C: Young ascocarp with paraphysoids and the first rows of excipulum cells (e; × 420). – D: *R. austroamericanum* (paratype), young apothecium with annular excipulum and connecting plectenchyma formed by the anchoring hyphae (a; × 220). – E: *R. neocaledonicum* (lectotype, H), basal part of an old apothecium, cupular excipulum partly in contact with adjacent thallus (× 190). – F: *R. austroamericanum* (paratype), marginal part of apothecium with cupular excipulum, the border between primary and secondary part of the excipulum indicated by an arrow (× 170).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not present in the soredia of *H. sorediosum*. This is, however, not surprising since haustoria are only rarely seen in the Collemataceae while they are abundant in *Lempholemma,* a genus of the Lichinaceae. Incidentally, the presence of haustoria is the best character to distinguish sterile specimens of *Lempholemma* from *Collema.*

Transitional forms of lichenized hormocysts with adjacent external hyphae have been reported for *Lempholemma albonigrum* (Henssen 1968). The main difference between the hormocysts of *Lempholemma* and the soredia of *Homothecium sorediosum* exists in the origin of the diaspores. The lichenized hormocysts are produced, together with unlichenized ones, in special organs, the hormocystangia (Degelius 1945), and may be, as in *L. vesiculosum* (Henssen 1969), almost free of fungal hyphae and are thus propagules merely produced by the phycobiont. The soredia of *H. sorediosum* and of *Peltula* species are not produced in swollen hormocystangia-like structures but arise from within the thallus, mostly adjacent to actively dividing hyphae of the mycobiont.

Superficially, the soredia of *H. sorediosum* may resemble isidia since they look less powdery than soredia of other lichens (Fig. 10 B, D, G). Fig. 8 reveals that these soredia develop successively from a particular area of the thallus. In general, the successional development of soredia is the best character to distinguish them from isidia, which arise singly as outgrowths from specific points on the thallus.

Anatomy of the thallus

The hyphae of the thallus are relatively thin, approximately 1–2 μm thick, and form a reticulum or they may be more or less horizontally arranged within the thallus centre (Fig. 11 B, 12 A).

In *H. chilense* and *H. sorediosum* the thallus is delimited by a distinct continuous cortex (Fig. 8 A–B, 9 D–E, 11 F). The cortical cells are mainly short, and their walls are strongly gelatinized. Seen in surface view the cell lumina are irregular (Fig. 9 G, H). The cortex may be in part mechanically separated from the thallus as in species of *Leptogium* or other genera of the Collemataceae with a similar primitive cortex.

In the other *Homothecium* species the thallus is either ecorticate or in parts irregularly delimited by periclinally orientated hyphae. Such structures may be interpreted as precursors of a true uniform cortex. The amount and extension of the delimiting horizontally arranged hyphae vary considerably. They may occur on both sides of the thallus (Fig. 9 F, 11 A–B, D–E, 12 B).

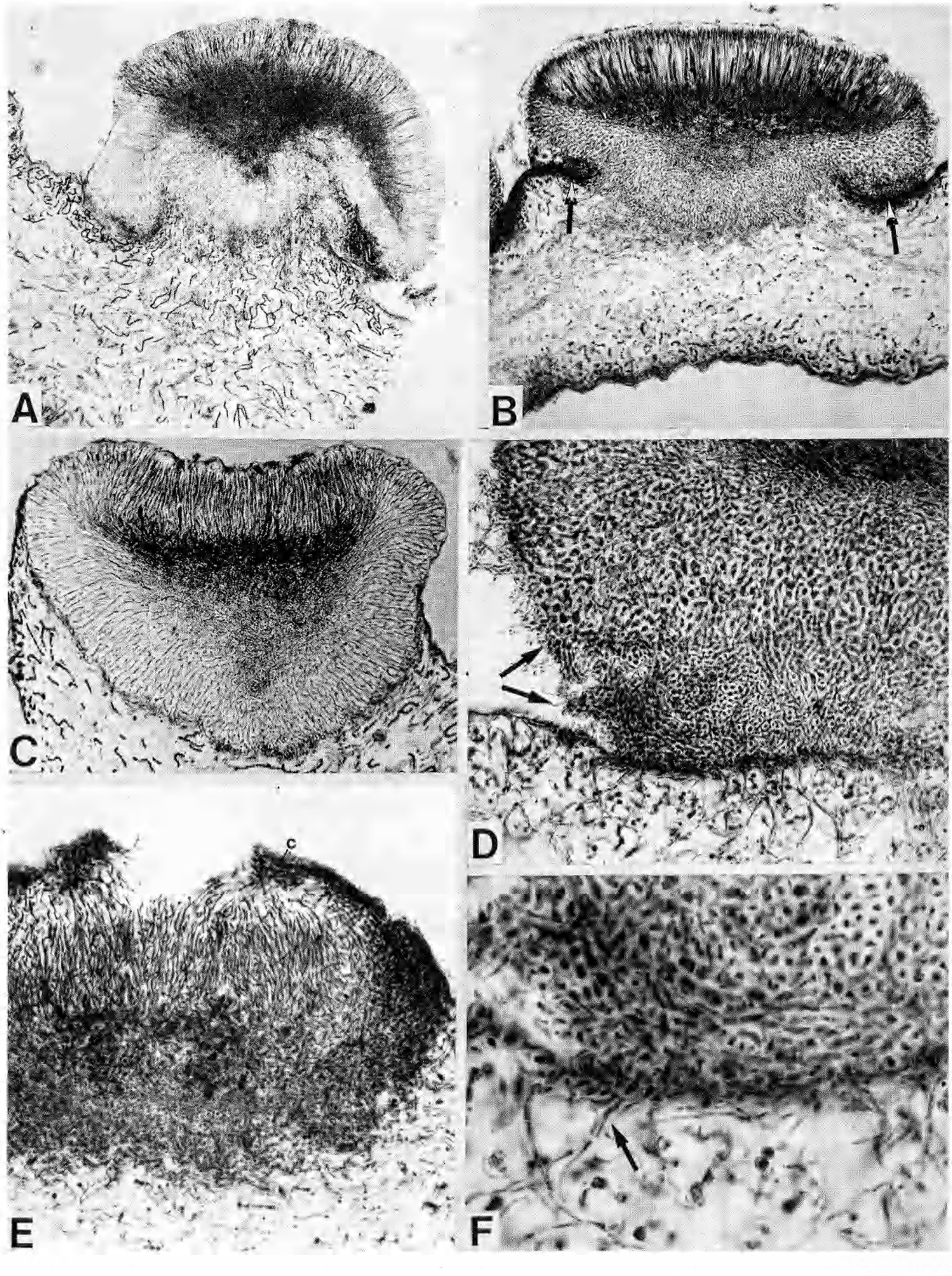
Around the developing ascocarp cortex-like structures of varying degree may be developed from the thallus itself or by the exciple hyphae invading the thallus. The differentiation of special supporting tissues adjacent to the developing ascocarp is a common feature in the Collemataceae (Henssen 1965, Henssen & Jahns 1973). In comparison to certain species of *Collema, Leptogium* and *Leightoniella,* the development of such structures is of rather restricted occurrence among *Homothecium* species.

Structure of the ascocarp

The development of the *Homothecium* ascocarp has been described in detail above. Basically, the mature apothecium is characterized by an annular excipulum proprium and a strand of anchoring hyphae arising from the subhymenium and bypassing the inner basal edges of the excipulum ring when invading the underlying thallus. Concerning the structure of the excipulum, two types may be distinguished: the reticulately connected hyphae may have either mainly narrow and elongated or short and broad cells (Fig. 4 C–D). The differences are best seen in the basal part of mature apothecia.

The asci and spores are rather uniform within the genus; the asci are seen to have an amyloid

Fig. 6. Ascocarp development in *Ramalodium*. – A: *R. japonicum* (syntype, TNS), partly degenerated apothecium (× 60). – B: *R. austroamericanum* (paratype), apothecium with cupular excipulum, arrows indicating connection between excipulum and thallus (× 100). – C: *R. succulentum* (holotype, H), immersed apothecium with cupular excipulum (× 100). – D–F: *R. austroamericanum* (holotype). – D: Plectenchyma formed between marginal excipulum and thallus (× 200). – E: Part of hemiangiocarpic apothecium, the covering layer (c) partly ruptured (× 200). – F: Connecting plectenchyma in higher magnification, anchoring hyphae invading the thallus (× 500).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ring-structure in the thickened apex when stained in iodine. The ring is conspicuous in young asci but becomes suppressed as the spores mature (Fig. 13 A–B). The simple, colourless spores are ellipsoid (lemon-formed) or somewhat fusiform. The shape of the spores may vary in a single ascus and fully mature spores seem to be rare. In their final state their walls become uneven and warted (Fig. 9 A). These warts are a secondary addition to the primary spore wall. In young spores the warts are rather large and ill-defined. The paraphyses are branched and partly anastomosing; their apices may be enlarged or not.

Structure of the pycnidia

The type of pycnidium agrees with that found in other members of the Collemataceae. The conidia are formed both terminally and laterally on short conidiogenous cells of the reticulately connected conidiophores. Pycnidia are rare and have not yet been seen in all species.

Subdivision of the genus

Within the genus two groups may be distinguished: Group I includes *H. chilense* and *H. sorediosum* and is characterized by the occurence of a distinct thalline cortex and by an excipulum composed mainly of broad and short cells. In group II, including the remaining species, no distinct continuous thalline cortex is developed, and the lumina of the cells of the excipulum are mainly narrow and elongated.

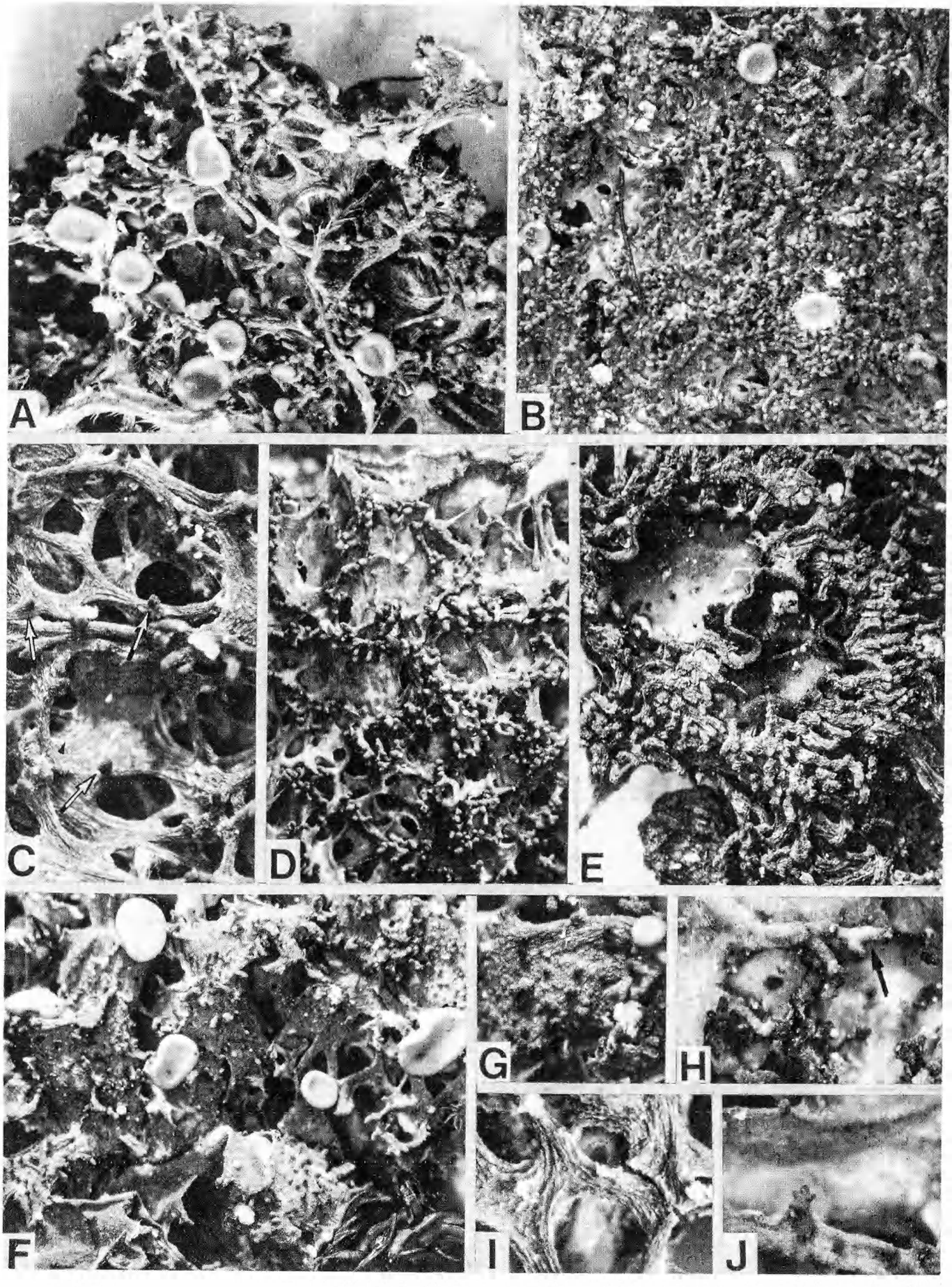
The two species of group I, *H. chilense* and *H. sorediosum,* are very distinct and not easily confused. *H. sorediosum* is unique in its production of soredia; *H. chilense* is well characterized by the terete, wrinkled lobes.

The species of group II are more difficult to recognize than those of group I being, obviously, closely related. *H. opulentum* is very polymorphic in regard to colour and surface structure. The violet-grey variety *redonii,* having strongly wrinkled lobes, resembles *H. chilense* and thus appears rather different from var. *opulentum* with an olive smooth thallus. The material from Juan Fernandez and Lago Argentino intergrade between these two extremes. *H. intermedium* is intermediate between *H. opulentum* and *H. patagonicum,* having a membranaceous thallus as in *H. opulentum* but which partly comprises flattened lobes as in *H. patagonicum.*

Key to the species of Homothecium

1. Thallus with a distinct cortex. Lumina of the excipulum cells mainly short and broad, the cell walls relatively thin (group I) 2
– Thallus without a distinct cortex. Lumina of the excipulum cells mainly narrow and elongated and embedded in a thick gelatinous matrix (group II) 3
2. Thallus granulose, minute, membranaceous or with thick swollen small lobes, more or less covered by soredia ..... *H. sorediosum*
– Thallus mainly composed of wrinkled terete lobes, not bearing soredia ..... *H. chilense*
3. Thallus membranaceous-fenestrate, lobes anastomosing; isidia mainly along the margin and on the intersecting ridges 4
– Thallus more or less distinctly lobate; isidia marginal or laminal 5
4. Thallus olive, greenish or rarely with a blue or violet tinge, surface smooth or in parts slightly wrinkled ..... *H. opulentum* var. *opulentum*
– Thallus bluish or violet-grey, surface strongly wrinkled ..... *H. opulentum* var. *redonii*
5. Thallus bluish or violet-grey; lobes more or less distinct, surface uneven or slightly rugose; isidia mainly laminal ..... *H. intermedium*
– Thallus dark olive-brown, almost transparent; lobes distinctly smooth; isidia marginal ..... *H. patagonicum*

Fig. 7. Habit photographs of *Homothecium* species. – A: *H. opulentum* var. *redonii* (holotype), part of the membranaceous-fenestrate thallus composed of anastomosing and wrinkled lobes (×8). – B: *H. opulentum* var. *opulentum* (Imshaug 37789), thallus centre with numerous small isidia (×7.5). – C: *H. opulentum* var. *redonii* (holotype), lobes bearing mainly marginal isidia (×15). – D: *H. opulentum* var. *opulentum* (James 1729), marginal part of thallus (×7.5). – E: *H. chilense* (holotype, H), two large urceolate apothecia surrounded by wrinkled lobes (×7.5). – F–G: *H. intermedium* (holotype). – F: Central part of the thallus (×7.5). – G: Lobe with laminal isidia (×20). – H: *H. patagonicum* (holotype, H), lobes bearing marginal isidia (×20). – I: *H. opulentum* var. *redonii* (holotype), wrinkled lobes (×20). – J: *H. opulentum* (Henssen 24596a), isidia on ridges of the thallus (×20).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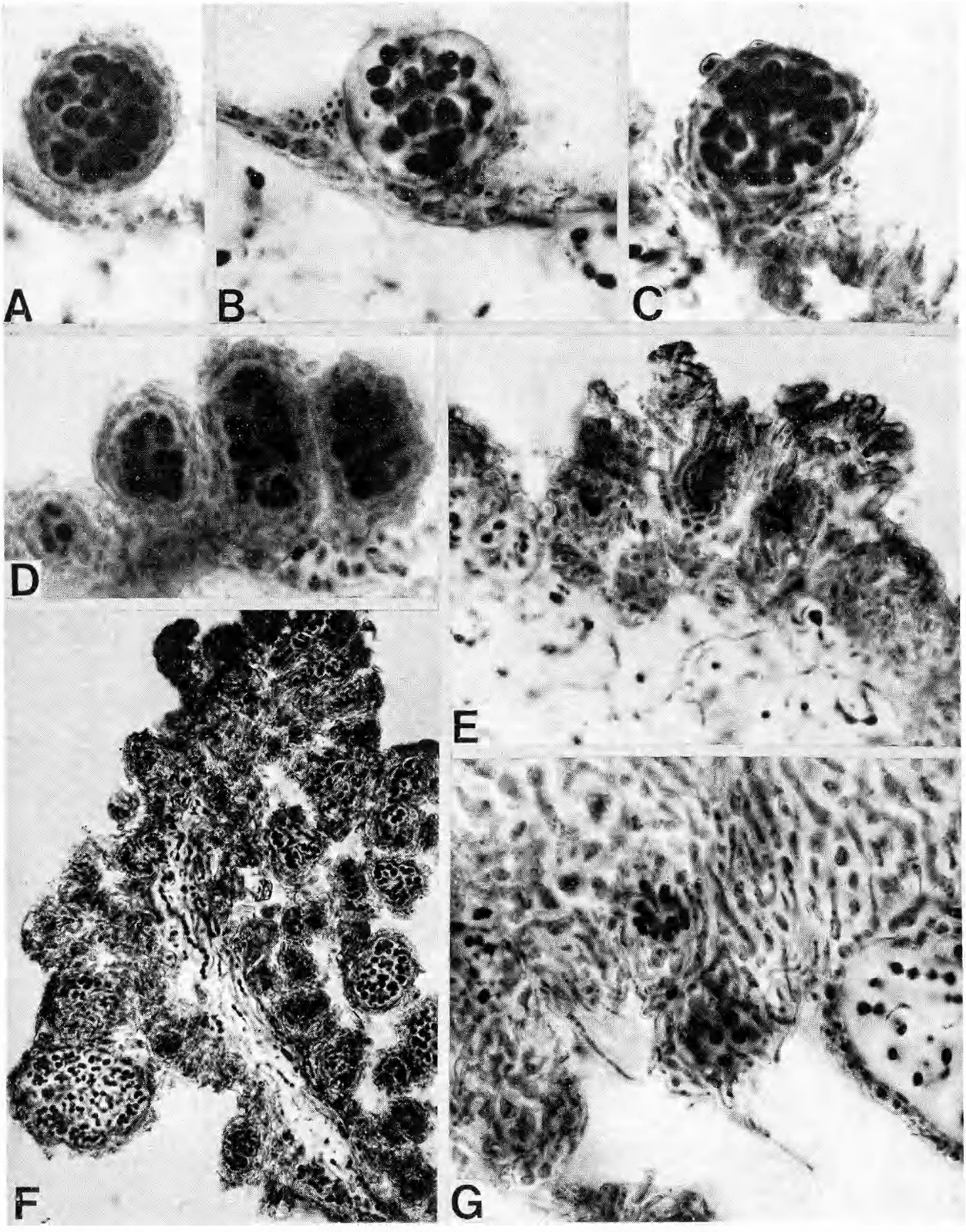


Fig. 8. Formation and incorporation of soredia in *Homothecium sorediosum* (microtome sections of the holotype). – A–B: Soredia lying on thallus surface, in A with some adjacent hyphae, in B "naked" (× 650). – C: Release of a soredium being surrounded by some fungus hyphae (× 650). – D: Group of soredia in different stages of development (× 650). – E: Group of soredia in successional production (× 500). – F: Lobe partly dissolved by soredia formation (× 225). – G: Excipulum hyphae enclosing soredia (× 500).

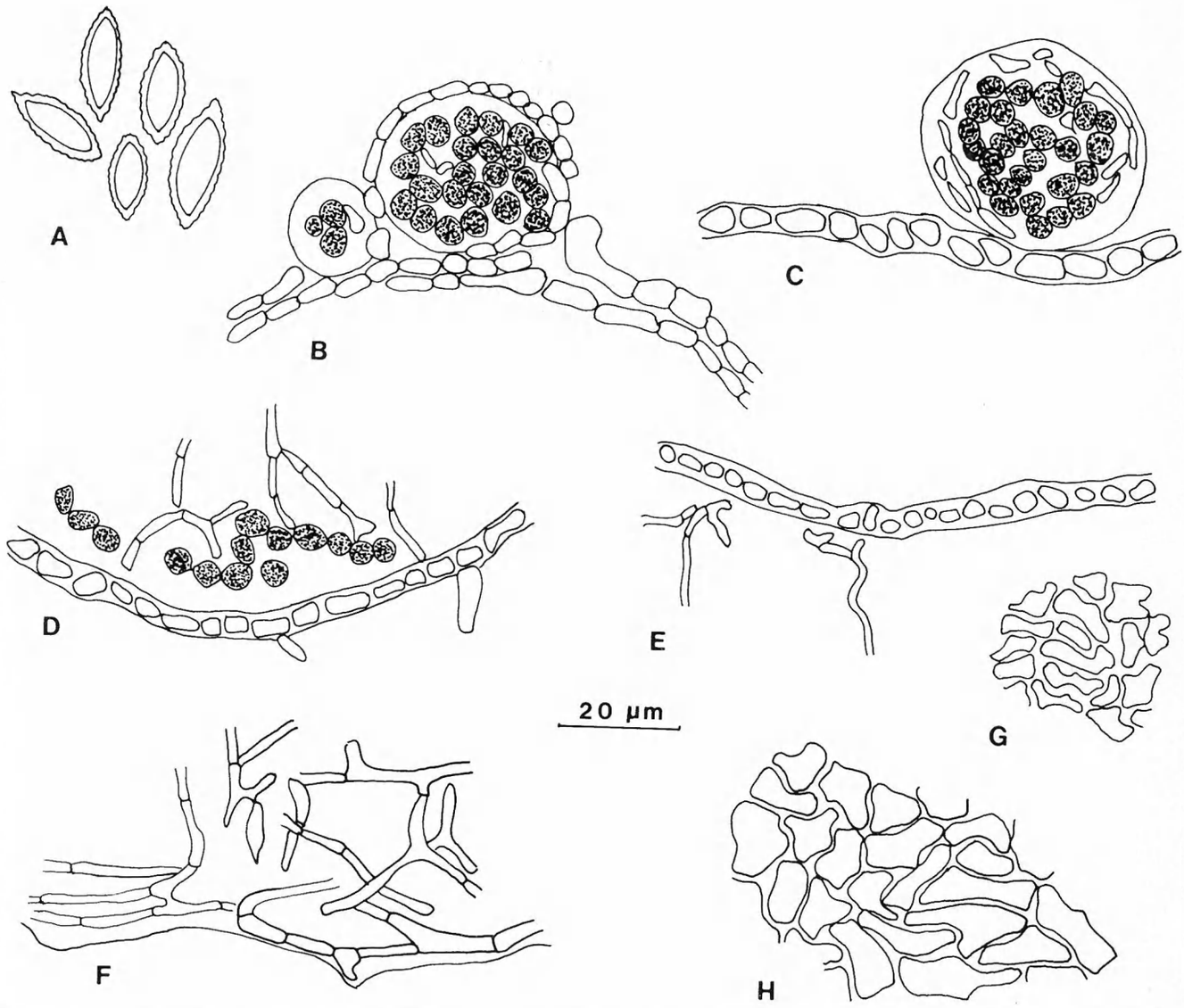


Fig. 9. Anatomy in *Homothecium*. – A–D: *H. sorediosum*. – A: Ascospores. – B: Two "naked" soredia being secondarily surrounded by hyphae developing from the thallus cortex. – C: "Naked" soredium lying on the thallus surface. – D: Corticated lower surface of thallus in cross section. – E: *H. chilense*, upper cortex of the thallus in cross section (algal cells omitted). – F: *H. opulentum*, t.s. of the lower side of the thallus delimited by periclinally arranged hyphae with elongated cells. – G: *H. sorediosum* and H: *H. chilense:* Upper cortex of the thallus in surface view; the cell lumina form an irregular pattern.

Homothecium sorediosum Henss., sp. nov.

Holotypus: Chile, Malleco, Contulmo, 1973 Henssen, Vobis & Redon 24271 (MB). Isotypus: Herbarium, Departamento Biología Universidad de Chile, Valparaiso; further isotypes will be distributed as *Lichenes Cyanophili Exsiccati*, Fasc. 2, no. 30.

Thallus parvus, granulosus, membranaceus vel lobatus, usque ad 20 mm latus, nigricans, soredia formans, corticatus. Apothecia usque ad 2 mm lata, fusca, margine proprio praedito. Excipulum annulare. Hymenium 95–100 µm altum. Asci cylindracei, 90–100× 8–9.5 µm, 8-spori; annulo amyloideo in apice asci incrassato. Sporae eseptatae, incolores, ellipsoideae, 12–19× 5–9.5 µm. Pycnidia 0.1 mm lata. Conidiophora ramosa et brevicellularia, conidia terminalia et lateralia formantia. Conidia bacilliformia, 2–2.5× 1 µm. Alga ad genus *Nostoc* pertinens.

Habit, Fig. 10 A–B, D, G; thallus anatomy and production of soredia, Fig. 8 A–F, 9 B–C; development and structure of the ascocarp, Fig. 1 E, 3 A–C, E–F, 4 A–C, E–F, 8 G; spores, Fig. 9 A; pycnidium, Fig. 3 D.

Thallus blackish, polymorphic, membranaceous, 5–20 mm in size or composed of several thick,

somewhat swollen lobes up to 3.5 mm long and 2 mm broad, or thallus granulose and granules 1–2 mm diam. Thallus secured by tufts of rhizoidal hyphae. Thallus surface more or less covered by developing or germinating soredia, often simulating globular isidia. Thallus with a distinct cortex on the upper and lower sides, one cell thick; cortical cells with strongly gelatinized walls, irregular in shape when seen from above. Hyphae within the thallus thin, either forming a reticulum or becoming aggregated and horizontally arranged at the centre. Thallus sections 190–340 μm thick. Phycobiont: *Nostoc* sp., cell chains more or less curved, concentrated towards the exterior of the thallus; cells 3–7 μm.

Apothecia up to 2 mm diam., disc brown, urceolate when young, with proper margin (Fig. 10 B). Hymenium 95–105 μm, staining first blue then vinose in iodine. Subhymenial layers 70–105 μm, including upper 45–55 μm, corresponding to the darker staining hypothecium sensu stricto (Fig. 4 F). Excipulum annular, incorporating adjacent soredia (Fig. 8 G), 90–100 μm thick, cells mainly short and broad, 9–12(–18) μm long, walls gelatinized. Marginal cells of the excipulum producing hyphal extensions, especially towards the basal part, which may form hyphal mats between the excipulum and thallus (Fig. 4 B) or foot-like structures invading the thallus (Fig. 3 F); the hyphae may also penetrate the thallus. Asci cylindrical, with an amyloid apical ring structure, 90–100 × 8–9.5 μm, containing 8, or occasionally fewer spores. Spores simple, colourless, 12–19 × 5–9.5 μm, often variable in shape and size within a single ascus, spore wall uneven, becoming minutely warty when mature. Pycnidia immersed, about 0.1 mm diam. Conidiophores branched and anastomosing, conidiogenous cells short, the conidia terminally and laterally produced. Conidia rod-shaped, 2–2.5 × 1 μm.

In the Contulmo National Park, this new species was abundant, overgrowing earth and brittle sandstone of a new road cutting in a humid *Nothofagus obliqua* forest. The substrate seemed to be at least temporarily moist. The material from Juan Fernandez is rather scanty, but is well in accord with the type collection.

H. sorediosum is distinguished from all other *Homothecium* species, as well as from all hitherto known Collemataceae, by the production of soredia. In habit the lichen resembles very much a species of *Collema* or *Leptogium*, especially when the thalli are predominantly composed of small swollen lobes and the developing soredia simulate isidia (Fig. 10 A, D). As a member of *Homothecium* the lichen is, however, easily recognized by the simple spores and the annular excipulum.

Localities. Chile, Malleco, Parque Nacional de Contulmo, *Nothofagus obliqua* forest, on earth and brittle sandstone of a road cutting, 1973 Henssen, Vobis & Redon 24271 (type) – Juan Fernandez, Valle Colonial, Trail de Portezuelo de Villagra, on soil and moss, 1965 Imshaug 37682 (MSC).

Homothecium intermedium Henss., sp. nov.

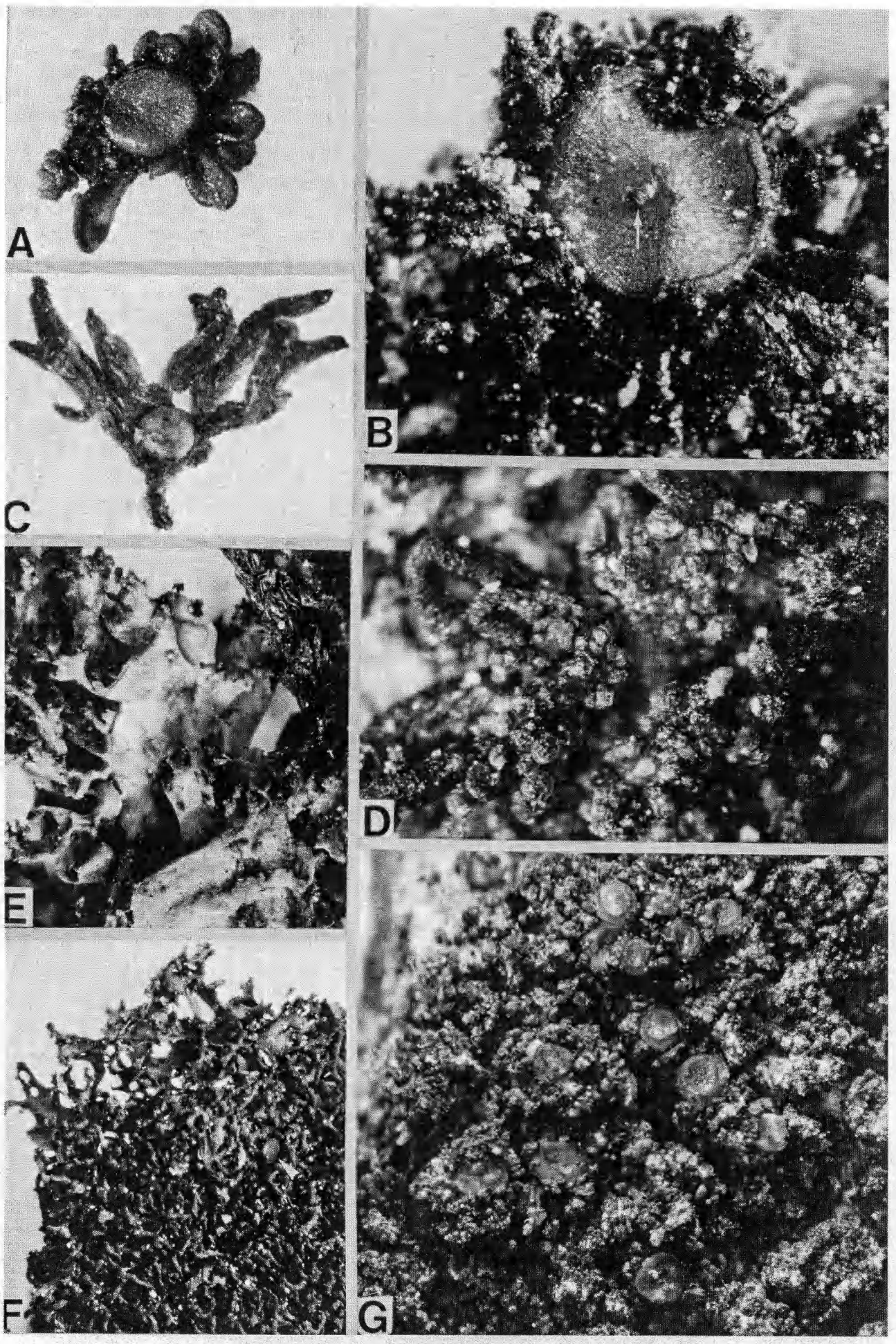
Holotypus: Argentina, Neuquén, Arroyo de Escorial, 1974 Henssen & Vobis 24589a (MB).

Thallus membranaceus vel lobatus, violaceo-griseus, inaequalis vel parum rugosus, 4.5 cm latus. Lobi 0.8 mm lati, isidia praecipue laminalia. Hyphae reticulum irregulare formantes. Apothecia ochracea, usque ad 2 mm lata, margine proprio praedito. Excipulum annulare. Hymenium 120–170 μm altum. Asci cylindracei, 95–100 × 10–12 μm, 8-spori; annulo amyloideo in apice asci incrassato. Sporae eseptatae, incolores, ellipsoideae, 9–15 × 5.5–8 μm. Pycnidia ignota. Alga ad genus *Nostoc* pertinens.

Habit, Fig. 7 F–G; thallus anatomy, Fig. 11 A–B; structure of excipulum, Fig. 11 G; asci with amyloid ring structure, Fig. 13 A–B.

Thallus bluish- to violet-grey, membranaceous-lobate, 4.5 cm large, secured to the substrate by tufts of rhizoidal hyphae. Lobes 0.8–2 mm

Fig. 10. Habit photographs of *Homothecium* species (A–D and G photographed in ± moist condition). – A–B: *H. sorediosum* (holotype). – A: Thallus with large thick lobes and central apothecium (× 10). – B: Large apothecium with prominent margin, disc partly covered by soredia which started germination (× 15). – C: *H. chilense* (holotype, H), wrinkled terete lobes bearing young apothecium (× 10). – D: *H. sorediosum* (holotype), large lobes covered by soredia (× 25). – E: *H. patagonicum* (holotype, H), lobes bearing marginal isidia (× 8). – F: *H. patagonicum* (Henssen 24588o), part of a thallus covered by aggregated lobes, apothecium indicated by an arrow; × 6). – G: *H. sorediosum* (holotype), granular thallus with numerous small apothecia (× 8).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broad, in sections 190–285 μm thick, often secured to one another by tufts of hyphae, surface uneven or slightly rugose. Isidia globular or elongated, mainly laminal, easily abraded when dry. Hyphae thin, forming mainly a loose reticulum, some hyphae extending horizontally just below the surface of both sides of the thallus. Phycobiont: *Nostoc* sp., cell chains more or less curved and concentrated towards the surface and margins; cells 3–7 μm.

Apothecia ochraceous-brown, up to 2 mm diam., disc at first urceolate with distinct proper margin, being first paler, later assuming the colour of the disc. Hymenium 120–170 μm, gelatine staining blue then vinose in iodine. Subhymenial layers 190–300 μm thick, including an upper darker staining hypothecium 70–95 μm thick. Excipulum annular, 180–240 μm thick, cells mainly narrow and elongated, walls strongly gelatinized, lumina (12–)18–26 μm long (Fig. 11 G). Asci cylindrical, 95–100 × 10–12 μm, with an amyloid ring in the thickened apex. Spores 8 per ascus, simple, colourless, ellipsoid, lemon-shaped or slightly fusiform, 9–15 × 5.5–8 μm, walls uneven. Pycnidia not seen.

On a large shaded lava boulder at the edge of a lava-field in a stand of *Nothofagus dombeyi*. Only known from the type locality.

H. intermedium is characterized by the bluish-grey thallus which is partly membranaceous and partly composed of thin flattened lobes, and by the predominantly laminal isidia. *H. opulentum*, the most similar species, differs in having a membranaceous thallus which is thicker (380–700 μm in section), and it bears its isidia mainly on its margins or upon the intersecting thalline ridges. *H. patagonicum* differs in the brown, almost transparent, distinctly formed lobes, in the marginal isidia and by its ecology: this species occurs on freely exposed, sunny situations.

Homothecium opulentum var. **redonii** Henss., var. nov.

Holotypus: Chile, Llanquihue, Mallín, 1974 Redon 03340 (MB). Isotypus: Herbarium, Departamento Biología Universidad de Chile, Valparaiso.

Thallus violaceo-griseus, saltem 3 cm latus, membranaceus et fenestralis lobis anastomosantibus. Lobi 0.1–0.2(–2) mm lati, rugosi. Isidia simplicia vel ramosa, praecipue marginalia. Differt a var. *opulento* thallo rugoso.

Habit, Fig. 7 A, C, I; anatomy of the thallus, Fig. 11 E; development and structure of the ascocarp, Fig. 2 A, C, 11 H.

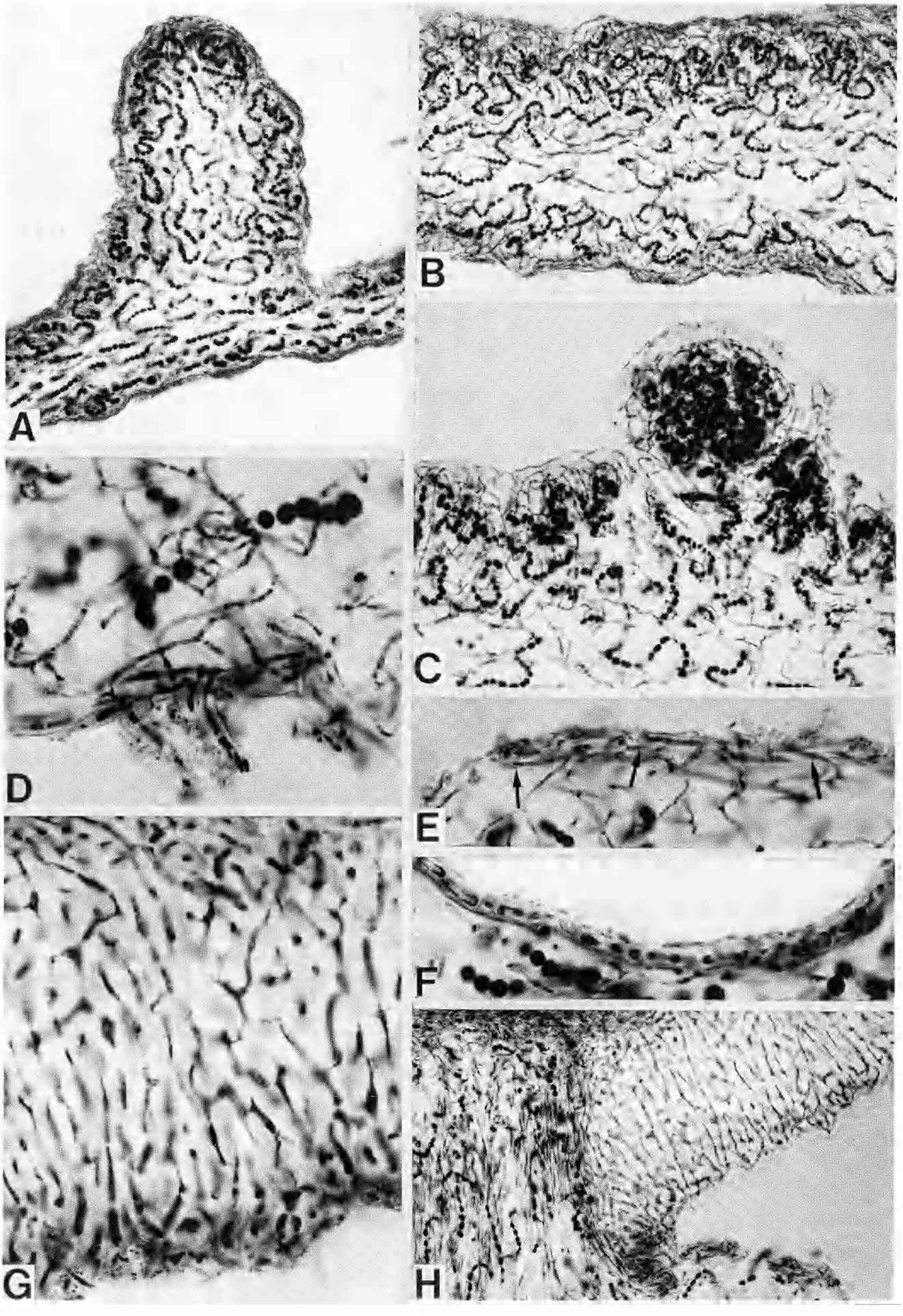
H. opulentum var. *redonii* is characterized by the membranaceous-fenestrate thallus with wrinkled anastomosing lobes, and by the bluish- or violet-grey colour. The lichen appears rather different from the main variety of the species which has an olive smooth thallus. *H. opulentum* var. *redonii* might by confused with *H. chilense* having also a wrinkled surface. In fact, the type specimen was recorded as *H. chilense* in Redon (1974). *H. chilense* may be distinguished, however, by the thick terete lobes provided with a distinct cortex; in var. *redonii* only precortical structures occur on both sides of the thallus (Fig. 11 E).

Localities. Argentina, Rio Negro, Parque Nacional de Nahuel Huapí, Bariloche, 1969 Dodge (MB, fragment communicated by J. Redon as no. 04579) – *Chile,* Llanquihue, Parque Nacional Vicente Perez Rosales, Mallín, on tree, 1974 Redon 03340 (type) – Valdivia, Cordillera Pelada, 520 m, Redon 04940 (Herb. Universidad de Chile, Valparaiso).

Homothecium opulentum var. **opulentum,** new records

H. opulentum var. *opulentum* is the only taxon of the genus which has been collected at all frequently. In addition to the localities listed in Henssen (1965), the following specimens have been examined:

Fig. 11. Anatomy of *Homothecium* species (microtome sections). – A–B: *H. intermedium* (holotype). – A: L.s. of thin lobe with isidium (× 200). – B: L.s. of thicker thallus with delimitations of periclinally orientated hyphae on both sides (× 200). – C–D: *H. opulentum* var. *opulentum* (Henssen 24569a). – C: L.s. of thallus bearing a young isidium (× 260). – D: Delimitation of periclinally orientated hyphae with outgrowing rhizoidal hyphae on the lower side of the thallus (× 650). – E: *H. opulentum* var. *redonii* (holotype), thallus upper surface with delimitation formed by periclinal hyphae (× 500). – F: *H. chilense* (holotype, H), l.s. of upper thallus surface with primitive cortex (× 650). – G: *H. intermedium* (holotype), part of excipulum (× 500). – H: *H. opulentum* var. *redonii* (holotype), inner edge of excipulum (× 200).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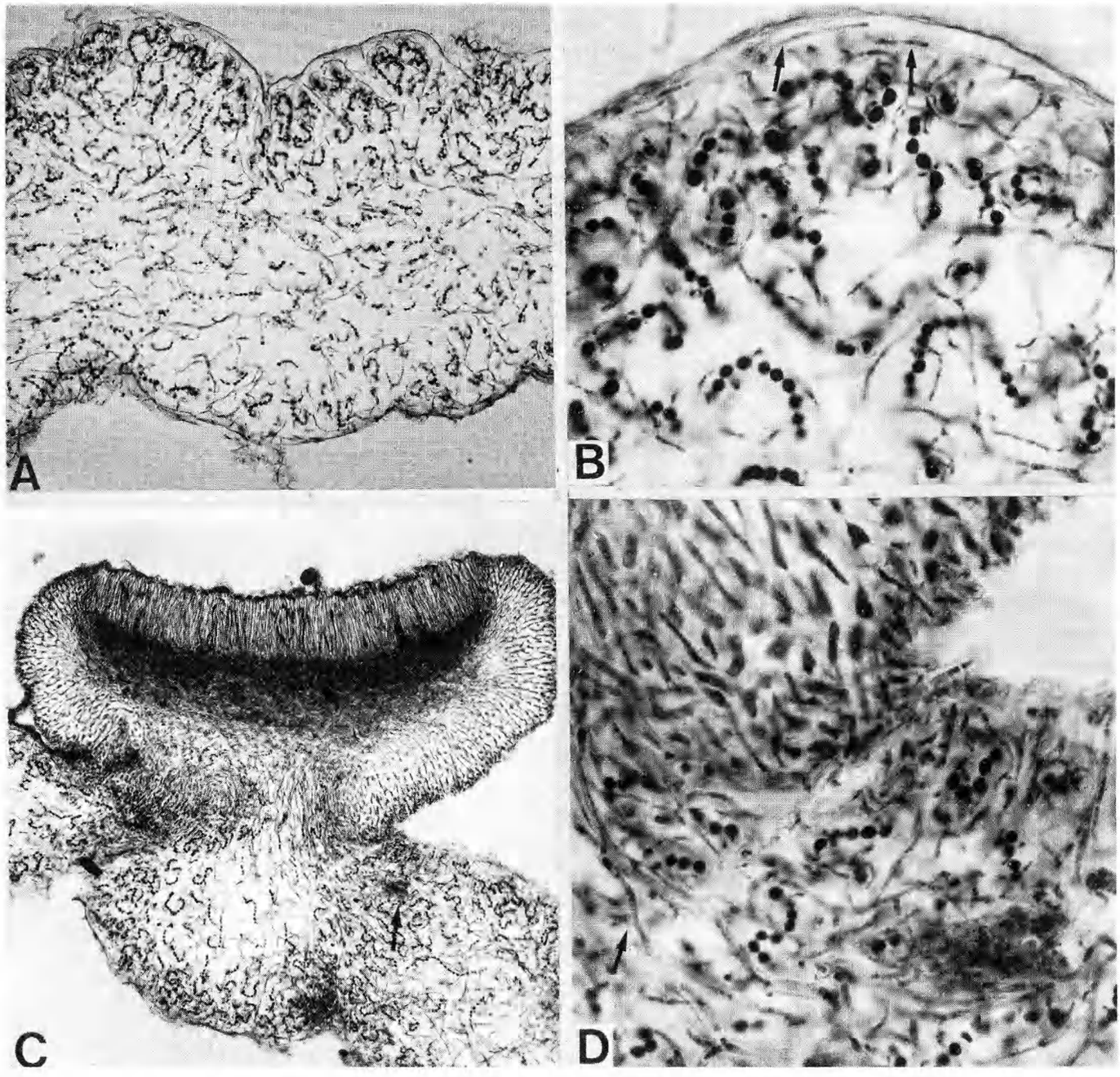
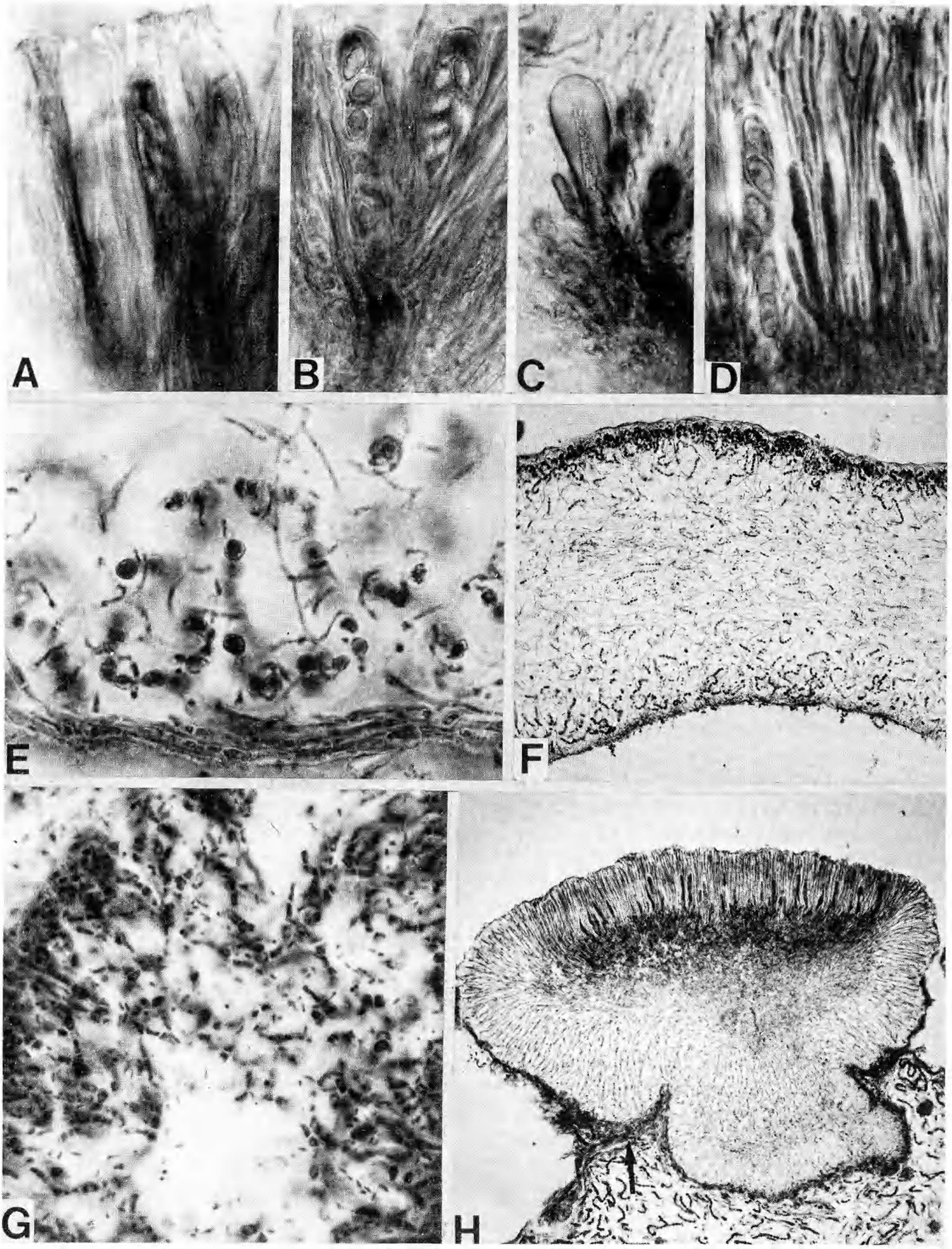


Fig. 12. Anatomy of *Homothecium patagonicum* (Henssen 24588o, microtome sections). – A: L.s. of thallus (× 120). – B: Thallus upper surface, arrows indicating periclinally extending hyphae (× 400). – C: Mature apothecium with annular excipulum, on the right degenerated ascogonium (× 80). – D: Sector in higher magnification, arrow indicating an anchoring hypha (× 400).

Fig. 13. Anatomy of *Homothecium* and *Ramalodium* species (A–C squash preparations stained in iodine, D–H microtome sections embedded in lactophenol cotton-blue). – A–B: *H. intermedium* (holotype), ascus apices with amyloid ring-structure (× 500). – C: *R. austroamericanum* (paratype), young ascus, mucous sheath of ascus wall stained blue (× 500). – D–G: *R. austroamericanum* (holotype). – D: Part of hymenium with asci in different stages of development and with simple or branched paraphyses (× 500). – E: L.s. of thallus lower side, delimitation formed by periclinal hyphae (× 650). – F: L.s. of thallus (× 100). – G: Part of pycnidium (× 500). – H: *R. succulentum* (isotype, BM), mature apothecium with enlarged stipe, arrow indicating contact of the excipulum to the adjacent thallus (× 100).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Argentina, Rio Negro, Parque Nacional Nahuel Huapí, Puerto Blest, on *Nothofagus dombeyi* in deep shade near the lake shore, 1973 Henssen & Vobis 24596a (MB) – Santa Cruz, Lago Argentino, Cerro Buenos Aires, near Moreno Glacier, overgrowing mosses on a dead *Nothofagus dombeyi* in shade, 1959 James 1729 (BM) – Cerro Mayo, opposite Mayo Glacier, 1959 James 1583 (BM) – *Chile,* Juan Fernandez, El Yunque, on *Nothomyrcia,* 1965 Imshaug 37789, 37798 (MSC) – Plazoleta del Yunque, 1965 Imshaug 37700 (MSC).

Specimens from Lago Argentino had a greenish colour while material from Nahuel Huapí is olive. In the specimens from Juan Fernandez the thallus was covered by relatively small isidia (Fig. 7 B), the surface smooth or slightly wrinkled and the colour greenish or partly bluish-grey thus resembling var. *redonii.*

Homothecium patagonicum, new record

H. patagonicum was known, hitherto, only from the type locality, Lago Moreno, near Bariloche. Although the lichen was not refound along the shores of this lake, it was collected further north.

Argentina, Neuquén, Parque Nacional de Lanín, Arroyo de Escorial, on free exposed boulders in a lava-field, 1973 Henssen & Vobis 24588o (MB).

The specimen is to be considered as a pulvinate form of *H. patagonicum* forming cushions of densely aggregated, short lobes (Fig. 10 F). The flattened smooth lobes, typical of the species are confined to the marginal area of the thallus. The anatomy of the thallus and the apothecium of the new collected specimen (Fig. 12 A–D) are well in accord with the type. While the other species of *Homothecium* so far known are all lichens of shady habitats, *H. patagonicum* shows marked preference for sunny and exposed substrates.

Ramalodium Nyl. in Cromb. emend. Henss.

Ramalodium Nyl. in Cromb., *J. Linn. Soc. (Bot.) 17:* 392 (1879) – Type species: *R. succulentum* Nyl. in Cromb.

Thallus membranaceous, or foliose to pulvinate fruticose, cartilaginous when dry, gelatinous when moist, olive or violet-grey. Lobes broad with ridges or veins, or narrow and wrinkled and then irregularly swollen or opuntioid when moist. Thallus ecorticate or with precortical structures formed by periclinally orientated hyphae; lower surface naked or with tomentum. Hyphae thin, forming a loosely branched reticulum or orientated horizontally in the thallus centre. *Nostoc* chains aggregated in the outer part of the thallus near the surface, cells green or violet.

Apothecia marginal or laminal, immersed or sessile, disciform or globose, disc dark red or reddish brown, with proper margin. Excipulum proprium annular when juvenile, becoming a closed cup-shaped layer when mature; hyphae reticulately connected, walls more or less strongly gelatinized, cell lumina rounded, angular or elongated. Asci cylindrical, containing 8 or fewer spores, gelatinous part of the ascus wall stained blue with iodine. Spores simple, colourless, thick-walled. Paraphyses partly branched, tips enlarged or not. Pycnidia sessile, conidiophores branched and anastomosing, conidiogenous cells producing short conidia terminally and laterally.

The development of the *Ramalodium* ascocarp, characterized by the gradual formation of the cupular excipulum proprium, has been described above. *R. japonicum, R. neocaledonicum* and *R. succulentum* are described in Henssen (1965). The new species *R. austroamericanum* differs from these in the external and internal morphology of the thallus and apothecium. It is the only species of the genus with rounded, smooth lobes (Fig. 14 A–F) and thus resembles certain members of the genera *Collema* and *Leptogium* for which it was taken when seen first in nature. The lower surface of the thallus is partly covered by a short tomentum as in *Leptogium* sect. *Mallotium,* and it is limited by a structure composed of one or two layers of periclinally aligned hyphae (Fig. 13 E, 15 D). The other *Ramalodium* species have wrinkled

Fig. 14. Habit photographs of *Ramalodium* species. A–F: *R. austroamericanum* (A–C, E holotype, D, F paratype). – A: Membranaceous lobate thallus (×5). – B: Hemiangiocarpic young apothecium (×20). – C: Apothecium with hairy proper margin (×20). – D: Part of richly fertile old thallus (×5). – E–F: Lobes with adnate apothecia (E×12, F×15). – G: *R. succulentum* (holotype, H), part of thallus, globose apothecia (×5). – H: *R. japonicum* (syntype, TNS), part of thallus with globose apothecia indicated by arrow (×5).


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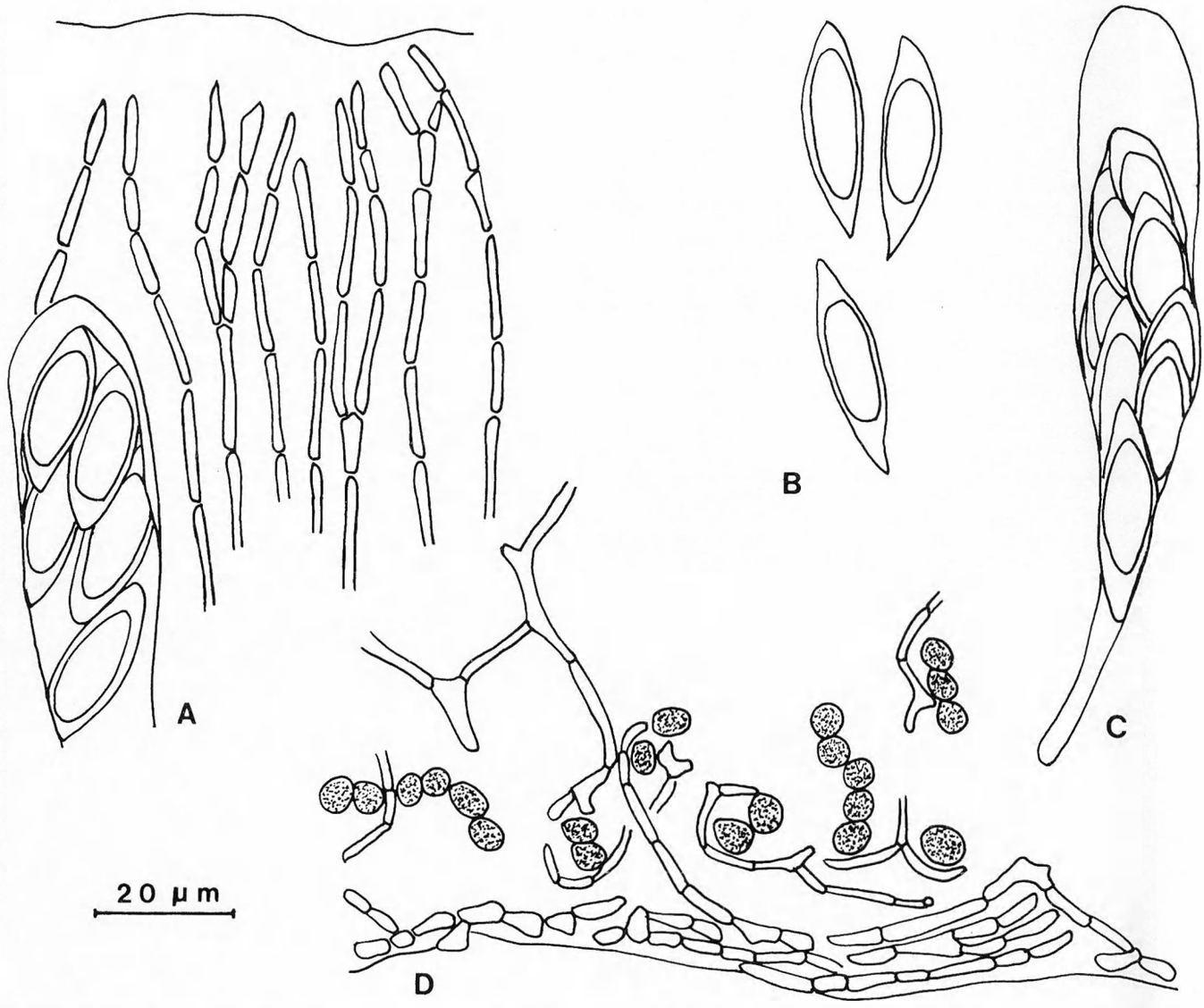

Fig. 15. Anatomy in *Ramalodium austroamericanum*. – A: Upper part of the hymenium. – B: Ascospores. – C: Ascus with spores. – D: T.s. of the lower side of the thallus, periclinally orientated hyphae with elongated or short cells forming a restricted irregular delimitation on the surface.

or swollen, narrow lobes and neither a tomentum nor a hyphal delimitation on the lower side of the thallus. The amorphous deposits which occur in *R. succulentum* have not been seen in *R. austroamericanum*.

In contrast to the Pacific species with globose ascocarps (Fig. 14 G, H), the apothecia in *R. austroamericanum,* at least at first, are flat and closely adnate to the thallus (Fig. 14 E). Their colour also differs in being red- to dark-brown but without a conspicuous red tinge. The apothecial margin is often tomentose (Fig. 14 C), and the excipular hairs may form a thick plectenchyma connecting the base of the marginal excipulum and the thallus (Fig. 6 D–F), a differentiation which has not been observed in the other species of the genus. The spores also differ in size and shape; they are twice as long as in the Pacific species, fusiform, and have thickened walls at both ends (Fig. 13 D, 15 A–C). The excipulum cells are shorter and broader than in the Pacific species, and the cell walls are less strongly gelatinized (Fig. 5, 6, 13 H). With regard to the structure of the excipulum *R. austroamericanum* resembles the *Homothecium* species included in group I above, while the excipular structure of *R. japonicum, R. neocaledonicum* and *R. succulentum* corresponds to that of *Homothecium* species placed in group II.

Key to the species of Ramalodium

1. Thallus olive; *Nostoc* cells green 2
– Thallus violet-grey; *Nostoc* cells violet 3
2. Thallus membranaceous with anastomosing, rounded, smooth lobes, lower side partly with a tomentum and a restricted delimitation of horizontally orientated hyphae. Spores fusiform, 18–31 μm long (S America) ..... *R. austroamericanum*
– Thallus pulvinate-fruticose with terete swollen lobes, lower surface without tomentum or a hyphal delimitation. Spores ellipsoid, 9–13.5 μm long (Japan) ..... *R. japonicum*
3. Thallus membranaceous to fruticose, at least 2.5 cm in diam., amorphous deposits present (Australia) ..... *R. succulentum*
– Thallus orbicular, foliose to fruticose, 0.5–1 cm in diam., no amorphous deposits present .. *R. neocaledonicum*

Ramalodium austroamericanum Henss., sp. nov.

Holotypus: Argentina, Neuquén, Parque Nacional Lanín, Lago Lacar, forest station Pucara, on *Nothofagus obliqua,* 1973 Henssen & Vobis 24547t (MB). Paratypus: Loc. cit. on *Nothofagus* sp., 1973 Henssen & Vobis 24569b (MB).

Thallus olivaceus, rosulatus, membranaceus vel lobatus, usque ad 2.5 cm latus. Lobi anastomosantes, rotundati, 4–7 mm lati, pagina infera subtomentosa, strato corticali praedita. Apothecia fusca, laminalia vel submarginalia, juvenilia immersa deinde adnata, usque ad 2.5 mm lata. Excipulum proprium initio annulare deinde cupulatum. Hymenium 90–120 μm altum. Asci cylindracei, 90–105 × 11–12 μm (6–)8-spori. Sporae simplices, incolores, fusiformes, 18–31 × 6.5–8 μm. Pycnidia immersa, 0.1 mm lata. Conidiophora ramosa et brevi-cellularia, conidia terminalia et lateralia formantia. Conidia bacilliformia, 3–4 × 1 μm. Alga ad genus *Nostoc* pertinens.

Habit, Fig. 14 A–F; thallus anatomy, Fig. 13 E–F, 15 D; development of the ascocarp, Fig. 5 B–D, F, 6 B, D–F; part of the hymenium, Fig. 15 A; asci and spores, Fig. 13 C, D, 15 B, C; portion of pycnidium, Fig. 13 G.

Thallus olive, rosette-shaped, membranaceous to lobate, c. 2.5 cm large, with ridges and holes, cartilaginous when dry, gelatinous when moist, fastened by tufts of rhizoidal hyphae, partly covered by short tomentum on the lower side. Lobes rounded, anastomosing, smooth, 4–7 mm broad. Hyphae thin, reticulately arranged or more or less horizontally extended in the inner parts of the thallus. Thallus in sections 300–500 μm high, partly with delimitations of horizontally extending hyphae at the lower surface, 1–3 rows of cells high. Phycobiont: *Nostoc* sp., cell chains concentrated in the upper and outer parts of the thallus; cells 3–7 μm diam.

Apothecia up to 2(–2.5) mm diam., laminal, submarginal or rarely marginal, adnate and often with a hairy proper margin, red-brown to dark-brown, flat or finally convex. Excipulum at first annular, secondarily cupular, 120–200 μm thick, composed of radiating and eventually reticulately connected hyphae composed of short cells. Plectenchyma between the thallus and excipulum 45–90 μm thick. Hymenium 90–120 μm, hypothecium 45–70 μm. Asci cylindrical, 90–105 × 11–12 μm, (6–)8-spored, mucous part of the ascus wall staining blue in iodine (Fig. 6 C). Spores simple, colourless, fusiform, 18–31 × 6.5–8 μm, often attenuated, walls thickened at both ends.

Pycnidia immersed, c. 0.1 mm broad, ostiole dark. Conidiophores branched and anastomosing, conidiogenous cells producing conidia terminally and laterally. Conidia rod- or dumb-bell-shaped, 3–4 × 1 μm.

On the bark of *Nothofagus* near the lake shore together with several species of *Collema* and *Leptogium*, and amongst other lichens.

R. austroamericanum is characterized by the olive, membranaceous thallus with rounded lobes bearing a tomentum on the lower side, the tomentum may disappear in old thalli. This new species is easily distinguished from similar species of *Collema* and *Leptogium* in having simple spores.

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for reading and correcting the manuscript and Dr G. Keuck for translating the summary into Spanish.

Resumen

Se describen cuatro nuevas Colematáceas de Sudamérica: *Homothecium sorediosum* Henss. de Chile, *Homothecium opulentum* var. *redonii* Henss. de Chile y Argentina así como *Homothecium intermedium* Henss. y *Ramalodium austroamericanum* Henss. de Argentina. – *H. sorediosum* es la única Colematácea conocida hasta ahora que produce soredios. El talo es negruzco, corticado y polimorfo: granuloso, membranáceo o formado por pequeños lobulos gruesos; el hábito es semejante a ciertas especies de *Collema*. – *H. opulentum* var. *redonii* tiene un talo gris-violáceo membranáceo, perforado, con lobulos anastomosados y estriados. *H. chilense* posee también un talo arrugado, pero los lóbulos son cilíndricos, más gruesos y corticados. – *H. intermedium* tiene un talo gris-violáceo, membranáceo con lóbulos distintamente aplanados e isidios laminales. – *Ramalodium austroamericanum* se parece en el hábito a especies de *Collema* o *Leptogium*. El talo es oliváceo de lóbulos anchos y cubierto en el lado inferior parcialmente con un corto tomento. Las esporas unicellulares son fusiformes, tienen un largo de 18–31 μm y poseen paredes engrosadas en los extremos.

El desarrollo de los apotecios de *Homothecium* y *Ramalodium* se ha descripto detalladamente. Los dos géneros son enmendados en base a las nuevas características constatadas. *Homothecium* se caracteriza por un excípulo anular y ascos con estructura anular amiloídes en los apices engrosados. En *Ramalodium*, solamente la cubierta mucilaginosa del asco es amiloides. El escípulo es primero anular y sólo secundariamente se hace cupular.

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Studies in the genus Endococcus (Ascomycotina, Dothideales)

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Hawksworth, D. L. 1979 09 30: Studies in the genus Endococcus (Ascomycotina, Dothideales). *Bot. Notiser 132:* 283–290. Stockholm. ISSN 0006-8195.

The generic name *Tichothecium* Flotow, widely used for lichenicolous fungi, is found to be typified by *Verrucaria nigrescens* Pers. and so must be placed as a synonym of the lichen genus *Verrucaria* Schrader nom. cons. A preliminary survey of the fungi formerly referred to *Tichothecium* shows that they fall into two groups on the basis of the structure of the asci. Those with 4- or 8-spored, bitunicate asci are placed in *Endococcus* Nyl. (syn. *Discothecium* Zopf), while ones with multispored asci discharging by a bursting of the apex are considered to belong to *Muellerella* Hepp ex Müll. Arg. A provisional key to the 12 species of *Endococcus* treated is provided and notes on their nomenclature included. The new combinations *E. alectoriae* (D. Hawksw.), *E. propinquus* (Körber), *E. ramalinarius* (Lindsay), *E. vermicularius* (Lindsay), *E. zahlbrucknerellae* (Henssen), *Muellerella lichenicola* (Sommerf. ex Fr.), *M. pygmaea* (Körber), and *Polycoccum arnoldii* (Hepp) are made.

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Recent investigations of the species referred to *Karschia* Körber (Hafellner 1979) and of the Hyphomycetes described from lichens (Hawksworth 1979 a) have clearly demonstrated the very extensive taxonomic revisions now necessary amongst the lichen-inhabiting (lichenicolous) fungi. The pyrenocarpous species with brown 1-septate ascospores and no interascal filaments are no exception to this tenet. Vouaux (1913), Smith (1926) and Keissler (1930) all placed species with 8-spored asci in *Discothecium* Zopf, and ones with multi-spored asci in *Tichothecium* Flotow; other characters were generally ignored.

Similar fungi with branched and anastomosing interascal filaments were referred by these authors to *Didymosphaeria* Fuckel but it is doubtful if they should be placed in that genus; Santesson (1960) consequently took up *Polycoccum* Körber for these fungi, in any case an earlier name than *Didymosphaeria*. As interascal tissues were generally omitted from descriptions by early authors, inevitably some species referred to *Discothecium* have proved to belong to *Polycoccum* on re-examination. A synopsis of the known species of *Polycoccum* has been provided by Vězda (1969) but there seem to be two elements in the genus as understood by him: one with rather unequally celled ascospores with smooth walls (this group includes the type species of *Polycoccum, P. trypethelioides* (Th. Fr.) R. Sant.), and the other with usually equal-celled ascospores with minutely echinulate walls (e.g. *P. galligenum* Vězda). Names of fungi in *Discothecium* which conform to Vězda's concept of *Polycoccum* are not considered further here.

Santesson (1960) pointed out that 8-spored vs. multi-spored asci was not a satisfactory criterion for generic separation and I concur with this view. An excellent example of a genus with various numbers of spores in the asci is *Coniochaeta* (Sacc.) Cooke which includes 4-spored, 8-spored and multispored species (Furuya & Udagawa 1977, Hawksworth 1978 a). Spore septation alone is equally unacceptable as a generic criterion, so it is necessary also to

consider *Muellerella* Hepp ex Müll. Arg., a genus von Arx & Müller (1975) considered as possibly close to *Tichothecium*. *Muellerella* comprises species with multi-spored asci, no interascal filaments, and brown non-septate spores; most species of *Muellerella* are lichenicolous. In *M. polyspora* Hepp ex Müll. Arg. (the type species of the genus) and *M. hospitans* Stizenb., the asci appear to discharge by a bursting of the outer wall and subsequent extrusion of the contents (Fig. 1 B) and not in the characteristically bitunicate manner. Henssen (1977) pointed out that the asci in the multispored *Tichothecium pygmaeum* Körber also were not bitunicate but opened by a bursting of the apical wall; my own observations confirm Henssen's conclusions and I have found the same method of discharge to occur in the other well-known species of *Tichothecium* with multispored asci, *T. lichenicola* (Sommerf. ex Fr.) R. Sant. Henssen (1977) further described a species she tentatively placed in *Tichothecium* with mainly 4-spored asci, *T. zahlbrucknerellae* Henssen, in which the asci were truely bitunicate; my studies indicate that this is so for several other species with 8-spored asci hitherto referred to *Tichothecium,* including *T. alectoriae* D. Hawksw., *T. gemmiferum* auct., *T. rugulosum* (Nyl.) Arnold (the type species of *Endococcus* Nyl.), and *T. stigma* Körber (Fig. 1 C). Ascus discharge is not always easy to demonstrate in aged herbarium specimens and further work on ascus structure in these groups should be carried out to fully determine the variation present.

A more satisfactory taxonomy for this group of fungi can, however, perhaps be achieved by broadening the concept of *Muellerella* so that it may comprise species with 1-septate ascospores (i.e. *Tichothecium lichenicola* and *T. pygmaeum*), and then separating it from the species with 4- or 8-spored asci previously placed in *Tichothecium* on the basis of the differences in ascus structure; the multispored asci of *Muellerella* are then considered a secondary character supporting this taxonomy. In *T. lichenicola* it is of interest that the septum develops rather late in sporogenesis; perhaps a further justification of this taxonomy.

Holm (1975 p. 485) drew attention to the fact that the generic name *Tichothecium* was first validly published by Flotow (1850) and not by

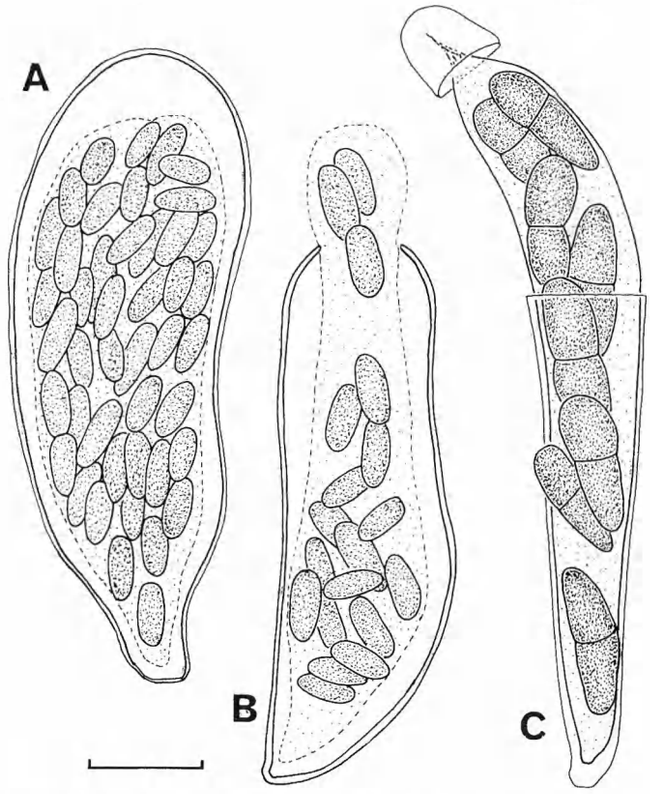

Fig. 1. Discharge of asci. – A–B: *Muellerella polyspora* (IMI 185015). – C: *Endococcus stigma* (L 910.195–403). – Scale 10 μm.

either Körber (1853) as supposed by Santesson (1960), or Körber (1848) as stated by Müller & von Arx (1962). No descriptions accompanied mentions of this name by Körber (1848), Flotow (1849) or Rabenhorst (1849).

Three species were cited in the protologue by Flotow (1850): *T. nigrescens* (Pers.), *T. fuscellum* (Turn.) and *T. verrucarioides* Ach. Flotow further clearly introduced the genus for lichen-forming pyrenocarpous fungi with a neatly areolate thallus: *T. nigrescens* is the species now known as *Verrucaria nigrescens* Pers., *T. fuscellum* is a synonym of *V. glaucina* Ach. (James 1965), and *T. verrucarioides* is a dubious corticolous species, *Pyrenula verrucarioides* Ach., described from India; this is unlikely to be congeneric with the other two species to judge from the original description and illustrations (Acharius 1814 pl. 2 fig. 20; original coloured paintings in BM also seen).

Holm (1975) correctly stated that the lectotype species for the genus *Tichothecium* must be one of the species mentioned by Flotow (1850); *T. pygmaeum* Körber, accepted as the type species of the genus by, for example, Clements & Shear (1931) and Santesson (1960), is not eligible

for consideration as it was not one of Flotow's originally included species. While *T. verrucarioides* is a doubtful taxon differing from the protologue in not being neatly areolate, *T. fuscellum* and *T. nigrescens* both have much to commend them as possible lectotypes as they are congeneric and conform to the original protologue of the genus; both were also mentioned by Flotow (1849). *T. nigrescens* is the first listed species in Flotow (1850), and Körber (1855 p. 342) clearly considered this as if the type stating "Herr v. Flotow gründete hierauf seine Gattung *Tichothecium*". The genus *Tichothecium* is consequently considered as lectotypified by *T. nigrescens* here.

Tichothecium Flotow thus becomes a later synonym of *Verrucaria* Schrader nom. cons. The generic name *Tichothecium* is consequently unavailable for use for the multispored, non-bitunicate lichenicolous fungi which are congeneric with *T. pygmaeum* Körber (i.e. *Muellerella* species). The earliest generic name available for the 4–8 spored bitunicate lichenicolous fungi formerly referred to *Discothecium* or *Tichothecium* appears to be *Endococcus* Nyl.

The fungi referred to *Tichothecium* auct. are in need of a monographic revision and it is quite impossible to provide a comprehensive account of them at this time. Following the discovery that the name of one common species was incorrect (Hawksworth 1979 b), I have examined type or authentic material of as many taxa as were easily available with a view to making a small contribution to the clarification of the taxonomy of this genus. As the generic name must also be changed, it is opportune to present my *preliminary* findings here in the form of a key to the accepted species and a synopsis of their nomenclature, particularly as these conclusions will be incorporated into the new check-list of British lichen-forming and lichenicolous fungi currently in the course of preparation.

Endococcus Nyl. (Loculoascomycetes – Dothideales)

Mém. Soc. Imp. Sci. Nat. Cherbourg 3: 193 (1855) – Type species: *E. rugulosus* Nyl.

Discothecium Zopf, Nova Acta Acad. Caesar. Leop. Carol. 70: 131 (1897) – Type species: *Discothecium stigma* (Körber) Zopf.

Sphaerellothecium Zopf, Nova Acta Acad. Caesar. Leop. Carol. 70: 184 (1897) – Type species: *Sphaerellothecium areneosum* (Rehm) Zopf.

Tichothecium auct. p. p., non Flotow, Bot. Ztg. 8: 361 (1850).

Ascomata arising singly, perithecioid, subglobose, immersed to erumpent, ostiolate, black; peridium carbonaceous, comprising 3–6 layers of radially compressed thick-walled dark brown pseudoparenchymatous cells; ostiole lined internally with distinct periphyses. Paraphyses, paraphysoids and pseudoparaphyses absent; asci originating in a gelatinized matrix. *Asci* elongate-clavate to subcylindrical, with a markedly thickened apex when young, bitunicate, originating in a basal fascicle, 4–8-spored. *Ascospores* irregularly arranged or distichous, ellipsoidal, with rounded or somewhat pointed apices, 1-septate, sometimes markedly constricted at the septum, dark brown, smooth-walled (by light microscopy).

Lichenicolous, parasymbiotic or parasitic on the thalli of lichen-forming fungi.

The generic name *Endococcus* was briefly mentioned in the first part of Nylander's *Essai* in 1854 (Nylander 1854 p. 15) but is considered as not validly published there (Art. 32).

Sorothelia Körber (type species *S. confluens* Körber) and *Lophothelium* Stirton (type species *L. acervatum* Stirton; see Hawksworth 1978 b) are both synonyms of *Polycoccum*. Von Arx & Müller (1975) placed *Endococcus* as a synonym of *Phaeospora* Hepp (in any case a much later name!). *Phaeospora* is traditionally separated from *Discothecium* and *Tichothecium* auct. in that its spores are 3- or more septate. I have not studied that genus in any detail and for the present prefer to retain it as distinct from *Endococcus* on the basis of the admittedly unsatisfactory character of the ascospore septation, and further the tendency of the spores to not be constricted at the septa. *Endococcus* might, however, eventually merit extension to include at least some taxa currently placed in *Phaeospora*.

The taxa referred to *Endococcus* below may be separated into two rather clear groups: one including the type species (*E. rugulosus*) in which the spores have rounded ends and are hardly constricted at the septum, and one including the type species of *Discothecium* (*D.*

stigma) where the spores have somewhat pointed apices and are very markedly constricted at the septum. As I have not been able to detect any further characters supporting this division, I regard these groups as congeneric.

Provisional key to the species treated

This key includes species with brown 1-septate spores and aparaphysate perithecioid ascomata conforming to Santesson's (1960) concept of *Tichothecium* but which are now referred to *Endococcus* or *Muellerella*.

1. Asci multispored 2
– Asci 4- or 8-spored 3
2. Ascomata 0.05–0.11 mm diam, usually ± completely immersed; ascospores brown, 5–7(–8) × 2–3(–4) μm; on *Caloplaca, Fulgensia* and *Lecanora* species, usually on calcareous rocks ... 14. *Muellerella lichenicola*
– Ascomata 0.15–0.2 mm diam, usually superficial; ascospores dark brown, 6–9 × 4–5 μm; on *Haematomma, Huilia, Lecidea,* and other crustose saxicolous lichens, usually on siliceous rocks ..... 15. *Muellerella pygmaea*
3. Asci 8-spored 4
– Asci 4-spored (rarely 8-spored); ascomata c. 100 μm diam; ascospores 10.5–13.5 × 5.5–6 μm; on *Zahlbrucknerella calcarea,* forming dark coloured galls to 0.3 mm diam ..... 12. *E. zahlbrucknerellae*
4. Ascospores with both ends rounded 5
– Ascospores with both ends, or rarely only one end somewhat constricted 10
5. Ascospores all exceeding 12 μm in length 6
– Ascospores mainly less than 12 μm in length 8
6. Ascospores ellipsoidal 7
– Ascospores narrowly ellipsoidal, pale brown, (12–)14–18(–20) × 3.5–5(–6) μm; on unidentified saxicolous crustose lichen ..... 4. *E. exerrans*
7. Ascospores not markedly constricted at the septum, 12–16(–18) × (5–)7(–9) μm; on a wide range of saxicolous crustose lichens ..... 9. *E. rugulosus*
– Ascospores clearly constricted at the septum, 10–13 × 4–4.5 μm; on *Ramalina leidoea,* New Zealand ..... 8. *E. ramalinarius*
8. Ascospores 4–7 μm wide 9
– Ascospores 8–11 × 3–4 μm; on *Thamnolia,* Falkland Islands ..... 11. *E. vermicularius*
9. Ascospores 6.5–8 × 5–6 μm; on *Rhizocarpon petraeum* and perhaps other saxicolous crustose lichens ..... 3. *'Discothecium' brachysporum*
– Ascospores (7–)9–10(–12) × 4–6(–7) μm; on a wide range of saxicolous crustose lichens ... 7. *E. propinquus*
– Ascospores 9–13 × 4–6 μm, cells unequal in size; on *Xanthoria parietina,* forming galls .... 6. *E. parietinus*
10. Asci exceeding 7 μm in width 11
– Asci 6–7 μm in width; ascospores 12–14 × 5–6 μm; on *Teloschistes,* Argentina . 5. *'Discothecium' infestans*
11. Ascospores mainly exceeding 5 μm in width 12
– Ascospores 10.5–15.5 × 3.5–4.5 μm; on *Alectoria ochroleuca,* Austria ..... 1. *E. alectoriae*
12. Ascospores 12–14 × 3–4 μm; on *Aspicilia,* and *Ochrolechia,* Europe ..... 2. *E. araneosus*
– Ascospores (12–)14–16(–20) × 4–6(–8) μm; on a wide range of saxicolous crustose lichens, widespread ..... 10. *E. stigma*

The following notes on the species are mainly nomenclatural. In the absence of a monographic study it would be premature to attempt to provide comprehensive descriptions or lists of host species. The diagnostic characters of the species are, however, indicated in the key and the ascospores of selected species are illustrated in Fig. 2.

Obligate synonyms and infraspecific names are omitted unless commonly used.

1. **Endococcus alectoriae** (D. Hawksw.) D. Hawksw., comb. nov.

Tichothecium alectoriae D. Hawksw., Trans. Br. Mycol. Soc. 57: 338 (1971) – Type: Austria, Salzburg, on *Alectoria ochroleuca,* July 1869, G. Davies (BM holotype!).

2. **Endococcus araneosus** (Rehm) H. Olivier

Bull. Acad. Intern. Géogr. Bot. 17: 127 (1907) – *Sphaerella araneosa* Rehm in Arnold, Ber. Naturh. Ver. Augsburg 26: 35 (1881) – *Discothecium araneosum* (Rehm) Vouaux, Bull. Soc. Mycol. Fr. 29: 55 (1913) – Type: 'Supra thallum et apothecia *Ochrolechia pallesc.* var. *upsaliensis* (L.) [i.e. *O. upsaliensis*] etc. in alpibus editoribus Tiroliensibus, leg. Dr. Arnold'.

This name was indicated to be a nomen nudum where it appears in Arnold (1874 p. 153) by

Keissler (1930 p. 398) but as spore measurements are given on p. 175 in Arnold's legend to his Table II it might be considered as validly published in 1874, not 1881.

3. **'Discothecium' brachysporum** (Zopf) Lettau

Hedwigia 61: 174 (1918) – *Tichothecium gemmiferum* var. *brachysporum* Zopf, Nova Acta Kaiserl. Leop.-Carol. Akad. 70: 283 (1898) – Type: 'Auf *Rhizocarpon excentricum* (Ach.) [i.e. *R. petraeum*], von Porphyr bei St. Ulrich in Gröden'.

I have not encountered such a small-spored species but from Zopf's figures it would appear to be a species of *Endococcus*. In the absence of any material it would be unwise to make the new combination in case Zopf overlooked any paraphyse-like structures present.

4. **Endococcus exerrans** Nyl.

Flora 62: 360 (1879) – *Microthelia exerrans* (Nyl.) A. L. Sm., Monogr. Br. Lich. 2: 332 (1911) – Type: Scotland, Ben-y-gloe, 'ad saxa quartzosa', J. M. Crombie (K isotypes!).

5. **'Discothecium' infestans** (Speg.) Vouaux

Bull. Soc. Mycol. Fr. 29: 56 (1913) – *Didymosphaeria infestans* Speg., An. Soc. Cient. Argent. 12: 176 (1881) – Type: Argentina, 'In thallo v. apotheciis languentibus *Teloschistidis flavicantis* ad palos vetustos, Conchas, 1 Maj. 1881'.

As this species was reported to lack paraphyses it seems possible it should be referred to *Endococcus* but without seeing material it would be premature to make the necessary combination.

6. **Endococcus parietinus** (Lindsay) Clauzade & Roux

Champ. Lich. Non-Lich.: 28 (1976) – *Microthelia parietina* Lindsay, Trans. R. Soc. Edinb. 25: 541 (1869) – *Didymosphaeria parietina* (Lindsay) Sacc., Syll. Fung. 17: 681 (1905) – Type: England, 'Cottishall, in Herb. Kew' (not traced).

? *Mycoporum physciicola* Nyl., Flora 56: 299 (1873) – *Discothecium physciicola* (Nyl.) Vouaux, Bull. Soc. Mycol. Fr. 29: 48 (1913).

Lindsay's material could not be located in BM, E or K. The status of this species requires further study.

7. **Endococcus propinquus** (Körber) D. Hawksw., comb. nov.

Microthelia propinqua Körber, Syst. Lich. Germ.: 374 (1855) – Type: 'In crusta Lecideae variegatae ad saxa porphyrica prope pagum Bruckhausen in Guesphalia', Lahm (K neotype, designated here!).

Tichothecium gemmiferum auct. p.p., non (Taylor) Körber – *Discothecium gemmiferum* auct. p.p., non (Taylor) Vouaux.

The typification of *Verrucaria gemmifera* Taylor, the basionym of *Tichothecium gemmiferum*, was investigated by Hawksworth (1979 b) who found it to be based on a mixture of species excluding this species as understood by recent authors. The usage of this name for a species recalling *E. rugulosus* but with smaller ascospores perhaps originates from Leighton (1851); the material illustrated by Leighton is labelled 'Miss Hutchins to Mr Turner. *Verrucaria gemmifera* Fl. Hib.' (K!) and is the smaller-spored taxon but there is no evidence this came from the type locality, Dunkerron.

The numerous synonyms listed by Keissler (1930 p. 385–386) under *Discothecium gemmiferum* almost all prove to belong to other species. The only exception is *Microthelia propinqua* as neotypified here; no material of this taxon is now present in Körber's herbarium in L but Lahm worked closely with Körber on this group of fungi and the specimen in K designated as neotype was sent to Leighton by either Lahm or Körber as authentic material of *M. propinqua*.

8. **Endococcus ramalinarius** (Lindsay) D. Hawksw., comb. nov.

Microthelia ramalinaria Lindsay, Trans. R. Soc. Edinb. 24: 440 (1866) – *Tichothecium ramalinaria* (Lindsay) D. Hawksw., Trans. Br. Mycol. Soc. 67: 55 (1976) – Type: New Zealand, Otago, on dead trunk of 'Goai', Greenisland Bush, on *Ramalina leiodea*, 26 October 1861, W. L. Lindsay (E lectotype!).

The lectotypification of this species is discussed by Hawksworth (1976 p. 54).

9. **Endococcus rugulosus** Nyl.

Mém. Soc. Imp. Sci. Nat. Cherbourg 3: 193 (1855) (Art. 72, Note 1) – *Verrucaria rugulosa* Borrer ex Leighton, Br. Angioc. Lich.: 47 (1851); nom. illegit. (Art. 64), non *Verrucaria rugulosa* Flörke 1808 – *Microthelia rugulosa* (Nyl.) Mudd, Man. Br. Lich.: 306 (1861) – *Tichothecium rugulosum* (Nyl.) Arnold, Flora 57: 143 (1874) – Type: England, 'old walls at Lewes,

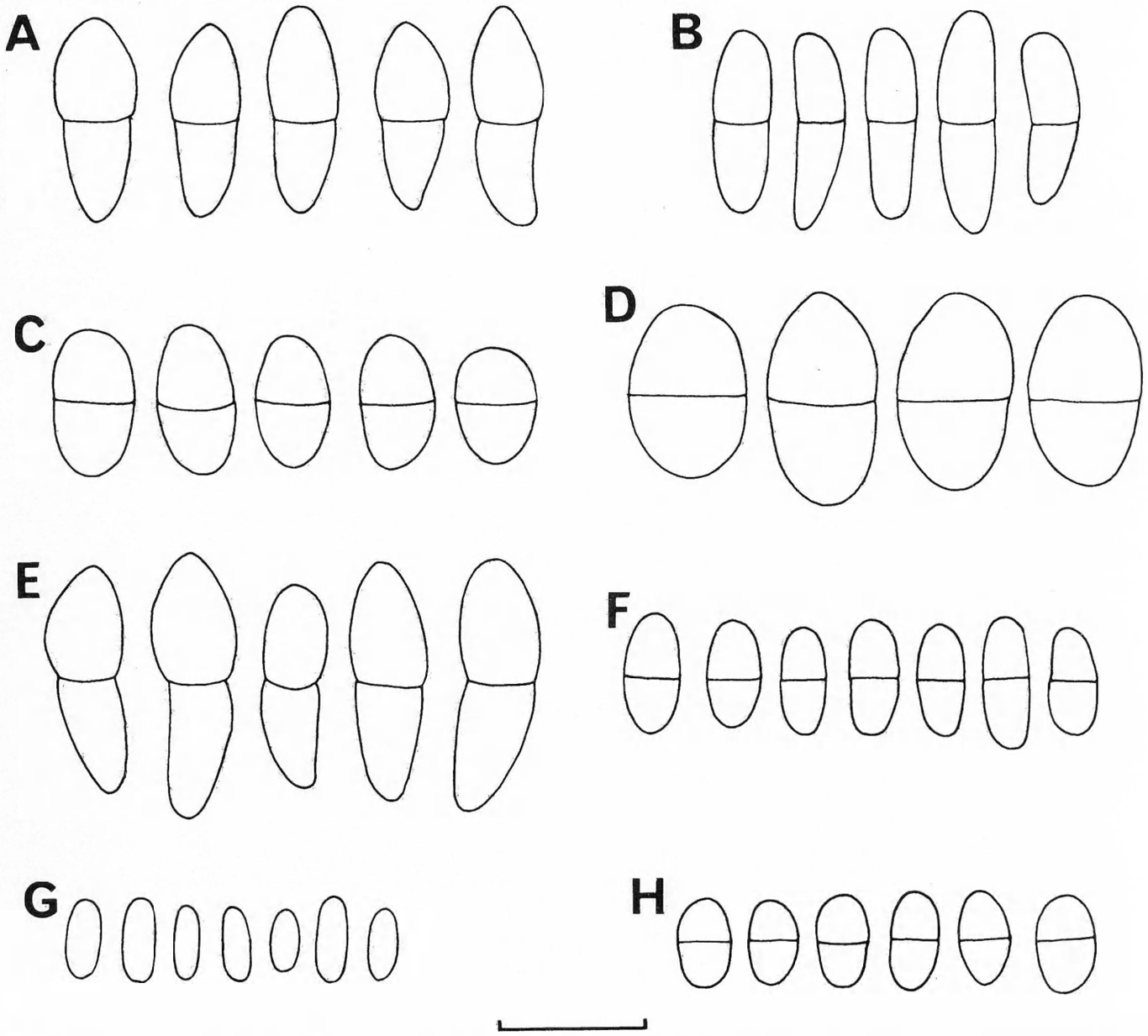

Fig. 2. Ascospores of selected *Endococcus* and *Muellerella* species (outlines only; all are olivaceous brown to dark brown). – A: *Endococcus alectoriae* (BM holotype). – B: *Endococcus exerrans* (K isotype). – C: *Endococcus propinquus* (K neotype). – D: *Endococcus rugulosus* (K holotype). – E: *Endococcus stigma* (L 910.195–403). – F: *Muellerella lichenicola* (K Anzi Lich. rar. Lang. no. 289). – G: *Muellerella polyspora* (IMI 185015). – H: *Muellerella pygmaea* (IMI 211480). – Scale 10 μm.

Sussex. Mr Borrer' (K holotype!).

Endococcus perpusillus Nyl., Mém. Imp. Sci. Nat. Cherbourg 3: 193 (1855), nom. inval. (Art. 32); Act. Soc. Linn. Bordeaux 21: 439 (1857), cum descript. – *Tichothecium perpusillum* (Nyl.) Arnold, Flora 57: 143 (1874) – Type: see Santesson (1960 p. 509).

Verrucaria larbalestieri Leighton, Trans. Linn. Soc. Lond., ser. 2, Bot. 1: 242 (1877) – Type: Ireland, Co. Galway, 'near Kylemore, 1877', C. Larbalestier (K holotype!).

? *Verrucaria fumosaria* Leighton, Trans. Linn. Soc. Lond., ser. 2, Bot. 1: 239 (1877) – Type: Wales, Pembrokeshire, nr Fishguard, Pen Cow, September 1876, W. A. Leighton (not traced).

? *Microthelia calcaricola* Mudd, Man. Br. Lich.: 306 (1861) – *Endococcus calcaricola* (Mudd) Norman, Sp. Loc. Nat. Norw.: 375 (1868) [not seen] – *Tichothecium calcaricola* (Mudd) Arnold, Flora 57: 143 (1874) – *Discothecium calcaricola* (Mudd) Vouaux, Bull. Soc. Mycol. Fr. 29: 49 (1913) – *Discothecium gemmiferum* var. *calcaricola* (Mudd) Keissler, Rabenh. Krypt.-Fl. 8: 389 (1930) – *Endococcus calcareus* Nyl. ex Crombie, Lich. Br.: 122 (1870); nom. illegit. (Art. 63) pro syn. *Microthelia calcaricola* Mudd – Syntypes: 'Killing, Ireland, Admiral Jones', 'near Lewes, Sussex, W. Unwin' (not traced).

? *Tichothecium pulvinatum* Eitner, Jahresb. Schles. Ges. Vaterl. Cult., Abt. II, 78: 26 (1901) – Type: Germany, 'Auf *Physcia stellaris*, Glatz, am Zollhaus hinter Birgwitz' (not traced).

At first (Hawksworth 1979 b) I thought the epithet *perpusillus*, used by Santesson (1960), could be saved as both were treated by Nylander in 1855; unfortunately subsequent study showed that Nylander did not validly publish this name until 1857 and consequently *rugulosus* must be taken up for this species. The epithet *rugulosus* was also not validly published in 1854 (Nylander 1854 p. 15) as the generic name is not considered to have been validly published then.

Endococcus rugulosus is a widespread species, almost certainly the commonest in the genus, although it has often been confused with the taxon widely called '*gemmiferum*' and treated as *E. propinquus* here. As pointed out by Santesson (1960), these species are clearly separated on the basis of the sizes of their ascospores.

10. **Endococcus stigma** (Körber) Stizenb.

Ber. Tät. St. Gall. Naturw. Ges. 22: 516 [p. 262 of reprint] (1882) – *Tichothecium stigma* Körber, Parerga Lich.: 468 (1865) – *Discothecium stigma* (Körber) Zopf, Nova Acta Kaiserl. Leop.-Carol. Akad. 70: 127 (1897) – Type: see Santesson (1960 p. 508).

Microthelia scabrida Lahm in Körber, Parerg. Lich.: 399 (1865) – Type: Germany, 'Kalkfelsen bei Stadtberge in Westphalen', Lahm (L 910.195–403 holotype!).

As my main concern at the onset of this study was the *rugulosus* group, I have not attempted to locate the type material of most of the names listed by Keissler (1930 p. 394) as later synonyms of this species. As some of these names are to be expected to be found to belong to other species (and genera!) they are not repeated here.

11. **Endococcus vermicularius** (Lindsay) D. Hawksw., comb. nov.

Lecidea vermicularia Lindsay, Trans. R. Soc. Edinb. 22: 143 (1859) – *Discothecium vermicularium* (Lindsay) Vouaux, Bull. Soc. Mycol. Fr. 29: 58 (1913) – *Tichothecium vermicularium* (Lindsay) Arnold, Flora 57: 142 (1874) – Type: see Hafellner (1979 p. 220).

12. **Endococcus zahlbrucknerellae** (Henssen) D. Hawksw., comb. nov.

Tichothecium zahlbrucknerellae Henssen, Lichenologist 9:44 (1977) – Type: see Henssen (1977 p. 44).

Excluded taxa

In addition to taxa previously referred to *Polycoccum*, one further species formerly treated in *Discothecium* must be added to that genus, and two species require transfer to *Muellerella* as discussed above.

13. **Polycoccum arnoldii** (Hepp) D. Hawksw., comb. nov.

Phaeospora arnoldii Hepp, Flecht. Eur. no. 701 (1860) – *Discothecium arnoldii* (Hepp) Vouaux, Bull. Soc. Mycol. Fr. 29: 58 (1913) – *Endococcus arnoldii* (Hepp) Trevisan, Consp. Verr.: 17 (1860) – Type: 'Auf steinigem Boden zwischen Winterhof w. Ruppertobuch, bei Eichstadt; F. Arnold' (K isotype!).

This species is rather close to *Polycoccum bryonthae* (Arnold) Vězda but has more clavate asci, somewhat smaller ascospores (9–11.5(–13)× 4.5–5(–7) μm), and occurs on *Diploschistes scruposus*.

14. **Muellerella lichenicola** (Sommerf. ex Fr.) D. Hawksw., comb. nov.

Sphaeria lichenicola Sommerf. ex Fr., Elench. Fung. 2: 103 (1828) – *Tichothecium lichenicola* (Sommerf. ex Fr.) R. Sant., Svensk Bot. Tidskr. 54: 507 (1960) – Type: see Santesson (1960 p. 507).

This is a very common species. Some synonyms are mentioned by Santesson (1960) but there are many others.

15. **Muellerella pygmaea** (Körber) D. Hawksw., comb. nov.

Tichothecium pygmaeum Körber, Denkschr. Schles. Ges. Vaterl. Cult. 1853: 231 (1853) – *Endococcus pygmaeus* (Körber) Th. Fr., Nova Acta Reg. Soc. Sci. Upsal., ser. 3, 3: 275 (1860) [preprint] – Type: see Santesson (1960 p. 506).

Many synonyms are listed for this common species by Keissler (1930 p. 411–412), several of which I have been able to confirm (e.g. *Tichothecium rehmii* Massal. ex Winter, *Microthelia ventosicola* Mudd). While *Muellerella lichenicola* tends to grow on lichens in basic or highly calcareous situations, *M. pygmaea* is commonest on species on siliceous rocks.

16. **Buellia minimula** Tuck.

Syn. N. Am. Lich. 2: 106 (1888).

This name was placed by Keissler (1930 p. 391) as a synonym of *Discothecium gemmiferum* var. *calcaricola*, but is correctly interpreted as the type species of a distinct discomycete genus, *Buelliella* Fink (see Hafellner 1979 p. 154).

Acknowledgements. I am very grateful to the curators of the herbaria cited in the text for permission to examine material in their care, and to Dr J. Hafellner and Dr L. Holm for comments on the manuscript.

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Asperula tragacanthoides Brullo, sp. nov. from Libya

Salvatore Brullo

Brullo, S. 1979 09 30: Asperula tragacanthoides Brullo, sp. nov. from Libya. *Bot. Notiser 132:* 291–293. Stockholm. ISSN 0006-8195.

Asperula tragacanthoides Brullo, sp. nov. (Rubiaceae) is described. It is a dwarf shrub growing in garigue on calcareous marl in N Cyrenaica (Libya). It is similar to *A. coa* Rechinger from the E Aegean area.

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Asperula tragacanthoides Brullo, sp. nov. – Fig. 1

Orig. coll. Cyrenaica, Uadi Schaaba sopra Tolmeta, 10.5.1974, Brullo & Furnari (CAT holotype, CAT, FI, G, W isotypes).

Planta perennis, 20–60 cm procera, suffruticosa, caespitosa, valde lignosa basi, cinereo-virescens vel glauca. *Caules* inferne ramosi, procumbentes, dense pruinoso-hispiduli, brevibus, pilis rigidis et incurvis muniti, plus minusve crasso-suberosi, subteretes, dense foliosi, foliis vetustis persistentibus, superne glabri vel subglabri, acute tetragoni, ramis prostrato-ascendentibus vel erecto-ascendentibus. *Internodia* inferiora valde approximata et incrassata, 2–20 mm longa, axillis bilateraliter breviter fasciculiferis seu foliis vel ramulis sterilibus, superiora elongata, rigida, subtilia, usque ad 50 mm longa, axillis fere fertilibus. *Folia* quaterna, angusta, linearia vel aciculato-subulata, basi breviter connata, uninervia, rigida, acuta, apicibus acuminato-pungentibus, et arista hyalina 1–1,5 mm longa praedita, marginibus laevibus, leviter revolutis et incrassatis, costa mediana subtus crasse prominenti. Folia basalia hispidula, 10–15 × 0,5–0,8 mm, subaequalia vel longiora quam internodia, superiora 4–10 × 0,8–1 mm, plus minusve glabra, quam internodia breviora. *Florescentia* simplex vel paulo ramosa, floribus in verticillastros plerumque valde remotos digestis, quosque 2–4 fasciculorum (2–)3–4(–5) floribus praeditos. *Bracteae* lanceolatae, 3–5 mm longae, basi dilatatae et leviter connatae, marginibus hyalinis angustis non revolutis, aristulatae, glabrae, fere breviores vel interdum quam flores subaequales. *Corolla* 4-mera, 5–6 mm longa, roseo-purpurescens, infundibuliformis, glabra, minutissime papillosa, lobis lanceolatis, 1–1,5 mm longis, distincte appendiculatis, intus incurvatis. *Stamina* 4, recondita, epipetala. Antherae biloculares, purpureo-nigricantes, c. 1 mm longae. *Stylus* sursum bifidus, stigmatibus globosis, purpureo-nigricantibus. Ovarium ovoideum, 0,8–1 mm longum, papillosum. Mericarpia ovoidea, 1,5–2,5 mm longa, brunneo-nigricantia, papillis densis et elongatis.

Othercollections: Cyrenaica, Ras el-Hilal, 25.5.1974, Brullo & Furnari (CAT); 23.3.1975, Brullo & Furnari (CAT).

A caespitose, grey-green to glaucous dwarf shrub 20–60 cm high. *Stems* branched below, procumbent–ascending; below subterete, ± suberous, pruinose and densely hispid with short, rigid and arcuate hairs, covered with dead leaves; above 4-angled and subglabrous to glabrous. Lower internodes 5–20 mm; upper ones rigid, elongate (up to 50 mm) and thinner. Basal nodes with vegetative short shoots; upper ones with clusters of flowers. *Leaves* in whorls of 4, 1-veined, linear to acicular or subulate, slightly connate at base, arcuate, hard and rigid; apex with hyaline awn 1–1.5 mm long; margins ± thick and slightly revolute; basal leaves finely hispid, 10–15 × 0.5–0.8 mm, upper ones ± glabrous, 4–10 × 0.8–1 mm. *Inflorescence* simple or few-branched, composed of verticillasters, with 2–4 clusters of (2–)3–4(–5) flowers in each whorl; each cluster supported by two bracts. Bracts lanceolate, 3–5 mm, shorter than or sometimes subequal to flowers, glabrous, aristate, slightly connate at base; margins hyaline, narrow and flat. *Corolla* 4-merous, 5–6 mm long, pink–purplish, infundibuliform, finely papillose;

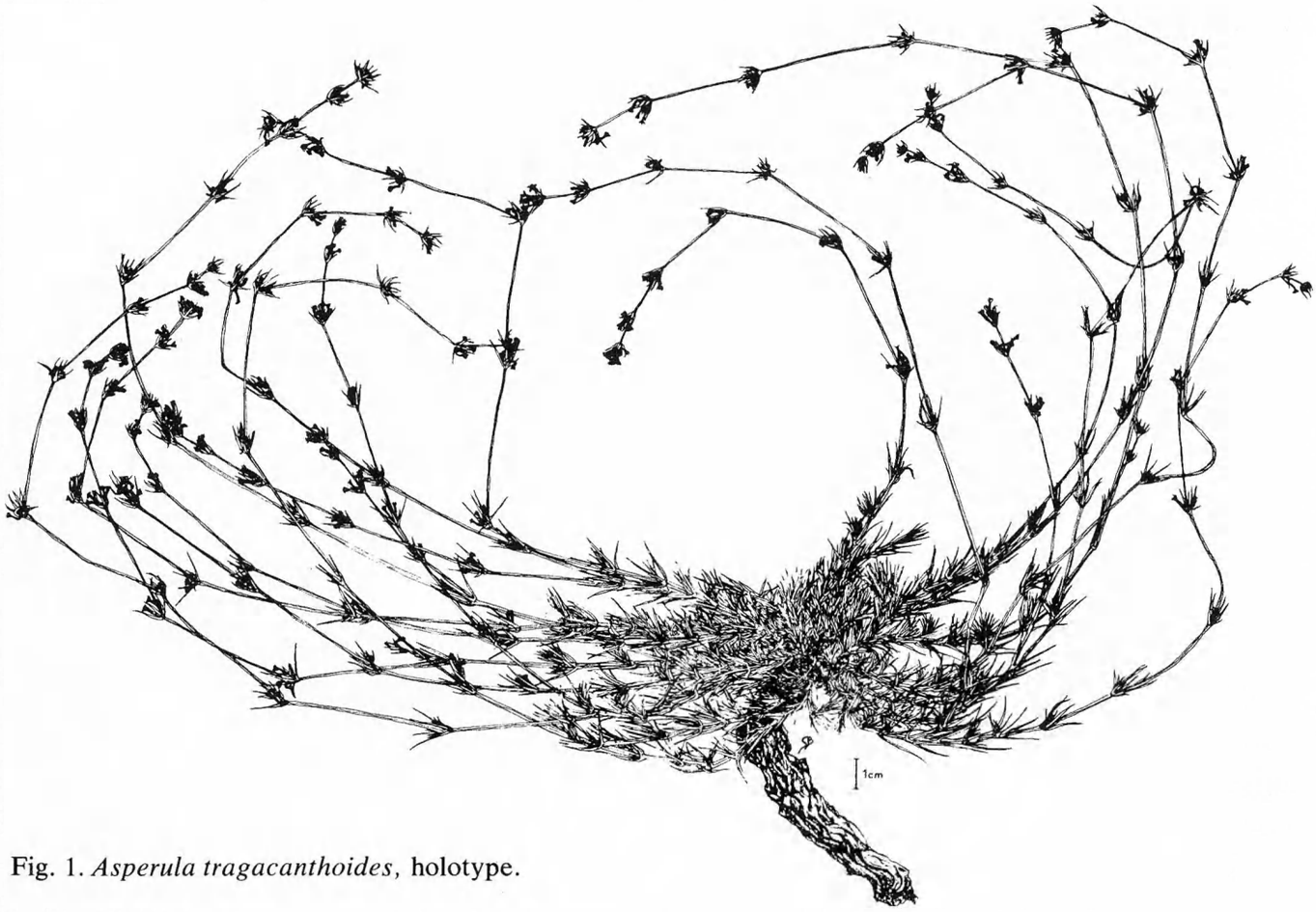

Fig. 1. *Asperula tragacanthoides*, holotype.

lobes lanceolate, 1–1.5 mm long, distinctly appendiculate, curved inwards. *Stamens* 4, included in tube; anthers purplish-black, c. 1 mm long. *Stigma* capitate, purplish-black. *Ovary* 0.8–1 mm, ovoid, papillose. *Fruit* brownish-black, 1.5–2.5 mm long, with dense and elongated papillae.

Distribution and habitat. Asperula tragacanthoides has been collected in N Cyrenaica during phytosociological research on the Gebel el-Ahkdar. It is quite rare and occurs in garigue on calcareous marl at 200–500 m altitude. *A. tragacanthoides* is associated with numerous xerophilous dwarf shrubs, e.g. *Rosmarinus officinalis* L. (dominant), *Erica multiflora* L., *Cistus parviflorus* Lam., *Helianthemum rubellum* C. Presl, *Lithodora hispidula* (S. & S.) Griseb. ssp. *cyrenaica* (Pamp.) Brullo & Furnari, *Teucrium barbeyanum* Aschers. & Taub., *Sarcopoterium spinosum* (L.) Spach, *Fumana arabica* (L.) Spach, *Phlomis floccosa* D. Don, *Polygala aschersoniana* Chodat, *Satureja thymbra* L., *Centaurea cyrenaica* Béguinot & Vacc., *Nepeta vivianii* (Coss.) Béguinot & Vacc., *Astragalus caprinus* L., *Hypericum empetrifolium* Willd., *Convolvulus oleifolius* Desr. and *Globularia arabica* Jaub. & Spach. This vegetation is evidently thermophilous and is typical of the sunniest slopes of the Gebel; the annual rainfall in the area is 350–600 mm. This vegetation has to be included in the class *Cisto-Micromerietea*, which has an E Mediterranean distribution.

Taxonomic relationships. Asperula tragacanthoides has to be included in sect. *Cynanchicae* (DC.) Boiss. Among the species of this section, *A. coa* Rechinger from the island of Kos (E Aegean) comes closest. It belongs to the E Mediterranean *A. lilaciflora* Boiss. group. *A. coa* differs from *A. tragacanthoides* in the following respects: it is larger; the basal leaves are broader than the upper ones; the leaf margins are strongly revolute; the apical awn of the leaves is shorter; the corolla is 3–4 mm and yellowish or pale pink; the fruit is larger.

Two other species of *Asperula* are known from Cyrenaica, viz. *A. cyrenaica* (Dur. & Barr.) Pamp. and *A. arvensis* L. The former is an

endemic, related to *A. hirsuta* Desf., and occurs exclusively in calcareous cliffs (Bartolo et al. 1977); the latter, which is new for Cyrenaica, is a weed of agricultural fields. In addition Sandwith & Simpson (1941) mention *A. aristata* L. fil., but the presence of this species in Cyrenaica has to be confirmed. *A. tragacanthoides* differs from all these species by its tragacanthoid habit.

Acknowledgements. My sincere thanks are due to Professor F. Ehrendorfer and Dr E. Schönbeck-Temesy, Vienna, for their kind help in solving the problems of the taxonomic relationships.

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Chromosome numbers in the tribe Rhipsalinae (Cactaceae)

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Gadella, T. W. J., Kliphuis, E. & Naber, J. 1979 09 30: Chromosome numbers in the tribe Rhipsalinae (Cactaceae). *Bot. Notiser 132:* 294. Stockholm. ISSN 0006-8195.

The chromosome number 2n = 22 is reported for 23 species of *Rhipsalis*, 2 species of *Lepismium* and for *Hatiora salicornioides* Web. 2n = 44 was found in *Rhipsalis cassytha* Gaertn.

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Most species of the Cactaceae are characterized by the chromosome number 2n = 22. The basic number of all species studied appears to be x = 11. Polyploidy is perhaps less frequent than in other families but in some genera high levels of polyploidy seem to occur: one species of *Opuntia* turned out to be 30-ploid (Yuasa et al. 1974); one species of *Mammillaria* appeared to be 24-ploid (Remski 1954).

The purpose of this communication is to present some new chromosome counts of Cactaceae, tribe Rhipsalinae, of which only two species were studied cytologically before: *Rhipsalis cassytha* (2n = 22, 44, Spencer 1955; Mangenot & Mangenot 1962) and *R. mesembryanthemoides* (2n = 22, Beard 1937).

The material (24 species of *Rhipsalis*, 2 species of *Lepismium* and 1 species of *Hatiora*) was obtained from the Botanical Garden of the State University of Utrecht, where the plants are in cultivation. Numbers given after each species indicate the collection studied. Mr L. Y. Westra kindly helped with the identification of the material. The counts were made on sectioned root tips, fixed in Karpechenko's fixative and stained with Heidenhain's haematoxylin method.

Species with 2n = 22 – *Hatiora salicornioides* Web., 3184 – *Lepismium anceps* Web., 3130, 3140, 3205 – *L. myosurus* Salm–Dyck, 1339 A – *Rhipsalis coriacea* Polak, 64–182 – *R. crispata* Hort., 13 – *R. dissimilis* (G. A. Lindb.) K. Schum., 3143 – *R. elliptica* G. A. Lindb., 3144 – *R. fasciculata* Haw., 3157 – *R. gibberula* Web., 3140 – *R. grandiflora* Haw., 3233 – *R. hadromosa* G. A. Lindb., 3164, 3199 – *R. houlletiana* Lemaire, 1343, 1704, 3154 – *R. megalantha* Loefgr., 3148, 3159 – *R. mesembryanthemoides* Haw., 3165 – *R. neves–armondii* K. Schum., 3168 – *R. oblonga* Loefgr., 3135 – *R. pachyptera* Pfeiff., 1352, 3169 – *R. paradoxa* Salm–Dyck, 1353, 3170 – *R. pentaptera* Pfeiff., 3173, 3187 – *R. prismatica* (Lemaire) Rümpl., 3178 – *R. puniceo-discus* A. G. Lindb. var. *chrysocarpa* (Loefgr.) Borg., 3132, 3146 – *R. rigida* Loefgr., 3142 – *R. shaferi* Britton & Rose, 3185 – *R. trigona* Pfeiff., 3234 – *R. tucumanensis* Web., 3203, 3231 – *R. warmingiana* K. Sch., 3129.

Species with 2n = 44 – *Rhipsalis cassytha* Gaertn., 3191, 3206.

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Pollen morphology and evolution in Psittacanthus (Loranthaceae)

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Feuer, S. & Kuijt, J. 1979 09 30: Pollen morphology and evolution in Psittacanthus (Loranthaceae). [Fine structures of mistletoe pollen II.] *Bot. Notiser 132:* 295–309. Stockholm. ISSN 0006-8195.

Pollen morphology of 32 species of *Psittacanthus* Mart. (including *Aetanthus* Engl.) was examined by light and scanning electron microscopy; 13 of these were additionally examined with the transmission electron microscope. *Psittacanthus* pollen is typically oblate and trilobate, deeply concave in polar view. Based on differences in sculpturing pattern three basic types are recognized: Type I, minutely spinulate; Type II, psilate; and Type III, scabrate-verrucate. Type I pollen is further divisible into subtypes based on differences in apertures which range from syncolpate and colpate to diplo- and syndiplocolpate configurations. Both Type I and II are columellate. Type I columellae are uniformly thickened and associated with supratectal spinules while Type II columellae are unevenly thickened, often exhibiting granular upper portions. The tectate-granular exine organization (Type III) is unique within the family. The pollen data cannot be used to delineate species groupings within *Psittacanthus*. However, they do indicate a close relationship between *Psittacanthus* and other large-flowered neotropical Loranthaceae, as well as an advanced position for the genus within this complex.

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The genus *Psittacanthus* (40–50 sp.), which has never been completely monographed, contains most of the large-flowered neotropical Loranthaceae. The genus extends from NW Mexico throughout tropical continental America to the Buenos Aires region of Argentina (Abbiatti 1946); Caribbean representatives are found on Jamaica, Guadeloupe, Dominica and Martinique (Urban 1898).

The generic boundaries as well as species relationships within *Psittacanthus* have been the subjects of much controversy. The original description of the genus (Martius 1830) was based on inflorescence, floral shape and anther morphology. A much better diagnostic feature, however, the lack of endosperm, was later discovered by Eichler (1868) and further corroborated by recent embryological data. Work on the seedling and early embryo shows that the embryo, particularly the massive cotyledons which range from 2–14 in number, has assumed the storage function from the endosperm (Kuijt 1967, 1970). In early embryogeny an extremely massive suspensor is formed which, though eventually crushed, remains recognizable in the seed. Though carpological data are unavailable for most *Psittacanthus* species, it is probably safe to assume that the lack of endosperm and the formation of a large suspensor are linked throughout the genus and are taxonomically significant for *Psittacanthus*.

Martius (1830) suggested a sectional subdivision with regard to dorsifixed versatile *versus* basifixed erect anthers. Using these same anther differences, Eichler (1868) proposed the first formal infrageneric classification dividing the genus into the subgenera *Eupsittacanthus* and *Aetanthus,* respectively. Undue emphasis on anther structure, however, led to much confusion. Van Tieghem (1895), for example, created 16 new genera in addition to *Psittacanthus* and *Aetanthus,* which he raised to

generic status. This plethora of accumulated generic names was later uncritically incorporated into *Psittacanthus* at the infrageneric level by Engler & Krause (1935). Recently, it has been shown that only one of the Van Tieghem genera (*Ligaria*) seems to be sufficiently distinct to warrant separate generic status (Barlow & Wiens 1973).

Despite the relatively clear generic boundary of *Psittacanthus,* defined by lack of endosperm, inflorescence and anther structure, no satisfactory statements can be made with regard to either species relationships or the position of the genus within Loranthaceae. Both these aspects might well be clarified by a detailed palynological study.

The present study has been undertaken within the context of extensive pollen investigations in New World, Australian and New Zealand Loranthaceae.

Material and methods

Flowers were collected from herbarium sheets taken from the following herbaria: F, GH, LEA, M, MO, S, UC, UMASS and UT. The flowers were first boiled in distilled water to facilitate pollen extraction. The extracted pollen was then washed twice in glacial acetic acid followed by a ten minute boiling in acetolysis fluid (Erdtman 1960). Pollen residues were then washed twice more in glacial acetic acid and once in distilled water. Acetolyzed pollen was processed for light microscopy, scanning and transmission electron microscopy (LM, SEM and TEM).

Material for LM was mounted in glycerine jelly. Determinations of size and shape were made with a Zeiss screwpiece micrometer. Measurements of 30 grains per population include: polar diameter (pole. dia.) and equatorial diameter (eq. dia.). The ratio between these two (P/E) provides an expression of overall shape.

Material for SEM was suspended in a drop of water, freeze-dried and sputter-coated with gold. Specimens were observed with a Cambridge Mark IIA scanning electron microscope.

Samples for TEM were first placed in .5% aqueous osmium tetroxide for two hours at room temperature, washed in distilled water and embedded in 2% agar (Skvarla 1966). The pollen/agar moiety was then minced into small pieces and subsequently dehydrated in acetone and embedded in Araldite 6005 (Electron Microscope Sciences). Thin sections were made with an LKB diamond knife, collected on uncoated grids, and stained in aqueous uranyl acetate (ten minutes, room temperature) and Reynolds' (1963) lead citrate (30 minutes, 50°C). Sections were viewed and photographed on an AE1 EM6B transmission electron microscope.

Exomorphology

Pollen grains radially symmetrical; isopolar; peroblate to oblate, rarely suboblate; triangular, slightly to deeply concave, and trilobate, deeply concave, rarely triangular and slightly convex in polar view; sculpturing minutely spinulate, psilate or scabrate-verrucate; exine imperforate at the polar faces, minutely perforate in equatorial areas; exine thickened directly at the centers of the polar faces usually in a triradiate pattern.

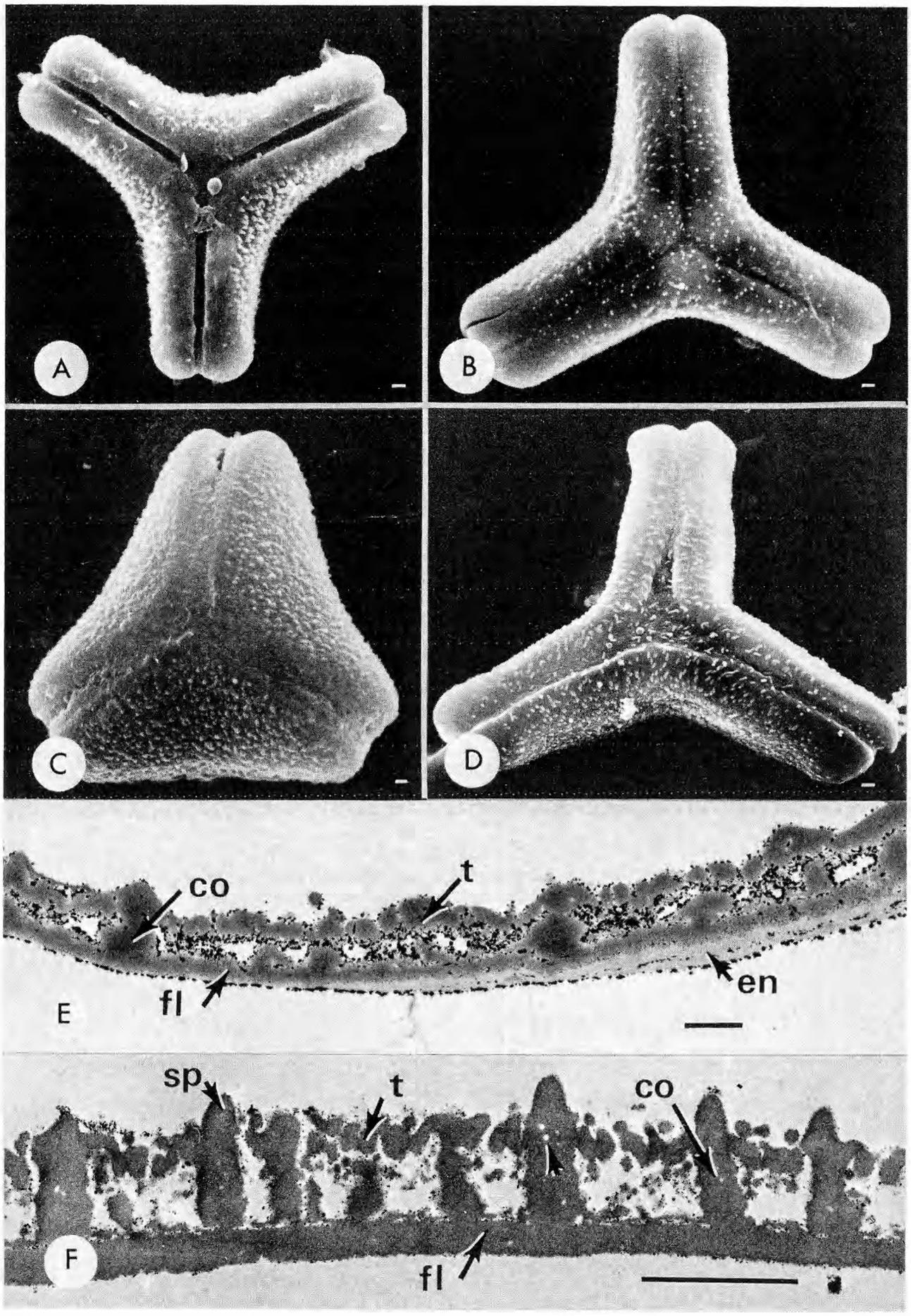
The genus is best divided exomorphologically according to differences in sculpturing patterns. Based on this character three basic pollen exomorphologies are recognized: Type I characterized by minutely spinulate sculpturing (30 spp.); Type II by psilate exine (1 sp.); and Type III by a scabrate-verrucate surface (1 sp.).

Type I. Spinulate

Sculpturing minutely spinulate; spinules narrow with acute or blunt apices, numerous in equatorial areas, sparse and scattered in polar regions; spinules usually dispersed randomly over polar faces but in some species consistently absent along margins of colpi and terminal portions of the pollen lobes; exine imperforate at polar faces, minutely perforate in equatorial regions; in equatorial areas often with small granules between spine bases.

Type I pollen is further divisible into four subtypes (A–D), based on differences in aperture types. The following aperture types occur in *Psittacanthus:* syntricolpate, tricolpate, diplotricolpate, and syndiplotricolpate.

Fig. 1. Type I, subtype A pollen (syntricolpate aperture type). – A: *Psittacanthus schiedeanus.* – B, E: *P. macranthus.* – C: *P. sonorae.* – D: *P. columbianus.* – F: *P. holtoni.* – A: Polar view. × 1600. – B: Slightly oblique polar view. × 1400. – C: Slightly oblique polar view. × 1400. – D: Slightly oblique polar view. × 1500. – E: Thin section through equatorial exine. × 8000. – F: Thin section through equatorial exine. The columellae are well developed and frequently exhibit small internal foramina (arrow). × 22,100. – Line in each micrograph equals 1 μm. – co columellae, en endexine, fl foot layer, sp spinule, t tectum.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Because of the diverse and complex nature of the apertures a brief explanation of apertural terms is given. The prefix *syn-* will be used to denote apertures fused at the center of the polar faces. The prefix *diplo-* will be used to denote two sets of apertures, each set of which is restricted to the polar face and is not continuous around the equator.

Each aperture type as well as concomitant variations in polar and equatorial shapes are described separately below proceeding from the most to the least prevalent type.

Subtype A. Syntricolpate – Fig. 1 A–F, Fig. 4 D, E

Colpi narrow, often broader at the center of the polar faces; colpal membranes occasionally disrupted in mid-regions of pollen lobes, otherwise smooth with occasional spinules; grains peroblate to suboblate; in polar view triangular or trilobate.

Species: *Psittacanthus auriculatus, P. brachynema, P. collum-cygni, P. columbianus, P. dichrous, P. holtoni, P. leptanthus, P. macrantherus, P. macranthus, P. nodosus, P. palmeri, P. schiedeanus, P. sonorae, P. zonatus.*

Specimens examined (not listed in Table 1): *Psittacanthus brachynema* Eichl., Venezuela, Wurdack & Adderley 43442 (GH) – *P. leptanthus* A. C. Smith, Brazil, Krukoff 4709 (MO) – *P. macrantherus* Eichl., Mexico, Gentry 5842 (UC) – *P. schiedeanus* (Cham. & Schl.) Blume, Costa Rica, Carlson 3584 (F); Costa Rica, Lent 1670 (F) – *P. sonorae* (Wats.) Kuijt, USA, Drouet et al. 3397 (F) – *P. zonatus* Diels, Ecuador, Asplund 18763 (S).

Subtype B. Tricolpate – Fig. 2 A, F

Colpi narrow, shallow, usually extending only slightly onto the polar faces (brevicolpate); apocolpium large; colpal membranes slightly granular in equatorial regions; grains peroblate to oblate; in polar view trilobate, deeply concave to rarely triangular, slightly concave.

Species: *Psittacanthus americanus, P. biternatus, P. calyculatus, P. cordiae, P. cucullaris, P. cupulifer, P. falcifrons, P. lateriflorus, P. linearis, P. scheryi, P. semiarticulatus, P. weberbaueri.*

Specimens examined (not listed in Table 1); *Psittacanthus calyculatus* (DC.) G. Don, Costa Rica, Burger & Liesner 6697 (F); Panama, Croat 12512 (F) – *P. lateriflorus* Woods. & Schery, Panama, Allen 3702 (F); Costa Rica, Feinsinger s. n. (acc. no. 1741106 (F)) – *P. linearis* (Killip) Macbridge, Peru, Hutchinson & Wright 3363 (UC) – *P. scheryi* Woods., Costa Rica, Utley et al. 2657 (F).

Subtype C. Diplotricolpate – Fig. 2 C, E, Fig. 3 A–G, 4 A–C

Two sets of three colpi each, each set restricted to a polar face; colpi usually short, narrow slits confined to the mid-region of the pollen arms; in *Psittacanthus cupulifer* colpi long, discontinuous only directly at the equator; colpal membranes slightly granular (occasionally expanded and split open during preparation); grains peroblate; in polar view trilobate, deeply concave.

Species: *Psittacanthus cupulifer, P. dilatatus, P. hamulifer, P. peronopetalus.*

Subtype D. Syndiplotricolpate – Fig. 2 B, D

Colpi consistently different at each of the polar faces; at one face colpi narrow, broadening only slightly just at the center of the polar face; at opposite face colpi broad, narrowing slightly near the ends of the pollen lobes and center of the polar face; colpi at both faces long, terminating just before the equator; grains oblate; in polar view triangular, slightly concave.

Species: *Psittacanthus clusiaefolius*

Type II. Psilate – Fig. 5 A–C

Surface of exine psilate (smooth), minutely perforate; perforations generally restricted to equatorial areas between apertures; grains syntricolpate; colpi narrow with slightly granular membranes; exine slightly thickened at the centers of polar faces; grains oblate, triangular, mesocolpia slightly convex in polar view.

Species: *Psittacanthus robustus.*

Type III. Scabrate-verrucate – Fig. 6 A–C

Sculpturing granular (scabrate) at the polar faces, psilate to slightly verrucate along the equator and on the raised apertural areas; granules on polar faces extremely small, densely clustered; grains tricolpate, brevicolpate; colpi restricted to rounded protruding portions of exine; in equatorial view, raised apertures lend a dumb-bell shaped appearance to grains; pollen

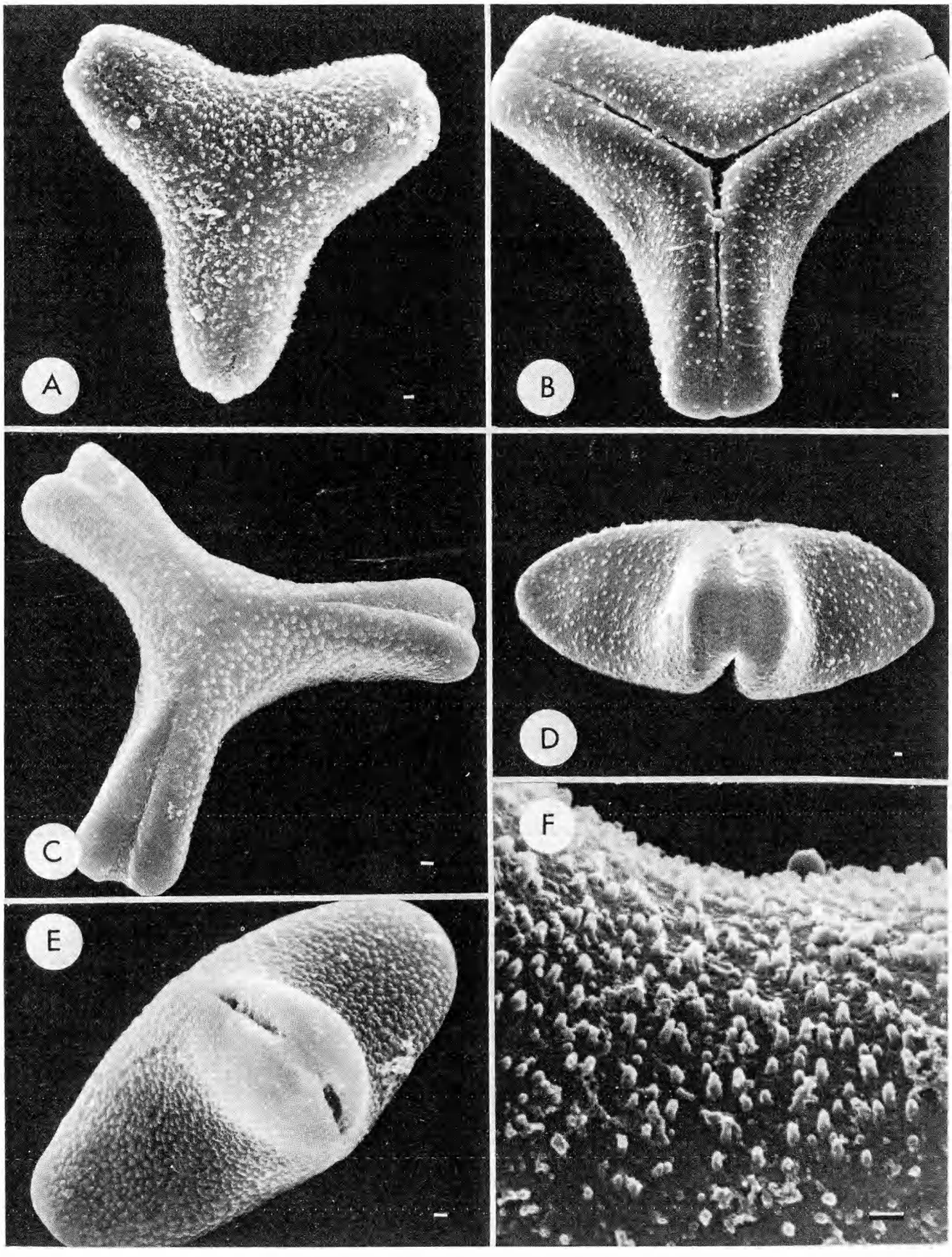


Fig. 2. Type I, subtypes B, C and D pollen (tricolpate, diplotricolpate and syndiplotricolpate aperture types). – A, F: *Psittacanthus calyculatus* (tricolpate). – B, D: *P. clusiaefolius* (syndiplotricolpate). – C, E: *P. cupulifer* (diplotricolpate). – A: Polar view. ×1200. – B: Polar view. ×850. – C: Polar view. ×1700. – D: Equatorial view. × 850. – E: Equatorial view. × 1700. – F: Detail of equatorial sculpturing. × 4800. – Line in each micrograph equals 1 μm.

peroblate, triangular, mesocolpia rounded convex in polar view.

Species: *Psittacanthus warmingii.*

Endomorphology

Psittacanthus pollen exhibits three basic endomorphologies, designated Type I, II and III which correlate respectively to the spinulate, psilate and scabrate-verrucate sculpturing patterns. Ektexine and endexine is present in all types.

Type I. Columellate – Figs. 1 E, F, 3 F, G, 4 E

Ektexine organized into tectum, columellae and foot layer; tectum either uniform or non-uniform in thickness; uniform tectum characterized by numerous, small perforations either vertically or randomly oriented; in the latter, the tectum broken into small irregular segments; non-uniform tectum composed of small rectangular ektexinous segments which alternate with similar size areas usually devoid of ektexine; upper and lower surfaces of these segments covered by an extremely thin but continuous layer of ektexine; tectum imperforate in polar regions; both uniform and non-uniform tecta with small, blunt or acute-tipped solid spinules; small, isolated unattached granules often present between spine bases; columellae short, evenly thickened occasionally exhibiting small internal foramina; columellae usually directly associated with supratectal spinules; columellae more numerous in equatorial areas, frequently clustered; granular areas composed of irregularly shaped ektexinous segments interspersed among columellae; foot layer as thick as tectum with granular upper and smoother lower surfaces; in apertural regions, columellae replaced by strictly granular areas; when present, equatorial endexine thin, homogeneous.

Endexine consistently present in apertural areas and directly beneath the centers of polar faces; endexine at polar faces extremely thick, thickest between the lobes.

Species: *Psittacanthus brachynema, P. biternatus, P. calyculatus, P. collum-cygni, P. columbianus, P. dilatatus, P. hamulifer, P. holtoni, P. macranthus, P. peronopetalus, P. schiedeanus, P. sonorae, P. weberbaueri.*

Type II. Columellate/granular – Fig. 5 D, E

Extexine organized into tectum, columellate-granular zone and foot layer; tectum thick, minutely perforate; perforations long, narrow vertical channels more numerous in equatorial areas; upper tectal surface smooth; lower surface granular and less electron dense; tectum supported by columella-like vertical elements irregular in outline; upper portions of columellae occasionally granular but still connected to tectum; granular zones, interspersed between columellae, composed of large, irregularly shaped masses of ektexine; foot layer discontinuous in equatorial areas, disrupted by numerous small gaps; foot layer continuous in apertural regions.

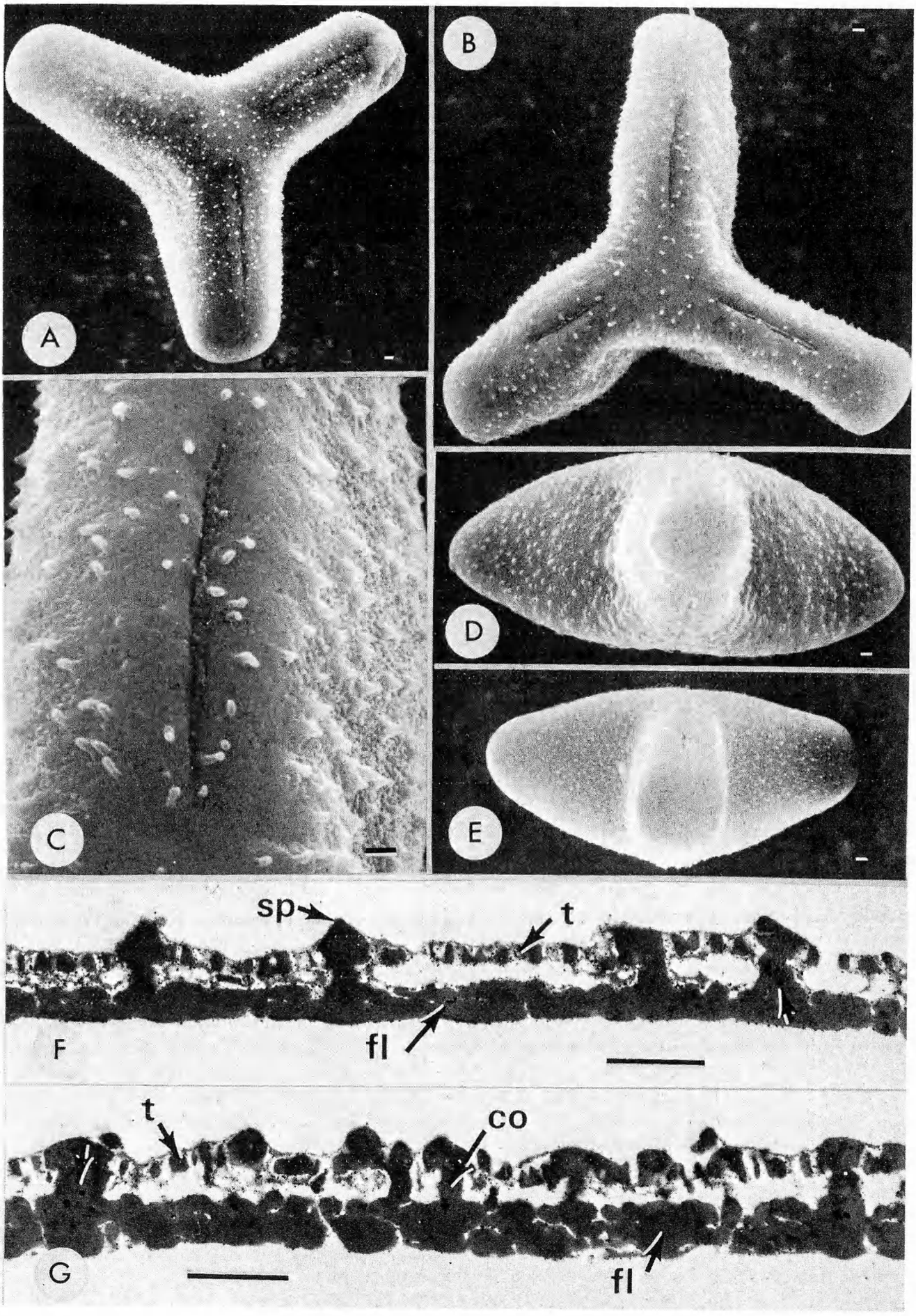
Endexine continuous around grain; non-apertural endexine homogeneous, filled with osmiophilic granules; upper surface interbedded with foot layer, lower surface smooth; apertural endexine thinner, disrupted, frequently lamellate, without osmiophilic granules.

Species: *Psittacanthus robustus.*

Type III. Partially columellate – Fig. 6 D–F

Ektexine organization disparate between equatorial and polar regions; equatorial ektexine organized into tectum, columellae and foot layer; tectum thick, minutely pitted (foveolate); columellae short, broader at the base, usually

Fig. 3. Type I, subtype C pollen (diplotricolpate aperture type). – A, E, G: *Psittacanthus hamulifer.* – B–D, F: *P. peronopetalus.* – A: Polar view. × 1000. – B: Polar view. × 1500. – C: Detail of aperture and surrounding exine. The psilate sparsely sculptured polar surface is in sharp contrast to the densely spinulate granular equatorial exine. × 5000. – D: Equatorial view. × 1500. – E: Equatorial view. × 1000. – F: Section through equatorial exine. Note the unevenly thickened tectum composed of small, regularly spaced ektexinous segments which are separated by areas of similar size usually devoid of ektexine. Small foramina often filled with osmiophilic material are visible in some columellae (arrow). × 14,600. – G: Section through equatorial exine. The foot layer is disrupted by small randomly oriented channels. Arrow indicates small, osmium-filled foramina present in some columellae. × 15,000. – Line in each micrograph equals 1 μm. – co columellae, fl foot layer, sp spinule, t tectum.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clustered; granular zones alternate with columellae; foot layer thick, up to three times the thickness of the tectum; upper surface of foot layer granular, lower surface smooth; polar ektexine organized into an upper granular zone and a solid basal stratum; granular zone composed of two to three layers of small elliptical granules; basal granules occasionally attached to solid lower stratum by short slender stalks; basal ektexine homogeneous, evenly thickened (comparable to foot layer?); basal ektexine thicker at periphery of polar faces.

Endexine continuous around grain; in equatorial and apertural areas thin, homogeneous; in polar regions, extremely thick, heavily lamellate.

Species: *Psittacanthus warmingii*.

Discussion

Psittacanthus is currently thought to be related to the large-flowered neotropical Loranthaceae once classified together in *Phrygilanthus*. As most of these putatively relictual genera exhibit a wide array of primitive features (Barlow & Wiens 1973) the status of pollen characters in *Psittacanthus* as well as the intra- and intergeneric relationships of the genus will be discussed in relation to the pollen characteristics of these large-flowered genera (unpubl. data).

Shape

All *Psittacanthus* pollen is typified by an elongate equatorial axis, the grains ranging in shape from peroblate to oblate, to more rarely suboblate. Though most species exhibit oblate pollen (P/E range .51–.75) several taxa possess only peroblate pollen (P/E range .31–.50) (see Table 1). In polar view the typical pollen amb is deeply concave and trilobed; only *Psittacanthus robustus* and *P. warmingii* have grains with triangular amb and convex mesocolpia.

The deeply concave trilobate shape is the least specialized among *Psittacanthus* species, showing the greatest similarity to the morphologically primitive large-flowered neotropical Loranthaceae (e.g. *Gaiadendron, Tripodanthus*). The rarely occurring slightly concave and convex pollen shapes, which resemble pollen shapes of the advanced small-flowered neotropical Loranthaceae, are probably derived conditions within *Psittacanthus*.

Apertures

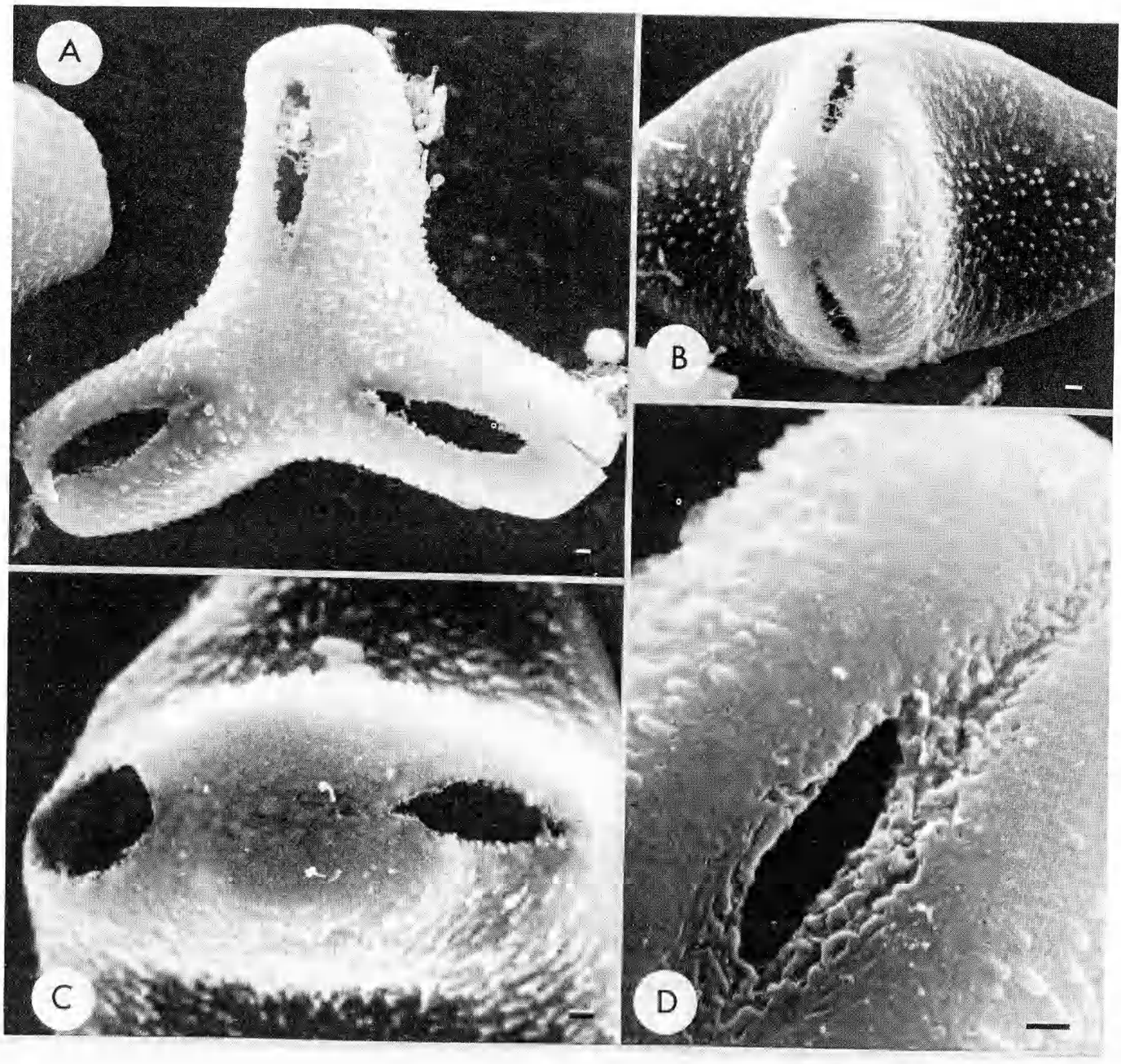
Psittacanthus pollen exhibits exclusively simple apertures. Most species possess either syncolpate (15 spp.) or tricolpate (13 spp.) (usually brevicolpate) pollen. The colpi are narrow and shallow with smooth or only slightly granular membranes. In some species with tricolpate pollen, the colpi, obscure and almost imperceptible at the equator, superficially resemble diploapertures (e.g. *Psittacanthus scheryi*).

Among the four remaining investigated species two aperture types are represented: diplotricolpate (*Psittacanthus dilatatus, P. hamulifer, P. peronopetalus*) and syndiplotricolpate (*Psittacanthus clusiaefolius*).

The data suggest the syncolpate aperture as basic within the genus; this aperture type characterizes not only a majority of species but all other large-flowered neotropical Loranthaceae as well. A well-defined tricolpate aperture type, though widespread among *Psittacanthus* species, is absent from all other large-flowered genera. The tricolpate condition may have developed independently in *Psittacanthus* by withdrawal of colpi from the centers of the polar faces.

Though the exact origins of particular aperture types in *Psittacanthus* are obscure, several general statements can be made concerning overall aperture evolution within the genus: (1) syncolpate pollen is the basic and least derived type in *Psittacanthus;* (2) the tricolpate condition is slightly more derived and most likely represents a well established transitional stage; and (3) the diplo- and syndiploaperturate conditions are advanced states. Since no other

Fig. 4. Type I, subtypes A and C (diplotricolpate and syntricolpate aperture types). – A–C: *Psittacanthus dilatatus* (diplotricolpate). – D, E: *P. collum-cygni* (syntricolpate). – A: Polar view. × 1800. – B: Equatorial view. × 1900. – C: Detail of aperture directly at the equator. × 3000. – D: Detail of colpal area. × 5000. – E: Section through non-apertural exine. Irregularly shaped ektexinous segments are frequently visible between columellae (arrow). × 13,100. – Line in each micrograph equals 1 μm. – co columellae, fl foot layer, sp spinule, t tectum.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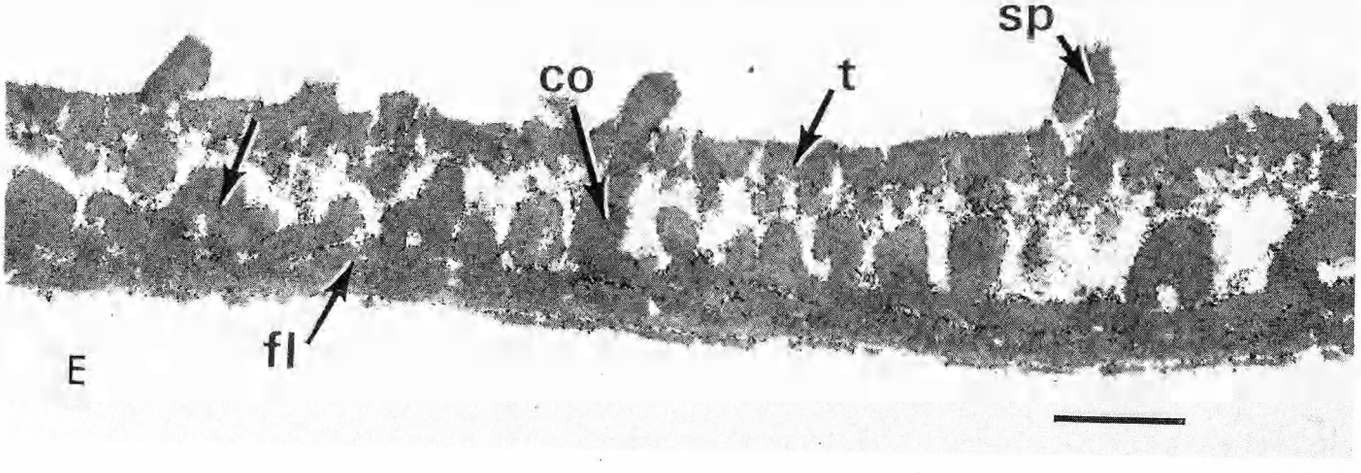
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closely related taxa exhibit diplo- or syndiplo-aperturate grains these types seem to have developed independently within *Psittacanthus*.

Sculpturing

Pollen of most *Psittacanthus* species is minutely spinulate with densely clustered spinules in equatorial areas and consistently fewer spines in polar regions (Type I sculpturing). The equatorial exine is perforate with an often slightly granular surface, while the polar surface and end portions of the lobes (in trilobate grains) are imperforate. In several species, the end portions of the lobes as well as the margins of the colpi are psilate. Only two species exhibit non-spinulate pollen: *Psittacanthus robustus* (psilate) and *P. warmingii* (scabrate-verrucate).

Spinulate sculpturing is probably the basic type within *Psittacanthus*. It characterizes a majority of species and shows the greatest similarity to other large-flowered neotropical Loranthaceae, particularly *Tristerix, Notanthera* and *Ligaria*. Though the tectum appears spinulate among these large-flowered taxa, however, closer inspection reveals an irregularly sculptured, highly divided surface, usually elaborated into crests and short ridges and in fact, only rarely, into spinules. Since no other large-flowered taxa possess a uniformly spinulate sculpturing combined with a thin, relatively imperforate tectum, it appears that these features have been selectively developed in *Psittacanthus*. Though less derived pollen characters for the genus as a whole, they are probably advanced features within the large-flowered complex. Psilate and scabrate-verrucate sculpturings are more derived. The former is similar to sculpturing types found among the advanced small-flowered neotropical mistletoes (e.g. *Struthanthus, Phthirusa, Cladocolea;* unpubl. data) while the latter is unique in the New World Loranthaceae.

Exine structure

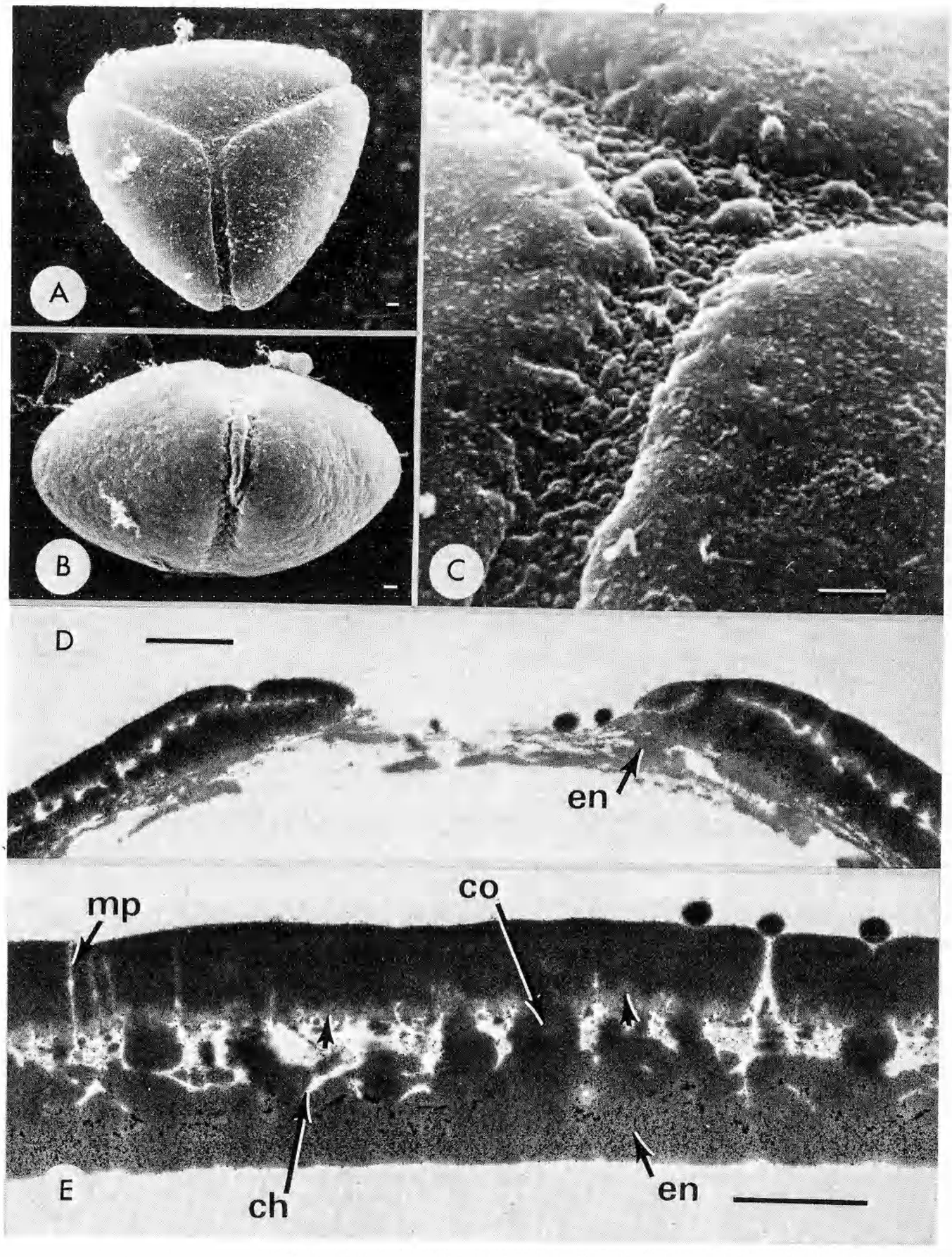
Tectum. All species of *Psittacanthus* exhibit a minutely perforate equatorial tectum with the perforations oriented either vertically (Fig. 5 E) or randomly throughout the tectum (Fig. 1 F). The most unusual tectal structure occurs in *Psittacanthus hamulifer, P. peronopetalus* and *P. brachynema*. Here the unevenly thickened tectum is composed of ektexinous segments which alternate with areas of similar size usually devoid of ektexine (Fig. 3 F, G). In *Psittacanthus robustus* the tectum is also non-uniform in thickness, exhibiting a considerably less electron-dense lower surface (Fig. 5 E arrows). The polar tectum is consistently imperforate in all taxa, except *Psittacanthus warmingii* where it is completely absent.

Columellae. *Psittacanthus* pollen is typically columellate. The columellae are regular in shape (excl. *P. robustus*), evenly thickened and usually directly associated with supratectal spinules (when present). The columellae range from extremely short to relatively large and well-developed, frequently showing small internal foramina (cf. Figs. 1 F, 3 C). The regularly spaced or slightly clustered columellae, usually more numerous in equatorial areas, are often surrounded by granular zones composed of large, irregular portions of ektexine. In pollen of *Psittacanthus warmingii* the small columellae are restricted to equatorial areas and are quickly replaced by a completely granular zone in polar regions (Fig. 6 D–F).

Foot layer. The foot layer is generally as thick as the tectum with a smooth lower surface and slightly granular upper surface. In several species the foot layer is disrupted by small, randomly arranged channels (Figs. 3 G, 5 E). The extremely thickened equatorial foot layer in pollen of *Psittacanthus warmingii* is anomalous within the genus (Fig. 6 E).

Endexine, present in all investigated species, is

Fig. 5. Type II pollen (*Psittacanthus robustus*). – A: Polar view. × 1500. – B: Equatorial view. × 1500. – C: Detail of exine surface directly at the center of the polar face. × 10,000. – D: Thin section through aperture. The endexine is thin, disrupted and slightly lamellate. × 13,000. – E: Section through non-apertural exine. The tectum is minutely perforate with a granular, slightly less electron-dense lower surface (arrows). The bases of the columellae are interbedded in an amorphous foot layer disrupted by numerous irregular channels. Note the slightly less electron-dense endexine filled with small osmiophilic granules. × 20,000. – Line in each micrograph equals 1 μm. – ch channels disrupting foot layer, co columellae, en endexine, mp minute perforations.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consistently found in apertural and polar areas, rarely in equatorial regions. In most species, the polar endexine is restricted to the centers of the polar faces, where it forms an extremely thickened lamellate plug visible as a triradiate thickening in the light and scanning electron microscopes. Only in *Psittacanthus warmingii* and *P. robustus* is endexine continuous around the grain. In the former, the equatorial endexine is thin and homogeneous in contrast to a thick and heavily lamellate polar endexine (Fig. 6 E, F).

An exine organized into supratectal spinules and a minutely perforate tectum supported by well-formed columellae appears to be the basic exine structure in *Psittacanthus*. This type of exine organization is similar to that found among other neotropical large-flowered Loranthaceae. In these genera the tectum is highly perforate, irregularly sculptured and supported by thin, sporadically occurring columellae usually interbedded in a finely granular matrix. Pollen of *Psittacanthus,* though retaining these basic features, has selectively developed a uniform tectum and well-developed columellae. The exine structure in *Psittacanthus robustus,* particularly the nature of the tectum and granular-fibrillar columellae, is reminiscent of species of *Phthirusa*. However, as there is no morphological continuity between the two genera, it is likely that these features have evolved independently within each taxon.

The Type III endomorphology (*Psittacanthus warmingii*) is without counterpart in the family. Though quite an advanced type, its very uniqueness suggests an independent, isolated development within the genus.

Interspecific and generic relationships

At the specific and subgeneric levels, pollen characters do not support differences based on anther morphology, precluding the subgeneric distinction between *Aetanthus* (basifixed anthers) and *Psittacanthus* ('*Eupsittacanthus*'; dorsifixed anthers); the pollen in both taxa is spinulate, trilobed, syncolpate and columellate.

Moreover, pollen data cannot be used to

Table 1. Pollen data of selected species of *Psittacanthus* arranged according to sculpturing and aperture types, respectively. Measurements in μm; means and its standard deviations; ranges in parentheses.

Taxon	pole. dia.	eq. dia.	P/E shape in eq. view	shape in pole. view	aperture type(s)
Psittacanthus auriculatus (Oliv.) Eichl. Mexico, Smith 805 (UC)	34.9± .12 (29.0–37.8)	45.6± .07 (43.4–48.4)	.76 (.65–.81) suboblate	triangular slightly concave	syntricolpate
P. columbianus A. C. Smith Colombia, Cuatrecasas 1291 (F)	24.4± .10 (21.0–28.0)	53.7± .13 (48.8–58.4)	.45 (.40–.48) peroblate	triangular deeply concave	syntricolpate
P. collum-cygni Eichl. Surinam, Rombouts 510 (UC)	30.0± .09 (26.8–33.0)	58.5± .12 (55.0–62.0)	.54 (.49–.57) oblate	trilobed deeply concave	syntricolpate
P. dichrous Mart. Brazil, Harley 17626 (MO)	40.0± .26 (37.1–43.8)	52.5± .19 (50.5–51.6)	.76 (.67–.87) oblate	trilobed deeply concave to triangular slightly concave	syntricolpate
P. holtoni (Eichl.) Engl. Colombia, Haught 5847 (F)	37.5± .14 (32.8–41.2)	65.1± .15 (61.2–70.0)	.57 (.53–.66) oblate	trilobed deeply concave	syntricolpate
P. macranthus Hook. Ecuador, Mille s.n. (MO)	28.5± .18 (25.6–31.1)	49.5± .11 (47.3–51.6)	.57 (.56–.63) oblate	trilobed deeply concave	syntricolpate
P. nodosus (Desr.) Engl. Ecuador, Solis 7328 (F)	36.2± .11 (33.0–40.0)	58.6± .13 (53.4–61.4)	.61 (.56–.65) oblate	trilobed deeply concave	syntricolpate

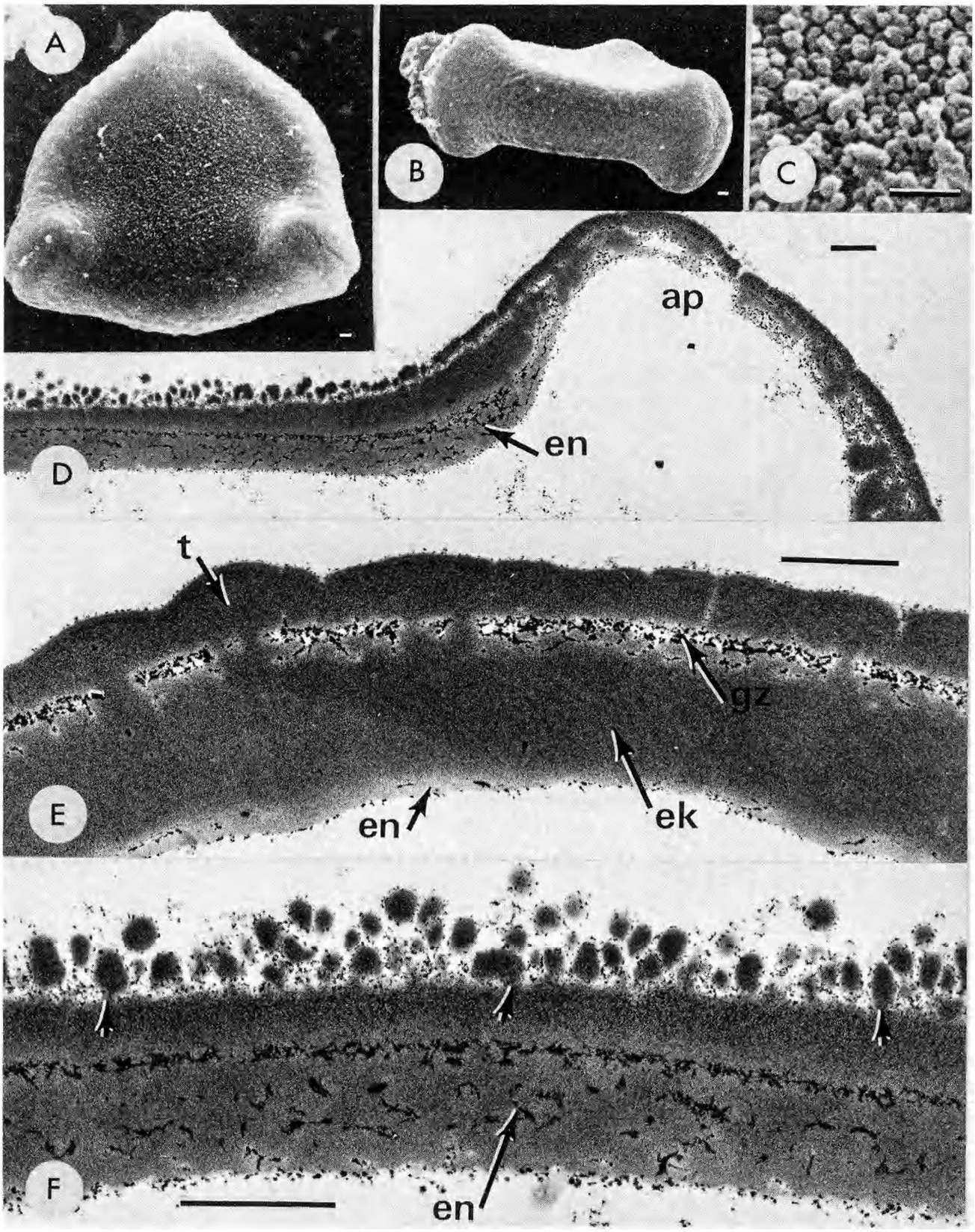

Fig. 6. Type III pollen (*Psittacanthus warmingii*). – A: Polar view. × 1300. – B: Equatorial view. × 1300. – C: Detail of polar surface. × 10,000. – D: Section through aperture and transitional zone between the equatorial and granular polar regions. × 6500. – E: Non-apertural equatorial exine. The minutely pitted (perforate?) tectum is supported by small columellae which are surrounded by granular zones. The endexine is thin and homogeneous. × 15,900. – F: Section through polar exine. The tectum and columellae have been replaced by a strictly granular zone composed of slightly elliptical granules occasionally attached to the foot layer (arrows). The endexine is thick and heavily lamellate. × 22,500. – Line in each micrograph equals 1 μm. – ap aperture, ek ektexine, en endexine, gz granular zone, t tectum.

Taxon	pole. dia.	eq. dia.	P/E shape in eq. view	shape in pole. view	aperture type(s)
P. palmeri (Wats.) Barlow & Wiens Mexico, Mexia 867a (MO)	25.7± .16 (23.5–27.1)	35.6± .11 (33.9–37.0)	.72 (.66–.79) oblate to suboblate	triangular slightly concave	syntricolpate
P. schiedeanus (Cham. & Schl.) Blume Costa Rica, Baker et al. 235 (F)	14.9± .10 (12.8–16.8)	40.0± .15 (36.7–42.0)	.37 (.31–.41) peroblate	trilobed deeply concave	syntricolpate
P. sonorae (Wats.) Kuijt Mexico, Gentry 4681 (F)	23.6± .19 (20.3–28.0)	37.3± .19 (35.0–41.2)	.63 (.57–.66) oblate	triangular slightly concave	syntricolpate
P. americanus (L.) Mart. Dominica, Hodge 1582 (MO)	21.6± .14 (19.4–23.8)	38.9± .16 (36.3–41.7)	.55 (.50–.62) oblate	triangular slightly concave	tricolpate
P. biternatus (Hoff.) Blume Brazil, Black 47-1766 (UC)	28.9± .05 (27.4–31.4)	47.7± .17 (41.4–51.4)	.60 (.55–.66) oblate	trilobed deeply concave	tricolpate
P. cordiae Krause Peru, Hutchinson & Wright (UC)	31.6± .06 (29.4–34.0)	47.5± .13 (44.8–54.4)	.66 (.60–.75) oblate	triangular slightly concave	tricolpate (brevicolpate)
P. cucullaris Blume Colombia, Zarucchi 1214 (LEA)	30.8± .12 (28.0–34.0)	57.0± .16 (52.2–61.8)	.54 (.49–.60) oblate	trilobed deeply concave	tricolpate
P. falcifrons Mart. Brazil, Froes 1718 (MO)	33.4± .31 (28.1–38.4)	52.5± .28 (47.3–56.6)	.64 (.57–.73) oblate	triangular slightly concave to trilobed deeply concave	tricolpate
P. semiarticulatus Rizzini Venezuela, Guevara 2223 (F)	18.9± .12 (16.6–20.5)	39.5± .18 (36.5–42.7)	.48 (.45–.52) peroblate	trilobed deeply concave	tricolpate (brevicolpate)
P. weberbaueri Patsch. Peru, Worth et al. 8874 (UC)	34.5± .16 (32.3–37.2)	55.0± .22 (52.1–58.1)	.63 (.58–.67) oblate	triangular concave; pollen lobes broad	tricolpate (brevicolpate)
P. cupulifer (H. B. K.) G. Don Ecuador, Wiens 3756 (UT)	24.2± .20 (21.8–27.4)	44.3± .09 (42.9–46.0)	.55 (.49–.61) oblate	trilobed deeply concave	diplotricolpate, tricolpate
P. dilatatus A. C. Smith Colombia, Lawrence 108 (UC)	31.7± .11 (29.0–35.8)	52.8± .09 (49.0–55.6)	.60 (.54–.69) oblate	trilobed deeply concave	diplotricolpate
P. hamulifer Kuijt Panama, Elias 13681 (MO)	35.6± .12 (30.8–39.2)	72.5± .13 (68.6–78.0)	.49 (.44–.53) peroblate	trilobed deeply concave	diplotricolpate
P. peronopetalus Eichl. Venezuela, Wurdack & Adderley 43429 (UC)	31.2± .33 (27.6–35.5)	63.9± .27 (60.9–67.7)	.49 (.44–.57) peroblate	trilobed deeply concave	diplotricolpate
P. clusiaefolius (Willd.) Eichl. Venezuela, Maguire et al. 37096 (MO)	55.6± .10 (52.5–58.7)	90.3± .25 (85.2–99.5)	.61 (.55–.69) oblate	triangular slightly concave	syndiplotri-colpate
P. robustus Mart. Brazil, Irwin et al. 11727 (F)	27.7± .11 (26.7–28.9)	40.1± .17 (39.6–41.1)	.69 (.65–.73) oblate	triangular convex	syntricolpate
P. warmingii Eichl. Venezuela, Wurdack & Adderley 43774 (F)	16.1± .14 (14.0–17.5)	44.5± .09 (42.9–45.1)	.36 (.34–.40) peroblate	triangular convex	tricolpate (brevicolpate)

delineate large species groupings. This is due in large part to the high degree of independent evolution undergone by a number of pollen characters, as illustrated by a distributional analysis of aperture types in *Psittacanthus*. The syncolpate aperture type, putatively the least derived, is not consistently associated with the more primitive pollen features and often occurs in conjunction with advanced pollen shapes (triangular slightly concave, triangular convex), sculpturing types (psilate), and exine structure (Type II). Conversely, advanced aperture types (diplo- and syndiplocolpate, tricolpate) are frequently combined with less derived pollen features, including trilobate pollen shape, spinulate sculpturing, and columellate ektexine. In the two instances where the pollen morphologies are clearly distinct from the bulk of *Psittacanthus* species (*P. warmingii, P. robustus*), a majority of the characters are so disparate that no inferences can be made with regard to species relationships based on these pollen data. In summary then, our pollen data do little to clarify interspecific relationships since no groups of species exhibit uniformly primitive or advanced pollen features.

At the intergeneric level, pollen data indicate a close relationship between *Psittacanthus* and the large-flowered neotropical Loranthaceae as well as an advanced position within this complex (see discussion on apertures, sculpturing and exine structure). Pollen evidence regarding ties between *Psittacanthus* and the large-flowered New World genera, and possible relationships with the primitive and relictual Australian Loranthaceae, will be the subjects of a subsequent paper.

Acknowledgements. We wish to thank the curators and staff of the herbaria who allowed removal of pollen material for this study. We are much indebted to Dr Michael Forster for his critical comments. Support by NRCC is gratefully acknowledged. We also wish to thank Dr E. B. Wagenaar for the use of the electron microscope and R. Wibel for SEM assistance.

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Cytology of Clematis gouriana and Naravelia zeylanica

K. V. Devar, G. Boraiah and T. F. Khaleel

Devar, K. V., Boraiah, G. & Khaleel, T. F. 1979 09 30: Cytology of Clematis gouriana and Naravelia zeylanica. *Bot. Notiser 132:* 310. Stockholm. ISSN 0006-8195.

Idiograms of *Clematis gouriana* Roxb. and *Naravelia zeylanica* DC. (Ranunculaceae) are presented. Both species have 2n = 16.

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Seeds for the present study were collected in the field in India and grown in the Botanical Garden, University of Agricultural Sciences, Bangalore; vouchers are in the herbarium at the same University. Root tips of *Naravelia zeylanica* DC. and leaf tips of *Clematis gouriana* Roxb. were pretreated for 3–4 hours in 0.002 M aqueous solution of 8-hydroxyquinoline at 10–15°C, fixed in acetic alcohol (1:3; root tips) or absolute alcohol, chloroform and acetic acid (6:3:1; leaf tips), stained in Feulgen and squashed in aceto-orcein. The slides were made permanent in Euparal. The idiograms are based on five good metaphase plates (representing all populations) for each species.

Localities. C. gouriana: Coorg Dt, Sampaje Forest, 19.2.1976 – Shimoga Dt, Agumbe Forest, 11.1.1978 – Kolar Dt, Nandi Hills, 20.2.1978.

N. zeylanica: Chikkamagalur Dt, Koppa Forest, 2.11.1976 – Shimoga Dt, Agumbe Forest, 12.1.1978 – N Kanara Dt, Gund Forest, 24.5.1978.

Both species have 2n = 16. The chromosome morphology of *Clematis gouriana* agrees well with that of other species of the genus with 2n = 16. The karyotype of *N. zeylanica* is rather similar to that of diploid species of *Anemone* with 2n = 16.

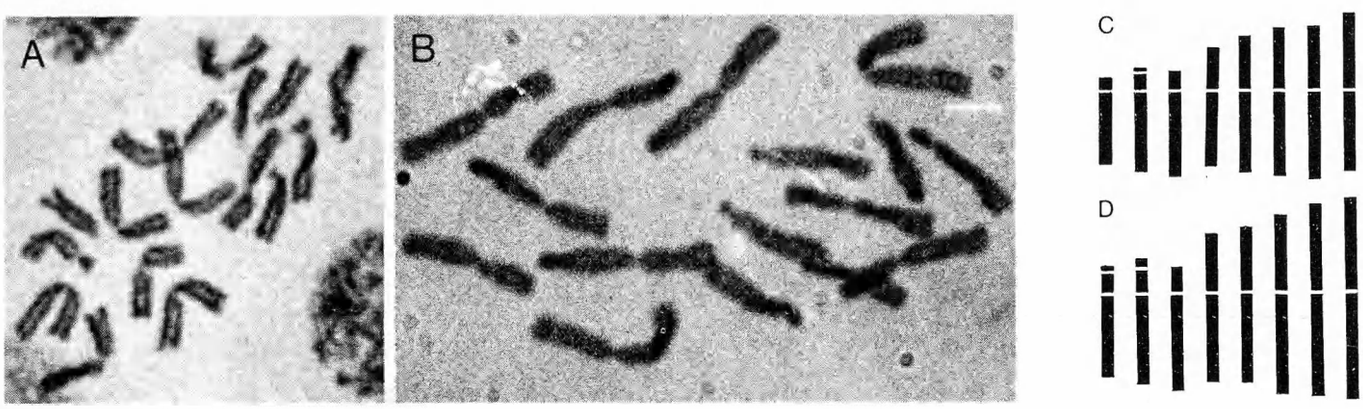

Fig. 1. Metaphase plates (× 650) and idiograms (× 2000). – A, C: *Clematis gouriana*. – B, D: *Naravelia zeylanica*.

Centaurea musakii: a new species from Thessalia (Greece)

Théodore Georgiadis

Georgiadis, T. 1979 09 30: Centaurea musakii: a new species from Thessalia (Greece). *Bot. Notiser 132:* 311–312. Stockholm. ISSN 0006-8195.

Centaurea musakii Georg., sp. nov., is described from calcareous rocks in the provinces of Trikala and Karditsa, Thessalia, Greece. Its chromosome number is 2n = 18. It belongs to *Centaurea* subg. *Acrolophus* (Cass.) Dobrocz.

Théodore Georgiadis, Institute of Botany, University of Patras, Patras, Greece.

Centaurea musakii Georg., sp. nov. – Fig. 1

Orig. coll.: Graecia, prov. Trikala, prope pagum Pili, in rupibus calcareis, alt. ca 200 m, 22-9-77 Georgiadis 1732 (UPA holotypus).

Biennis vel perennis, tota planta adpresse albo-tomentosa. *Caules* erecti, superne corymboso-pauciramosi 20–40 cm alti, plerumque usque ad inflorescentiam plurifoliati. *Folia* adpresse albo-tomentosa, basalia petiolata, bipinnatisecta, segmentis lanceolatis vel ovatis; caulina inferiora petiolata, bipinnatisecta, segmentis utrimque 4–6, superiora pinnatisecta, segmentis utrimque 1–2. *Capitula* solitaria, cylindrico-ovata; involucrum 13–15 × 12–14 mm. *Ungues phyllorum* virides, sparse araneosi vel glabri, nervis 3–5 distincte striatis; appendices triangulares, nigrae, pectinato-ciliatae, ciliis utrimque 10–12, 3 mm longis, in spinam terminalem 1–1,5(–2) mm longam excurrentes. *Flores* rosei, marginales radiantes. *Pappus* 4(–5) mm longus, achaenio aequilongus vel longior.

Affinis *C. niederi* Heldr. et *C. wettsteinii* Deg. & Dörfl.; a prima segmentis foliorum angustioribus capitulis minoribus et appendicibus non oblongis sed triangularibus differt ab altera foliis majoribus segmentis manifeste angustioribus, caulibus robustioribus inter alia valde divergit.

This new species belongs to the subgenus *Acrolophus* (Cass.) Dobrocz., sect. *Pannophyllum* Hayek. It grows on calcareous rocks at the foot of Mt Agrapha (Thessalia). It resembles *C. niederi* Heldr. from the cliffs of Klissoura near Mesolonghi and *C. wettsteinii* Degen & Dörfl., known from Macedonia in Yugoslavia. However, it differs from both these species in having longer and narrower leaves and smaller capitula. The appendices of the phyllaries are black with black cilia and a terminal spine only 1–1.5 mm long; *C. niederi* has brown, white-ciliate appendices with a terminal spine 2.5 mm long; in *C. wettsteinii* the appendices are black with black cilia, but the terminal spine is even longer than in *C. musakii*.

C. musakii has the same chromosome number as *C. niederi*, 2n = 18; that of *C. wettsteinii* is not known.

Other collections: Greece. Prov. Karditsa, prope pagum Musaki, in rupestribus calcareis, alt. ca 200 m, 22.9.1977 Georgiadis 1731 (UPA) – Rochers à Pili et rochers à Musaki, 6.7.1963, J. Contandriopoulos, G. Deleuil & P. Quézel (Université Aix-Marseille III).

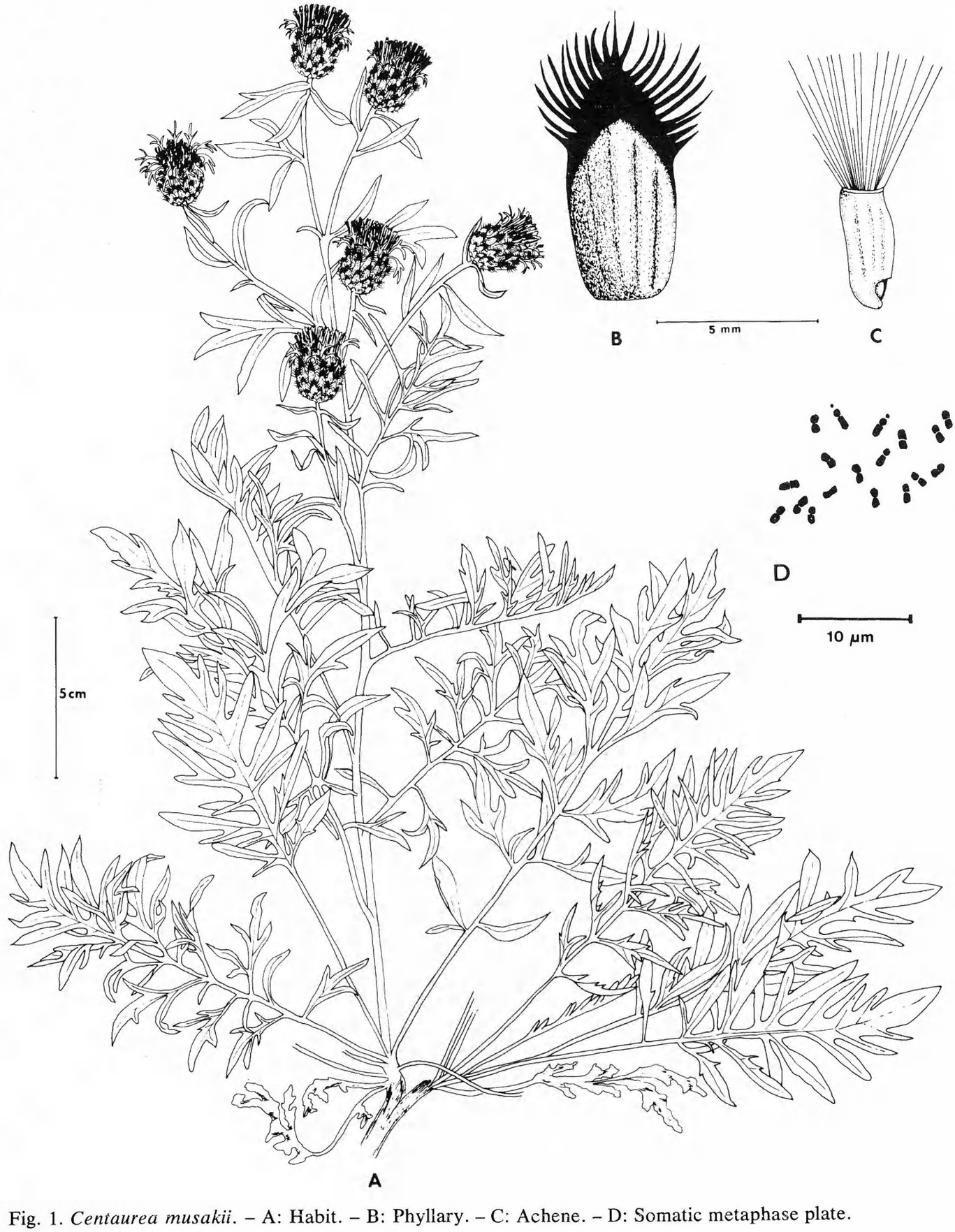

Fig. 1. *Centaurea musakii*. – A: Habit. – B: Phyllary. – C: Achene. – D: Somatic metaphase plate.

Matsushimomyces (Hyphomycetales), a new genus of forest microfungi

V. G. Rao and K. I. Mani Varghese

Rao, V. G. & Varghese, K. I. M. 1979 09 30: Matsushimomyces (Hyphomycetales), a new genus of forest microfungi. [Contribution No. 672 from the Department of Mycology and Plant Pathology.] *Bot. Notiser 132:* 313–314. Stockholm. ISSN 0006-8195.

Matsushimomyces indicus Rao & Varghese, gen. et sp. nov. is described and illustrated. It has been collected on decaying leaf litter from the Ponmudy forests of Kerala (S India).

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Matsushimomyces indicus Rao & Varghese, gen. et sp. nov. – Fig. 1

Etym. After Dr T. Matsushima, Japan
Deuteromycotina, Hyphomycetales, Dematiaceae

Orig. coll.: India, Kerala, Ponmudy, on decaying leaf litter of a dicot plant, 10.11.1976, K. I. Mani Varghese (AMH 3359 holotype, IMI 210313 isotype).

Coloniae saprophyticae, effusae vel punctiformes, pallide griseo-brunneae. Mycelium plerumque in substratum immersum ex hyphis laevibus ramosis, septatis, 3.5–7 μm crassis pallide brunneis vel brunneis compositum. Stromata erumpentia pseudoparenchymàtica, raro intra- vel sub-epidermalia, brunnea vel atrobrunnea. Conidiophora macronemata vel micronemata, caespitosa ex stromatibus orientia, recta vel flexuosa, septata, ad apicem ramosa, brunnea vel atrobrunnea, apicem hyalina et laevia, usque ad 160 μm longa, 4–5 μm crassa, basi saepe ad 5.5–7.5 μm inflata. Conidiophora micronemata recta vel curvata, hyalina vel pallide-brunnea, raro ramosa, laevia, 15–25.5 × 3.5–4.5 μm. Cellulae conidiogenae discretae vel in conidiophoris et in ramis positae, polyblasticae, sympodiales, hyalinae vel subhyalinae, cylindricae vel doliiformes, usque ad 5-denticulatae. Conidia solitaria, sicca, acropleurogena, falcata, laevia, hyalina, medio 1-septata, extremis acutis, 25–36.5 × 1.5–2.5 μm.

Colonies saprophytic, effuse or punctiform, greyish brown. Mycelium immersed in substrate, composed of flexuous pale brown to brown, branched, smooth-walled, septate, 3.5–7 μm thick hyphae. Setae and hyphopodia absent. Stromata rarely intra- or subepidermal and then erumpent, composed of round or angular, brown to dark brown cells. Conidiophores macronematous as well as micronematous, often caespitose, arising from the stroma. Macronematous conidiophores erect, straight or slightly flexuous, septate, smooth, branched at the apex, brown to dark brown except at the apex which is hyaline, up to 160 μm long, 4–5 μm thick, slightly swollen (5.5–7.5 μm) at the base. Micronematous conidiophores simple, erect, straight or slightly curved, smooth-walled occasionally branched, hyaline to pale brown, 15–25.5 μm long, 3.5–4.5 μm thick in the broadest part. Conidiogenous cells integrated and terminal on conidiophores and branches, polyblastic, sympodial, hyaline to subhyaline, cylindrical or doliform with one to five denticles, 10–20.5 × 3–4.5 μm. Conidia solitary, dry, falcate, hyaline, smooth, acropleurogenous, uniseptate, pointed at each end, 25–36.5 × 1.5–2.5 μm.

The present fungus resembles *Microdochium* Syd. (Sutton et al. 1972) in having polyblastic sympodial conidiogenous cells and hyaline falcate conidia. But all the species of *Microdochium* possess ampulliform to lageniform, hyaline conidiogenous cells borne on a hyaline to subhyaline, pseudoparenchymatous epidermal stroma. The micronematous conidiophores of the present fungus are similar to those of *Microdochium caespitosum* Sutton et al. (1972), but the multiseptate, branched macronematous

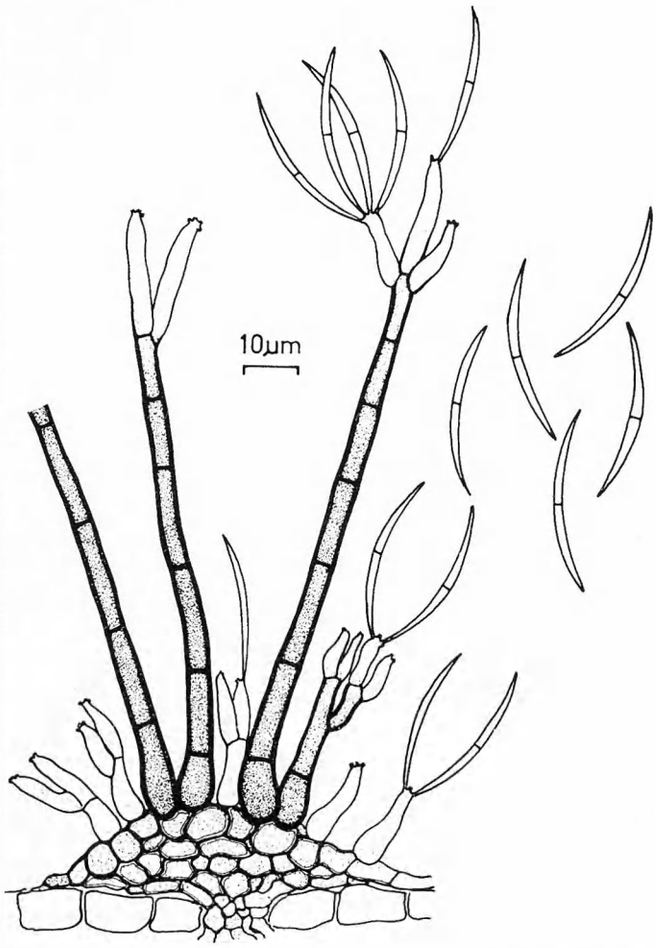

Fig. 1. *Matsushimomyces indicus*. Stroma, conidiophores and conidia.

conidiophores are not seen in any species of *Microdochium*.

Matsushimomyces indicus has some resemblance to *Idriella vandalurensis* Vittal (1970) in the shape of the conidia, but characters of the conidiophores and stroma differ.

The genus *Matsushimomyces* is readily distinguishable from *Idriella* Nelson & Wilhelm (1956), *Chloridiella* Arnaud (cf. Nicot & Charpentie 1971) and *Microdochium* Syd. in possessing typically branched, multiseptate, brown to dark brown conidiophores which are borne on a pseudoparenchymatous, dark brown, erumpent stroma.

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Festuca minutiflora Rydb., a neglected species

Signe Frederiksen

Frederiksen, S. 1979 09 30: Festuca minutiflora Rydb., a neglected species. *Bot. Notiser 132:* 315–318. Stockholm. ISSN 0006-8195.

Festuca brachyphylla Schult. & Schult. in the southern parts of the Rocky Mountains consists of two taxa; one is closely related to *F. brachyphylla* s.str. but probably distinct (not further discussed here); the other is a well-defined species, *F. minutiflora* Rydb. Both seem to be tetraploids (2n = 28), while *F. brachyphylla* s.str. is a hexaploid (2n = 42).

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Two species of *Festuca* with short anthers (1.2 mm or less) have been reported from the southern parts of the Rocky Mountains, viz. *F. baffinensis* Polun. and *F. brachyphylla* Schult. & Schult. (Weber 1967). *F. saximontana* Rydb. has often been confused with *F. brachyphylla* since the anthers are only slightly longer in the former (1.0–1.6 mm). Nevertheless they are easily separated by the sclerenchymatic tissue, which is strongly developed in *F. saximontana* and weakly developed in *F. brachyphylla* and its allies (Saint-Yves 1925, Holmen 1964, Frederiksen 1977). *F. baffinensis* is easily distinguished from *F. brachyphylla* on account of the densely pubescent culm. It was reported from Colorado by Weber (1961); it is rare with a scattered distribution throughout most of the Rocky Mountains and seems identical with *F. baffinensis* from the Arctic. *F. brachyphylla* is more complex; it is morphologically heterogeneous within the southern parts of the Rocky Mountains and plants from this area differ from material from the Arctic (Holmen 1964, Frederiksen 1977).

Material. This paper is mainly based on material from Colorado, but specimens from other areas have also been studied. Collections from the following herbaria were studied: C, CAS, COLO, G, L, NY, P; a few collections of living material have also been available. A list of specimens studied of *F. minutiflora* Rydb. will be sent on request.

Discussion

Two distinct taxa can be identified within *F. brachyphylla* s.lat. from Colorado. One matches fairly well *F. brachyphylla* s.str. from the Arctic although it has somewhat shorter spikelets (4.4–5.6 mm, for the lowermost three florets excl. arista), fewer florets (3–5) per spikelet, and a longer arista (1.6–)2.4–3.2 mm (Fig. 1 A, B). According to Holmen (1964) 2n = 28 was found in such a plant (a single count), whereas *F. brachyphylla* s.str. is known to be a hexaploid with 2n = 42 (Frederiksen 1977). The length of the guard cells corroborates the difference in ploidy level, those of the southern taxon being slightly but clearly shorter than those of *F. brachyphylla* s.str. (Fig. 2). It thus seems to be closely related to *F. brachyphylla* s.str. although not identical with it. The rank of subspecies was proposed by Holmen (1964), but a final conclusion requires more intense studies within *F. brachyphylla* in the Rocky Mountains.

The second taxon from Colorado deviates very much. It is characterized by small spikelets (three-flowered spikelets 3.0–4.8 mm long, lemma 2.2–3.4 mm) with 2–3(–4) florets only, and a very short arista (0–1.5 mm) (Fig. 1 C). It is also a tetraploid with 2n = 28 (based on a few counts only, but the length of the guard cells seems to

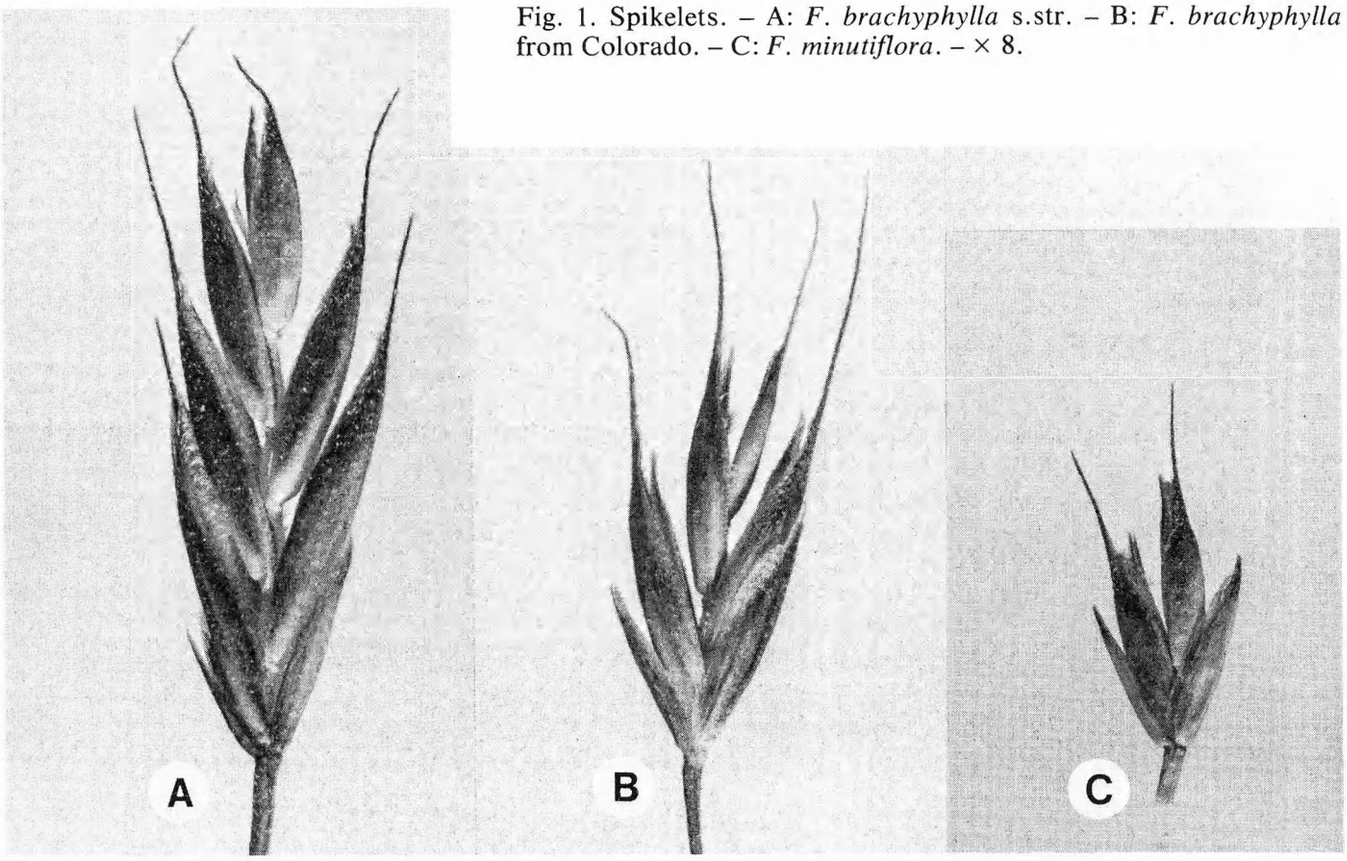

Fig. 1. Spikelets. – A: *F. brachyphylla* s.str. – B: *F. brachyphylla* from Colorado. – C: *F. minutiflora*. – × 8.

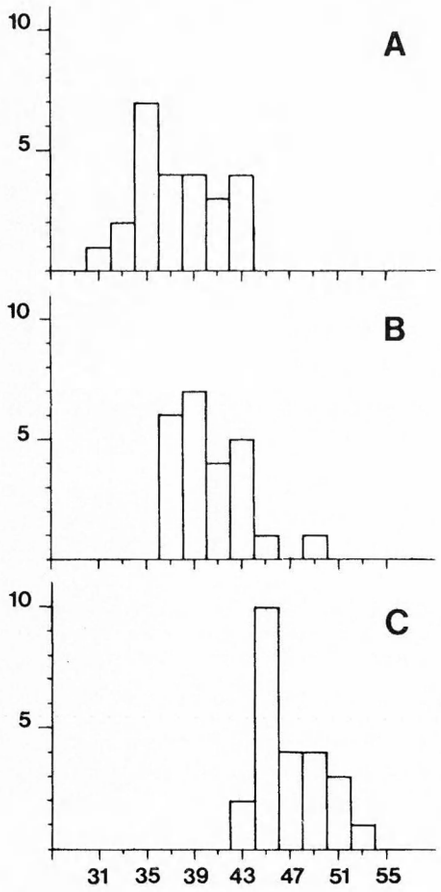

Fig. 2. Histograms showing the length of the guard cells in μm. – A: *F. minutiflora*. – B: *F. brachyphylla* from Colorado. – C: *F. brachyphylla* s.str. – Vertical axis: no. of specimens.

confirm the tetraploid level; Fig. 2). The top of the caryopsis is hairy in this taxon (Fig. 3) and glabrous in *F. brachyphylla*. I have studied this character within *F. brachyphylla* and its nearest allies (*F. hyperborea* Holmen ex Frederiksen, *F. brevissima* Jurtz. and *F. baffinensis*) as well as in *F. saximontana*. The top of the caryopsis is hairy only in *F. baffinensis*, glabrous in the other species. It seems to be a constant character which has been used previously within *Festuca* (Saint-Yves 1925, Krečetovič & Bobrov 1934); Hackel (1882) considered it to be a non-variable character within most *Festuca* species. Consequently it would be reasonable to regard the taxon in question as a separate species.

Rydberg (1917) mentions two taxa of interest: *F. brachyphylla* and *F. minutiflora* Rydb. The type specimen of *F. minutiflora* was found to match the taxon with hairy caryopsis and the original description fits well (Rydberg 1905).

Saint-Yves (1925) demonstrated the heterogeneity of *F. brachyphylla*, named *F. brevifolia* R. Br. by him. Three varieties were published: var. *arctica*, var. *endotera* and var. *utahensis*. Var. *arctica* was divided into subvar. *genuina* (based on *F. brevifolia* s.str. and thus conspeci-

fic with *F. brachyphylla* s.str.) and subvar. *pubiculmis* (one specimen only was cited; it was from Greenland; I have not been able to trace it but it does undoubtedly belong to *F. baffinensis*). Saint-Yves based his subdivision mainly on the presence or absence of hairs on the top of the caryopsis. Var. *utahensis* and subvar. *pubiculmis* were found to be hairy; subvar. *genuina* was glabrous; var. *endotera* was sometimes glabrous, sometimes hairy. Reexamination of most specimens cited by Saint-Yves as var. *endotera* shows that the northern specimens belong to *F. brachyphylla* s.str. The remaining collections, all from Oregon, California and Colorado, include plants with hairy and glabrous caryopses, matching the two taxa proposed here.

Festuca minutiflora Rydb.

Rydberg 1905 p. 608 – *F. ovina* L. var. *minutiflora* (Rydb.) Howell 1951 p. 151 – Type: Baker, Cameron Pass, July 13, 1896 (NY holotype).

F. brevifolia R. Br. var. *endotera* Saint-Yves 1925 p. 254 p.p., type incl. – *F. brachyphylla* Schult. & Schult. var. *endotera* (Saint-Yves) Litardière 1945 p. 108 p.p. – Type: Baker 176, near Pagosa Peak, August, 1899 (G lectotype, selected here).

F. brevifolia R. Br. var. *utahensis* Saint-Yves 1925 p. 257 – *F. brachyphylla* Schult. & Schult. var. *utahensis* (Saint-Yves) Litardière 1945 p. 108 – Type: Baker 175, near Pagosa Peak, August, 1899 (G lectotype, selected here).

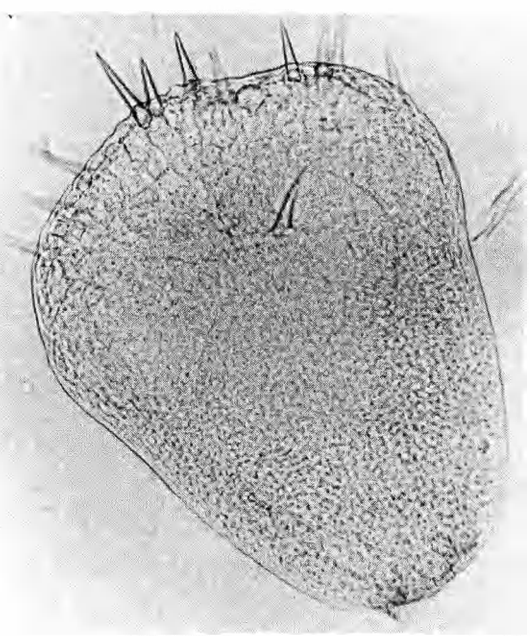

Fig. 3. Young caryopsis from *F. minutiflora*. Styles removed. – × 100.

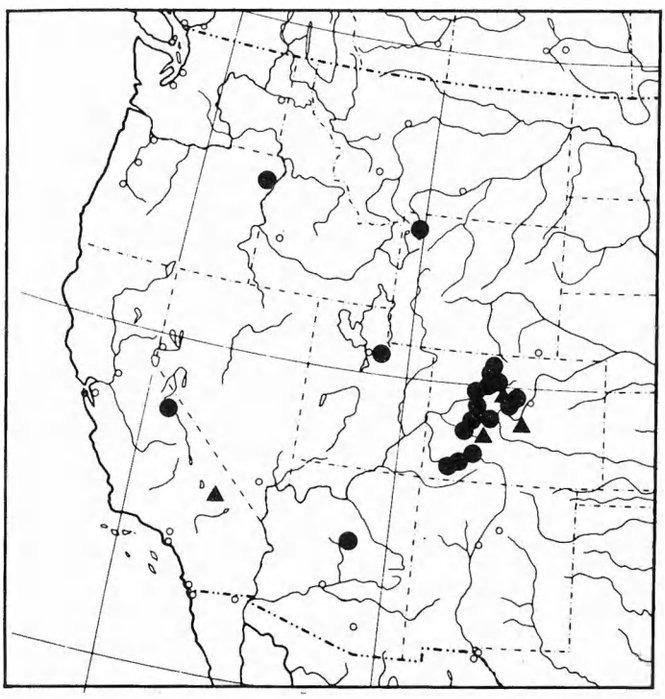

Fig. 4. Distribution of *F. minutiflora*. ▲ indicates specimens cited by Rydberg (1905) or Howell (1951), not seen by the author.

To the description by Rydberg (1905) can be added: top of caryopsis hairy, branches of the panicle glabrous or only slightly scabrous.

I include *F. brevifolia* var. *utahensis* in this species only with some hesitation. The top of the caryopsis is hairy, but it deviates especially in having more florets per spikelet and broader leaves. However, there are transitional specimens even among the few specimens examined.

F. minutiflora has a very scattered distribution, as it grows in high alpine areas between 3000 and 4000 m. Outside Colorado only few specimens were found (Fig. 4).

Acknowledgements. The author wishes to thank Professor W. A. Weber, curator of the Herbarium of the University of Colorado Museum, for sending living material of *F. minutiflora*. Moreover I wish to thank Professor A. Strid and Dr K. Jakobsen, Copenhagen, for valuable discussions during the work on the manuscript.

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Leaf sclereids – occurrence and distribution in the angiosperms

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Angiosperm genera known to possess leaf sclereids are listed, and their distribution in Dahlgren's twodimensional diagram of the angiosperm system is shown. Leaf sclereids seem to be rare or absent in groups which for other reasons are regarded as being derived, such as the monocotyledons, Asteranae and Caryophyllanae.

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The objective of this review is threefold, viz. (1) to show the general distribution of leaf sclereids among the angiosperms; (2) to check their distribution in Dahlgren's (1975) twodimensional system (Fig. 1); and (3) to decide whether leaf sclereids are taxonomically valuable at higher levels of classification.

The data are compiled from the works of Solereder (1908), Metcalfe & Chalk (1950) and Rao & Bhattacharya (in press), supplemented with many articles published during the last three decades. It has not been possible to map the different types of sclereids separately. Some comments are, however, included at the end of the lists of genera for each superorder.

The sclereids may either be found at the end of veins only: *terminal* sclereids; or they may be irregularly distributed: *diffuse* sclereids.

Magnolianae

Magnoliales: Winteraceae: *Bubbia, Zygogynum* – Himantandraceae: *Himantandra* – Magnoliaceae: *Aromadendron, Kmeria, Magnolia, Manglietia, Michelia* – Annonaceae: *Anaxogorea, Annona, Asteranthe, Cyathocalyx, Desmos, Goniothalamus, Guatteria, Habzelia, Heteropetalum, Phaeanthus, Popowia, Segeretia, Unona, Uvaria* – Canellaceae: *Canella, Cinnamosma, Pleodendron, Warburgia* – Myristicaceae: *Gymnocranthera, Horsfieldia, Knema, Iryanthera.*

Laurales: Lauraceae: *Actinodaphne, Ocotea, Ravensara, Persea.*

Terminal sclereids are recorded in Magnoliaceae and Canellaceae. In the other five families they are diffuse. Nests of sclereids occur in Himantandraceae and Winteraceae.

Ranunculanae

Ranunculales: Menispermaceae: *Abuta, Adeliopsis, Albertisia, Anomospermum, Anamirta, Arcangelisia, Burasaia, Chlaenandra, Chondrodendron, Coscinium, Detandra, Husemannia, Limacia, Parabaena, Penianthus (Heptacyclum), Rhaptonema, Stephania, Tinomiscium.*

The sclereids are diffuse and polymorphic.

Nymphaeanae

Nymphaeales: Nymphaeaceae: *Euryale, Nuphar, Nymphaea, Victoria* – Barclayaceae: *Barclaya.*

Diffuse, ramiform to polyramous sclereids have been found in four genera of Nymphaeaceae. *Barclaya* has ramiform sclereids. The sclereids are crystalliferous and strongly scattered in the mesophyll.

Rutanae

Rutales: Rutaceae: *Boronella, Boronia* – Simaroubaceae: *Eurycoma, Hannoa, Hyptiandra, Irvingia, Mannia, Odvendra, Perrieria, Picramnia, Picrasma,*

Quassia, Samadera, Simaba, Simarubopsis – Meliaceae: *Dysoxylum, Khaya.*

Polygalales: Vochysiaceae: *Vochysia* – Trigoniaceae: *Lightia, Trigoniastrum* – Polygalaceae: *Asteropeia, Badiera, Monnina, Montabea, Polygala* – Emblingiaceae: *Emblingia.*

Sapindales: Sapindaceae: *Cupaniopsis, Haplocoelum, Matayba, Paullinia, Seriania, Xerospermum* – Anacardiaceae: *Bouea* – Hippocastanaceae: *Billia.*

Geraniales: Nitrariaceae: *Nitraria* – Erythroxylaceae: *Erythroxylum* – Humiriaceae: *Sacoglottis* – Hugoniaceae: *Hugonia* – Ixonanthaceae: *Ochthocosmus.*

Terminal sclereids are recorded in *Vochysia* (Vochysiaceae), *Boronia* and *Boronella* (Rutaceae), *Montabea* (Polygalaceae) and *Hannoa* (Simaroubaceae).

Dillenianae

Dilleniales: Dilleniaceae: *Hibbertia, Tetracera, Wormia.*

Malvales: Malvaceae: *Goethea, Pavonia.*

Urticales: Moraceae: *Balanostreblus, Ficus, Sahagunia.*

Euphorbiales: Euphorbiaceae: *Acalypha, Actephila, Actinostemon, Alchornea, Chaetocarpus, Chondrostylis, Givotia, Conceveiba, Dalechampia, Erismanthus, Euphorbia, Mabea, Pausandra, Phyllanthus, Sebastiana, Tragia, Trigonostemon* – Pandaceae: *Centroplacus.*

The sclereids are diffuse; in the majority of genera idiofibrosclereids sensu Rao & Bhupal (1971) are present. Terminal sclereids are recorded for *Hibbertia* (Dilleniaceae, Rao & Das 1979).

Thymelaeanae

Thymelaeaceae: *Enckleia, Daphne, Daphnopsis, Gyrinops, Lasiosiphon, Linostoma, Stephanodaphne.*

Terminal as well as diffuse sclereids have been reported. Idiofibrosclereids are present in *Enckleia* and *Linostoma* (Rao & Bhupal 1973).

Violanae

Violales: Flacourtiaceae: *Calantica, Casearis, Erythrospermum, Homalium, Patrisia, Tuelania.* – Passifloraceae: *Passiflora* – Turneraceae: *Turnera* – Begoniaceae: *Begonia* – Datiscaceae: *Octomeles.*

Tamaricales: Tamaricaceae: *Hololachna, Reaumuria* – Frankeniaceae: *Frankenia.*

Capparales: Salvadoraceae: *Azima, Dobera, Salvadora* – Capparidaceae: *Boscia, Cadaba, Capparis, Courbonia, Niebuhria, Thylachium.*

Leaf sclereids are apparently most common in Violales. The occurrence of terminal ramiform sclereids in *Reaumuria* (Tamaricaceae) is unusual. Terminal, polymorphic sclereids are known from *Capparis* and *Niebuhria* (Capparaceae).

Celastranae

Celastrales: Aquifoliaceae: *Ilex* – Celastraceae: *Hippocratea, Kokoona, Lophopetalum, Maurocenia, Maytenus, Microtropis, Pterocelastrus, Salacia, Schaefferia* – Goupiaceae: *Goupia* – Sphenostemonaceae: *Phlebocalymna.*

Santalales: Olacaceae: *Eganthus, Endusa, Heisteria, Minguartia, Ochanostachys, Olax, Ptychopetalum, Schoepfia, Scorodocarpus, Ximenia* – Opiliaceae: *Agonandra, Cansjera, Lepionurus, Opilia* – Loranthaceae: *Dendrophtora, Loranthus, Nuytsia, Stachyphyllum* – Viscaceae: *Oryctanthus, Viscum* – Santalaceae: *Acanthosyris, Buckleya, Jodina, Osyris, Quinchamalium, Thesium.*

Rhamnales: Rhamnaceae: *Ceanothus, Microrhamnus* (= *Condalia*), *Rhamnus, Zizyphus (Sarcomphalus).*

Diffuse, monomorphic as well as polymorphic sclereids have been reported from this superorder. Spicular cells as well as terminal tracheids occur in Olacaceae. The records of terminal vesiculose sclereids in *Goupia* (Goupiaceae; Rao & Bhattacharya 1975) and *Ptychopetalum* (Olacaceae) are noteworthy. These sclereids were formerly considered to be enlarged storage tracheids (Solereder 1908 p. 877). In *Oryctanthus* (Viscaceae) restricted bundle sheaths at the minor veins possess crystalliferous sclereids.

Solananae

Solanales: Convolvulaceae: *Dicranostyles, Erycibe, Humbertia, Ipomoea, Lysiostyles, Maripa, Prevostea* – Ehretiaceae: *Cordia.*

Hamamelidanae

Trochodendrales: Trochodendraceae: *Trochodendron* – Eupteleaceae: *Euptelea.*

Hamamelidales: Hamamelidaceae: *Eustigma, Exbucklandia, Disanthus, Distylium, Hamamelis, Loropetalum, Sycopsis, Trichocladus* – Rhodoleiaceae: *Rhodoleia.*

Cunoniales: Cunoniaceae: *Cunonia, Pancheria, Weinmannia* – Bruniaceae: *Linconia, Lonchostoma.*

Diffuse sclereids are recorded in Trochodendrales, whereas in Hamamelidales and Cunoniales many genera have terminal sclereids. Idiofibro-

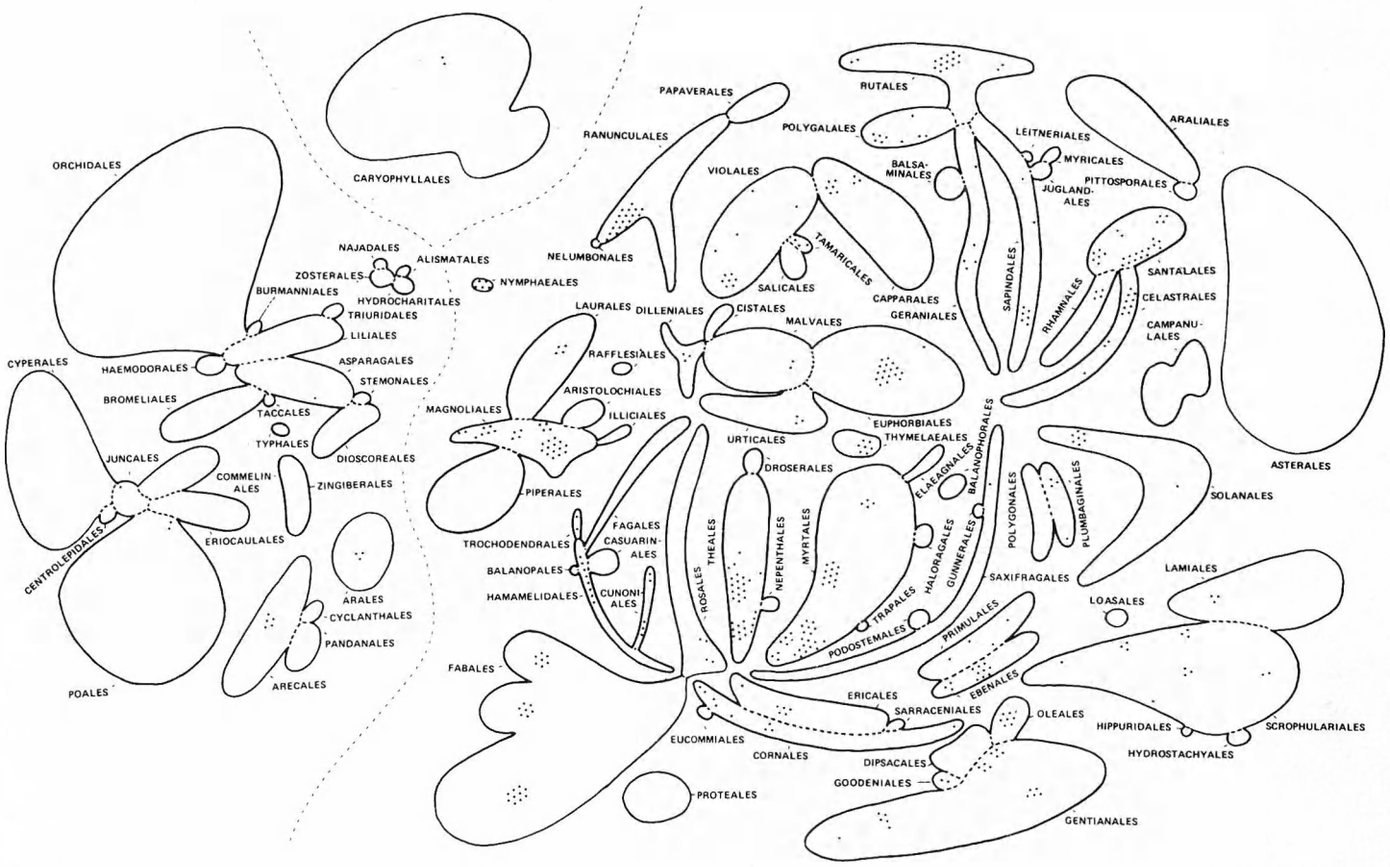

Fig. 1. Distribution of leaf sclereids in the angiosperms (the diagram from Dahlgren 1975). Each dot represents one genus in which leaf sclereids have been reported.

sclereids are reported from *Distylium, Loropetalum, Sycopsis* and *Trichocladus* (Hamamelidaceae; Rao & Bhupal 1973).

Rosanae

Rosales: Connaraceae: *Pseudoconnarus, Rourea* – Chrysobalanaceae: *Couepia, Licania*.

Fabales: Mimosaceae: *Affonsea, Calliandra, Inga, Piptadenia, Prosopis, Pithecolobium, Stryphonodendron* – Caesalpiniaceae: *Cassia, Cynometra, Dimorphandra, Macrolobium, Mora, Oxystigma, Saraca* – Fabaceae: *Ammodendron, Andira, Bossiaea, Bowdichia, Buchenroedera, Dillwynia, Ormosia, Platymiscium, Pultaea, Swartzia*.

Diffuse sclereids as well as terminal ones (in *Cynometra, Cassia, Dimorphandra* of Caesalpiniaceae and in *Ormosia* of Fabaceae) have been reported. Idiofibrosclereids occur in *Cynometra* (Caesalpiniaceae; Rao & Bhupal 1973).

Proteanae

Proteales: Proteaceae: *Adenanthos, Banksia, Bellendena, Dilobeia, Dryandra, Grevillea, Hakea, Isopogon, Leucospermum, Paranomus, Petrophila, Roupala, Sorocephalus, Stenocarpus, Xylomelum*.

Diffuse sclereids are most common, but *Bellendena* has terminal sclereids.

Myrtanae

Myrtales: Lythraceae: *Alzatea, Rhynchocalyx, Sonneratia* – Rhizophoraceae: *Bruguiera, Ceriops, Kandelia, Poga, Rhizophora* – Crypteroniaceae: *Alzatea, Crypteronia, Dactylocladus, Rhynchocalyx* – Combretaceae: *Anogeissus, Buchenaria, Bucida, Combretum, Ramatuella, Thiloa* – Oliniaceae: *Olinia* – Melastomataceae: *Coryphadenia, Gravesia, Henrietella, Huberia, Lavoisiera, Leandra, Medinilla, Memecylon, Microlicia, Miconis, Mouriri, Plethiandra* – Penaeaceae: *Brachysiphon, Endonema, Glischrocolla, Penaea, Saltera* (=*Sarcocolla*), *Sonderothamnus, Stylapterus* – Myrtaceae: *Angophora, Eucalyptus, Eugenia, Jambosa*.

Diffuse sclereids are most common and have been reported from Lythraceae (Sonneratiaceae), Rhizophoraceae, Crypteroniaceae, Combretaceae, Penaeaceae and Myrtaceae, whereas terminal sclereids have been observed in *Bruguiera* and *Kandelia* (Rhizophoraceae), *Olinia* (Oliniaceae) and *Memecylon, Mouriri* and *Coryphadenia* (Melastomataceae). Nests of sclereids

or sclerocysts are present in *Plethiandra* (Melastomataceae).

Saxifraganae

Saxifragales: Fouquieriaceae: *Fouquieria*.

The genus *Fouquieria* is better placed in the Cornalean-Ericalean complex (Dahlgren et al. 1976). The sclereids occur along minor veins and vein endings together with isolated clusters of tracheary elements (Lersten & Carvey 1974).

Plumbaginanae

Plumbaginales: Plumbaginaceae: *Aegialitis* – Limoniaceae: *Limonium, Limoniastrum, Goniolimon*.

Diffuse sclereids are rare, and terminal ones is the common type in Limoniaceae. In a few species of *Limonium*, interrupted sheaths are present along the veins from the base to the apex of the lamina.

Primulanae

Primulales: Myrsinaceae: *Ardisia* – Aegiceratacеae: *Aegiceras* – Theophrastaceae: *Theophrasta* – Primulaceae: *Dionysia*.

Ebenales: Ebenaceae: *Diospyros, Euclea, Maba* – Sapotaceae: *Amorphospermum, Bumelia, Chrysophyllum, Labourdonnaisia, Madhuca, Manilkara, Mimusops, Pouteria, Sideroxylon*.

Diffuse sclereids are most common, but terminal sclereids occur, together with diffuse ones, in a few species of *Dionysia* (Primulaceae).

Theanae

Theales: Ochnaceae: *Blastemanthus, Luxemburgia, Ochna, Cespedesia, Elyasia, Hilairella, Poecilandra, Trichovaselia, Vaselia* – Theaceae: *Adinandra, Annesleya, Camellia, Cleyera, Eurya, Franklinia, Freziera, Gordonia, Laplacea, Nabiasodendron, Pyrenaria, Schima, Ternstroemia, Visnea* – Marcgraviaceae: *Marcgravia, Norantea, Ruyschia, Souroubea* – Caryocaraceae: *Anthodiscus, Caryocara* – Pelliceriaceae: *Pelliceria* – Bonnetiaceae: *Bonnetia*.

Symplocaceae is probably better placed in Cornales. Diffuse sclereids are the most common.

Cornanae

Ericales: Actinidiaceae: *Saurauia* – Ericaceae: *Craibiodendron, Diplycosia, Erica, Gaultheria, Leucothoe*.

Cornales: Garryaceae: *Garrya* – Alangiaceae: *Alangium* – Cornaceae: *Griselinia, Mastixia* – Nyssaceae: *Nyssa* – Icacinaceae: *Desmostachys, Discophora, Stemonurus* – Sambucaceae: *Viburnum*.

The occurrence of terminal spheroidal sclereids in *Leucothoe* and *Craibiodendron* (Ericaceae) is interesting. The sclereids in Cornales are diffuse.

Gentiananae

Oleales: Oleaceae: *Jasminum, Ligustrum, Linociera, Myxopyrum, Notelaea, Olea, Osmanthus, Schrebera*.

Goodeniales: Goodeniaceae: *Dampiera, Scaevola*.

Gentianales: Loganiaceae: *Anthocleista, Fagraea, Potalia, Strychnos* – Rubiaceae: *Burchellia, Chomelia, Coffea, Scyphiphora, Jovetia* – Menyanthaceae: *Limnanthemum, Liparophyllum, Nymphoides, Villarsia* – Apocynaceae: *Aspidosperma, Bousigonia, Micrechites, Neocouma, Trachelospermum* – Asclepiadaceae: *Dischidia*.

Most taxa have diffuse sclereids, but terminal ones are known from *Schrebera* (Oleaceae), *Scaevola* (Goodeniaceae) and *Scyphiphora* (Rubiaceae).

Lamianae

Scrophulariales: Globulariaceae: *Globularia* – Orobanchaceae: *Kopsiopsis* – Bignoniaceae: *Colea, Crescentia, Phyllarthron* – Gesneriaceae: *Cyrtandra, Hemiboea, Stauranthera* – Acanthaceae: *Elytraria, Staurogyne* – Scrophulariaceae: *Dopatrium, Lindernia, Torenia*.

Lamiales: Verbenaceae: *Citharexylum, Clerodendrum, Nyctanthes, Petrea*.

The sclereids are diffuse.

Caryophyllanae

Caryophyllales: Chenopodiaceae: *Arthrocnemum, Salicornia*.

Diffuse as well as terminal sclereids have been found in the palisade parenchyma of these two genera.

Lilianae

Asparagales: Agavaceae: *Agave*.

The sclereids of *Agave* occur at the leaf tips.

Commelinanae

Juncales: Thurniaceae: *Thurnia*.
Poales: Restionaceae: *Anarthria, Ecdeiocolea*.

The sclereids are diffuse (Cutler 1969).

Arecanae

Arecales: Arecaceae: *Bactris, Daemonorops, Eugeissona, Licuala, Lodoicea.*

The sclereids of the palms are diffuse. Idiofibrosclereids have also been reported from *Bactris* and *Licuala.*

Aranae

Arales: Araceae: *Monstera, Rhaphidophora, Scindapsus.*

The sclereids of *Scindapsus* and *Rhaphidophora* are large fusiform ones or trichosclereids. Zosterosclereids have been reported in *Monstera.* Septa are present in scattered sclereids of *Scindapsus.*

Discussion

Sclereids appear to be very rare in the monocotyledons, where they are confined to some genera of Arecaceae, Araceae, Agavaceae, Restionaceae and Thurniaceae.

Sclereids in the dicotyledons are so far *not reported* in the superorders Rafflesianae, Aralianae, Saxifraganae (except for Fouquieria; see above), Asteranae, Campanulanae, Balanophoranae and Loasanae.

Sclereids are moreover *not reported* to occur in the orders Aristolochiales, Piperales, Illiciales (Magnolianae), Nelumbonales, Papaverales (Ranunculanae), Juglandales, Myricales, Leitneriales, Balsaminales (Rutanae) Cistales (Dillenianae), Salicales (Violanae), Casuarinales, Fagales, Balanopales (Hamamelidanae), Elaeagnales, Trapales, Haloragales (Myrtanae), Polygonales (Plumbaginanae), Nepenthales, Droserales (Theanae), Sarraceniales, Eucommiales (Cornanae), Dipsacales (Gentiananae), Hippuridales and Hydrostachyales (Lamianae).

Sclereids seem to be of *limited distribution* in some orders of dicotyledons. They are known only from Menispermaceae in Ranunculales, from one genus of Anacardiaceae in Sapindales, from seven genera of Convolvulaceae and one genus of Ehretiaceae in Solanales, from a few taxa of Actinidiaceae and Ericaceae in Ericales, from a few genera of Malvaceae in Malvales, from some genera of Verbenaceae in Lamiales, and from two genera of Chenopodiaceae in Caryophyllales.

Richness of sclereids is conspicuous in most Nymphaeales, in Capparaceae of the Capparales, in Hamamelidaceae (incl. Rhodoleiaceae) of the Hamamelidales. Its abundance is also noteworthy in Magnoliales, Proteales, Plumbaginales and families of Santalales, Myrtales, Primulales, Ebenales, Theales, Cornales, Oleales and Goodeniales.

The sclereids thus show a scattered distribution. However, they tend to be rare or absent in those orders which tend to be advanced in various other respects (peripheral in the diagram). They are much more common in woody than in herbaceous groups, such as Caryophyllales and the monocotyledons.

The physiological role of sclereids must be considered when phylogenetic trends are under discussion. Since the days of Francken (1890), emphasis has been placed on the protective role of sclereids, but it remains a working hypothesis in the absence of experimental work (Rao & Bhattacharya in press).

The scattered occurrence of sclereids in different taxonomic and ecological groups makes it difficult to understand their evolutionary and functional significance (Fahn 1969 p. 100). Francken (1890) concluded that the presence of sclereids did not correlate with physiological conditions or the environment. However, complex formation of sclereids in *Dionysia* (Primulaceae) may be considered as part of a syndrome of characters connected with xerophytic adaptations (Bokhari & Wendelbo 1976). On the other hand, terminal idioblasts have been recorded in many species of mesic *Hibbertia* (Dilleniaceae) where their significance is unclear (Rury & Dickison 1977). Lersten & Carvey (1974) consider that the variation in number of sclerified veinlet elements in different parts of the geographical range of a species of *Fouquieria* casts doubt on their importance for the normal physiological activity of the leaf.

Idioblasts in the form of tracheoids and sclereids as well as transitional cells at the vein endings occur in many genera. Their terminal relationship has been confirmed by ontogenetic studies in *Mouriri* (Foster 1947), *Memecylon* (Rao 1951, 1957, Bhupal 1971), *Boronia* (Foster 1955) and *Niebuhria* (Rao 1958).

It is tempting to speculate that terminal sclereids are transformed terminal tracheoid

cells. Rao & Mody (1961) suggested that genera which have well developed terminal tracheoids at the vein endings would include species with well developed terminal sclereids. Foster (1947), however, argued that even if a complete transitional trend from tracheoids into sclereids could be demonstrated, a phylogenetic connection is not proved. Foard (1958, 1959) is of the opinion that the formation and development of idioblastic sclereids is genetically controlled. This is a question of great interest and experimental as well as analytical research is needed.

Phylogenetic speculations based on the distribution of sclereids do not seem warranted as yet. Whether they have any functional significance is uncertain. Superficially it seems to be a truly fortuitous anatomical character, but this view is partly contradicted by the pattern of distribution within the angiosperms. Leaf sclereids may not have any major phylogenetic significance although they may be of some taxonomic interest in certain groups of plants.

Acknowledgements. We wish to thank Lise Bolt Jørgensen and Professor Rolf Dahlgren, Copenhagen, for taking interest in reviewing the manuscript and preparing the diagram.

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Structural heterozygosity in tetraploid Allium platyspathum

R. N. Gohil

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The somatic complement of *Allium platyspathum* Schrenk var. *falcatum* Regel (2n = 4x = 32) comprises 2 median, 25 submedian and 5 subterminal chromosomes. Male meiosis is characterized by the formation of multivalents involving up to 16 chromosomes. This implies that in this cytotype translocations have been superimposed on polyploidy.

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Allium platyspathum Schrenk var. *falcatum* Regel grows wild in the Ladakh Himalayas up to 3300 m. So far only a diploid cytotype of this species has been recorded (Fedorov 1969, Moore 1970, 1971, 1974). The two populations studied in the present investigation were tetraploid with 2n = 32. In the present communication its karyotype and details of male meiosis are described.

Material and methods

Bulbs collected from two geographically isolated localities in Ladakh, viz. Drass (3050 m) and Bodh Kharbu (3300 m) were cultured in the Botanical Gardens, Kashmir University. Root tips were fixed in acetic alcohol (1:3) after pretreatment in 0.3% aqueous colchicine solution for 3 hours at room temperature. After fixation in 24 hours they were hydrolysed in 9 drops of aceto-orcein and one drop of 1N HCl at 60°C for ten minutes. Squashes were made in 1% aceto-orcein. For meiotic studies young inflorescences were fixed in absolute ethanol, acetic acid and chloroform (1:1:1). Anthers were squashed in 1% aceto-orcein. All the studies were made from temporary mounts. Ten plants from each locality were studied. The karyotype and male meiosis have been studied in the same individuals.

Karyotype

Root tip mitosis showed 2n = 32 chromosomes in all cells. Of these 2 are median, 25 submedian and 5 (the smallest ones) are subterminal (Fig. 3). Four of the five subterminal chromosomes bear small *cepa* type satellites. The non-satellited subterminal chromosome is the smallest one (5.0 μm). The longest chromosome is 9.2 μm. The total and mean chromatin length is 224.6 and 7.019 μm, respectively.

Male meiosis

The prophase configurations could not be resolved. At metaphase I, only ten cells could be analysed. The multivalent associations became more complex owing to the interlockings between multivalents (Fig. 1). The various associations met with are given in Table 1.

The highly complex chromosome pairing did not influence the subsequent course of meiosis very much. At anaphase I the following segregation patterns were found: 16/16 (7 cells), 17/15 (3 cells), 17/14 and one laggard (4 cells) and 18/14 (9 cells). A few cells had bridges and laggards also. The pollen viability does not seem to be very much affected. 70% of the pollen produced stained with acetocarmine or iodine.

The most characteristic feature of the cytology of *Allium platyspathum* is the occurrence of associations of up to 16 chromosomes during male meiosis. 23% of the chromosomes formed quadrivalents, a feature expected in a tetraploid cytotype.

The formation of associations involving more

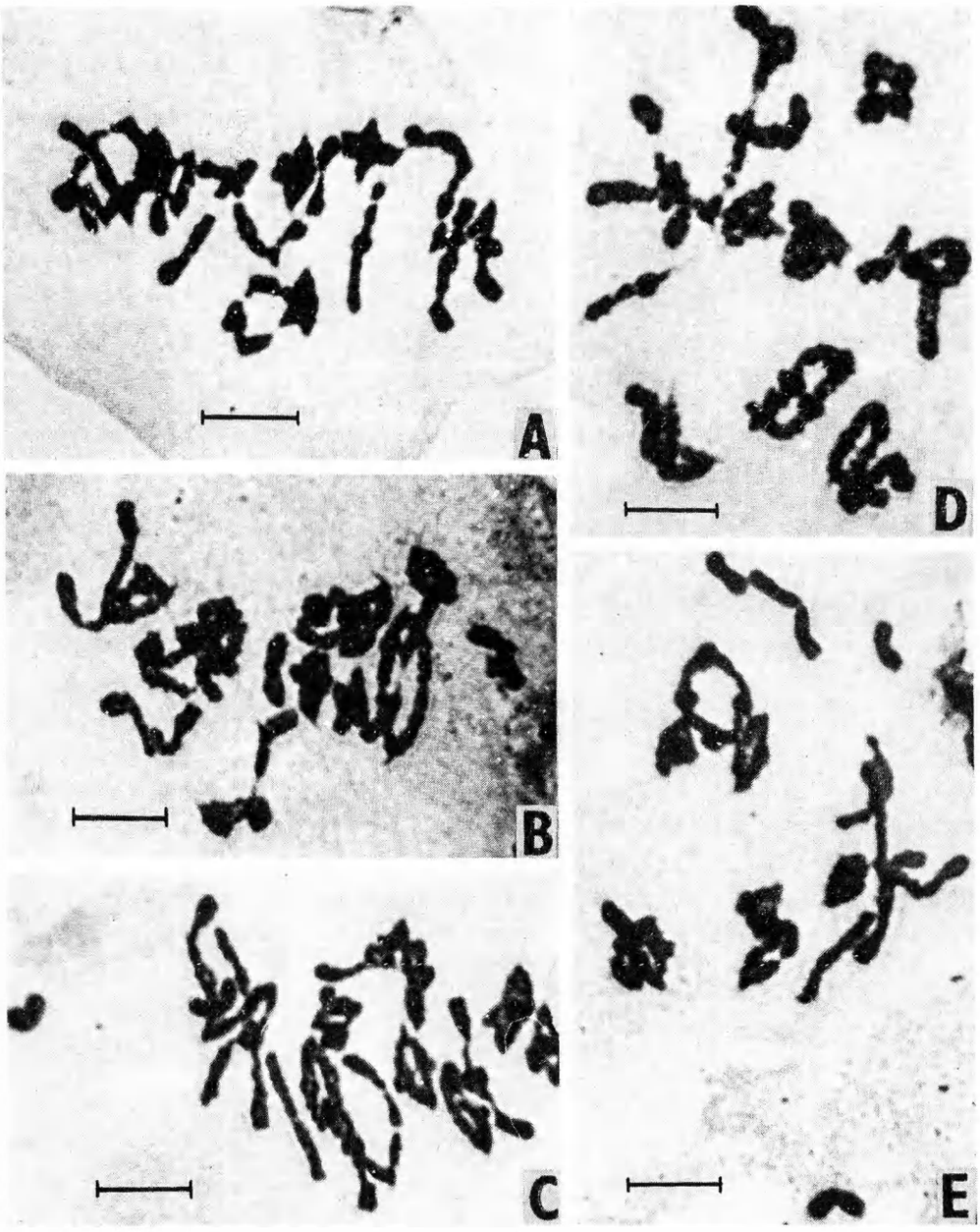

Fig. 1. Metaphase I in *Allium platyspathum*. For details see Table 1. Scales 10 μm.

Table 1. Multivalent associations at M1 in tetraploid *Allium platyspathum*. – The last line gives percentage of chromosomes (of totally 320) involved in the different associations.

Cell no.	Associations										Fig.
	XVI	XIII	XI	VIII	VI	V	IV	III	II	I	
1	1	.	.	.	.	.	.	2	3	4	
2	.	1	1	.	.	.	.	2	.	2	
3	.	.	.	1	.	.	2	.	8	.	
4	.	.	.	.	1	1	2	1	5	.	1 A
5	.	.	.	.	1	.	2	1	7	1	1 B
6	.	.	.	.	1	.	2	.	8	2	
7	.	.	.	.	.	1	2	4	2	3	1 C
8	.	.	.	.	.	.	3	4	4	.	1 D
9	.	.	.	.	.	.	3	2	6	2	
10	.	.	.	.	.	.	2	2	8	2	1 E
Sum	1	1	1	1	3	2	18	18	51	16	
%	5	4	3	3	6	3	23	17	32	5	

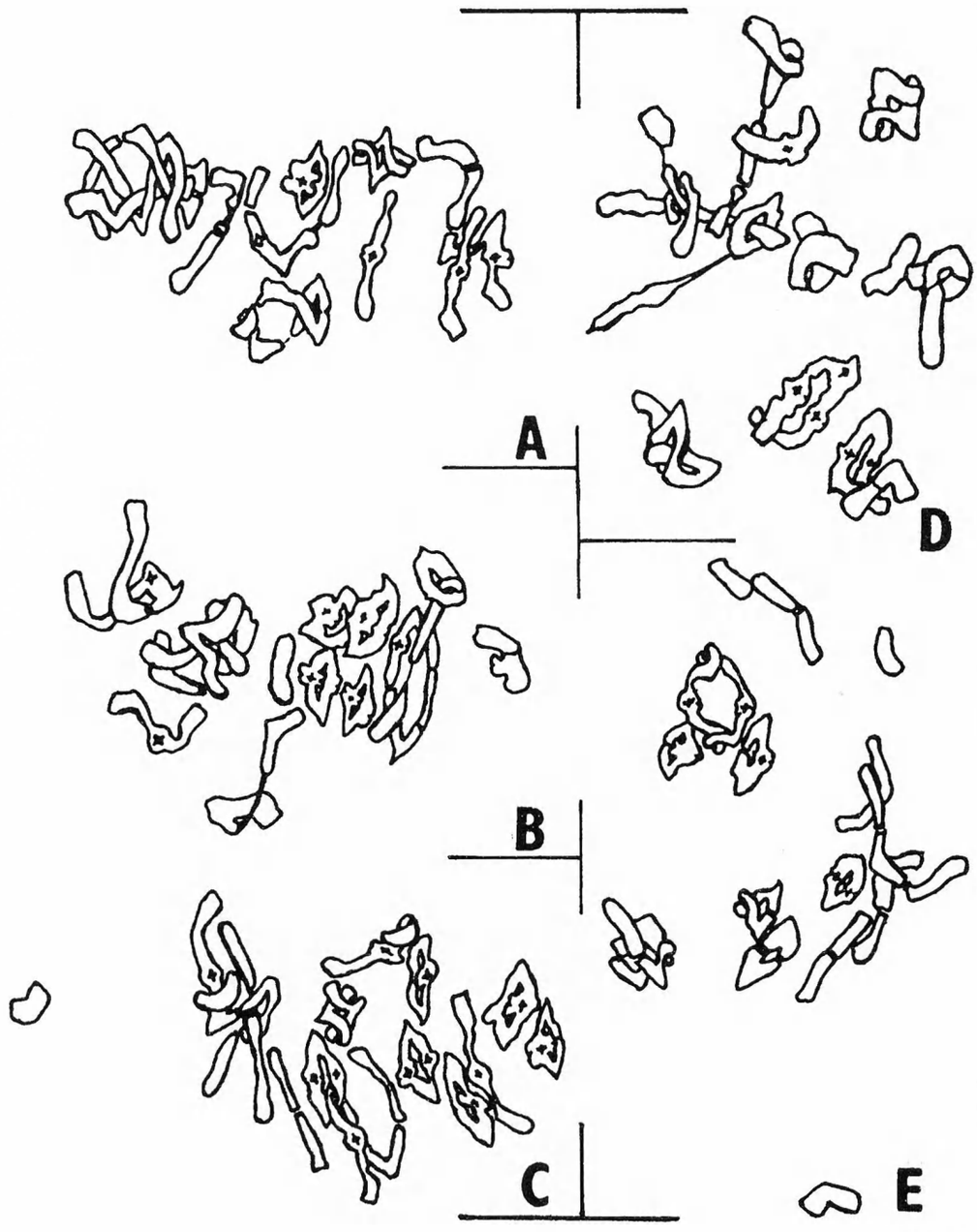

Fig. 2. Explanatory diagrams for Fig. 1.

than four chromosomes is evidence that several chromosomes have undergone reciprocal interchanges after the original formation of the tetraploid. This fact is also evident from the presence of five subterminal chromosomes in the karyotype.

Reciprocal translocations in polyploid *Allium* is previously known (Håkansson & Levan 1957, Gohil 1973). However, the number of chromosomes forming multivalents in these cases is not so high. Håkansson & Levan (1957) recorded association of 12, 8, 6 and 5 chromosomes in tetraploid *Allium odorum*. Despite the large chromosomes of this genus, translocations are rather rare even in the diploid taxa (Gohil & Koul 1978).

Acknowledgements. I am grateful to Dr A. K. Koul for advice and to Professor P. Kachroo for providing facilities.

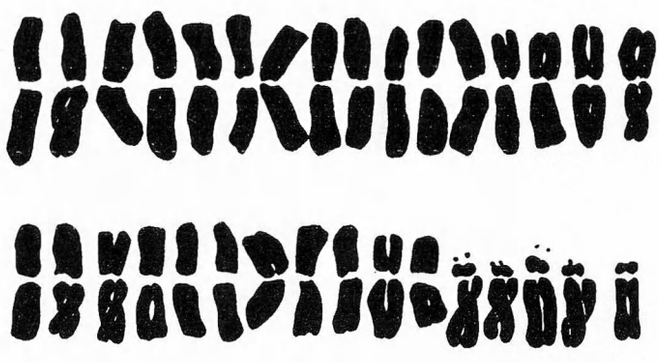

Fig. 3. The somatic complement of *Allium platyspathum*.

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Anthecological studies on the Lady's Slipper, Cypripedium calceolus (Orchidaceae)

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A four-year field study of the relations between *Cypripedium calceolus* L. and anthophilous insects on the island of Öland, S Sweden, is presented. Seasonal and dial activity, approach, alighting, entering and escape of different flower-visitors were studied. Solitary bees (*Andrena, Lasioglossum* and *Halictus*) were pollen vectors. The most frequent and regular vectors were females of *Andrena haemorrhoa* (F.). Male bees visited flowers sparsely. The crimson spotted floral structures are false nectar guides which are important for the attraction and entering of bees. The floral fragrance is dominated by acetates. Chemical correspondence with pheromone secretions in *Andrena* suggests that the fragrance might interfere with pheromone controlled alighting reactions and thereby increases entering into the labellum. The large expanded stigma acts as a "key" to the vectors' freedom as it provides the essential support for bending down the elastic basal hinge of the labellum. The duration of bees' imprisonment was affected by the age of the flower, microclimate and the bees' morphology and physical strength. Considerable losses of vectors towards a successful pollination point to an extreme dependence of local bees with regular habits. Functional details and escape routes of bees indicate that the populations studied belong to a small-flowered anthecotype.

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Since the famous work by Charles Darwin (1862) the pollination mechanisms in the genus *Cypripedium* L. have been a source for speculation. Darwin assumed that pollination was effected by an insect sitting on the outside of the labellum, piercing with its mouthparts into either of the two small posterior orifices. His American colleague Asa Gray (1862), however, became convinced that the work was carried out by some insects which crawl into the labellum, perhaps entering through one of these orifices or, more likely through the large central opening, and then escaping by crawling past the stigma, making their exit by the posterior openings and so transferring the pollen. A few years later Hermann Müller (1868, 1869) verified the latter theory when he observed solitary bees of the genus *Andrena* F. pollinating *C. calceolus* L.

The presence or absence of food in the labellum has been a subject of continuous debate. Kurr (1833) found no nectar but Darwin (1862) drew attention to the hairs on the bottom of labellum and noted that their tips secreted small drops of viscid fluid which was possibly nectar. This "nectar-like fluid" (Smith 1863) was interpreted by Müller (1869) as nectar although he had stated previously "keinen Honig dar" (Müller 1868). The occurrence of nectar is unfortunately still reported in modern works (Brenner 1910, Godfery 1933, Summerhayes 1951, Proctor & Yeo 1973). Müller (1868) also mentioned that feeding might occur on the "saftigen Haare", an assumption which later became treated as a fact (Müller 1873, Kerner 1891, Knuth 1898, Porsch 1906, Kirchner 1911). It has since been proved that the fluid is oil and not nectar (Knoll 1922, Daumann 1932, 1941, Ziegenspeck 1936) and that the hairs on the vegetative parts of the plant also produce a similar (identical?) secretion (Nestler 1907). Ac-

cording to Ziegenspeck (1936) and Daumann (1968) the trichomes inside the labellum are not eaten or chewed. Stoutamire (1967) however, writes that "these hairs are often chewed". Faegri & Pijl (1971) pointed out the possibility of such "emergency reactions" of an imprisoned visitor. To sum up, there is no reliable observation of feeding on hairs or secretions in the flowers. This justifies the conception of "Täuschblume" in this case (Daumann 1968) i.e. the flowers act by deceit (Faegri & Pijl 1971).

Müller (1868) propounded that the attraction of pollinators to *C. calceolus* was due to colour and fragrance. Several authors have characterized the fragrance as being sweet or fruity (Ziegenspeck 1936, Füller 1955). The site of production is the redbrown sepals and petals (Ziegenspeck 1936, Daumann 1968). Experiments have indicated that far attraction is visually guided (Daumann 1968) while the function of the scent is unknown. The crimson spotted infertile stamen in *Cypripedium* has been supposed to take part in attraction as a nectar guide (Delpino 1867, Brenner 1910, Arzt 1954, Gibson 1964) and also act as a landing-stage (Godfery 1933, Summerhayes 1951), a shelter for the stigma (Füller 1955), a part of the sliding zone (Ziegenspeck 1936) and as a shading screen to make the posterior openings visual for imprisoned bees (Müller 1868). Arzt (1954) put forward the theory that the spotted veins lining the bottom of the labellum of *C. calceolus* were also a nectar guide.

Müller (1868) and Darwin (1869) interpreted the inflected margins of the entrance in the labellum of *C. calceolus* as being a structure which prevented the bees which had entered from escaping. This view has often been adopted (e.g. Summerhayes 1951, Proctor & Yeo 1973). Knoll (1922) and Daumann (1968), however, demonstrated that bees remained imprisoned even when the inflection was cut away. Bees visiting *Cypripedium* must be of a certain size to be able to escape via the narrow passage and remove pollen (Robertson 1924, Ziegenspeck 1936, Summerhayes 1951). Bees which are too large often perish in the labellum (Baxter 1889, Summerhayes 1951, Gibson 1964) and so do the small weak insects (Müller 1869, Brenner 1910, Kirchner 1911, Ziegenspeck 1936). The light windows of the labellum – transparent lateral areas of the posterior wall without pigmentation and intercellular spaces – are supposed to induce phototaxis in pollinators and lead them the correct way (Webster 1886, Troll 1951). However, if the light windows are covered, bees are nevertheless able to pass the mechanism of the flower (Daumann 1968).

Hitherto in Europe the only pollinators of *C. calceolus* observed have been females of the genus *Andrena* (Müller 1868, 1869, 1873, Daumann 1968). Daumann (1968) once saw a *Halictus* female visit the flowers. By contrast, the N American variety *pubescens* (Willd.) Correll is known to be visited by males of *Ceratina* (Stoutamire 1967), and females of 10 genera of solitary bees (Guignard 1886, Cockerell 1915, Robertson 1924, Swezey 1945, Stoutamire 1967).

The primary purpose of the present study was to reveal details in the adaptation of the flowers of *C. calceolus* to the visiting insect fauna. Attention has also been paid to the principle of attraction of the pollinators.

Material and methods

Observations regarding *C. calceolus* and its relations with anthophilous insects were carried out in the central part of the island of Öland, S Sweden, during the first half of June, 1975–78. The localities are situated at Gillsätra, Långlöt and Halltorp in Glömminge, Långlöt and Högsrum parishes respectively. In Gillsätra two stands c. 200 m apart produced c. 5 and 60 flowers each year and are referred to as Gillsätra 1 and 2. In Halltorp some single flowering specimens occurred (c. 5 flowers) representing the survivors of a formerly large population. The population at Långlöt had c. 25 flowers. In the richest localities, i.e. Gillsätra 2 and Långlöt, the flowering specimens grew within a few metres from each other which suggests successful vegetative multiplication. The extent to which clone formation occurs is not known. As preliminary studies revealed Gillsätra 2 to be the most promising observation site, efforts were concentrated on this locality in order to obtain as much data as possible. Thus, the results reported in this paper are largely based upon observations from Gillsätra 2.

The three populations constitute field layer elements in deciduous forest vegetation of the *Ulmo-Fraxinetum* type (Kielland–Lund 1971). In Gillsätra 2 *Corylus avellana* L. and shoots of *Fraxinus excelsior* L. dominated the shrub layer around *C. calceolus*. Vegetatively important field layer species were *Aegopodium podagraria* L., *Convallaria majalis* L. and *Cardamine bulbifera* (L.) Crantz. Concurrently blooming entomophilous species in the immediate vicinity of *C. calceolus* were predominantly *Geranium sylvaticum* L. and *Convallaria majalis*. The distance to surrounding fields was about 150 m. Other important flowering

species, such as *Anthriscus sylvestris* (L.) Hoffm., *Crataegus laevigata* (Poir.) DC., *Taraxacum* sect. *Taraxacum* and *Ranunculus acris* L., occurred along the borderlines of these fields and interspersed here and there along crossing tracks etc.

On sunny days at Gillsätra 2 a shifting mosaic of illuminated spots, due to the canopy, passed over the field layer as the position of the sun changed. Consequently, the rate of illumination on a flower and thereby the intensity of the reflected light drastically changed within minutes and many times during a day. During the period 1975–78 the canopy gradually became denser and lowered the illumination. Data on the spring weather have been obtained from measurements at the Ecological Station of Uppsala University, Ölands Skogsby, situated 11 km SSE of Gillsätra. As practically no pollinators were active in cloudy weather, observations were concentrated to warm and sunny days. The total observation time was 69 hours.

The behaviour of insects was recorded from the moment they entered the scene around the flowers until they left for other activities. A stop watch and a tape recorder were of great help. Some vital behaviour steps observed need to be defined. *Approach* means that an insect directs its flight and comes within 10 cm of a flower. *Alighting* means that an approaching insect grasps the labellum or flies directly on to the front opening. *Entering* means that the visitor, passively or actively, comes inside the labellum while *creeping* is the term used when is passes the reproductive floral organs and leaves through one of the two exits. The term *climbing* means escape in one way or another through the entrance opening.

As much care as possible was taken not to disturb the pollinator–plant relations. Consequently, insects were collected only when it was absolutely necessary for identification purposes. Some of the visiting bees were impossible to determine at species level with certainty in the field. In such cases samples were taken in order to cover the diversity of species. Accordingly, bees were often identified in the field as belonging to a certain group of species or "type" only. For instance "*Andrena nigroaenea*-type" means that during field conditions the bee agreed in all perceptible characters with this species. A few pollen loads from bees which entered the labella were investigated.

The floral fragrance was collected in pre-column tubes and analysed by gas chromatography–mass spectrometry (GC–MS) (see Nilsson 1978). In 1975 the scent emitted by four flowers which had not been isolated from insect-visits was analysed. In 1976 two flowers were used which had been isolated prior to anthesis to prevent possible contamination of scent from visitors. As the bees showed an interest in the staminode, two pentane extracts of three flowers were prepared, one from the staminodes and one from the remaining parts. The volatiles in the extracts were compared by GC.

The populations of *C. calceolus* used in this study are among the few still left on Öland which means that many people come to enjoy the beauty of the plant. This had a slight negative effect on pollinator frequency during this investigation.

Floral fragrance

A typical gas chromatogram showing 9 fragrance compounds is presented in Fig. 1. Most of these compounds could be tentatively identified. Additional runs gave two further components viz. ethyl acetate and traces of one unknown sesquiterpene hydrocarbon. All GC–MS analyses indicate that a series of acetates dominate the composition of the scent. In particular octyl and decyl acetate were present in large amounts. Only one sesquiterpene made a prominent constituent viz. α-farnesene. The peak was identical with the mass spectrum of the compound isolated from the natural coating of apples (Murray 1969). Linalool, a monoterpene alcohol common in the scents of various flowers and fruits, and hydroquinone dimethyl ether were also present. Comparisons between analyses from 1975 and 1976 revealed no principal differences in composition, i.e. the scent was definitely produced by the flowers. A mixture of pure octyl and decyl acetate closely resembles the odour given off by the flowers under natural conditions on a sunny day. The somewhat fruity smell may originate from linalool and α-farnesene.

When the extract of the staminodes was run no volatiles in the region of Fig. 1 appeared on the chromatogram. However, the extract of the remaining parts of the flowers contained several volatile compounds in this region.

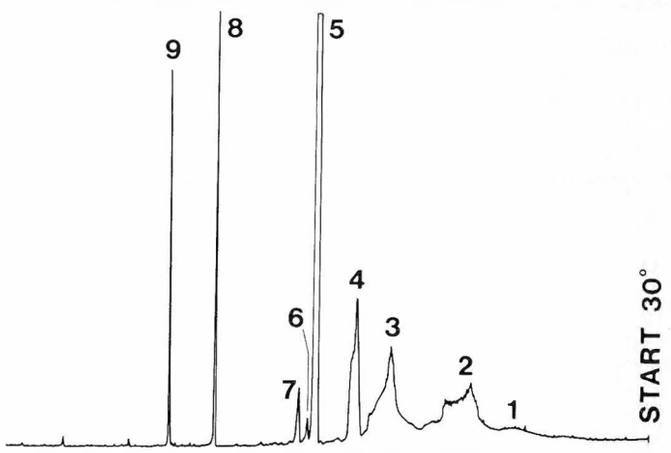


Fig. 1. Gas chromatogram of the floral fragrance of *Cypripedium calceolus* emitted from 4 flowers during 6 hours and collected in a pre-column tube packed with Porapak Q 50–80M as a collecting material. GC-equipment: LKB OV-101 25 m capillary column programmed from 30° to 220° at a rate of 8° per minute. Tentative identification: 1 Monoterpene hydrocarbon. 2 Hexyl acetate. 3 Linalool. 4 Hydroquinone dimethyl ether. 5 Octyl acetate. 6 do isomer. 7 β-phenethyl acetate. 8 Decyl acetate. 9 α-farnesene.

Flower visitors

Over 50 species of insects were found to visit the flowers i.e. they alighted on floral parts (Table 1). With the exception of parasitic wasps the list represents approximately the normal anthophilous insect fauna to be expected in such a biotope. Females of the solitary bee *Andrena haemorrhoa* (Andrenidae), the hoverfly *Melanostoma scalare* (Syrphidae) and the fly *Thricops semicinerea* (Muscidae) were the most frequent. Approximately 70% of the bees belonged to the genus *Andrena* (7 species), 15% were bumblebees (6 species), 13% belonged to the family Halictidae (5 species) and 2% to the genus *Nomada* (Anthophoridae) (2 species). About 90% of all bees and 85% of *Andrena* were females. Males of three species visited flowers i.e. *A. haemorrhoa, A. subopaca* and *Nomada ruficornis*. Also worth noting is the fact that all visiting Nematocera were males.

Both flowers and vegetative parts are remarkably often consumed by slugs and snails (not listed), a fact noted already by Müller (1868). Large species of *Arion* sometimes ate the stems causing withering while smaller species attacked various parts of the labellum and made extra holes in it. At Gillsätra in 1977, 17 flowers (20%)

Table 1. Insects visiting *Cypripedium calceolus* on Öland and species recorded as pollen vectors. Number of insects entering labella is given within parenthesis. – * Observed but not collected. – ** Captured before escape.

Species	No.	With pollen smear
Thysanoptera		
Taeniothrips picipes (Zett.)	(several)	.
Lepidoptera		
Pararge aegeria (L.)*	1♂	.
Micropterix calthella (L.)	1♂(1)	.
Coleoptera		
Meligethes aeneus (F.)	14(13)	.
Epuraea aestiva (L.)	3♂♂(3)	.
Eusphalerum sorbi (Gyll.)	4♂♂(4), 2♀♀(2)	.
Byturus ochraceus (Scr.)	3♂♂(3), 3♀♀(3)	.
Dasytes plumbeus (Müll.)	5♂♂(2), 2♀♀(2)	.
Grammoptera ruficornis (F.)	4(2)	.
Pria dulcamarae (Scop.)	1♀(1)	.
Diptera		
Melanostoma scalare (F.)	1♂(1), 22♀♀(17)	.
Syrphus ribesii (L.)	12	.
Heringia heringi (Zett.)	2♀♀(2)	.
Platychirus albimanus (F.)	1♀(1)	.
Dasysyrphus venustus (Meig.)	1♀(1)	.
Syritta pipiens (L.)	1♂(1)	.
Pipiza bimaculata Meig.	1♀(1)	.
Volucella bombylans (L.)*	1	.
Eristalis Latr.*	1	.
Syrphidae*	1	.
Thricops semicinerea (Wied.)	17♀♀(14)	.
Lucilia R.-D.*	1(1)	.
Calliphoridae*	1	.
Rhamphomyia umbripennis Meig.	2♂♂(2)	.
Rh. nigripennis (F.)	1♂(1)	.
Empis bicuspidata Coll.	1♂(1), 6♀♀(5)	.
E. tessellata F.*	3	.
E. nigripennis Meig.	1♂(1)	.
E. pennipes L.	1♀(1)	.
E. nigripes F.	1♂(1)	.
E. lamellicornis Beck.	1♂	.
Empididae (Empidini)*	23(6)	.
Aedes cataphylla Dyar	7♂♂(6)	.
Coboldia fuscipes (Meig.)	2♂♂(2)	.
Swammerdamella brevicornis (Meig.)	1♂(1)	.
Hymenoptera		
Bombus hortorum (L.)	3☿☿(2), 4♀♀	.
B. lucorum (L.) coll.*	5♀♀(1)	.
B. sylvarum (L.)*	4♀♀(1)	.
B. pratorum (L.)*	1♀	.
B. lapidarius (L.)*	1♀	.
B. pascuorum (Scop.)*	1♀	.
B. Latr.*	4♀♀(1)	.
Psithyrus Lep.*	2♀♀	.
Symphyta*	3	.
Lasioglossum albipes (F.)	5♀♀(5)	+
L. morio (F.)	2♀♀(2)	+
L. calceatum (Scop.)	1♀(1)	+
L. quadrinotatum (K.)	1♀(1)	+
Halictus tumulorum (L.)	1♀(1)	+
H. Latr. (s.l.)*	11♀♀(10)	.
Nomada bifida Th.**	1♀(1)	.
N. ruficornis L.**	1♂(1)	.
N. Scop.*	2(2)	.
Andrena haemorrhoa (F.)	9♂♂(9), 56♀♀(47)	+
A. fucata Sm.	2♀♀(2)	+
A. subopaca Nyl.	2♂♂(2)	.
A. helvola L.	1♀(1)	+
A. nigroaenea (K.)	1♀(1)	+
A. tibialis (K.)	1♀(1)	+
A. carantonica Pér.	1♀(1)	+
A. Latr.*	43(33)	.
Andrenidae & Halictidae*	6(2)	.

were damaged in such a way that they could not be useful in the pollination process.

Abundance of visitors

Spring weather conditions differed considerably during the period 1975–78. In 1977 and 1978 a cool period in combination with few sunny days occurred in April–May which delayed or extended the swarming of insects compared with the two previous years. Therefore males of *Andrena haemorrhoa,* normally most abundant in April–May, took part in pollination in 1977 and 1978 (Table 2). *A. helvola,* an early spring species, was recorded in 1977 only.

Bees were present only on sunny days and generally only approached flowers which were illuminated. During most of the time of anthesis in 1975 and 1977 the maximum day temperature was above 20° and the frequency of visitors was highest during these years (Table 2). In 1976 the weather was cool and unfavourable and few bees were recorded. In 1978 a very warm period occurred before and during the first 10 days of flowering. In spite of this, the number of bees was rather low.

The frequency of approaching and entering bees was highest in the middle of the day, 12–2 p.m., i.e. during the warmest part of the day (Fig. 2 A–E). The activity of halictid bees on *C. calceolus* showed a distinct peak shortly after one p.m. (Fig. 2 C) in connection with foraging on some nearby flowers of *Geranium sylvaticum* which then became exposed to the sun.

Circumstances concerning visiting and approach

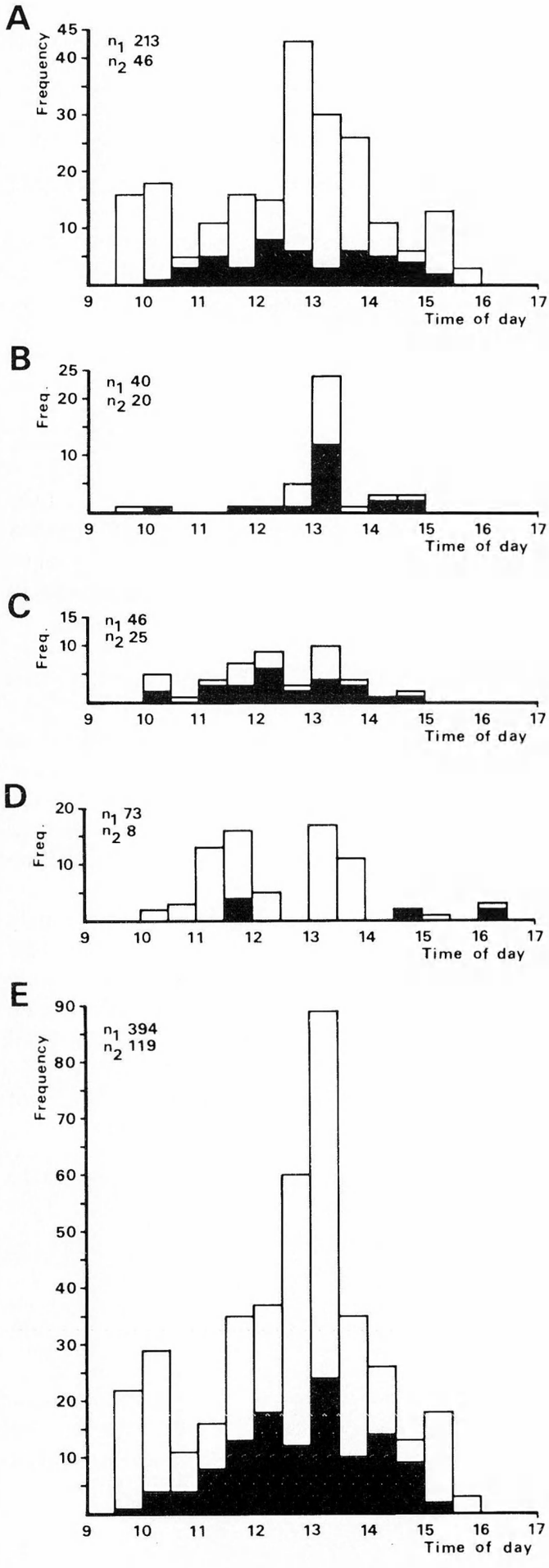
Around the stands of *C. calceolus* flight paths of bees and other insects were influenced by the topography of the surrounding vegetation. A system of regular routes and "cross-roads" existed which were frequented by flying insects and where they met and passed one another, within their habitats. Some male bees were observed to make odour marks along their routes. The small males of *Andrena subopaca* perfumed strips of the leaf-edges of *Aegopodium podagraria* and *Fraxinus excelsior,* sometimes only a few dm from flowers of *C. calceolus.* Males of *Andrena haemorrhoa* flew at a higher level, often vertically patrolling foliage and stems. Isolated inflorescences of *Cardamine*

Table 2. Maximum day temperatures during anthesis and frequency of approaches (number of insects per hour) by bees and bumblebees to the flowers of *Cypripedium calceolus* observed at Gillsätra 2 in June 1975–78. – * Maximum temperatures, measured at the Ecological Station, Ölands Skogsby. – ** *Andrena nigroaenea, A. tibialis* and *A. carantonica.*

	1975	1976	1977	1978
Day temperature during anthesis (mean)*				
5 first days	13.6°	14.7°	17.2°	26.1°
5 next days	20.9°	17.6°	22.4°	24.9°
Last days	20.4°	19.4°	22.7°	15.4°
Approaches per hour				
Bumblebees	1.0	0.7	1.3	0.7
Large *Andrena*** ♀♀	0.8	0.2	1.0	0.7
Andrena haemorrhoa ♂♂			1.1	0.5
A. haemorrhoa ♀♀	5.2	1.8	3.2	2.4
Halictidae	0.4	0.5	1.2	0.3
Nomada			0.2	0.1
Unidentified bees	0.7	1.2	1.3	0.6

bulbifera were sometimes used as landmarks. An attempt at copulation was seen only once near *C. calceolus.* On this occasion a female of *A. haemorrhoa,* after approaching one labellum, had alighted on a hazel leaf about 2 m above the flowers. After she had been basking and grooming for about 60 seconds a patrolling male pounced violently at her and the couple tumbled down to a lower leaf after which the male quickly left the scene.

Some insects visited concurrently blooming plants nearby and in that connection often became attracted by the labella of *C. calceolus* (e.g. halictid bees on *Geranium sylvaticum,* see above). The flowers of *G. sylvaticum* were also frequented by bumblebees, empidids, syrphids and butterflies which behaved in a similar manner towards *C. calceolus.* For example two females of *Rhingia campestris* (Meig.) (Syrphidae) approached 6 and 5 labella respectively after taking nectar from *G. sylvaticum.* Three bumblebees approached 5, 2 and 2 labella, etc. Females of *Andrena* were only seen on three occasions foraging near *C. calceolus,* every time on *Convallaria majalis.* Two were *A. haemorrhoa* and one a *A. nigroaenea*-type; at least one of the former and the latter were collecting pollen. These females did not approach *C. calceolus* but passed by without noticing, one of them at a distance of about 5 dm from the labella. The pollen loads from some females



captured in labella also indicated that bees mainly or at least partly foraged for pollen on distant sources and not near *C. calceolus*. Two *A. haemorrhoa* had 100% and 96% pollen of *Crataegus*-type respectively, the last also 4% *Anthriscus*. One *Lasioglossum calceatum* had 59% *Anthriscus*, 33% *Crataegus*-type, 7% *Stellaria holostea* L. and 2% Cruciferae while one *L. quadrinotatum* had 58% Liliaceae, 42% *Bellis perennis* L. and some *Geranium* pollen. One *Halictus tumulorum* had 51% Liliaceae, 38% *Ranunculus* and 9% *Bellis* pollen.

The majority of bees entering the spaces around *C. calceolus* directed their flight towards one or more labella (Fig. 3 A, 4 A). Of 118 bees (Andrenidae & Halictidae) which passed within 1 m from a group of 19 flowers 95 (80.5%) were attracted. From the point of directional change, flight paths of bees and other insects normally went straight towards a labellum. Far attraction did not show any sign of being odour influenced. However, during the final stage of approach bees sometimes performed an undulating flight and on three occasions specimens of *A. haemorrhoa* circled around flowers which indicated near-by chemical stimulation. Sometimes bees visited exactly those labella which were already occupied by one or even more bees which suggested that they were chemically stimulated by the prisoners. For example, two males and one female *A. haemorrhoa* entered labella containing one conspecific female. Once a female *Lasioglossum quadrinotatum* entered a labellum occupied by one male and a female *A. haemorrhoa*. In another case one *A. haemorrhoa* female had passed through and left the labellum but after 6 minutes the same flower was entered by a male of the nest parasite *Nomada ruficornis*.

Alighting and behaviour on the labellum

Approach to the labellum often led to alighting but the ratio was different for different bees.

Fig. 2. Dial activity of bees on the flowers of *Cypripedium calceolus* at Gillsätra, Öland 1975–78. The histograms represent the number of approaches (unfilled bars from the base line) and enterings (filled bars) observed per half-hour during the day. – A: *Andrena haemorrhoa* ♀♀. – B: Halictidae ♀♀. – C: Large *Andrena* ♀♀ (*A. nigroaenea* - *A. tibialis* - *A. carantonica*). – D: Bumblebees. – E: Andrenidae and Halictidae.

Table 3. Behaviour of bees towards flowers, mode of escape and morphology of bees visiting *Cypripedium calceolus*. The bee-groups are: 1 Bumblebees. 2 Large *Andrena* bees. 3 Medium-sized *Andrena* bees. 4 Large *Lasioglossum* bees. 5 Small halictid and andrenid bees. – * This value represents the small workers of *Bombus hortorum*. – **Measurements were made proportionally to frequency of species found within each group.

Bee-group	No. of approaches	Alightings of approaches (%)	Enterings of alightings (%)	Mode of escape (%)			Body-length Mean (mm)	Height of thorax Mean (mm)	Number of bees measured**
				By climbing	Through snail-hole	By creeping			
1	76	86	12	100	0	0	14.0*	4.2*	3
2	43	79	65	81	5	14	13.8	3.5	6
3	287	22	69	18	5	77	11.3	3.0	16
4	28	61	76	9	18	73	8.1	2.7	7
5	14	64	89	0	0	100	6.3	1.4	5

In Table 3 the approaching bees have been separated into 5 size groups. These groups also partly represent taxonomic affinities. Bumblebees (Group 1) had the highest ratio of alighting but Group 2, 4 and 5 also show high values. Surprisingly, medium sized *Andrena* bees (i.e. mainly *A. haemorrhoa*) (Group 3) alighted almost three times less often than any other group. On one occasion only did a bee (*A. haemorrhoa*, female) alight on the redbrown petals. This represents 0.5% of all alightings by bees on floral parts.

Bumblebees always landed on the lateral margins of the front opening (Table 4). It could be established that at least 7 individuals searched for food on the flowers i.e. probed around the staminode or on other parts of the labellum. For example, the large queens of *Bombus hortorum* sat across the entrance probing with their long proboscis downwards and under the stigma. Each individual bumblebee alighted on up to six subsequent labella but normally only on one or two before leaving ($\bar{x} = 2.6$, $n = 25$).

Large *Andrena* bees (*A. nigroaenea – A. tibialis – A. carantonica*) (Group 2) landed on the margins and occasionally on the staminode. On several occasions, when entering did not occur, they probed the staminode with their mouthparts.

Medium sized *Andrena* bees (*A. haemorrhoa – A. fucata – A. helvola*) alighted on the margins but frequently flew also directly into the central opening near the staminode which they tried to reach with their stretched-out legs as if trying to get a foothold. Sometimes they managed to alight on the staminode and it was obvious that the majority of bees tried to reach this part of the flower before they fell to the bottom. Four specimens of *A. haemorrhoa* crept about on the lateral margins for several seconds as if they were seeking. No feeding reactions were seen but might have occurred as the mouthparts of this group are short and difficult to observe.

Larger *Lasioglossum* species (*L. albipes – L. calceatum – L. quadrinotatum*) (Group 4) and the smallest bees (*Lasioglossum morio – Halictus tumulorum – Andrena subopaca*) (Group 5) frequently "alighted" directly into the entrance. On several occasions when bees landed on the lateral margins they stretched themselves out over the front opening in the direction of the staminode.

Some of the dipterous visitors were obviously trying to feed on the flowers. Thus a *Volucella bombylans* (Syrphidae) probed the staminode for several seconds. Empidids were often seen investigating various parts of the labellum and the column with their mouthparts.

Bees sometimes landed on vegetative parts of

Table 4. Place of alighting and behaviour of bees on the labellum of *Cypripedium calceolus*. The numbers refer to clear cases only. Bee-groups as in Table 3.

Bee-group	Number of bees observed to			
	land into the entrance	land on the lateral margins	probe the staminode	crawl into labellum
1	.	20	7	4
2	3	19	4	7
3	28	26	.	1
4	6	11	.	3
5	4	2	.	.

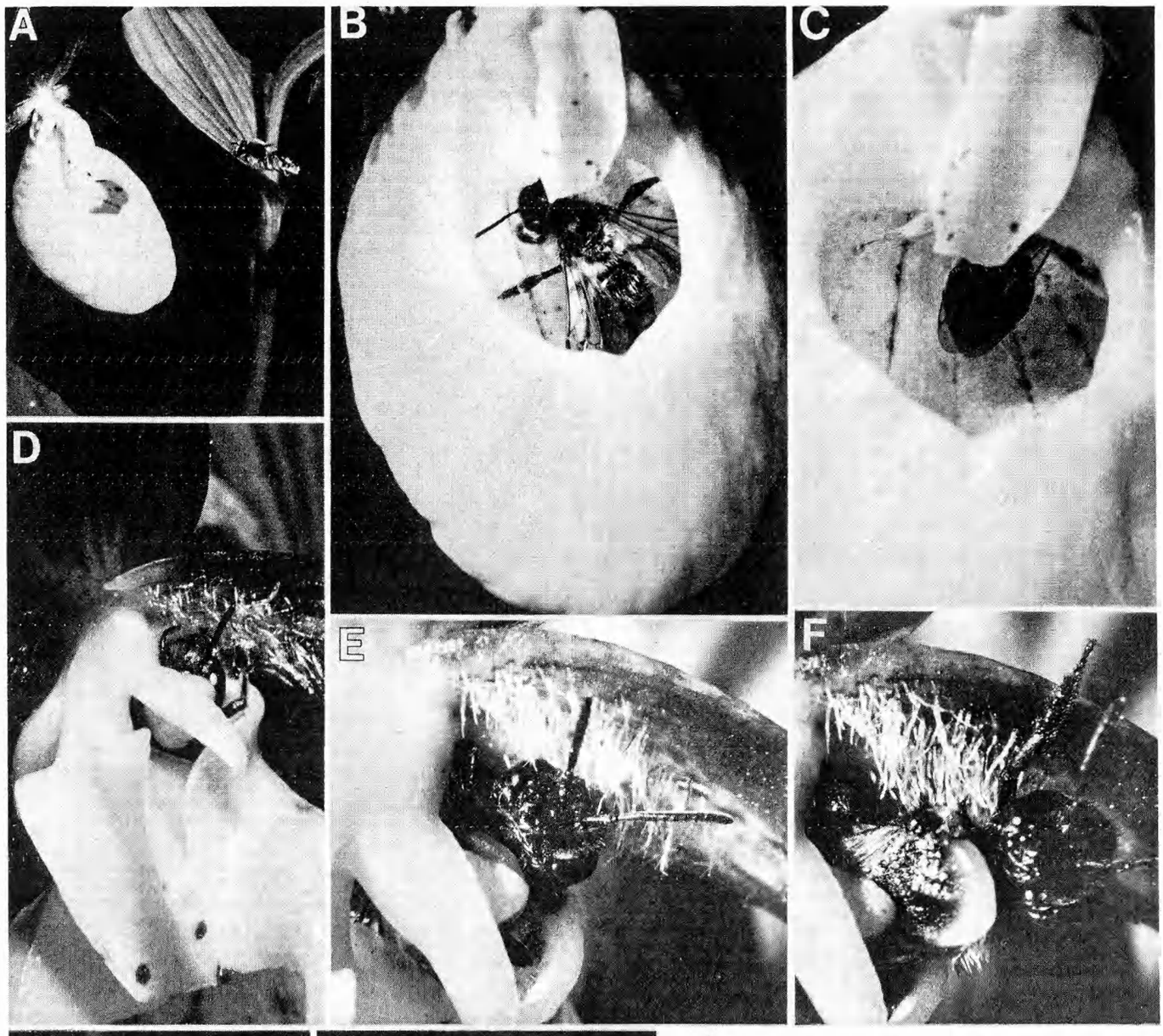


Fig. 3. The visiting of *Cypripedium calceolus* by bees. All photos are taken under natural conditions in the field. – A: *Andrena haemorrhoa* ♀ approaching labellum. – B: *A. carantonica* ♀ shortly after entering, restlessly walking around with her wings still spread. – C: *A. haemorrhoa* ♀ in the beginning of prizing under the stigma. Note the resting position of wings, the angle of abdomen and the spread hind legs to get foot-spurn. – D: Do., with her head under the anther. – E: Do., with thorax under the anther. Note also the position of her body in relation to the stigma which is visible down to the left. – F: Do., some seconds later. The pollen smear has been accumulated and deposited on her thorax. – G: Do. female reaching freedom, climbing the right petal. – H: Exhausted after passing the mechanism, worn and wet (rainwater bath in labellum!) *A. haemorrhoa* ♀ with a beautiful deposition of pollen smear dangles on the edge of leaf unable to synchronize her movements.

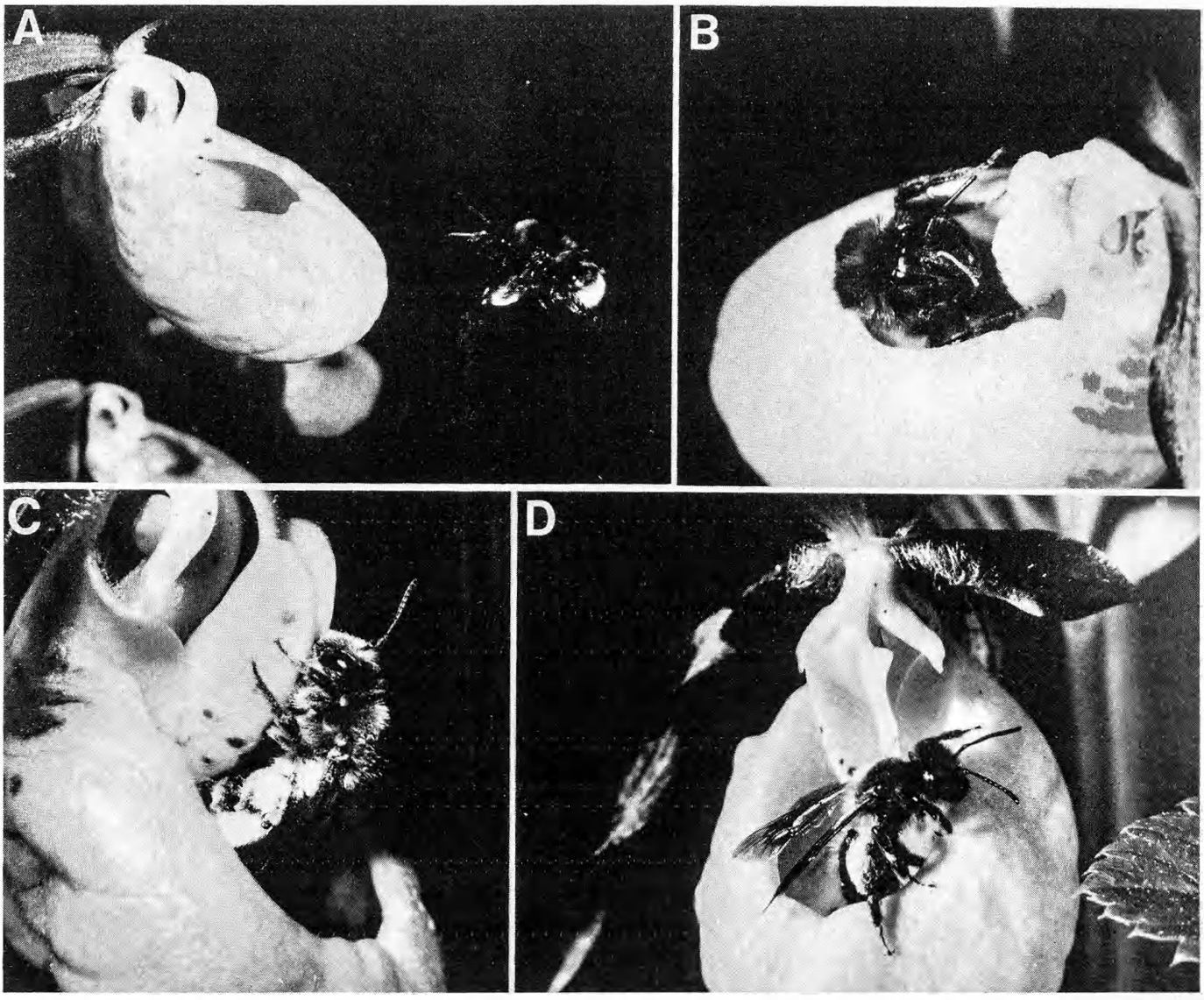


Fig. 4. The visiting of *Cypripedium calceolus* by bees which escape the wrong way. All photos are taken under natural conditions in the field. – A: Worker of *Bombus hortorum* approaching the labellum. – B: The same specimen climbing the staminode after a short inspection of the inside. In the face between the antennae a pollinarium of *Orchis mascula* L. is visible. – C: *Andrena haemorrhoa* ♀ leaving by climbing the staminode. Note that the labellum of this flower is a little malformed (see down to the left) which was enough to lose a potential pollinator. – D: *A. carantonica* ♀ lifting herself out of the labellum by the claws on the margins.

C. calceolus without a preceding approach of the flowers, apparently to bask and groom only. *A. haemorrhoa* landed on leaves (7 occasions) and on pedicels (3 occasions). From these and similar observations made during the 4 years the impression is that these parts of the plant may also have some mysterious attraction to bees. Once a female became attracted by a withered bud and inspected it repeatedly.

Entering into the labellum

The smaller the size of alighting bees, the higher the ratio of entering the labellum (Table 3). Large bumblebee queens often tried to squeeze themselves through the front opening but they seldom entered. However, queens of smaller species and workers e.g. of *Bombus hortorum* (Fig. 4 B) sometimes went down for a short inspection of the inside. Entering by bumblebees was a process with little or no element of involuntariness such as sliding, etc., but was an act performed largely under control.

Large *Andrena* bees often "crawled" into the labellum as if they wanted to explore something interesting on the bottom (7 observations). Individuals stretching themselves out in the air above the front opening towards the staminode

often tumbled down when they had too few claws left on the margins to maintain an efficient grip. They seldom entered by flying right into the entrance. Thus, during entering by this bee-group there was often a moment when the visitor lost control over the events.

Compared with the previous group medium sized *Andrena* bees usually entered more directly without crawling or clinging to the lateral margins of the entrance (Table 4). When the latter behaviour occurred they frequently lost their balance and grip and fell on their heads. Only once was a female seen to crawl down into the labellum.

Smaller bees (Groups 4 and 5) entered in a similar way to the previous group. However, several females of *Lasioglossum albipes* and *L. calceatum* crawled into the labellum as if interested in the bottom.

Captivity and escape

The behaviour of insects inside the labellum varied. Smaller flies crept about in an unconcerned manner. Bees, however, more or less immediately tried to return through the entrance, stretching out to their full length towards the lateral margins while crawling with their front legs to gain a hold. Bumblebees and many of the large *Andrena* bees managed to get a foothold with their claws on the margins and/or on the staminode and could easily lift themselves out (Fig. 4 B, D). Normally, this took place already within a few seconds after entering (Table 5). The regular climbers often visited more than one flower (Table 6) and did not seem to be frightened by their experiences. However, a drastic difference was noted in the percentage of climbing between the large and the medium sized *Andrena* bees (Groups 2 and 3) although the difference in body-length was only 2.5 mm (Table 3). Occasionally smaller bees such as *A. haemorrhoa* succeeded in escaping by climbing the staminode (Fig. 4 C). Still smaller bees were seldom (Group 4) or never (Group 5) observed to use this method. The chances of climbing obviously decreased with decreasing body-length. As the depth of the labellum was approximately 15.5 mm (n = 28) the bees must be about 3–4 mm shorter to become imprisoned frequently. Only once was a bee seen to leave through the entrance by a combined action of its wings and a

Table 5. Time spent by bees in the labellum of *Cypripedium calceolus* for their two ways of escape. Bee-groups as in Table 3.

	Time spent in labellum														
	Seconds		Minutes												
	10	30	1	2	3	4	5	6	7	8	9	10	15	20	x̄
Creeping out (passing anther)															
Andrena tibialis ♀ (Gr 2)	.	.	.	.	1	.	.	.	.	.	.	.	.	.	3.43
A. nigroaenea-type ♀♀ (Gr 2)	.	.	.	.	.	.	1	1	.	.	.	.	.	.	
A. haemorrhoa ♀♀ (Gr 3)	2	.	.	.	1	4	.	1	2	3	1	.	.	1	3	11.13
A. haemorrhoa ♂♂ (Gr 3)	.	.	.	.	.	.	.	.	1	.	1	.	.	.	1	
A. helvola ♀ (Gr 3)	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	
A. spp. ♂♂, ♀♀ (Gr 3)	.	.	.	.	.	.	1	2	.	1	.	.	2	.	.	
Lasioglossum albipes ♀♀ (Gr 4)	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	2.56
L. spp. ♀♀ (Gr 4)	.	.	.	.	2	1	1	.	.	.	.	.	.	.	.	
L. morio ♀ (Gr 5)	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1.28
L. spp. + *Halictus* sp. ♀♀ (Gr 5)	.	.	2	1	1	1	.	.	.	.	.	.	.	.	.	
Climbing (entrance escape)															
Bombus spp. ☿☿, ♀♀ (Gr 1)	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Andrena nigroaenea-type ♀♀ (Gr 2)	11	3	1	1	.	.	.	.	.	.	.	.	1	.	.	
A. haemorrhoa ♀♀ (Gr 3)	.	3	.	.	2	.	.	.	.	.	.	.	.	.	.	
A. fucata ♀ (Gr 3)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	
A. spp. (Gr 3)	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	
Lasioglossum sp. ♀ (Gr 4)	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	

Table 6. Individual behaviour of bees visiting labella of *Cypripedium calceolus* more than once on the same occasion. The time spent in labellum is given in minutes and seconds within parenthesis. Flights between flowers are indicated by arrows. – Abbreviations; Ap approach, Al alighting, Cr creeping and Cl climbing. – * Captured after entering. – ** Falls to the ground, exhausted.

Observation No.	Species	Behaviour
Creeping through two successive labella		
75:232	*Andrena haemorrhoa* ♀	Ap-Al-E-Cr(00.05)→Ap-Al-E-Cr or Cl (>43.00)
77:97	*Lasioglossum quadrinotatum* ♀	Ap-Al-E-Cr→Ap→Ap-Al-E*
77:100	*Andrena haemorrhoa* ♂	Ap-Al → Ap-Al-E-Cr(04.45)→Ap→Ap→Ap-Al-E-Cr(11.48)**
77:138	*Lasioglossum morio*-type ♀	Ap-Al-E-Cr(00.44)→Ap-Al-E-Cr(03.50)
Climbing out of the first, creeping through the second		
75:178	*Andrena nigroaenea*-type ♀	Ap-Al-E-Cl(00.05)→Ap-Al-E-Cr(05.00)
76:43	*Lasioglossum albipes* ♀	Ap-Al-E-Cl(snail-hole)→Ap-Al-E-Cr(03.40)
77:86	*Andrena nigroaenea*-type ♀	Ap-Al-E-Cl(01.10)→Ap-Al-E-Cr(04.10)
Climbing out of two or three labella		
75:153	*Bombus hortorum* ☿	Ap-Al-E-Cl→Ap-Al-E-Cl
76:4	*B. sylvarum* ♀	Ap-Al-E-Cl→Ap-Al-E-Cl
77:24	*Andrena nigroaenea*-type ♀	Ap-Al-E-Cl(00.05)→Ap-Al-E-Cl(00.10)
77:145	*Bombus hortorum* ☿	Ap-Al→Ap-Al→Ap-Al→Ap-Al→Ap-Al→Ap-Al-E-Cl→Ap-Al-E-Cl
78:30	*Andrena tibialis*-type ♀	Ap-Al-E-Cl(snail-hole)→Ap-Al-E-Cl(≈00.03)→Ap-Al-E-Cl(≈00.03)
78:38	*A. nigroaenea*-type ♀	Ap-Al-E-Cl(≈00.03)→Ap→Ap-Al-E-Cl(≈00.03)

sudden jump. On the contrary smaller flies, e.g. *Thricops semicinerea* and empidids flew in and out of the labellum more or less freely. The extra holes in the labella made by snails and slugs were of course immediately used by bees as ways of escape thus giving rise to a clear loss of potential pollen vectors (Table 3).

With the exception of bumblebees no bees were seen to probe the bottom or any other part of the inside for food. However it was almost impossible to observe the mouthparts of bees immediately after entering so feeding reactions might often as well have occurred.

Bees that failed to climb out were very "upset" and ran around on the bottom making rushes against the entrance. This state, characterized by violent, unrestrained behaviour, was often accompanied by an irritated wing-buzzing or interrupted by intense grooming. The wings were not held in a resting position (Fig. 3 B). After c. 1–2 minutes, however, a clear change occurred in the mood of the bees (typical cases) which caused them to "cool down" and to put their wings to rest. Meanwhile, for some reason, their attention became mainly directed towards the upper part of the labellum beyond the stigma. They began to prize methodically with the thorax under the stigma which was indicated by the body being bent at an angle and the bee striving to push itself forwards by foot-spurn (Fig. 3 C). Their rhythmic prizing soon caused the whole labellum to move and to become bent downwards like with an elastic (but indeed stiff) hinge at the very base which gradually, as they forced forwards, enlarged the distance between the stigma and the bottom. Thus, the large, convex and somewhat depressed stigma which came to clasp the thorax dorsally was not only an obstacle; it also supplied necessary support for bees to make a way out for themselves. The dorsal hair clothing of the thorax became flattened down anteriorly during these efforts showing that the height of the thorax made the greatest resistance and that the upper part of the stigma became placed between head and thorax as a temporary barrier. Normally, repeated failure to press the body past the stigma was made with short retreats in between. Observations and close-up photography revealed that the thorax was forced to pass under one of the two upper curvings of the stigma (Fig. 5). The nearest light window perhaps induces phototaxis towards that side, past the stigma. As the bees penetrated higher up and out (Fig. 3 D), the

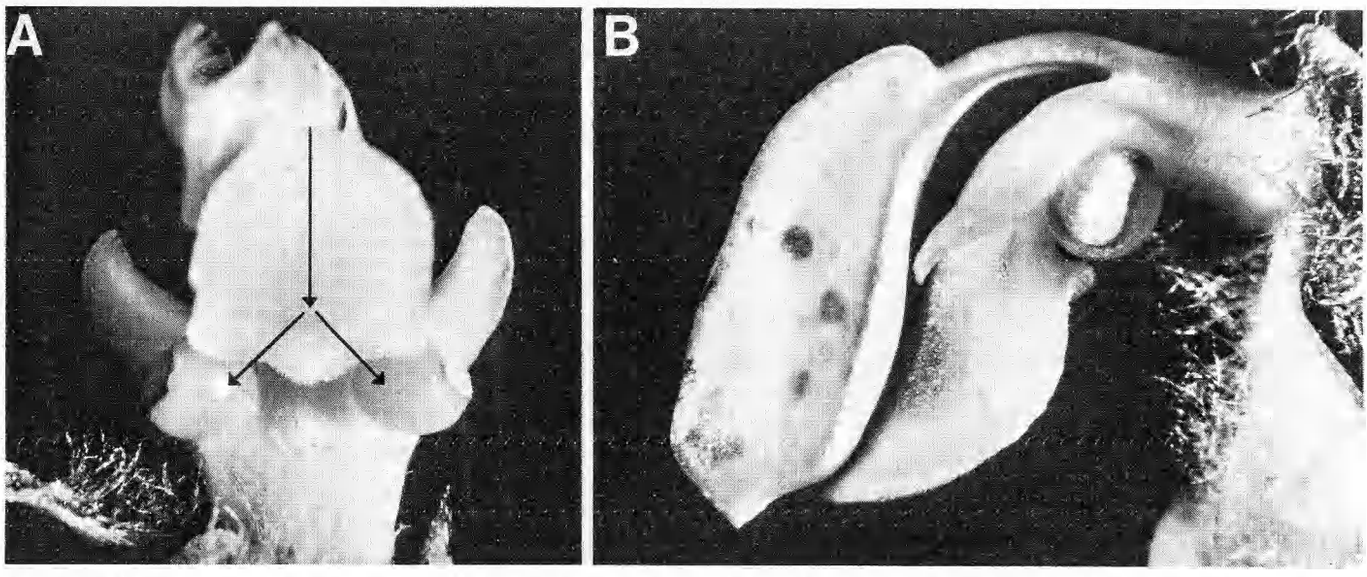


Fig. 5. Close view of the column of *Cypripedium calceolus* (5×). The paths taken by pollinators are indicated by arrows. – A: "Bee's view" of the column. Note the two small curvings in the posterior margin of the stigma. – B: Lateral view.

second obstacle, the anther, narrowed the passage (Fig. 3 E). In this position bees often drew their heads back several times into the labellum due to the narrowness of the passage. However, as their thorax had come underneath the anther the bees had advanced so far that they practically never tended to back. When the thorax had finally squeezed past the anther a portion of the pollen smear was scraped off and accumulated like a pad on the anterior dorsal part of the mesonotum (Fig. 3 F). Meanwhile the claws behind the hind margins made it possible for bees to draw themselves out and climb a lateral petal rather quickly (Fig. 3 G).

A deviation from the normal course of events mentioned above often occurred. If bees failed to pass the stigma for a longer time they made now and then new attempts to get out via the entrance. Once a female of *A. haemorrhoa* had reached beyond the anther with her head but then backed all the way down past the stigma. In another case a female of *A. fucata* backed several times in a similar way. After 65 minutes she managed to climb the staminode but an examination showed that there was no pollen smear on her thorax, only that the dorsal hairs had been adpressed.

The time spent in the labellum by creeping bees varied from a few seconds up to days but normally it did not take more than 10 minutes (Table 5). The large, robust *Andrena* bees (Group 2) passed relatively quickly (only 3 observations). Between bee-groups 3–5 the time was obviously correlated to the height of the thorax. Small halictid bees passed without obvious prizing and consequently several times faster than the medium sized *Andrena* bees but on the other hand they removed much less pollen, if any at all (Fig. 6 C). These bees eventually got the smear on top of their thorax. In larger bees the deposition of the smear became larger and more and more accumulated anteriorly on the sloping part of the mesonotum (cf. Fig. 6 A–D). In the bee-groups 3–4 the hairs on the thorax became glued to the body by the viscid smear (Fig. 3 F, 6 A).

The age of the flower also influenced the duration of imprisonment of the bees, e.g. bees of Group 3 passed through 9–12 day old flowers 5 times quicker than through flowers 4–5 day old ($\bar{t} = 2.43$ minutes ($n = 6$) and $\bar{t} = 13.12$ ($n = 8$) respectively). During early anthesis the basal connecting part of the labellum was stiff but later on it became slacker so that the labellum became easier to bend down. Towards the end of anthesis the labellum tended to droop. Consequently, the mechanism was maximally hard to pass during the first days of flowering which resulted in efficient early removal of the pollen smear by creeping bees.

Another factor affecting the time of escape was the physical condition of the bees. Creeping sometimes reduced their strength so much that they were unable to fly afterwards (see below).

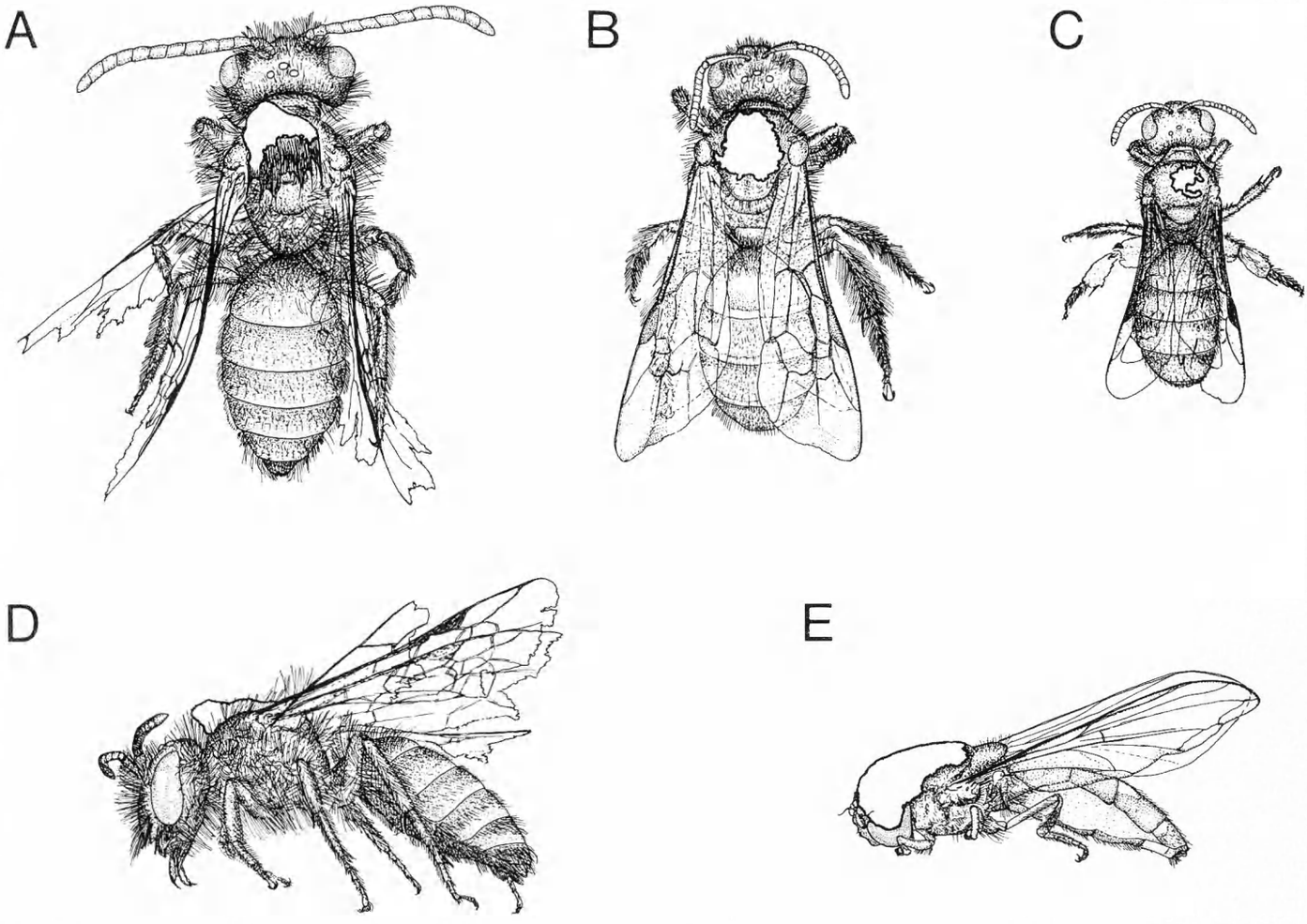


Fig. 6. Deposition of pollen smear on different insects visiting the flowers of *Cypripedium calceolus*. Drawings of authentic specimens (5×). – A: *Andrena haemorrhoa* ♂, with smear accumulated on the anterior part of mesonotum. – B: *Lasioglossum albipes* ♀, with smear dorsally on mesonotum. – C: *Lasioglossum morio* ♀, with a little smear on top of thorax. – D: *A. haemorrhoa* ♂. – E: *Melanostoma scalare* ♀, removed from anther to which it was deadly glued.

Two bees which passed through two successive labella needed 7 and 3 minutes longer to creep out of the second (Table 6, No. 77:100, 77:138).

The time of day and the weather conditions were also important. Bees which entered late in the afternoon or in cool weather often became inactive and sometimes stayed until the next day or longer in labellum.

In no case was it witnessed that visitors escaped by gnawing themselves through the wall. However, a hole in the "window" of one labellum made from the inside by some chewing insect (bee?) indicated that some visitors, though rarely, practised this method.

Bees very seldom died in the labellum. On only one occasion a small bee, *Andrena subopaca* male, was found dead. On the other hand, females of *Melanostoma scalare* which tried to escape through the exits were too weak and became trapped by the sticky smear and perished (Fig. 6 E). Then their dead bodies blocked the exits for potential pollen vectors. At Gillsätra 2 in 1977 7% of the flowers were "plugged" in this way. Also male mosquitoes died in the labella (*Aedes cataphylla*, 5 observations). *Meligethes aeneus* was once found glued to death on to an anther.

Bees of the genera *Andrena, Lasioglossum* and *Halictus* were the only insects observed to leave the flowers with pollen smear (Table 1). A large proportion of the smaller species passed the floral reproductive organs properly (Table 3). For various reasons it could not be established whether *Nomada* bees and the small *Andrena subopaca* were able to pass the mechanism and remove pollen. Their habitus suggests, however, that they might act as pollen vectors as well.

After creeping, the bees normally sat on the

petals or flew to the leaves of surrounding vegetation for grooming after which they left the place. In contrast, some individuals of *A. haemorrhoa* were dead-tired and crawled about, dangling on the edges of leaves etc. e.g. No. 76:62 (Fig. 3 H), a worn specimen which also got a bath in remaining rainwater after she had entered. Another time a male fell to the ground unable to fly after passing through two flowers. In 9.5% of the cases immediately after creeping the bees entered and crept out of a second labellum (Table 6). Climbing out of the first labellum and creeping through the second was observed twice. One *Lasioglossum albipes* first escaped via a snail-hole and thereafter passed through the mechanism of the next flower. More frequently bumblebees and large *Andrena* bees climbed out of two or more flowers (Table 6).

Pollination

As a few bees backed after reaching the anther, transfer of pollen within the same flower was not excluded. According to the low frequency of such behaviour, however, self-pollination must be rare. It could not be proved that such a transfer ever took place.

Pollination occurred when a bee with a pollen smear on its thorax forced itself against the stigma (Fig. 3 C). Obviously the pollen smear became "worked on to" the surface of the upper part of the stigma during the prizing by the vector. As the smallest bees (Group 5) easily passed the stigma without obvious prizing they were probably of little or no importance as pollinators.

As we have seen c. 9.5% of the bees could directly act as pollinators as they immediately entered a new labellum. The rest left the place for other activities within their territories. If we use the field data on the series of events (Table 3) and assume that all of these bees later returned and approached the labella we can estimate how many approaches by each bee-group were (theoretically) needed to produce pollination. Accordingly, the bee-groups 2, 3, 4 and 5 had to make 200, 71, 9 and 3 approaches respectively, to produce one single pollination each. During the four years, large *Andrena* bees (Group 2) were only seen to make 43 approaches which indicates that they very seldom, if ever acted as pollinators. Evidently bee-groups 3 and 4 were responsible for the majority of pollinations.

The pollination system

If the percentage of "right events" (Fig. 7), behaviour of bees and morphological interactions are compared, the effectiveness of the flowers with different bee-groups can be taken into consideration. Regarding anther and stigma contact the flowers are best adapted to medium sized *Andrena* bees (Group 3). On the other hand a mysterious bottleneck existed between approach and alighting with this group. Somewhat unexpectedly, alighting and entering functioned best with the extreme groups 1 and 5 respectively.

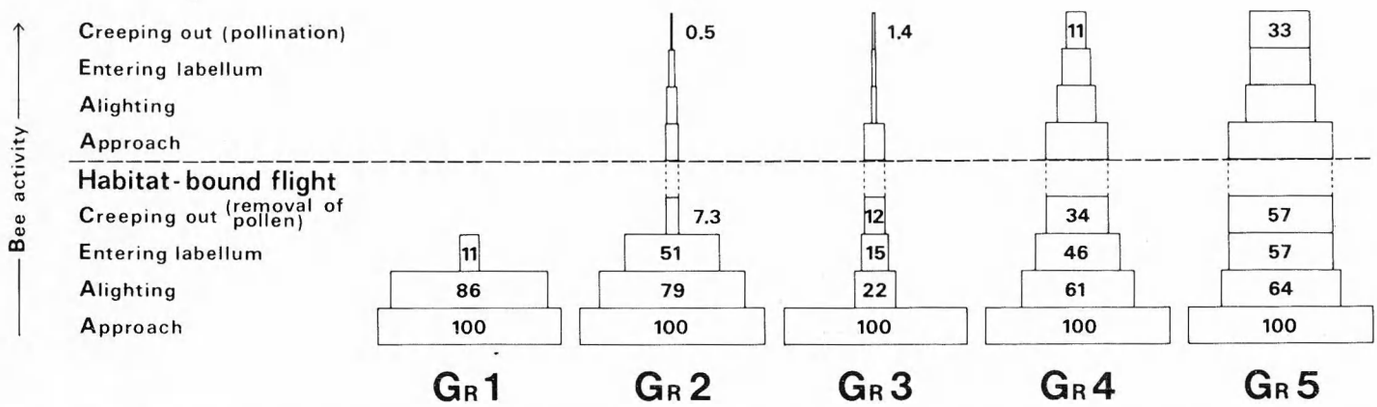


Fig. 7. Model of the pollination system of *Cypripedium calceolus* on Öland in relation to functional groups of bees. Each step ("right event") is based on field data given in percent of a common denominator (100 approaches). For the groups 2–5 the upper pyramides have been calculated with the optimistic assumption that all bees creeping out of the first labellum later approach a second. Bee groups as in Table 3. Note that the system of these isolated plant populations is extremely dependent on regular habits ("revisiting situations") of bees as the losses before a successful pollination are considerable.

As all plant populations studied were small and isolated a self-evident critical point existed in the pollination system i.e. a strong dependence on a local bee-fauna with regular habits. The data indicate that any loss of bees which carried pollen smear during the habitat-bound flight could be extremely serious for the plant due to the great chances for the bees to avoid the mechanism of the flowers in various ways (Fig. 7). This is also underlined by Daumann's (1968) observations that only 2 of 17 alighting bees had pollen smear.

Fruit set

Regular fruit set occurred only at Gillsätra 2 and Långlöt (Table 7). The populations producing only a few flowers each year were practically devoid of sexual reproduction. At Gillsätra 2 the highest relative fruit set was in 1976 (almost 20%) which is somewhat surprising as in both 1975 and 1977 the frequencies of visiting bees were higher (cf. Table 2).

Discussion

The visitor fauna on Öland shows great similarities to those found by others further south in Europe (Table 8). The pollination by *Andrena* males, the frequent visiting by halictid bees and the records of *Nomada* spp. are important differences. Bumblebees, by Daumann (1968) noted only to make approaches, often visited the flowers. Under normal conditions males of *A. haemorrhoa* seldom face the flowers as anthesis occurs during the final part of their flight-period April–beginning of June. Females of this species occur from May until July i.e. they have a somewhat later flight period and probably a greater longevity. The anthesis, in the first half of June, seems to coincide rather well with an intense nest constructing and foraging period in this *Andrena* species and also with the flowering of important pollen plants for this bee on Öland such as *Crataegus, Anthriscus* and *Convallaria*. Pollen of Rosaceae forms a prominent constituent in its brood-food (Alfken

Table 7. Fruit set of *Cypripedium calceolus* on Öland.

Locality	Year	No. of flowers	No. of fruits	Fruit set (%)
Halltorp	1975	9	1	11
	1976	3	0	0
	1977	3	0	0
	1978	5	0	0
Gillsätra 1	1975	7	0	0
	1976	4	0	0
	1977	4	0	0
	1978	3	0	0
Gillsätra 2	1975	49	6	12
	1976	46	9	20
	1977	83	15	18
	1978	63	6	10
Långlöt	1976	29	2	7
	1977	43	5	12
	1978	4	1	25

Table 8. Previously recorded insects visiting *Cypripedium calceolus* in Europe. – * D Germany, CS Czechoslovakia, GB Great Britain.

Species	Country*	Observer
Hymenoptera		
Andrena tibialis (K.) (*A. atriceps* (K.)) ♀	D, CS	Müller 1868, Daumann 1968
A. nigroaenea (K.) ♀	D, CS	Müller 1873, Daumann 1968
A. flavipes Pz. (*A. fulvicrus* (K.)) ♀	D, CS	Müller 1868, Daumann 1968
A. vaga Pz. (*A. pratensis* Nyl.) ♀	D	Müller 1869
A. haemorrhoa (F.) (*A. albicans* (K.)) ♀	D	Müller 1873
A. minutula (K.) (*A. parvula* (K.)) ♀	D	Müller 1869
A. bicolor F. ♀	CS	Daumann 1968
A. gravida Imh. ♀	CS	Daumann 1968
A. hattorfiana (F.) ♀	CS	Daumann 1968
Halictus sp. ♀	CS	Daumann 1968
Diptera		
Tubifera sp.	CS	Daumann 1968
Syrphus sp.	CS	Daumann 1968
Syritta pipiens (L.)	GB	Webster 1886
Cheilosia sp.	D	Müller 1873
Thricops semicinerea (Wied.)	D	Müller 1873
Anthomyia sp.	D	Müller 1873
Empis punctata F.	D	Müller 1873
E. sp.	CS	Daumann 1968
Coleoptera		
Meligethes sp.	D, CS	Müller 1868, Daumann 1968
Cetonia sp.	D	Füller 1955
Araneida		
Misumena vatia (Cl.)	D	Arzt 1954

1913, Chambers 1946, Anasiewicz & Warakowska 1971).

The frequency of visiting bees at different times of the day seems similar to the dial activity of solitary bees in general (cf. Käpylä 1974). Obviously, weather conditions and the presence of food-plants nearby influence visiting and consequently the pollination. For the individual flower, the possibility of direct sunlight is probably a factor of great importance.

Observations made here fully support Daumann's results (1968) that bees become optically far attracted by the yellow labellum. The bee-visited concurrently blooming plants give no reason to believe that the orientational response on the labellum is an expression of colour based constancy towards an expected food-plant i.e. that the flowers act by colour resemblance. The other possibility is that reflected light from the labellum releases a spontaneous reaction due to an inborne sensitivity to this particular colour quality. The bees must also be in the mood for being attracted by such cues. Scouting honeybees fly spontaneously towards yellow (Oettingen-Spielberg 1949) and so do *Eristalis* (Ilse 1949) and *Meligethes* (Nolte 1959). The very strong far attraction of passing bees to the labella (80.5%) also suggests that a similar spontaneous reaction may be involved especially in halictid bees whose constancy on *Geranium* was often broken by *C. calceolus*. According to Caron (1972) many solitary bees are attracted to artificial yellow-coloured traps.

Observations indicated that the patterns of crimson spots on the staminode and on the veins in the bottom are false nectar guides. Such contrasting "Tüpfenmale" and "Strichmale" are known to stimulate visiting and probing reactions (Kugler 1970). Thus, the deceptive spots evidently stimulate the pollinators to alight at near-by flight and, if entering does not instantly occur, to advance towards the staminode or to crawl down to the bottom. During the whole process floral fragrance is present but is not at all, as indicated by GC, produced by the conspicuous staminode, which apparently is only an optically–mechanically functioning device. Accordingly any guidance by scent after alighting is unlikely. The function of the fragrance is probably to lower the threshold for optically oriented reactions such as alighting and/or searching for food on the deceptive nectar guides. The composition of the fragrance makes it unlikely that *C. calceolus* should imitate the odour of one or more of the concurrently blooming bee-plants even if they may have some components in common. For example, linalool and phenethyl acetate are present in the floral fragrance of *Convallaria* (Mack & Köpsel 1973). Many flower scents with linalool as a small or large constituent stimulate visiting by honeybees (Frisch 1920). Thus, at least the presence of linalool might deceive bees.

According to literature and a number of other fragrance analyses (Nilsson unpubl.), the presence and domination of the series of acetates are very rare. Reasonably, these compounds should rather "appeal" to some other behaviour pattern in bees than to the acquired behaviour towards food sources. Tengö & Bergström (1977) found that acetates are present in the cephalic pheromone secretions in at least two of the *Cypripedium*-visiting *Andrena* species (both sexes). *A. haemorrhoa* has decyl, dodecyl and tetradecyl acetate as constituents while *A. nigroaenea* has octyl acetate. Thus, these two pollinators have *the same* substances in their pheromone secretions as those present in the floral fragrance of *C. calceolus*. The cephalic secretions are used by *Andrena* males to odour-mark objects (leaves etc.) in their habitat which attract the females and probably also attract and aggregate the males themselves (Tengö & Bergström 1977). The secretions, which are species-specific, also give these bees their characteristic body-perfume. Bergström & Tengö (1974) have also analysed the volatile part of the secretion from the abdominal Dufour gland in *Andrena* females and found farnesene to be a constituent in 4 of the *Cypripedium*-visiting species i.e. *A. haemorrhoa, A. nigroaenea, A. helvola* and *A. bicolor* (one of the farnesenes is α-farnesene, Tengö pers. comm.). According to the same authors the Dufour secretion in solitary bees has obviously a dual function i.e. to serve as a lining material in the nest and – in its volatile part – as a signal on the nest-site. Butler (1965) has shown that the soil by the nest entrances of *Andrena flavipes* is scented by the females and that this odour stimulates both sexes to alight on the ground by the nest-site. Thus, on the basis of odour correspondence, there exist some indications that *C. calceolus* might interfere with pheromone controlled behaviour patterns in

some of its pollinators. Inborn alighting reactions might perhaps be released during a near-by flight over its labellum. Bees visiting already occupied flowers suggest that the addition of bee-perfumes to the labella enhances the deceptive ability. In *Cypripedium californicum* Gray, pollinators of the genus *Ceratina* rest on the labellum and drive away approaching insects which suggests that some active compound in the floral fragrance elicits bees' actions (Kipping 1971).

From the laborious work of bees in the labella it is very probable that some of their often strong body-perfume is adsorbed by touched structures, especially on the hairs which are longest and most dense under the stigma where the pollinators spend most of their time. The fatty secretion on the trichomes may also retain pheromones from the visiting bees. The trichomes are very soft and about as high as the thorax of the pollinators (2–3 mm) (Fig. 5) which means that the clothing of bees becomes efficiently rubbed during their exertion. That these hairs would function solely as a foothold (Summerhayes 1951, Proctor & Yeo 1973) seems very unlikely. According to Ziegenspeck (1936), their cellular construction speaks in favour of easy flexibility and deformation capacity. Their strong light-refractive ability might also possibly stimulate phototactic behaviour of bees under the stigma in addition to the light windows. They may also lower friction against the bottom for creeping visitors. That the hairs would force bees to press against the stigma (Ziegenspeck 1936) or to "einem gewissermassen hochbeinigen Schreiten" (Füller 1955) is not supported – stigmatic contact is effected by the stiff but elastic basal hinge of the labellum. If the trichomes are "contrivances" for adsorbing bee perfumes and thereby enlarging the deceptive capacity of the flower is a matter requiring further investigation.

The comparatively low alighting frequency by medium sized *Andrena* bees (practically *A. haemorrhoa*) is a riddle. The observations indicate that at least bee-groups 1, 2, 4, and 5 were in a foraging mood when they became attracted to *C. calceolus* viz. they came directly from *G. sylvaticum,* often probed for food etc. However, bees of Group 3 obviously had their regular food-plants elsewhere, and in most cases did not seem to be in that mood, but rather on the way to or from their nests, in mate searching flight etc. The males of *A. haemorrhoa* were definitely in a mating flight mood. Since far attraction of all groups functioned well and flower scents are known to be of great importance for alighting reactions in bees (Kugler 1970), it seems as if the fragrance had a special meaning for Group 3. The fragrance might interfere with odour-controlled behaviour patterns in these bees and release spontaneous (inborne) alighting reactions. The multi-component fragrance might operate differently among species, individuals or even in the same individual bee on different occasions. Bees perhaps "associate" some of the compounds with food (e.g. linalool), their nests (e.g. α-farnesene) or with scent-marks in their habitat (e.g. acetates). Evolution of fragrance compounds in a plant in direction to such a broad attraction system is quite probable – if the reason for the pollinators' visits becomes totally unimportant due to flower morphology. The latter is exactly what happens the moment suitable bees enter the labellum of *C. calceolus* – they face a fixed pollination route.

The very large, expanded stigma is not only an adaptation for pollination by temporarily imprisoned bees, it is also the key to their freedom. As the pollen is worked on to its surface, no sticky exudate is necessary. That the smear normally becomes deposited on the anterior sloping part of the thorax, where it is protected in the crevice between the head and thorax, is perhaps an adaptation for protection against the loss of pollen when the females work in their nest burrows.

From the one-way-traffic and the spacing between stigma and anthers, Faegri & Pijl (1971) considered the flowers to have a functional protogyny. The stiffness of newly opened flowers perhaps also points to a functional male phase. Macior (1974) suggested that bees visiting *Cypripedium acaule* Ait. frequently caused self-pollination by backing from the anther. In *C. calceolus* this is obviously a rare phenomenon. That bees sometimes chew their way out through the wall is known from *C. reginae* Walt. (Guignard 1886) and *C. acaule* (Stoutamire 1971).

The change of mood in bees which have entered, and which makes them begin to prize under the stigma, is one of the most important events for the function of the pollination system. According to Knoll (1922), the grooming of

insects in the labellum is induced by the oil which becomes adhered to their tarsi. Consequently there is a possibility that the fatty secretion on the hairs gradually greases the bees' antennae and thereby, temporarily, inactivates the olfactory receptors. A minimization of all chemical stimulation should slow down the bees and contribute to a change in mood.

The difficulty in escaping as experienced by the bees has been supposed to keep bees from revisiting the labella (Webster 1886, Baxter 1889). Repeated visits by *Ceratina* bees to *C. californicum* suggest that bees do not mind the effort of passing the mechanism (Kipping 1971). In *C. acaule* pollination is thought to be dependent on "a few chance encounters with naive *Bombus* queens" which "seem to learn to avoid the flowers" (Stoutamire 1971). If floral allurement in *C. calceolus* is adapted to exploit inborn reactions in bees, such effects are not to be expected. In fact cross-pollination is based upon a minimized learning.

The observations indicate that a slight change in deepness or distance between column and bottom in the labellum would cause that other bees than the medium sized ones can be effectively exploited as pollinators. The construction suggests that adaptation to larger or smaller vectors could easily occur. According to Daumann (1968), the most frequent pollinators in Czechoslovakia are *Andrena tibialis* and *A. nigroaenea* i.e. bees of Group 2 in this study. An adaptation to large *Andrena* bees in that area is also supported by the fact that he never saw bees that had entered leave the wrong way (except once in tests). No other authors mention wrong way escape with the exception of Ziegenspeck (1936), who states that it "recht selten" occurs. Obviously, climbing is much more common in the populations on Öland than further south in Europe which probably means that the plant on Öland belongs to a somewhat small-flowered anthecotype (intraspecific type adapted to pollination by a certain vector-group). Many facts in this study support that *C. calceolus* on Öland is anthecologically adapted to females of *A. haemorrhoa*.

Fruit set of *C. calceolus* on Öland is rather low and the small populations will certainly have to rely largely on vegetative growth for their survival. In a German locality Detto (1905) found 65% fruit set. As a contrast Gumprecht (1974) mentions that in a rich locality with hundreds of specimens less than half a dozen set fruit. The unexpected high value at Gillsätra 2 in 1976 could have been a result of unfavourable weather which increased revisiting due to shorter flight ranges for local bees which had their nests adjacent to the isolated orchid population.

The entering by pollinators into the labellum of *C. calceolus* often occurs by their striving to explore the inside and not as an involuntary act caused by the inflected rim. In *C. californicum* bees either slip or crawl into the labellum (Kipping 1971) and in *C. acaule* bumblebees even "force an entrance and investigate the floor" (Stoutamire 1971). In *C. arietinum* the pollinator was observed to "slowly enter" (Stoutamire 1976). The species within the genus are obviously adapted to various degrees of voluntariness in the pollinators to enter the labellum. This must in turn be intimately coupled to the evolution of deceptive floral allurements e.g. odour, colour and false nectar guides.

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Botanical literature

Alexander, M. (ed.) 1977: *Advances in microbial ecology. Vol. 1.* 268 pp. Plenum Press, New York and London. ISBN 0-306-38161-3.

The aim of this new review series is to present monographs "that will deal with diverse problems and all major categories of microorganisms – bacteria, algae, protozoa and virus". Thus, all topics in microbial ecology will be covered, which makes this series very welcome. Microbial ecologists work with quite diverse fields, such as plant pathology, aquatic biology, waste management, medical and oral microbiology, and microbiology and biology in general. If the editor is successful in gathering data and knowledge from these diverse fields, then the series will fill a long-standing need. – The first volume contains five papers.

Detritus food chains in aquatic ecosystems: the role of bacteria by Fenchel and Barker Jørgensen (49 pp. + 195 refs.) deals with the breakdown of detritus, mainly in marine environments. The review covers all aspects of detritus decomposition, from primary decomposition by bacteria to more complex interactions between animals and bacteria. The authors also critically analyse some of the methods used to study detritus food chains.

Ecological studies with the chemostat by Veldkamp (30 pp. + 144 refs.) is a rather elementary introduction to the theory of the chemostat. The author also gives some examples of the use of this equipment in ecological studies of bacteria and algae, and of microbial interactions. The examples chosen provide insight into the possible uses of chemostat techniques in ecology.

Cosgrove's paper *Microbial transformations in the phosphorous cycle* (32 pp. + 164 refs.) deals with a subject which we feel has been rather overlooked in the past. It deals mainly with phosphorous transformations in the soil, but those in waste-water treatment plants and inland basins are also included, as well as a chapter dealing with the microbial breakdown of organophosphorous pesticides.

Biochemical ecology of nitrification and denitrification by Focht and Vershaute (63 pp. + 408 refs.) is a comprehensive paper which not only deals with biochemical aspects but also with species diversity and the influence of environmental factors on both these soil processes. Furthermore, the authors discuss global aspects of nitrification and denitrification and the applications in e.g. waste treatment.

Waste treatment is also the subject of la Rivière's paper *Microbial ecology of liquid waste treatment* (41 pp. + 188 refs.). Besides reviewing the literature on the biology of active sludge, trickling filter, anaerobic digestion and oxidation ponds, the author emphasizes the importance of developing new methods of waste treatment aimed at recovering the energy sources and the minerals present in waste. He concludes that "this provides microbial ecology in a felicitous manner with a wealth of tasks, not only scientifically interesting, but also directly corresponding to urgent societal needs".

We very much hope that the editor, for the volumes to come, will be able to select as good and well-written papers as those found in the first volume.

Erland Bååth and Bengt Söderström

Pollen from bills of African sunbirds (Nectariniidae)

Mattias Iwarsson

Iwarsson, M. 1979 09 30: Pollen from bills of African sunbirds (Nectariniidae). *Bot. Notiser 132:* 349–355. Stockholm. ISSN 0006-8195.

Pollen samples from the bills of 54 museum-skins of 18 species of African sunbirds (Nectariniidae) were analysed. Thirty-four birds distributed among 14 species carried a quantity of pollen which suggested that flower visits had occured. Pollen grains of *Leonotis* (Labiatae) were found in 15 samples and Liliaceae pollen (probably *Aloe* or *Kniphofia*) in 11 samples. *Erythrina, Erica, Protea, Opuntia* and Compositae pollen were also present. In a few cases it was possible to determine which plant species the bird had visited. The majority of the birds carried one pollen grain type only, which indicates flower constancy. The method of pollen analysis used is suggested for field investigations on plant–bird relationship when sunbirds are captured and then released.

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Field observations of sunbirds in various localities in Africa have shown that most species are regular flower visitors. The birds' dependence on nectar as food has been demonstrated in studies on available nectar resources and sunbirds' territoriality (Gill & Wolf 1975, 1977). The benefit of their visits is reciprocal since they effect cross-pollination of a number of plants. Many African birdflowers have been listed by Porsch (1929). Faegri & van der Pijl (1971) presented the syndrome of ornithophily.

The aim of the present study was to test the value of pollen analysis on samples from museum skins of sunbirds as an indication of the importance of bird pollination and floral constancy.

Material and methods

Pollen was sampled from skins of 18 species of African sunbird males in the collections of the Zoological Museum, Uppsala University (Table 1 no. 1, 2, 11, 16, 26–31 and 33) and the Swedish Museum of Natural History, Vertebrate Zoology, Stockholm (3–10, 12–15, 17–25, 32 and 34) by using small pieces of paper (c. 2 cm^2). These were moistened in distilled water and carefully drawn over the bill, the forehead and sometimes the chin of the birds. The paper was put in a glass tube, dried and the tube was corked. After acetolysis (the paper dissolves) according to Erdtman (1969), the material was mounted in glycerol and sealed with paraffin-mastix (1:1) and nailpolish. No destruction of the pollen was observed under the light microscope although some of the skins were more than 100 years old (7, 13, 14).

The pollen grains could as a rule be determined to family and genus by comparison with published figures and descriptions. Reference preparations in lactic blue from herbarium material was made for control. Using my own and published field observations and knowledge of plant distribution, it was sometimes possible to infer even which species had most probably been visited.

The number of pollen grains has been subjectively classified into three groups (Table 1 and 2). Out of 54 samples, 34 (14 species) contained more than 10 grains/preparation which was set as the lower limit for the assumption that the bird had visited flowers. Among the 20 samples with lower frequencies a few identified pollen grains are also mentioned in the results. Out of the 20 excluded samples, 8 were found to contain no pollen.

Pollen terminology follows Erdtman (1969). The names of the sunbirds follow Skead (1967) and Williams (1963, 1967).

Results

General comments on the morphology of the pollen grains are given in Fig. 1. Under each

pollen grain type the birds on which it was found are listed. The bracketed number mentioned in Fig. 1 and in the main text refer to the bird specimens enumerated in Table 1.

The pollen found in the preparations at a low frequency (less than 10 grains/preparation) includes pollen of some birdflowers such as *Erythrina, Leonotis,* Proteaceae and Liliaceae. One additional example of identified pollen grains was the *Cinnyris bifasciatus* (5) which had six large Cactaceae pollen (cf. Fig. 1 U). The pollen grains are very similar to those of *Opuntia quitensis* A. Web. (cf. Tsukada 1964).

Coniferous pollen grains (anemophilous) were found in 10 samples but in no case more than 2 grains/preparation.

The 20 excluded pollen samples were taken from the following birds. * samples totally deficient of pollen grains.

Chalcomitra fusca (*Nectarinia fusca;* Dusky Sunbird), *Cinnyris mediocris* (Eastern Double-collared Sunbird), *C. minullus* (Tiny Sunbird; 1* out of 2 samples), *C. venustus* (Variable Sunbird; 2* out of 4 samples), *C. violacea* (*N. violacea;* Orange-breasted Sunbird; 1* out of 2 samples), *N. famosa* (Malachite Sunbird; 3 samples), *N. johnstoni* (Scarlet-tufted Malachite Sunbird), *N. pulchella* (Beautiful Sunbird; 2* samples), *N. reichenowi* (Golden-winged Sunbird; 1* out of 2 samples), *N. tacazze* (Tacazze Sunbird; 1* out of 2 samples).

A. **Liliaceae** – Fig. 1 A, B

Chalcomitra fusca, Cinnyris afer (Greater Double-collared Sunbird), *C. venustus, Nectarinia johnstoni, N. famosa.*

The two common bird pollinated genera in this family are *Aloe* and *Kniphofia*. Unfortunately their pollen grains could not be distinguished morphologically.

However, the sunbirds from high altitudes (3, 4, 10, 18–20, 23, 24) have probably visited *Kniphofia* flowers. The shortbilled *Chalcomitra fusca* is reported to visit *Aloe littoralis* Bak., *A. zebrina* Bak., *A. grandidentata* Salm-Dyck, *A. hereroensis* Engl. and *A. gariepensis* Pillans in Namibia (Skead 1967). *Lachenalia* is a South African genus with some bird-pollinated species which have a similar type of pollen grains.

B. **Proteaceae, Protea** – Fig. 1 E–G

Chalcomitra senegalensis (*Nectarinia senegalensis;* Scarlet-chested Sunbird), *Nectarinia johnstoni.*

These sunbirds (2, 22) have been collected at high altitudes in Mts Elgon and Kilimanjaro, carrying pollen grains morphologically similar to that of *Protea* (cf. Zinderen Bakker 1953). The plant species most probably visited are *Protea gaguedi* J. G. Gmel. and *P. kilimandscharica* Engl. Volkens (1899) reported visits by *Cinnyris* and *Nectarinia* species to *P. gaguedi* (as *P. abyssinica* Engl.).

C. **Leguminosae, Erythrina** – Fig. 1 O–S

Cinnyris mediocris, Nectarinia famosa.

The pollen grains of *Erythrina* were easily identified (cf. Zinderen Bakker & Coetzee 1959 and Graham & Tomb 1974). The sunbirds (8, 15) have visited the same species, *E. abyssinica* Lam. ex DC., with very variable flower morphology (Verdcourt 1971) in East Africa. It is notable that the bill of *N. famosa* is c. 9 mm longer than that of *C. mediocris*.

D. **Labiatae, Leonotis** – Fig. 1 J–L

Cyanomitra verticalis (Green-headed Sunbird), *Nectarinia famosa, N. kilimensis* (Bronze Sunbird), *N. reichenowi.*

The *Leonotis* pollen grains have been compared to published descriptions (Wunderlich 1967) and my own unpublished data. It has not been possible to distinguish the species on acetolysed pollen grains. In the field two distinct colours of the pollen can be discerned: pink–orange (*L. raineriana* Vis. (=*L. mollissima* Gürke) and *L. leonitis* (L.) R. Br.) and pale yellow (*L. nepetifolia* (L.) R. Br. var. *nepetifolia* and *L. decadonta* Gürke).

The genus is an important source of food for the sunbirds, especially *N. reichenowi* which often frequents *L. nepetifolia* (L.) R. Br. var. *nepetifolia* in Kenya (Gill & Wolf 1975, 1977, own observations, Fig. 2). This sunbird has a bare groove on the forehead which can "store" large quantities of pollen (cf. Friedmann & Stager 1969). In Kenya *L. nepetifolia* occurs at altitudes lower than 2500 m and *N. famosa* (21), *N. kilimensis* (26–31) and *N. reichenowi* (33) have probably all visited this species.

At higher altitudes (usually over 2500 m) a woody species of the genus occurs, i.e. *L. raineriana* s.l. It is represented by two corolla

Table 1. Frequency of pollen grains identified from bills of sunbirds. An Angola, Et Ethiopia, Ke Kenya, Na Namibia, Rw Rwanda, SA South Africa, Ta Tanzania, Ug Uganda, Za Zaïre. – Frequency: * 10–50 pollen grains/preparation, ** 50–150, *** > 150. Pollen types A–H refer to the text.

No.	Sunbird	Locality	Date	Pollen type	Frequency
1	*Chalcomitra fusca*	Na, Kleinkaras	1931-07-22	A	***
				F	***
				F	**
2	*Chalcomitra senegalensis*	Ke, Mt Elgon	1948-03-31	B	*
3	*Cinnyris afer*	Za, Kivu, Mt Karisimbi	1921-03-18	F	***
				G	*
4	Do.	Rw, Mt Sabino	1921-02-20	A	**
5	*Cinnyris bifasciatus*	An, Catete	1953-12-01	F	***
6	Do.	An, Catete	1953-12-27	F	***
7	*Cinnyris chalybeus*	SA, Cape Town	1839-02-19	F	**
				H	*
8	*Cinnyris mediocris*	Ta, Kilimanjaro, 3000 m	1906-02-26	C	***
9	*Cinnyris regius*	Za, Kivu, Burungu	1921-03-09	G	*
				E	*
10	*Cinnyris venustus*	Za, Kivu, Kibati	1921-03-07	A	**
				F	*
11	*Cyanomitra verticalis*	Ke, Kapenguria	1964-03-15	D	**
12	*Nectarinia erytrocerca*	Za, Kivu, Goma	1921-03-01	F	**
13	*Nectarinia famosa*	SA, Port Natal	1840-08-19	A	*
14	Do.	SA, Cape, Kalk Bay	1845-02-28	A	*
				D	*
15	Do.	Za, Kivu, Nyamulagira, 1700 m	1933-11-01	C	**
				A	*
16	Do.	Ke, Molo, 3000 m	1964-12-16	D	**
17	Do.	Et, 30 km N Addis Ababa	1958-10-03	D	***
18	Do.	Rw, Mt Muhavura, 3000 m	1921-02-11	A	*
19	Do.	Rw, Mt Sabino	1921-02-21	A	**
20	Do.	Rw, Mt Sabino	1921-02-20	A	***
21	Do.	Ug, Kitende	1921-01-25	D	***
22	*Nectarinia johnstoni*	Ta, Kilimanjaro, 3000 m	1906-02-21	B	***
23	Do.	Za, Kivu, Mt Karisimbi	1921-03-19	F	*
				A	*
24	Do.	Za, Kivu, Kabare	1913	A	*
25	*Nectarinia kilimensis*	Ta, Kilimanjaro, Kibonoto	1905-11-01	D	**
26	Do.	Ke, Kiambu	1957-03-18	D	**
27	Do.	Ke, Kiambu	1957-03-18	D	***
28	Do.	Ke, Kiambu	1957-03-17	D	*
29	Do.	Ke, Kiambu	1957-03-17	D	***
30	Do.	Ke, Kiambu	1957-03-17	D	**
31	Do.	Ke, Kiambu	1957-03-18	D	***
32	*Nectarinia reichenowi*	Ta, Kilimanjaro, Kibonoto	1905-08-04	D	*
33	Do.	Ke, Kiambu	1957-03-17	D	*
34	Do.	Ke, Mt Elgon, 2500 m	1948-03-04	D	**

colour forms (pale orange buff and orange). *C. verticalis*, *N. famosa* (16, 17) and *N. reichenowi* (32, 34) have in all likelihood visited this species (cf. Sjöstedt 1910).

N. famosa from South Africa (14) may have frequented *L. leonurus* (L.) R. Br., which was mentioned as a source of food by Skead (1967) but there are also other *Leonotis* species in this area.

E. **Compositae, Anthemideae** – Fig. 1 I

Cinnyris regal (Regal Sunbird).

Pollen from this sunbird was identified as a species belonging to the Anthemideae (cf. Skvarla & Larson 1965). No birdflower is known in this usually anemophilous group and as only 11 grains were seen, they may represent contaminations.

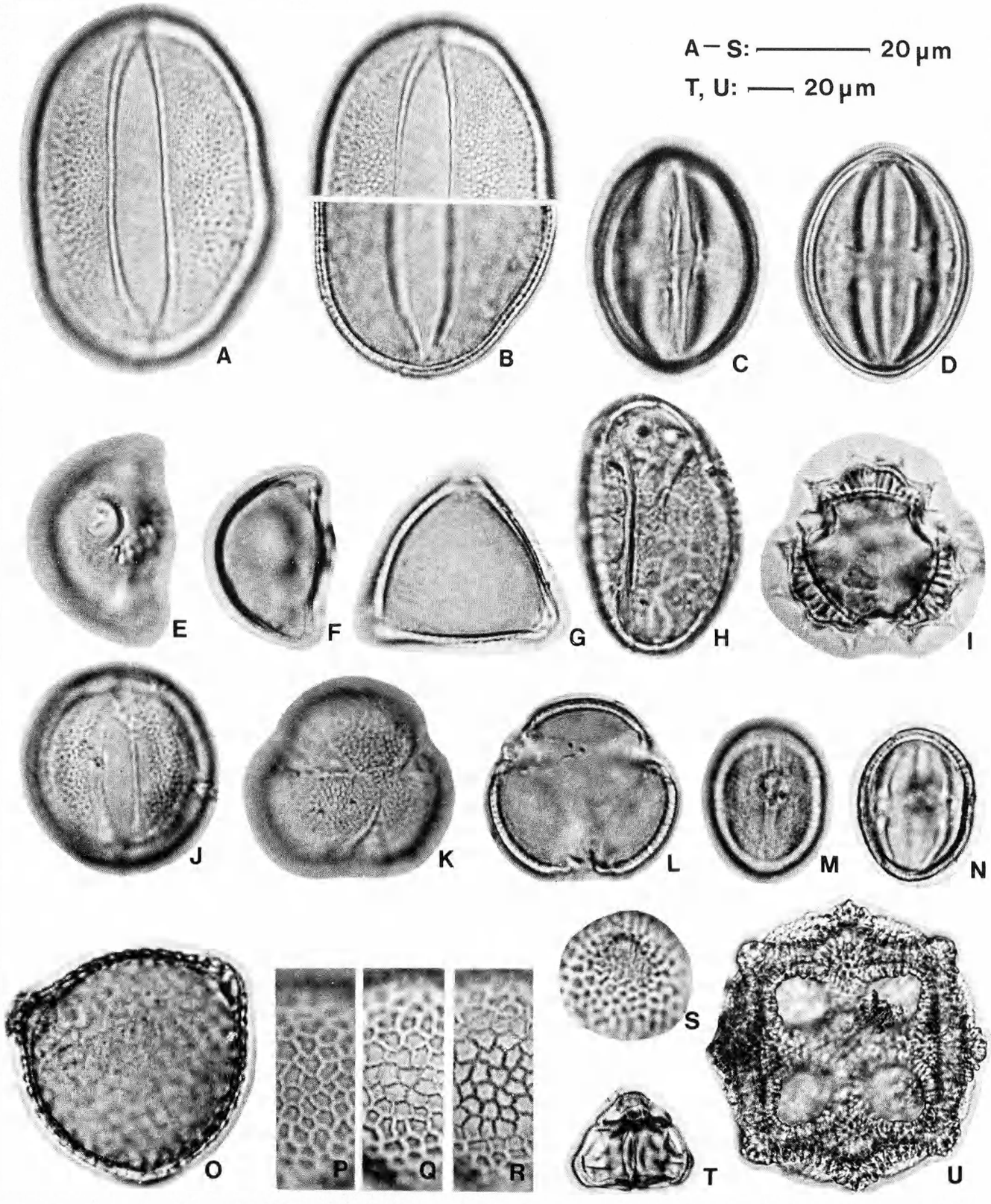

Fig. 1. Pollen types. – A, B: Liliaceae (bird 20), monocolpate, microreticulate OL-pattern; B lower half, optical section. – C, D: 3-colporate type (7), colpus narrow, os rounded, sexine almost smooth. – E–G: *Protea* (22), E circular pore with faintly sculptured operculum; F sexine almost smooth, grains anisopolar, equatorial view; G grains triangular, triporate, polar view. – H: Fern spore (3), monolete, oblate with granulate ornamentation. – I: Compositae, Anthemideae (9), 3-colporate, os rounded, sexine thick, no cavea, columellae at two levels. – J–L: *Leonotis* (27), 3-colpate, central sculptured portion of colpus membrane missing due to acetolysis (sexine thicker at the poles in equatorial view), microreticulate. – M, N: 3-colporate type (5), colpus narrow, os rounded, sexine sculptured. – O–S: *Erythrina* (8), O polar view, 3-porate, triangular (suboblate in equatorial view); P–R sexine reticulate, S lumen smaller at pores with granular operculum. – T: *Erica* (7), pollentetrad, sexine faintly ornamented. – U: *Opuntia,* 12–15-porate, polyhedral, sexine coarsely reticulate with elongated bacula.

F. **3-colpate unidentified pollen grains** – Fig. 1 C, D, M, N

Chalcomitra fusca, Cinnyris afer, C. bifasciatus (Little Purplebanded Sunbird), *C. chalybeus* (*Nectarinia chalybea;* Lesser Double-collared Sunbird), *C. venustus, N. erythrocerca* (Red-chested Sunbird), *N. johnstoni.*

This category includes at least three different types of pollen grains: 15–25 μm, sculptured (1, 6, 10, 12, 23; Fig. 1 M, N), 25–40 μm, sculptured (3, 5), 30–40 μm, almost smooth (1, 7; Fig. 1 C, D).

All attempts to identify these pollen grain types have failed. My working hypothesis gained from Hedberg (1964 p. 38) that *N. johnstoni* (23) had visited some giant *Lobelia* in this area cannot be verified by comparison of the pollen grain morphology.

G. **Fern spore** – Fig. 1 H

Cinnyris afer, C. regius.

It is difficult to explain the presence of wind dispersed fern spores on these sunbird skins. Probably they represent contamination after capture; both bird skins were collected by the same expedition.

H. **Ericaceae, Erica** – Fig. 1 T

Cinnyris chalybeus.

The pollen tetrad was identified as Ericaceae by comparing it with published descriptions, in which endexine cracks are noted (Oldfield 1959). The genus *Erica* shows great variation in South Africa and some species seem to be adapted to sunbird pollination (cf. Skead 1967).

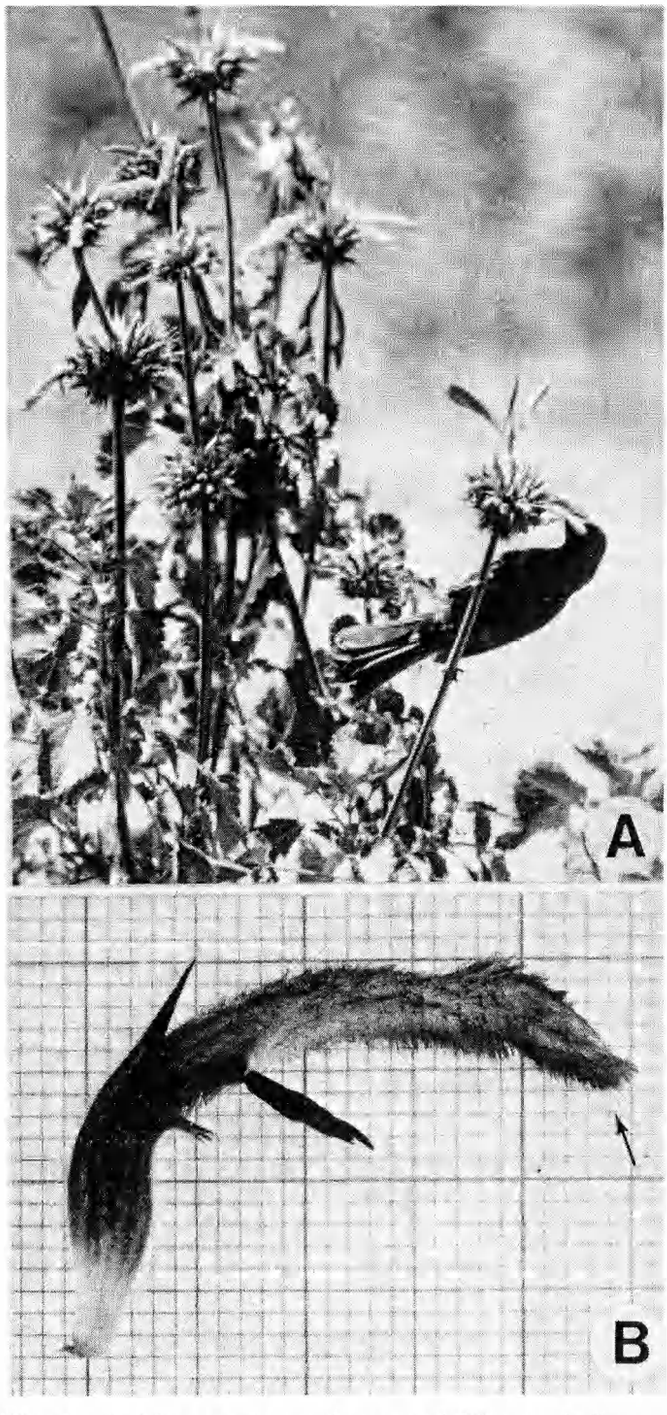

Fig. 2. A: *Nectarinia reichenowi* visiting an inflorescence of *Leonotis nepetifolia* (Loita Plains, Masai Distr., Kenya, 21.III.1973). The normal behaviour is to successivly move around, inserting the bill in the curved corolla tubes, probing all for nectar at the base. – B: Flower. The upper lip of the corolla covers anthers and stigma. This part is touched by the forehead of the bird and pollen is spread out by the surrounding hairs (arrow).

Discussion

One way to find out bird–plant relationship is to collect pollen from the bills of bird skins. It will however often be difficult to identify the pollen grains. In most cases family or genus could be determined but for the very common pollen grain type F not even this was obtained. To determine the plant species visited, it is necessary to make reference preparations of pollen.

When pollen grains are present only at a frequency of 10–50 grains/preparation the records must be treated with some caution. The bird sometimes visits a flower which is also frequented by insects and small amounts of foreign pollen may be exchanged. Out of 17 pollen grain records (Table 2) three might be the result of contamination. The sunbird *Cinnyris*

Table 2. Records of bird–flower contact. Pollen types A–H, see text. ′ exclusively one pollen type found. ″ found together with other pollen types. * contamination.

Frequency	Pollen types																				
	A′	A″	B′	B″	C′	C″	D′	D″	E′	E″	F′	F″	G′	G″	H′	H″	Σ′	Σ″	Σ
10– 50/prep.	3	3	1	0	0	0	3	1	0	1*	0	2	0	2*	0	1	7	10	17
50–150/prep.	2	1	0	0	0	1	6	0	0	0	1	2	0	0	0	0	9	4	13
>150/prep.	1	1	1	0	1	0	5	0	0	0	2	2	0	0	0	0	10	3	13
Sum	6	5	2	0	1	1	14	1	0	1	3	6	0	2	0	1	26	17	43

regius (9) with two types of anemophilous pollen grains on its bill had obviously been contaminated.

Pollen grains present at a frequency of over 50 grains/preparation (the majority) are unlikely to be present due to chance or contamination i.e. they must come from flower visits.

The scarcity or lack of pollen grains on the 20 sunbirds mentioned in the Results can be explained by careful cleaning of the skins by the collectors, or, indeed, by the sunbirds themselves since they are often observed cleaning bills and forehead of pollen and nectar while resting between foraging tours. The sample 25–31 from the same locality may illustrate the variation: there were 18–721 *Leonotis* pollen grains/preparation found on these birds.

In 8 preparations of the 20 samples not reported in Table 1, no pollen was found. This is an indication that pollen is not transferred from one bird to another in the collections and that contamination between the probes when sampling does not occur.

In 14 out of 15 records of sunbirds (Table 2) with *Leonotis* pollen, the birds exclusively visit this genus. In dense stands of the weedy *L. nepetifolia* (autogamous in absence of pollen vector), sunbirds keep small feeding territories (Gill & Wolf 1975). Considering this behaviour and the almost pure *Leonotis* stands it is natural to expect only one pollen grain type on the bill. The woody *Leonotis* species are more evenly distributed, often mixed with other birdflowers such as *Aloe, Protea, Faurea, Tecomaria* and Loranthaceae. Here it would be expected to find mixed types of pollen grains, but the few birds (14, 16, 17, 32, 34) examined in this study do not suggest this, an exception being *Nectarinia famosa* (14) from South Africa which had also visited Liliaceae flowers.

A majority of the birds in Table 1, 26 out of 34, have one pollen type on the bill, seven birds have two types and only one bird was found with three pollen types. This speaks for floral constancy. In connection with this, it is notable that with low numbers of pollen grains in the samples, the majority are mixed (Table 2). At high numbers on the contrary, most samples consist of one pollen grain type only. The seven *Nectarinia famosa* from Tropical Africa (15–21), captured at various months and localities seem to rely respectively on nectar from species of *Erythrina, Leonotis* and Liliaceae which have overlapping flowering seasons in this area.

The method of collecting pollen used here can be elaborated and conveniently applied in the field. To elaborate, certain parts of the bird are to be investigated. These parts should be chosen with respect to expectation of pollen deposits indicated by the flower morphology. Field observations on pollination of *Erythrina* have revealed that pollen is deposited on throat and breast of the bird (in S America, Cruden & Toledo 1977). If this is the case with sunbirds in Africa visiting *Erythrina,* some pollen grain records might have been overlooked, since pollen sampling was not done on breast and throat of the skins in the present study. When used in studies on plant–bird relations, the pollen sampling on sunbirds captured and then released, has to be supported by observations on flower visits and comparative studies of reference pollen samples from the available bird-visited flora in the neighbourhood.

Acknowledgements. I would like to thank Mrs Ulla-Britt Sahlström and Mrs Gun-Britt Örlander for photographic and laboratory assistance. The Curators at the Zoological Museum, Uppsala University and the Swedish Museum of Natural History, Vertebrate Zoology, Stockholm have kindly put the bird skins at my disposal. The staff at the Palynological Laboratories in

Stockholm and Montpellier are acknowledged for help with pollen identifications. Thanks are also due to colleagues at my institute for discussions on the manuscript. Dr Ray M. Harley helped me with the linguistic revision.

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Botanical literature

Ettl, H. 1979: *Die Gattungen Carteria Diesing emend. Francé und Provasoliella A. R. Loeblich (Chlamydomonas und die nächstverwandten Gattungen III).* 226 pp., 28 pl. Beihefte zur Nova Hedwigia 60. J. Cramer Verlag, Vaduz. ISBN 3-7682-5460-7. Price DM 100.–.

This final part of Dr Ettl's treatise deals with the genera *Carteria* and *Provasoliella*. Both have four flagella but *Carteria* has a pyrenoid whereas *Provasoliella* lacks one. In this respect they form an analogue to *Chlamydomonas* and *Chloromonas*. Both genera are rather small. *Carteria* has 62, and *Provasoliella* 16 species. In addition there is quite a number of insufficiently described taxa, some of which have been transferred to other genera. Members of both genera are widespread, although many are seldom recorded. They occur in various kinds of freshwater bodies; one is cryophilous, and some belong to the soil algae.

There are 28 plates with very useful illustrations, some of them made by the author. Drawings are essential in phycology, and the lack of adequate drawings often renders records quite useless.

The book concludes with an index for this part, and another one which covers all three volumes. There is also a supplement to the preceding parts, which brings them up-to-date.

The everlasting value of this manual cannot be questioned, and the author deserves our admiration. The treatment – a mine of invaluable information – is a monument of dispassionate scholarship.

Like its predecessors, which appeared in 1970 and 1976, this volume is very handsome, and it is a special pleasure to note that it has been issued as a hardback. The total price for the three volumes is high. Yet this treatise should be within reach of every limnologist, for it is conscientious, exhaustive, informative and instructive throughout. It is a real joy to consult it, because whatever you wish to know is there.

Kuno Thomasson

Dorycnium fulgurans, a neglected species from the Balearic Islands

Per Lassen

Lassen, P. 1979 09 30: Dorycnium fulgurans, a neglected species from the Balearic Islands. *Bot. Notiser 132:* 357–358. Stockholm. ISSN 0006-8195.

The combination *Dorycnium fulgurans* (Porta) P. Lassen is made, based on *Anthyllis fulgurans* Porta. It is related to *D. pentaphyllum* Scop.

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Porta (1887) described *Anthyllis fulgurans* from near Fornells, Menorca. The species has since been found also on the N coast of Mallorca and on Isla de Cabrera (Palau 1952) off the S coast of Mallorca. Knoche (1922) said "je croirais volontiers que cette plante n'est qu'une variété de l'*A. Hermanniae* si le fruit n'était pas absolument different". Porta described the fruit only briefly and did not comment upon its peculiarities. The species is not mentioned in *Flora europaea* (Cullen 1968).

The fruits of *A. fulgurans* are dehiscent and quite different from those of any species of *Anthyllis*. Most floral characters also differ. On the contrary the flowers and fruits are almost indistinguishable from those of *Dorycnium pentaphyllum* Scop. ssp. *pentaphyllum* (Fig. 1). The leaves are also very similar. *Anthyllis fulgurans* is obviously a *Dorycnium* and thus the following new combination is proposed:

Dorycnium fulgurans (Porta) P. Lassen, comb. nov. – Fig. 1 A

Basionym: *Anthyllis fulgurans* Porta 1887 p. 303 – Type: "Balearium insula Minore, in pascuis petrosis maritimis prope pagum Fornells (loco unico!) 6. Jul. 1885. Porta et Rigo" (LD isotypus!)

D. fulgurans differs from *D. pentaphyllum* by being a spiny cushion plant (similar to *Launaea cervicornis* (Boiss.) Font Quer & Rothm., *Smilax aspera* L. var. *balearica* Willk., and other Balearic endemics in the same habitat), by the mostly 3- to 4-foliolate leaves with caducous leaflets, and by the inflorescences, which are almost sessile (peduncle 0–2 mm), few-flowered (2–4 flowers/peduncle) and often occur in pairs in the axils.

There is another species related to *D. pentaphyllum* with almost sessile inflorescences, viz. *D. axilliflorum* Huber-Morath from Anatolia. According to the description and figure in Huber-Morath (1939) this species is similar to *D. pentaphyllum* in habit and in having a many-flowered inflorescence.

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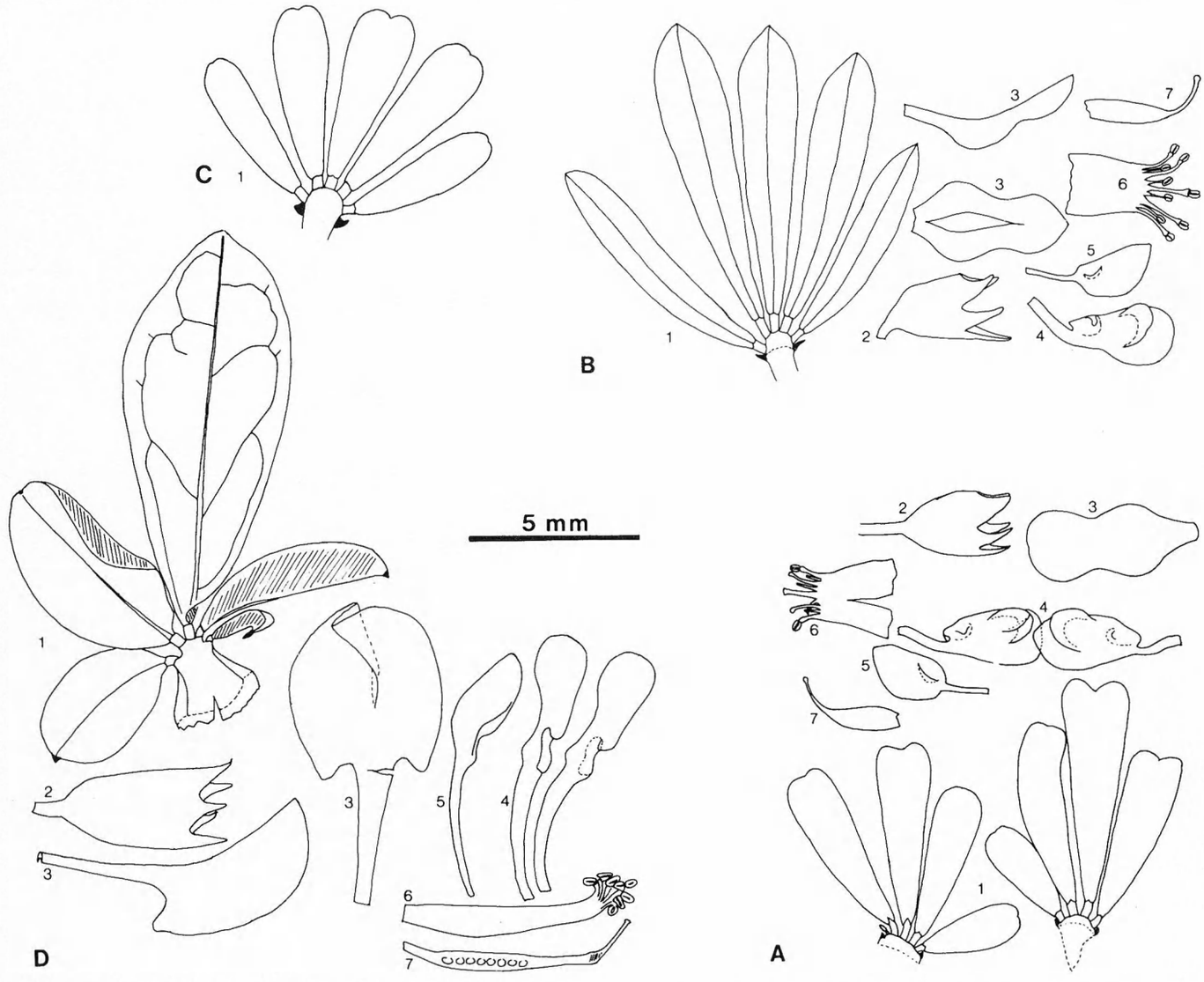

Fig. 1. A: *Dorycnium fulgurans* (Mallorca, Dahlgren et al. 1969: 252, LD). – B: *D. pentaphyllum* ssp. *pentaphyllum* (Mallorca, Dahlgren et al. 1969: 957, LD). – C: *D. pentaphyllum* ssp. *pentaphyllum*, another common leaf form (Spain, N. Hj. Nilsson 101, LD). – D: *Anthyllis hermanniae* (Corsica, M. Sundqvist s.n., LD). – 1 leaves, 2 calyx, 3 vexillum, 4 alae, 5 carina, 6 staminal sheath, 7 pistil.

Cerastium smolikanum Hartvig, sp. nov. and C. vourinense from N Greece

Per Hartvig

Hartvig, P. 1979 09 30: Cerastium smolikanum Hartvig, sp. nov., and C. vourinense from N Greece. [Materials for the Mountain flora of Greece, 1.] *Bot. Notiser 132:* 359–361. Stockholm. ISSN 0006-8195.

Cerastium smolikanum Hartvig is described from ophiolithic rocks in the summit area of Mt Smolikas, N Pindhos, Greece. It is similar to *C. ligusticum* and *C. pumilum,* but differs e.g. in the long papillae on the seeds. *C. vourinense* Möschl & Rechinger is reported from the same mountain; information on its petal morphology is presented.

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Cerastium smolikanum Hartvig, sp. nov. – Fig. 1

Orig. coll.: Greece, N Pindhos, Mt Smolikas, summit area from the cairn on the E plateau and 1.5 km N, 2400–2500 m, serpentine rocks, 27.7.1977, Christensen, Kjær & Hartvig 7267 (ATH holotype, C, G, LD, M, W isotypes).

Collections: Mt Smolikas, E slope of great E plateau, c. 5 km W of Samarina, 2300–2450 m, serpentine rocks and screes, 19.8.1975, Hartvig & Seberg 4479b (C) – W-facing steep, rocky slope below the cairn on the great E plateau, 2500 m, substr. serpentine, 21.8.1975, Hartvig & Seberg 4537 (C) – Summit area 5.5 km W of Samarina, W-facing, steep, rocky slope below the cairn on the great E plateau, 2500 m, substr. serpentine, 14.7.1976, Hartvig, Baden & Christiansen 5865 (ATH, C, K) – 8 km W of Samarina, S-facing slope of summit ridge, 2500 m, *Festuca* heath on serpentine scree, 14.7.1976, Hartvig, Baden & Christiansen 5885 (ATH, C, G) – In latere boreali verticis orientalis (2556 m), 2400–2500 m. In clivis lapidosis et rupestribus ophiolithicis. 17.8.1976, Greuter 14522 (herb. Greuter, C, G, UPA).

Herba annua glandulosa complures caules adscendentes emittens. *Folia* basalia late ovata, petiolata; media et superiora spathulata. *Bracteolae* herbaceae, infimae foliacea. *Sepala* margine scariosa. *Petala* bifida, glabra, 1.3 sepalorum longitudine. *Capsula* recta, 3–3.5 mm lata, calycem paulumum superans, dentibus suberectis margine revolutis. *Placenta* bacilliformis. *Semina* reniformia, 1.0–1.4 mm longa, margine compluribus seriebus tuberculorum cylindricorum longorum armata.

Annual with few to several ascending, up to 15 cm long flowering branches from lower part of the stem, rarely simple. All parts of plant with a dense indumentum of straight, spreading, c. 5-celled glandular hairs, 0.25–0.5 mm long on the leaves, somewhat shorter on stems and on pedicels. End-cell shortly clavate to almost globose, c. 60 × 50 μm, yellowish on dried material. Eglandular hairs few, similar to the glandular ones, but end-cell long, pointed and hyaline. Stems, sepals and sometimes leaves ± tinged with purple. *Stems* 0.7–1.0 mm in diameter at base, with 10–18 (usually 12) internodes. Basal leaves crowded, early withering, ± persistent; lower leaves 6–10 × 4–7 mm, broadly ovate, subacute, abruptly narrowed into a 5–18 mm long petiole; middle and upper leaves spathulate, (12–)15–20(–25) × 3–7 mm. Inflorescence with up to 10 flowers. *Pedicels* (8–)10–20(–23) mm, 0.15–0.35 mm in diameter, straight, erect at anthesis, reflexed after anthesis; fruiting pedicels erect and straight, sometimes slightly curved below the calyx. Pedicels on ultimate branches with 1.5–2.5 mm long, elliptical, herbaceous bracteoles; lower bracteoles leaf-like. Flowers broadly campanulate. *Sepals* narrowly ovate, acute, 5–7(–7.5) × (1.6–)2(–2.3) mm, with a scarious margin which is c. 0.4 mm wide near the apex and extends almost to the base on the two inner sepals, narrowed and confined to the distal third in the outer two. *Petals* white, occasionally tinged with purple, obovate, 7–

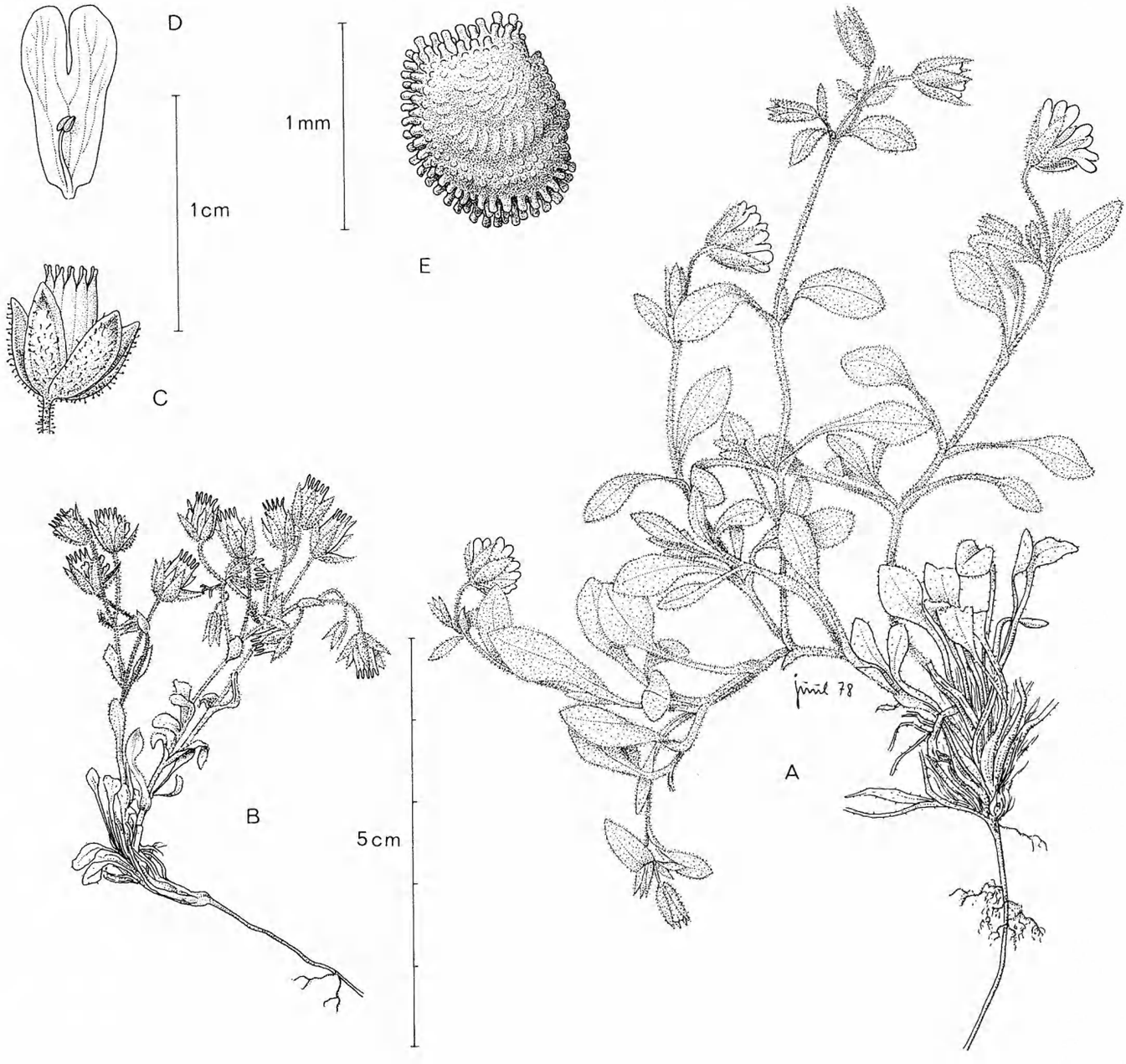

Fig. 1. *Cerastium smolikanum*. – A: Habit of flowering plant. – B: Habit of fruiting plant. – C: Capsule. – D: Petal and stamen. – E: Seed. – A, D Hartvig et al. 5865, B, C type.

8.5 × 3.0–3.8 mm, bifid for 1/3–2/5, glabrous. *Stamens* 10, subulate, 3–3.5 mm, glabrous, those opposite the sepals with dilated, swollen, nectar-producing bases. Anthers dorsifixed, yellow, c. 0.65 mm long. *Ovary* almost globose at anthesis, glabrous. *Styles* 5, c. 2 mm, white, papillose in the upper 3/5. *Capsules* straight, 5.5–8 mm, slightly narrowed from the 3–3.5 mm wide, rounded base, equalling or exceeding calyx with 2 mm, with 10 nerves. Capsule-teeth c. 1.2 mm, c. 0.5 mm wide at base, suberect; margins revolute. Placenta rod-shaped, c. 2.5 mm, with short funicles (up to 0.5 mm at apex). *Seeds* 1.0–1.4 mm, pale yellowish brown, roundish-reniform; rim with several rows of cylindrical to clavate, rounded, basally rugose tubercles up to 0.2 × 0.08 mm, which gradually decrease in length and change to low, rugose ridges on the faces; testa close.

Cerastium smolikanum is only known from Mt Smolikas in the N Pindhos range, where it grows on ophiolithic rocks and screes in the alpine zone between 2300 and 2500 m. It is found only within a small area in the E part of the summit region. It grows on steep, rocky slopes, in cavities, on small ledges and in the sparse mineral soil accumulating among boulders and

rough scree. It is usually associated with species such as *Minuartia verna, Silene pindicola, Alyssum smolikanum, Aubrietia gracilis* var. *degeniana, Draba athoa, Potentilla speciosa, Saxifraga paniculata, Artemisia eriantha, Crepis guioliana, Doronicum columnae, Omalotheca hoppeana* and *Senecio doronicum*.

The well developed basal rosette, which at time of flowering is ± withered, indicates that *C. smolikanum* is a winter annual. Abundant flowering is observed from the middle of July. In the extraordinarily dry and warm summer of 1977 the capsules of most flowers had already ripened by the end of July; in normal years the flowering is supposed to last to late August.

Taxonomic relationships

The type of capsule, the annual habit and the glabrous petals and filaments suggest that *C. smolikanum* should be placed within subsection *Leiopetala* of section *Fugacia*. Of the species with rod-shaped placenta, short funicles and shortly clavate end cells on the glandular hairs only *C. ligusticum* and *C. pumilum* ssp. *pumilum* have some resemblance with *C. smolikanum*. They all have herbaceous or almost herbaceous bracteoles, spathulate to petiolate basal leaves, often a dark green colour with purplish stems and lower leaves, a glandular indumentum with few glandular hairs, and ± long petals. There are, however, several differences. *C. smolikanum* has obovate to spathulate primary bracteoles (not ovate to elliptical), a shorter and wider capsule and roundish-reniform (not trapeziform-reniform) seeds with narrower dorsal rim and densely covered with long, cylindrical–clavate (not low, conical) tubercles, which are considerably longer on the dorsal edge than on the faces.

In fact, no other European annual species of subgenus *Cerastium* (*Orthodon* Ser.) shows closer resemblance with *C. smolikanum* than the species mentioned above. Among W Asian *Fugacia, C. longifolium* Willd. has some similarity with *C. smolikanum*. It has, however, typical *Fugacia* seeds, 20-nerved capsule and ciliate petals. The only other annual species from Europe and W Asia with long cylindrical tubercles on the seeds is *C. vourinense*. This is, however, a *Strephodon* (with circinately outrolled capsule-teeth), and it has narrow, entire petals, herbaceous outer sepals, elliptical upper leaves and a more irregular, freely branched inflorescence. The seeds of *C. vourinense* have four rows of tubercles, which are fewer, wider and usually longer than those of *C. smolikanum*.

Seeds with long tubercles are much more common among the perennial species of *Cerastium* and maybe the relationships of *C. smolikanum* is with a perennial species complex rather than with the *Fugacia*.

Cerastium vourinense Möschl & Rechinger

Collections: Mt Smolikas, the peak Bogdanis, 3.5 km W of Samarina, 2240 m, serpentine rocks and screes, 26.6.1976, Hartvig, Baden & Christiansen 5312 (C) – Mt Vourinos, 17 km SW of Kozani, summit area, 1700–1870 m, mainly rocky slopes with *Buxus* and *Juniperus*, substr. serpentine, 5.7.1977, Hartvig & Christensen 6423 (C).

This is a very distinct species which takes an isolated position within sect. *Strephodon*. It has only been known from two collections from the type locality, where it is still present. The collection from Mt Smolikas, a single weak plant, represents an extension to the Pindhos range.

Petal characters were previously insufficiently known, but the following observations could be made on the Smolikas plant:

Petals narrowly oblong to narrowly obovate, 6.3 × 1.9 mm, truncate, narrowly cuneate at base, c. 1.3 times as long as sepals. The whole plant has a conspicuously pale green colour. Apart from slightly longer styles, a difference which could merely be a variation by chance, the plant from Mt Smolikas matches in all observed characters my own material from Mt Vourinos as well as the original description of *C. vourinense* perfectly well.

Acknowledgements. I wish to thank Dr T. Christensen for the Latin translation. The drawing was made by Mr P. Juul. The field-work has been supported by grants from the Arnstedt family foundation.

A mountain flora of Greece

Arne Strid

A project to produce a critical flora of the Greek mountains has been started in January, 1979. Botanists in several countries including Greece, Sweden, Denmark and W Germany participate in the project. There is a board of advisors consisting of Werner Greuter (Berlin), Georgios Lavrentiades (Thessaloniki), Karl Heinz Rechinger (Vienna), Hans Runemark (Lund) and William T. Stearn (London). Project co-ordinator is Arne Strid, Institute of Systematic Botany, University of Copenhagen, 140 Gothersgade, DK-1123 Copenhagen K, Denmark.

Small articles including descriptions of new taxa, new combinations, lists of chromosome numbers, etc., will appear in *Botaniska Notiser* at irregular intervals during the next three or four years under the common heading *Materials for the Mountain Flora of Greece*.

A new species of Chondrilla from Mt Pangaion

Kostas Papanicolaou

Papanicolaou, K. 1979 09 30: A new species of Chondrilla from Mt Pangaion. [Materials for the Mountain flora of Greece, 2.] *Bot. Notiser 132:* 363–365. Stockholm. ISSN 0006-8195.

Chondrilla lenae Papanicolaou, sp. nov. is described from Mt Pangaion in NE Greece. It grows in subalpine meadows and is related to *C. chondrilloides* (Ard.) Karsten from the Alps. The chromosome number is 2n = 10.

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Chondrilla lenae Papanicolaou, sp. nov. – Fig. 1

Orig. coll.: NE Greece, Mt Pangaion, NW part of summit area, place called Dena, dry stony elevation within grassland, c. 1600 m. Limestone. 24.7.1977 Papanicolaou 467 (C holotype, Herb. Univ. Thessaloniki isotype).

Herba perennis, 20–35 cm alta, e rhizomate verticali surgens. *Folia basalia* 8–16, 30–70 × 3–18 mm, subglabra, oblanceolata, dentata, petiolis brevibus. *Caulis* 1–3, erectus, striatus, in media planta et supra laxe ramificatus. *Folia caulina* 0–3, linearia, glabra. *Pedunculi* terminales, glabri. *Capitula* terminalia, longe pedunculata et paucula lateralia subsessilia, circiter 11-flora. *Involucrum* cylindricum. *Involucri phylla* 2-seriata, 7–11 × 1.4–2.2 mm magna, plus minus tomentosa, in summa sexta parte papillas nigras praebens in phyllis interioribus longas, in exterioribus parvas. *Receptaculum* planum, foveolis exannulatis, eciliatis. *Flores* 9–15 mm longi, homogami, lingulati, flavi. *Achenium* glabrum, longitudinaliter pluricostatum-tuberculatum, curvum prope basin, 5-squamosum ad apicem, fuscum, 3.0–3.5 mm longum. *Rostrum* 2.5–3.5 mm longum, deciduum. *Pappus* albus, 3–4 mm longus, biserialis, pili scabrosi.

Perennial herb 20–35 cm tall with a short, stout, not or sparingly branched woody stock. *Basal leaves* 8–16, forming a rosette, ascending to suberect, 30–70 × 3–18 mm, oblanceolate, ± acute, gradually attenuate into a winged petiole c. 1/4 as long as the blade; blade irregularly incise-dentate with characteristic rounded incisions and short, acute to acuminate teeth, sparsely eglandular-puberulent on both sides; margin narrowly hyaline and sometimes brownish-red. *Stems* 1–3 (1 from each leaf rosette), erect, unbranched or more often branched at the middle and above, terete, 1.4–1.8 mm in diameter, solid, striate, glabrous throughout. *Cauline leaves* 0–3, linear, bract-like, entire, 5–15 × 0.8–1.0 mm. *Main branches* 1–4, alternate, forming an angle of c. 40° with the stem. *Flowering heads* usually terminal, solitary, suberect to erect on rather long peduncles, occasionally lateral on short peduncles. *Involucre* cylindrical, 7–11 × 3.5–5.0 mm. *Involucral bracts* in 2 series, white-tomentose especially at the margins in bud stage, almost glabrous in fruiting stage. *Outer involucral bracts* 6–7, 1/5–1/4 as long as the inner ones, ovate-lanceolate, c. 0.7 mm wide at the base, acute, dark green to blackish-green, usually with blackish papillae near the apex. *Inner involucral bracts* 8, lanceolate, 1.4–2.2 mm wide, acuminate, not as dark as the outer ones, with long blackish papillae on the back in the apical 2–3 mm; the 3 outermost of the inner involucral bracts without scarious margins, followed by 2 bracts with the outer margin non-scarious and the inner margin scarious, and finally 3 bracts with both margins scarious (most clearly visible in fruiting stage). *Receptacle* flat, alveolate; the pits without scales and not ciliate. *Florets* 11, all ligulate, 9–15 × 2.5–3.2 mm, hermaphrodite, glabrous, yellow; tube 3.0–3.2 mm long; teeth of the limb c. 0.7 mm long, subacute. *Anther tube* c. 7 × 0.4 mm;

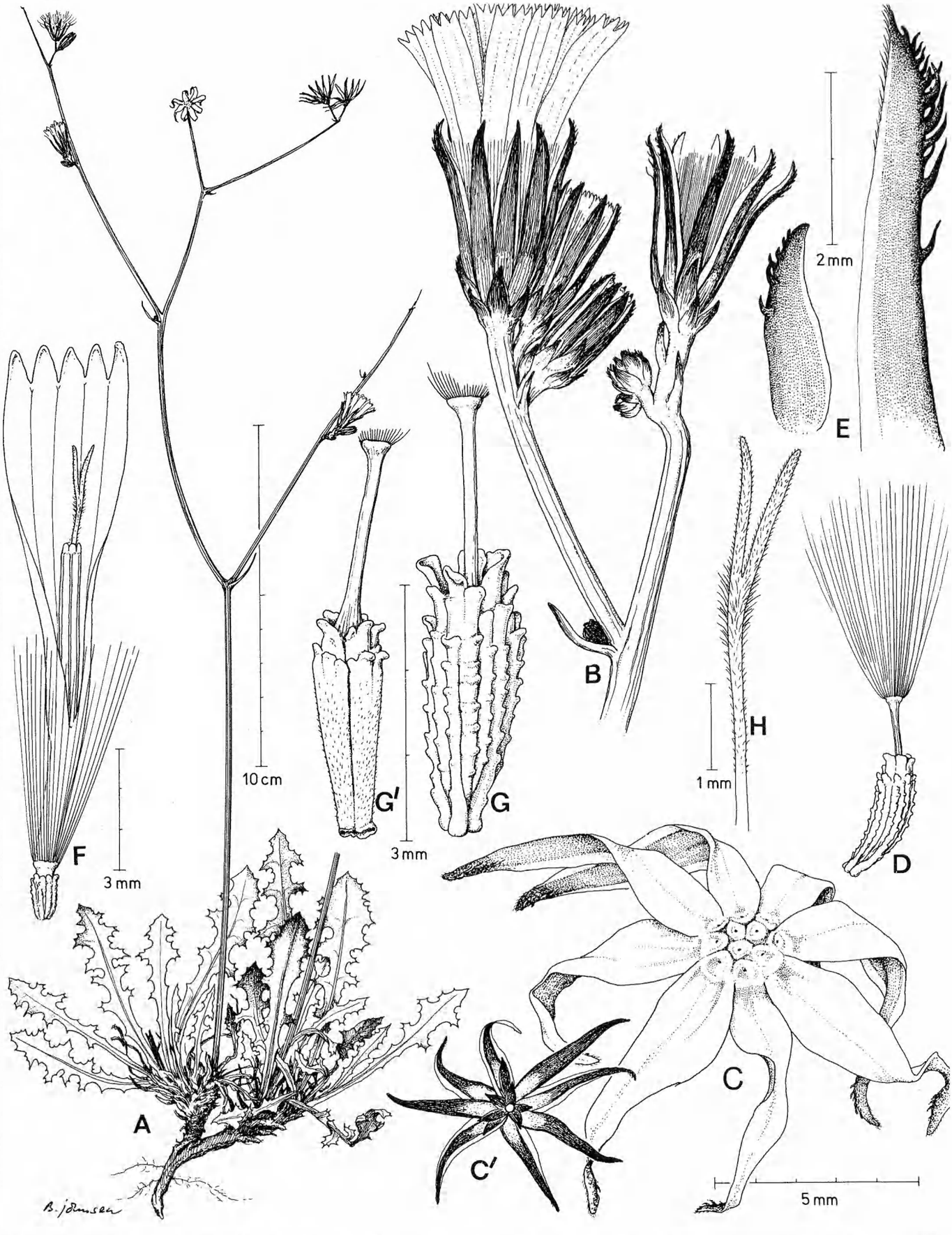

Fig. 1. *Chondrilla lenae*. – A: Habit. – B: A group of lateral capitula. – C: Receptacle of a fruiting head to show alveolate structure. – C′: Same fruiting head seen from the back to show short outer involucral bracts and scarious margins of some of the inner involucral bracts. – D: Achene at the same magnification as C. – E: Outer and inner involucral bracts in side view. Note the long, dark papillae towards the apex. – F: Floret. – G: Mature achene. – G′: Almost mature achene of *C. chondrilloides* for comparison. – H: Style.

Table 1. Differences between *Chondrilla lenae* and *C. chondrilloides*.

C. lenae	*C. chondrilloides*
Basal leaves incise-dentate with rounded incisions and shortly acuminate teeth	Basal leaves entire or remotely dentate
Capitula 8–12(–14) per stem	Capitula 15–25 per stem
Capitula terminal and sometimes lateral	Capitula always terminal
Involucral bracts with long blackish papillae near the apex	Involucral bracts without papillae
Achene glabrous, with 14–16 distinctly tuberculate ribs	Achene appressed-pubescent, without ribs, without or sometimes with a few tubercles near the apex

appendages very small, somewhat hyaline, subacute. *Style branches* 1.3–1.8 mm long, uniformly thick, subobtuse, with erecto-patent scabridity, dark-brown to blackish-brown. *Achenes* beaked; body of achene 3.0–3.5 × 1.1–1.3 mm, often curved in the lower third, somewhat attenuate towards the base, 14- to 16-ribbed with 6–10 tubercles on each rib and a crown of 5 thick scales c. 0.6 mm long at the apex, dark-brown to blackish-brown when fully mature, light-brown when half mature; beak distinctly set off from the body, 2.5–3.5 mm long. *Pappus* hairs in 2 series, 3–4 mm long, scabrid, white. *Chromosome number* 2n = 10.

Taxonomic relationship. Of the four European species of *Chondrilla, C. lenae* is undoubtedly related to *C. chondrilloides* from the Alps, but differs in a number of characters (Table 1).

Cytology. Ten plants were raised from seeds taken from herbarium specimens and kept in cultivation in the experimental field of the Copenhagen University Botanical Garden. Four of them were examined cytologically. The plants were kept overnight at c. 5°C; root tips were fixed in the Svalöv modification of the Navashin-Karpechenko fixative, sectioned with a microtome and stained with crystal violet. The chromosome number was found to be 2n = 10 which agrees with the number reported for *C. chondrilloides*. The size of the chromosomes varies between c. 5 and 8 μm. All the chromosomes are more or less metacentric; satellites were observed on one pair.

Distribution and habitat. On Mt Pangaion, *C. lenae* was found on a gravelly slope of a small limestone ridge in a non-closed plant community with *Polygala supina* Schreb. subsp. *rhodopaea* (Velen.) McNeill, *Viola delphinantha* Boiss., *Genista carinalis* Griseb. and *Aethionema saxatile* (L.) R. Br.

A second collection was found by A. Strid, Copenhagen, in the personal herbarium of W. Greuter in Berlin. It was gathered by Greuter on Mt Orvilos (Ali Botuš) near the Bulgarian border in 1978.

Acknowledgements. The Latin diagnosis was prepared by Dr T. Christensen, and the illustration by Mr B. Johnsen.

Botanical literature

Bănărescu, P. & Boşcaiu, N. 1978: *Biogeographie*. VEB Gustav Fischer Verlag, Jena. 392 pages, 48 figures. Bestellnummer 532 917 6. Price DDR 45 M.

Biogeography is a science of utmost importance for the understanding of the processes of evolution and for the conception of the history of living beings. It may seem strange, therefore, that even most of its recently published introductory textbooks have shunned all mentioning of the new explanations of its basic processes that cytogeneticists have unravelled during the past three-quarters of a century, that these texts seem to prefer taxonomic concepts lacking in exactness and sometimes even based on socalled phenetics that is opposite to genetics, that they are largely concerned with speculations based on the superstitions of the stability of the oceans and the lability of the species, and that they tend to put much emphasis on the unproven conjecture of long distance dispersal to explain the distribution of the biota.

Recently a very different approach to a biogeographical introductory text has become available, a book that puts emphasis on modern results of genetics and plate tectonics and downplays many of the classical explanations that history has found to be inadequate. It is a teamwork by a zoologist, Petru Bănărescu, and a botanist, Nicolae Boşcaiu, and it was originally written in Romanian. It has now, five years after its first publication, become available in a good German translation, and it is to be hoped that it will also be translated into English for the numerous students confined to this language in which nothing even remotely so modern is available.

The first chapter discusses the objectives of biogeography, its connection with other sciences and its historical interpretation, followed by a review of the phenomena of speciation in the perspective of genetical and historical biogeography. These parts are succeeded by one on cytogeography and by another on the area that leads to a chapter on the faunas and floras and their origins and to another that discusses the paleogeographical factors that have influenced the distribution of biota. The Quaternary glaciations and their biogeographical effects are discussed in a section of their own, and so is the reconstruction in time and space of the areas of some selected groups of animals and plants. The marine biogeographical regions and their evolution receive a detailed interpretation, followed by a section on the biogeographical regions of the landmasses, and by a chapter reviewing questions regarding the distribution of animals living in freshwater. There is a comprehensive bibliography, lists of authors and subjects and a register of scientific animal and plant names. The book is amply illustrated with distribution maps, either new or from recent publications.

As this enumeration indicates, the authors approach biogeography from several new points of view. Those looking for classical ideas will find most of them to be sympathetically mentioned, although he is likely to find more stimulation in modern surveys of continental drift and cytogenetics as these affect biogeographical concepts, and also to enjoy the fresh and critical approach to several classically observed phenomena.

The book is nicely produced and reasonably priced, and there seem to be few major misprints. The most disturbing of the latter may be the reference to polyploidy in the fauna, rather than the flora, of Macquarie Island on p. 70, and the dropping from the bibliography of a few references mentioned in the text.

Áskell Löve

Veronica bornmuelleri (Scrophulariaceae) new to Europe

Per Hartvig

Hartvig, P. 1979 09 30: Veronica bornmuelleri (Scrophulariaceae) new to Europe. [Materials for the Mountain flora of Greece, 3.] *Bot. Notiser 132:* 367–369. Stockholm. ISSN 0006-8195.

Veronica bornmuelleri Hausskn. (subsect. *Biloba* Römpp), a W and C Asian species, is reported from Mt Smolikas in NW Greece as new to the European flora and as introduced to Colorado, N America. A description of the plant is given.

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Veronica subsect. *Biloba* belongs to the mainly annual section *Alsinebe* and includes according to Stroh (1942) and Borisowa (1955) some 15 species, all restricted to W and C Asia. They are primarily characterized by the sepals, which are connate in pairs, the deeply emarginate capsule and the rugose, hollow seeds. They occur on open soil in mountain areas, frequently in cultivated places and fields.

Four species reach Anatolia on the W limit of their distribution: *V. biloba* Schreber, *V. bornmuelleri* Hausskn., *V. campylopoda* Boiss. and *V. intercedens* Bornm. (Fischer 1978). They are among the most widespread in the subsection, and some of the species have occasionally been reported as introduced far outside their natural area; *V. campylopoda* from Europe near Berlin in 1940 (Hartl 1968) and from N America in Utah (Rydberg 1922) and New York (Gleason 1958). *V. biloba* has been found in Washington, Idaho and Utah (Rickett 1973). I am not able to confirm these records, but I have seen two collections in Copenhagen (C) of "*V. biloba*" from N America. The one was *V. campylopoda* from Utah (Cottam 7619), the other *V. bornmuelleri* from Colorado: Boulder, mouth of Bear Canyon, 5800 ft (Lanham & Weber 23.5.1965).

In 1976 *V. bornmuelleri* was discovered in NW Greece as new for the European flora.

Collections. W Macedonia, Nom. and Ep. Grevenon, Mt Smolikas, E ridge, 2 km SW of Samarina. Plateau with grazed meadow among *Carduus tmoleus* s.l., 1880 m, ophiolithic substr., 10.7.1976, Hartvig, Baden & Christiansen 5722 (ATH, C, G, K, LD) – 4 km S of Samarina by the road to Armata. Rocky, SE-facing slope in open woodland of *Pinus nigra* with scrub of *Buxus* and *Juniperus*, 1400 m, ophiolithic substr., 12.7.1976, Hartvig, Baden & Christiansen 5863b (C).

Description. Usually erect annual with several long ascending branches from lower part of the stem. *Stems* 25–30 cm, glandular-hairy. *Leaves* sparsely pubescent, petiole 0–5 mm, lamina ovate, 25–35 × 12–18 mm, remotely serrate. *Racemes* long, with 12–30 flowers and with up to 1.3 mm long, glandular hairs. *Bracts* ovate, acuminate, glandular-hairy, petiolate, gradually decreasing in size, lower ones up to 17 × 8 mm, subincise-serrate, with 2–3 pairs of acute–acuminate teeth, the uppermost with one pair of teeth or entire. *Calyx lobes* ovate, acuminate, 7–10 × 3.5–5 mm, entire or the lower with 1–2 pairs of acute teeth, connate for c. 1 mm, with glandular hairs. Fruiting pedicels subpatent, 4–8(–15) mm long, straight to slightly recurved, reflexed below the calyx. *Capsule* 4–4.5 × 5–6.5 mm, 2-lobed, sinus 2.5–3 mm deep, acute, lobes not or slightly divergent. Style 1.1–1.4 mm. Pedicels and capsule with short, 0.1–0.2 mm long, ± crispate eglandular hairs and 0.3–0.7(–

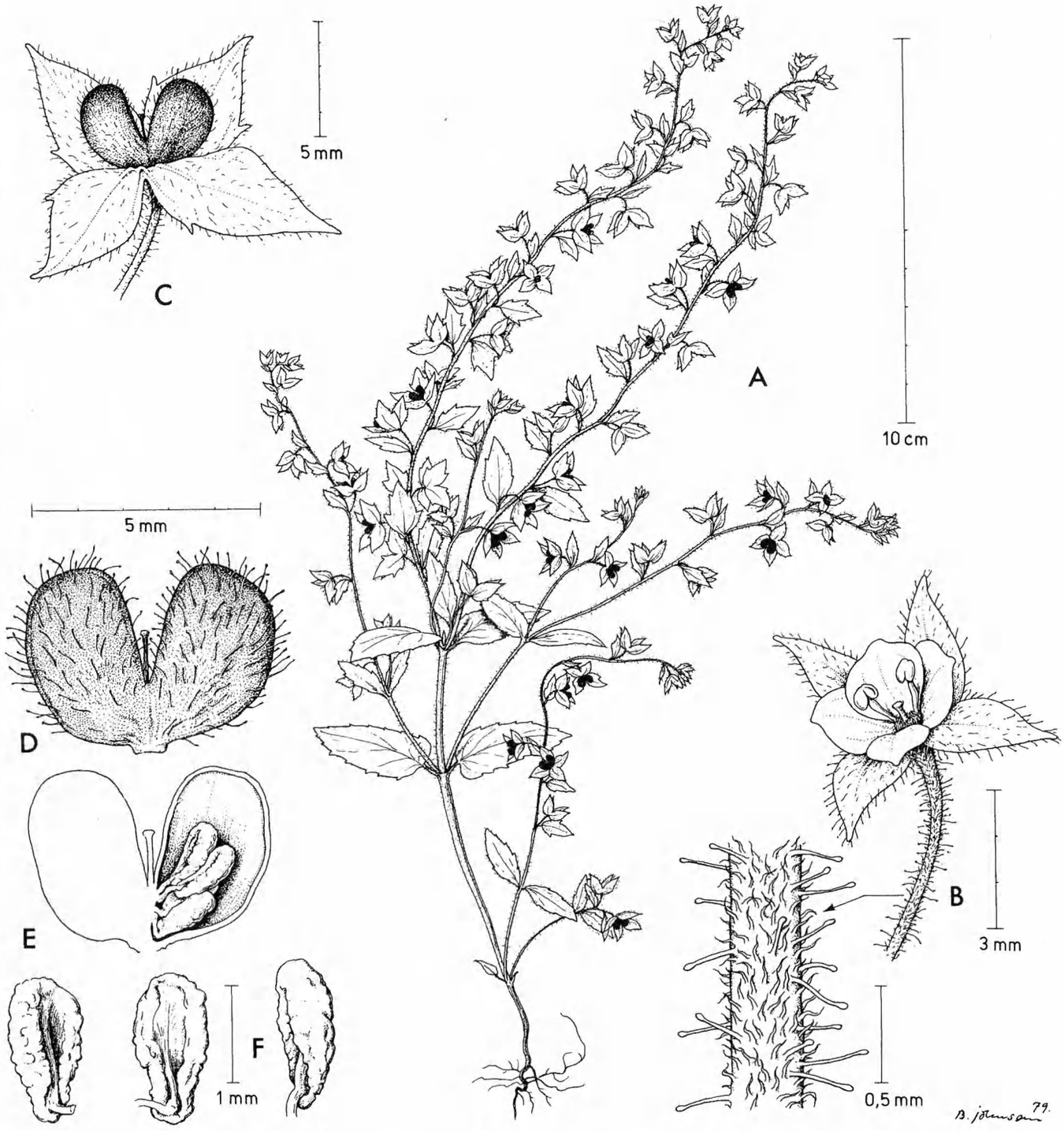

Fig. 1. *Veronica bornmuelleri* (Hartvig, Baden & Christiansen 5722). – A: Habit of fruiting plant. – B: Flower and part of pedicel. – C: Fruit. – D: Capsule. – E: Opened capsule lobe with 4 seeds. – F: Seeds.

0.9) mm long, spreading glandular hairs. – Fig. 1.

The plants match material from the type locality of *V. bornmuelleri* in Anatolia well (Amasya: Akdagh, Bornmüller no. 1808 (C); type not seen).

Affinities. *V. bornmuelleri* has often been confused with *V. biloba* and *V. campylopoda*, and mixed collections are frequent from places where the species occur together. Small plants of *V. bornmuelleri* with entire calyx lobes, less serrate bracts or with divergent capsule lobes have often been misinterpreted. A useful treatment of the Turkish taxa has recently been published by Fischer (1978). According to him *V. bornmuelleri* is best distinguished from *V. biloba* on the longer, usually glandular hairs on the capsule and the inflorescence, and on the bracts with 1–4

teeth (*V. biloba* has only short hairs and entire bracts), and from *V. campylopoda* on the wider calyx lobes and on the bracts, which in *V. campylopoda* are narrower and entire, the lower sometimes crenate-serrate.

Phytogeography. The find of *V. bornmuelleri* in NW Greece almost 1000 km from the nearest locality in Anatolia is phytogeographically interesting. It adds to the increasing number of Irano-Turanian plants with an isolated occurrence in the Balkans found during the last few years of intense floristic exploration of the mountains of N and C Greece. Other examples of the same kind are the discoveries of *Trigonella strangulata* and *T. velutina* (Greuter 1975), *Thesium brachyphyllum* (Aldén 1976) and *Thlaspi kotschyanum* (Gustavsson 1978).

Acknowledgement. I wish to thank Mr Bent Johnsen for the skilful drawing.

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Almost a quindecennial ago, a volume consisting of two large books on the distribution of the ferns, gymnosperms and dicotyledons of C Europe, from Salicaceae to Fabaceae in the classical Engler system, was published by Professor Hermann Meusel and his cooperators of Halle in E Germany. This is a comparative review of the areas of the numerous boreal species of this flora, a work comparable to, but widely more comprehensive than the maps of the circumpolar and amphiatlantic plants worked out by Professor Eric Hultén. The first of these impressive books includes almost 1000 maps. Many of these cover several species and also extra-European relatives, so the number of taxa mapped probably surpasses 2000. The second book is a monumental text describing and discussing the maps and evaluating the various floristical areas they represented.

Although a second and final volume of this immense review of plant distribution areas was said to be in preparation for an early publication, it was not published until late in 1978. It reaches only to the family Plantaginaceae, so the remaining families, the important bibliography and the registers have been left for a third volume, which hopefully will appear soon, since the authors indicate that it is almost completed. The second volume comprises 656 maps representing about 1700 species so the set already widely surpasses the coverage of any atlas of plants ever published.

The beginning chapter of the present volume – 145 pages of concentrated information – continues the review of the forms and types of areas of distribution which characterizes the families included. This part is followed by 110 pages of diagrams of the areas and descriptions of the flora elements, whereas almost 170 pages are devoted to short but comprehensive explanations of the maps and detailed discussions of the taxonomy and relationship of the particular species and their variations.

Nobody who scrutinizes this superb text and its accompanying maps can avoid to be impressed by its quality and quantity, or by the rare ability of the authors to concentrate detailed informations that otherwise are available in numerous books, and still add own observations and evaluations. Such a book cannot be but praised even by those many, who wish they had themselves been able to do even a fraction of the work basic to the atlas. But as all excellent accomplishments, it is a godsend also to those who prefer to judge the works by others from their own limited experience, since points of disagreement have not been avoided by the authors. That, however, is of minimal significance in a work packed with old and new information of the highest exactness. It will be regarded as the standard in its field for generations, an atlas that no botanical library can afford not to have on its shelves. Those who recognize its importance and realize its superiority will wait eagerly for the third and last volume of this magnum opus of an unusual visionary.

Áskell Löve

Embryology of Arctotideae-Gorteriinae (Compositae)

Lennart Ahlstrand

Ahlstrand, L. 1979 09 30: Embryology of Arctotideae-Gorteriinae (Compositae). *Bot. Notiser 132:* 371–376. Stockholm. ISSN 0006-8195.

Macrosporogenesis and embryo sac development of three species of *Gazania* Gaertn., two species of *Hirpicium* Cass., and one species of *Berkheya* Ehrh. were studied. The archespore is 1-celled in *Berkheya* and *Gazania*, and 1- or rarely 2-celled in *Hirpicium*. Embryo sac development is monosporic of the 8-nucleate Polygonum type. Slender hair-cells at one side of the micropylar canal are observed in *Gazania* and *Berkheya;* in mature embryo sacs these cells decompose forming a coherent mucuous area. The synergids do not reach far into the micropylar canal; no synergid haustoria are present. There are three antipodes; in *Berkheya* they divide repeatedly and often become 2-nucleate. Antipode haustoria are never developed. In *Gazania* and to some extent in *Berkheya* the integumentary tapetum becomes many-layered around the lower half of mature embryo sacs; the upper half of the tapetum remains one-layered. Characteristic for *Gazania* is a large empty chamber half-way encircling the embryo sac in level with the antipodes. The endosperm formation in *Gazania* and *Berkheya* is Cellular. The chromosome number for *Hirpicium gorterioides* (Oliv. & Hiern) Roessler is n = 5.

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The present investigation deals with the macrosporogenesis and embryo sac development of some species of *Berkheya* Ehrh., *Hirpicium* Cass. and *Gazania* Gaertn. These genera have their main distributional areas in S and W Africa. They are also represented in tropical and E Africa and one *Berkheya* species is even found in Nigeria (Roessler 1959, 1970, 1973, Norlindh 1977). The genera comprise 73, 12 and 16 species, respectively (Norlindh 1977).

Material and methods

Fixations were made of material from flowering plants in the Royal Botanic Gardens, Kew (*Gazania maritima, Berkheya adlami* Hook. f. = *Berkheya radula;* 1966), in the Botanical Garden of Copenhagen (*Gazania rigens* var. *uniflora;* 1966, 1967), and in the Botanical Garden of Uppsala (*Gazania rigens* var. *rigens;* 1967). The material of *Gazania jurineifolia* and the *Hirpicium* species was collected in 1963 in SW Africa by Dr L. E. Kers, Stockholm.

The *Gazania* specimens were identified by Dr H. Roessler, München. Kers's specimens (Kers 23 *Gazania jurineifolia,* Kers 483 *Hirpicium gorterioides,* Kers 884 *H. echinus*) are at S. All other specimens and the slides studied are at GB.

The technique used was described by Ahlstrand (1978).

Results

Gazania maritima Levyns. The archespore is 1-celled (Fig. 1 A). The megasporogenesis (Fig. 1 A–C) results in the formation of a linear tetrad (Fig. 1 C). The lowermost megaspore develops into an embryo sac. The other ones degenerate (Fig. 1 D). The embryo sac development is monosporic and of the Polygonum type (Fig. 1 D–G). The nucellar epidermis remains unchanged up to the 2-nucleate stage of the embryo sac (Fig. 1 E), but since it is only very rarely present in the 4-nucleate stage (Fig. 1 F) it seems to succumb rapidly.

The integumentary tapetum begins to develop already at the stage of embryo sac mother cells. In early mature embryo sac stages the tapetum is

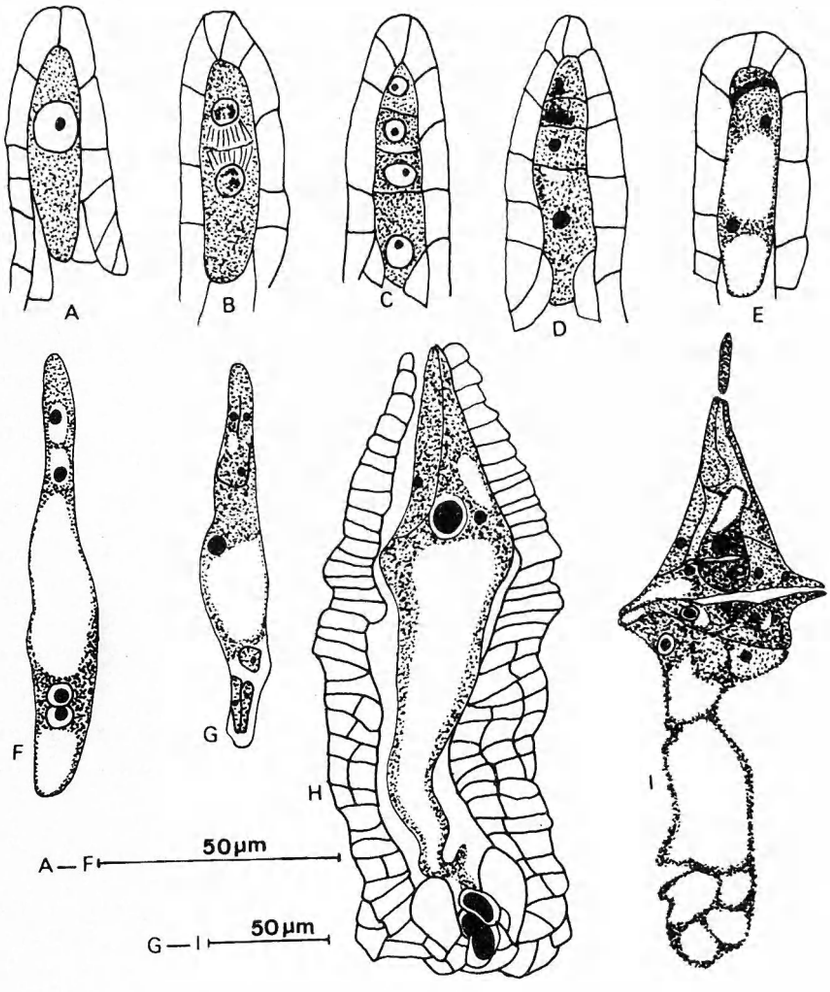

Fig. 1. *Gazania maritima*. – A: Megaspore mother cell. – B: Dyad formation. – C: Tetrad. – D: Old tetrad; upper megaspores degenerating. – E: 2-nucleate embryo sac; degenerating megaspores, nucellar epidermis unchanged. – F: 4-nucleate embryo sac. – G: Organized embryo sac. – H: Old embryo sac; integumentary tapetum, degenerating antipodes surrounded by an empty chamber outside the embryo sac. – I: Embryo sac with proembryo, endosperm cells, richly vacuolated plasma at the chalazal end.

one-layered; in later stages the cells of the lower half of the tapetum divide periclinally resulting in a rather thick embryo sac cover. The upper tapetum cells do not divide (Fig. 1 H).

The synergids are comparatively small in organized embryo sacs (Fig. 1 G); they do not extend into the micropylar canal. There are three antipodes; two of them usually lie side by side and the third one on the top of them (Fig. 1 G). They degenerate long before the endosperm formation starts up (Fig. 1 H). There is a large empty chamber on a level with the antipodes, between the integumentary tapetum and the embryo sac halfway surrounding the latter. On one single microscopical section this chamber looks like two separate rooms (Fig. 1 H). Serial sections, however, reveal that they are coherent.

The endosperm formation is probably ab initio Cellular as early occurring divisions of the endosperm nuclei are accompanied by cell wall formation (Fig. 1 I). In endosperm stages the central part of the embryo sac expands outwards (Fig. 1 I). At the same time the embryo sac elongates at the chalazal end and the plasma becomes vacuolized (Fig. 1 I). Probably the expanding parts of the embryo sac function as haustoria.

Other Gazania species. *G. rigens* (L.) Gaertn. var. *uniflora* (L. f.) Roessler (Fig. 2 A–F), *G. rigens* var. *rigens* (Fig. 2 G–O) and *G. jurineifolia* DC. ssp. *scabra* (DC.) Roessler (Fig. 3). The embryology of these species is very similar to that of *G. maritima*. There are no synergid haustoria, the integumentary tapetum is more than one cell-layer thick around the lower part of the embryo sac, and there is a prominent empty chamber in the chalazal region of the embryo sac. Tall, extended cells, hair cells, are present at one side of the micropylar canal (see Schnarf 1929 p. 288). In later stages of the embryo sac development their cell walls are sometimes dissolved; the cell plasma thus forms a coherent mucilaginous mass (Fig. 3 E).

Hirpicium echinus Less. The archespore is 1-celled (Fig. 4 A). The embryo sac development

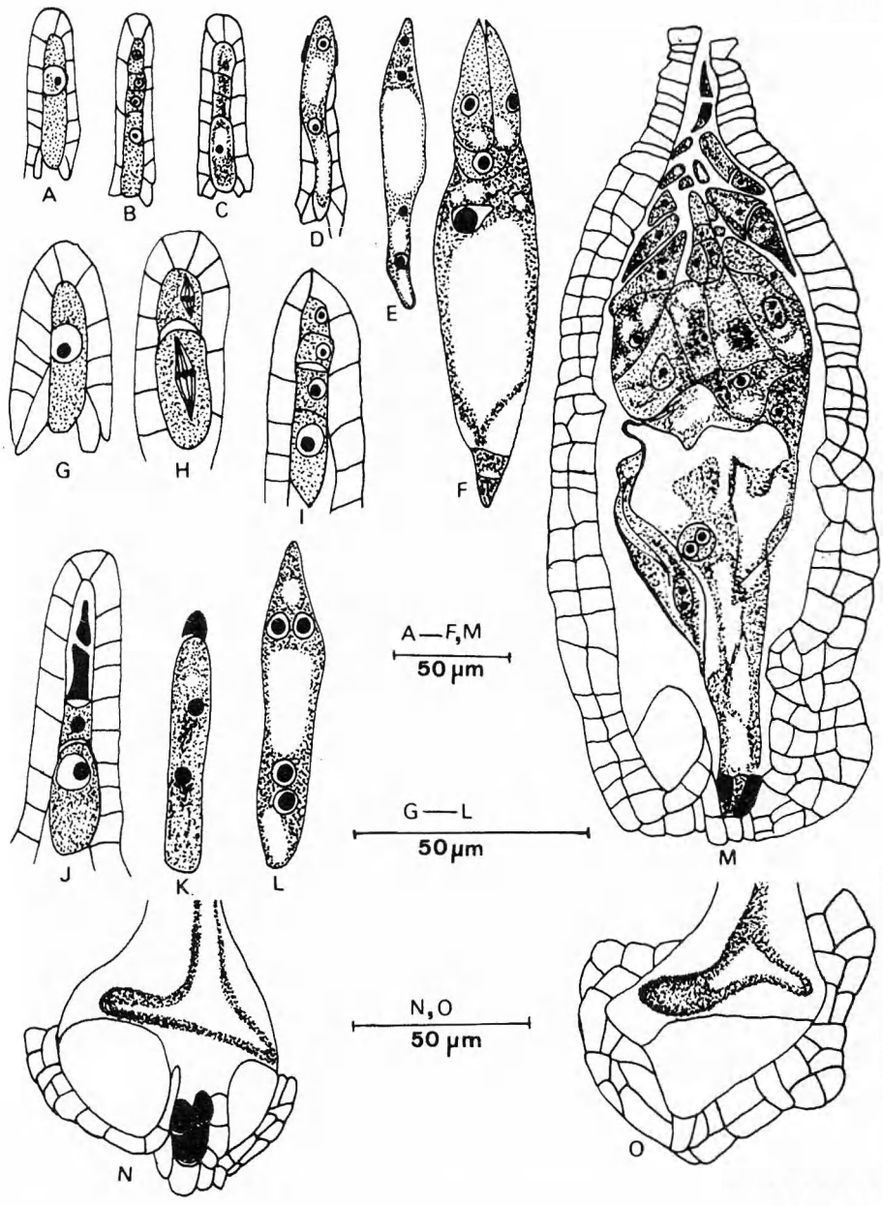

Fig. 2. A–F: *Gazania rigens* var. *uniflora*. – G–O: *G. rigens* var. *rigens*. – A, G: Megaspore mother cell. – B, I: Linear tetrad. – C, J: Old tetrad with functional megaspore. – D: 2-nucleate embryo sac, part of the nucellar epidermis degenerating. – E, L: 4-nucleate embryo sac. – F: Organized embryo sac; vacuolated synergids. – H: Homotypic divisions of dyad cells; metaphase. – K: 2-nucleate embryo sac; degenerating megaspores, no remainders of nucellar epidermis. – M: Embryo sac with endosperm cells and proembryo; degenerating antipodes, the integumentary tapetum several cells thick in chalazal direction. – M–O: Serial sections of an embryo sac reveal the existence of one single, large, empty chamber outside the embryo sac chalazally.

is of the monosporic Polygonum type (Fig. 4 B–D). The nucellar epidermis has not become quite degenerated in 4-nucleate embryo sac stages (Fig. 4 D). Organized embryo sacs have not been met with in this material.

Hirpicium gorterioides (Oliv. & Hiern) Roessler. The archespore is usually 1-celled (Fig. 4 E). Only once an archespore of several cells was found (Fig. 4 F). Megasporogenesis (Fig. 4 G, H) results in a linear tetrad (Fig. 4 H). The lowermost megaspore germinates to produce an embryo sac (Fig. 4 I). The embryo sac development is of the Polygonum type (Fig. 4 I–L). The organized embryo sac has tall synergids but they do not extend into the micropylar canal (Fig. 4 L). There are three 1-nucleate antipodes (Fig. 4 L). The chromosome number n = 5 has been determined in pollen mother cells (Fig. 4 M).

Berkheya radula (Harv.) De Wild. The archespore is probably one-celled. Some potential archesporial cells are often seen beneath the functioning megaspore mother cell (Fig. 5 A). Usually (Fig. 5 A) but not always (Fig. 5 B) the lowermost megaspore develops into an embryo sac. The embryo sac development is monosporic of the Polygonum type (Fig. 5 A–F). The synergids are comparatively small. The antipodes divide repeatedly and become numerous (Fig. 5 F, I). The cells at one side of the micropylar canal elongate. In later stages of mature embryo sacs they degenerate and their cell walls begin to dissolve (Fig. 5 G). Cytoplasma may

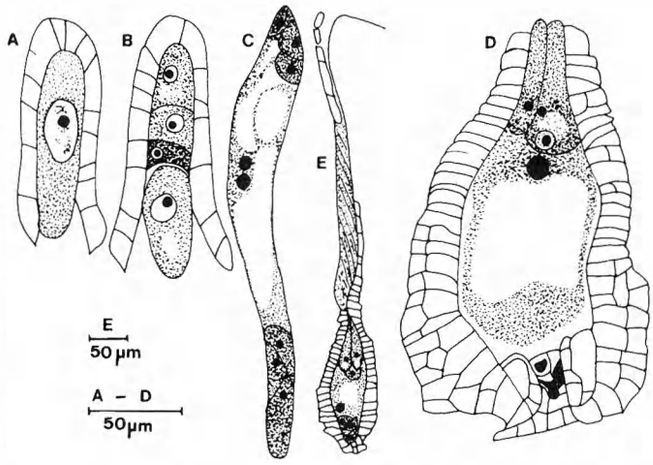

Fig. 3. *Gazania jurineifolia* ssp. *scabra*. – A: Megaspore mother cell. – B: Linear tetrad; the basal megaspore is functioning. – C: Early stage of an 8-nucleate embryo sac. – D: Embryo sac stage with the integumentary tapetum thickened chalazally; degenerating antipodes; empty chamber between the integumentary tapetum and a single row of cells in level with the antipodes. – E: Organized embryo sac stage; polar nuclei fused; integumentary tapetum cells still undivided; cells in the micropylar canal decomposing, forming a coherent mucuous area.

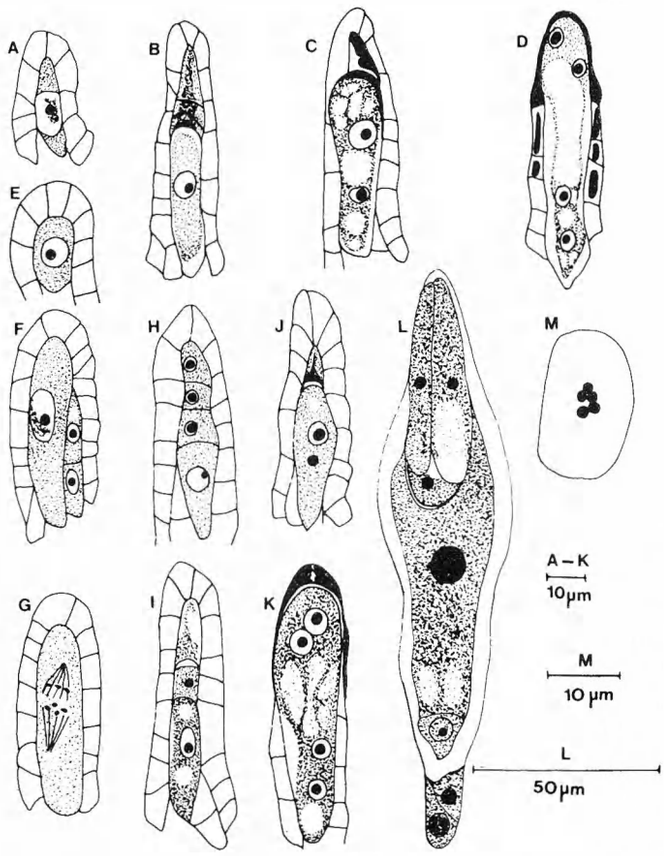

Fig. 4. A–D: *Hirpicium echinus*. – E–M: *H. gorterioides*. – A: Megaspore mother cell. – B: Functioning megaspore mother cell; the other three megaspores degenerating. – C: 2-nucleate embryo sac stage; degenerated megaspores, nucellar epidermis still unchanged. – D: 4-nucleate embryo sac stage; degenerating nucellar epidermis. – E: Megaspore mother cell. – F: Archespore of three megaspore mother cells. – G: Megaspore mother cell in anaphase. – H: Linear tetrad. – I: Tetrad; the chalazal megaspore functioning. – J: 2-nucleate embryo sac; rests of degenerating megaspores. – K: 4-nucleate embryo sac; degenerating nucellar epidermis. – L: Organized embryo sac; polar nuclei fused, three antipodes. – M: Pollen mother cell, metaphase, n = 5.

then accumulate so as to fill up the micropylar canal. Double fertilization occurs (Fig. 5 H). The integumentary tapetum in the chalazal part of the embryo sac becomes thickened due to cell divisions (Fig. 5 I). The endosperm formation seems to be Cellular (Fig. 5 J).

Discussion

Hoffmann (1894) placed the three genera in the subtribe Gorteriinae of the tribe Arctotideae, a subtribe characterized by more or less connate involucral bracts. The same author also recognized the subtribes Arctotidinae (with free involucral bracts) and Gundeliinae (with the flowerheads gathered into heads of a second order). On behalf of style similarities he regarded the Arctotideae as being related to the Cynareae. Some species of the Gorteriinae are also similar to the Cynareae in habit. Roessler (1959) and Norlindh (1977) included the genera *Berkheya, Cullumia* R. Br., *Didelta* L'Hérit., *Heterorhachis* Sch. Bip. ex Walpers, *Cuspidia* Gaertn., *Gorteria* L., *Hirpicium* and *Gazania* in the subtribe Gorteriinae. Moreover Norlindh (1977) also accepted *Heterolepis* Cass.

The pollen grains of *Berkheya* species are either echinate, echinolophate or lophate with non-caveate exines. The always lophate pollen grains of *Gazania, Gorteria* and *Hirpicium* have caveate exines (Stix 1960, Skvarla et al. 1977 p. 147). Leins & Thyret (1971) regarded the irregularly echinate pollen grain type of *Berkheya* to be the most primitive, and they recognized three evolutionary lines in the Gorteriinae, one of them including *Berkheya,* another one *Gazania* and *Hirpicium.*

The chromosome numbers 2n = 14 and 16 have been found in *Berkheya* (Gelin 1936, Turner & Lewis 1965). Nordenstam (1967, 1969) found 2n = 10 and 20 in *Gazania* and 2n = 10 in *Hirpicium.*

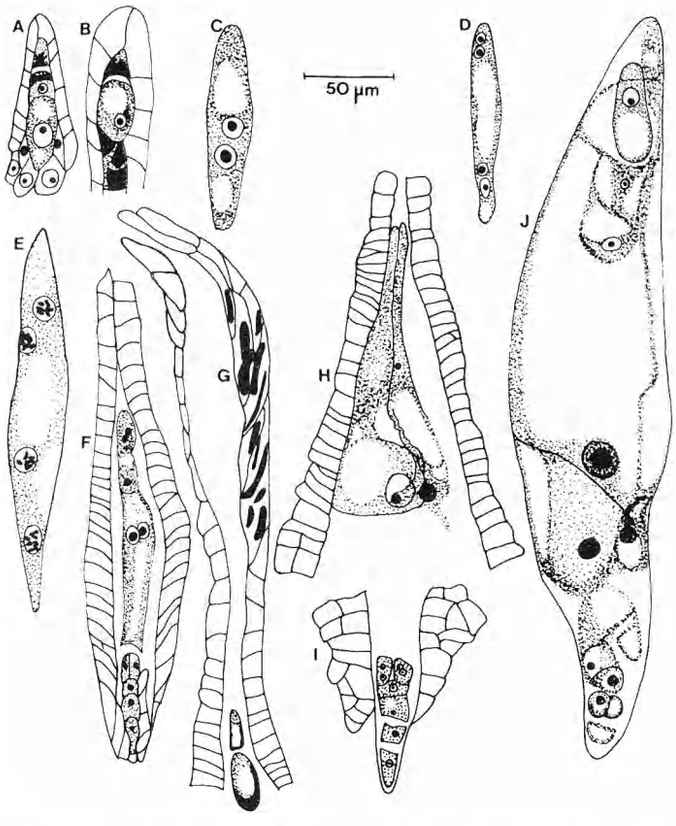

Fig. 5. *Berkheya radula*. – A: Functioning megaspore mother cell of a degenerating linear tetrad; potential megaspore mother cells below the tetrad. – B: 1-nucleate embryo sac and degenerating megaspores. – C: 2-nucleate embryo sac. – D: 4-nucleate embryo sac. – E: 4-nucleate embryo sac preparing for division. – F: Organized embryo sac; antipodes divided before fusing of the polar nuclei, the integumentary tapetum of one single row of cells. – G: Decomposing mucilaginous slender cells of one side of the micropylar canal. – H: Egg apparatus and the primary endosperm nucleus; fertilization process is accomplished. – I: Chalazal part of the same embryo sac as in H; six antipodes, two of them 2-nucleate, the integumentary tapetum thickened through cell divisions. – J: Embryo sac with proembryo and endosperm, probably of the Cellular type; antipodes degenerating.

Schürhoff (1926) stated that "*Gazania longifolia*" had no synergid haustoria. Gelin (1936) found a 1-celled archespore and an embryo sac development of the Polygonum type in *Berkheya bergiana* Söderb. He presumed that the synergids did not develop into haustoria. The cell walls of one part of the micropylar canal became mucilaginous which probably helped the penetration of the pollen tube. Primarily three antipodes were developed which divided repeatedly; no less than 14 antipodes were observed in one embryo sac.

In the present investigation *Gazania, Hirpicium* and *Berkheya* are found to have the Polygonum type of embryo sac development with primarily three antipodes. In mature embryo sacs *Gazania* differs from *Berkheya* in number of antipodes, in a considerably thicker integumentary tapetum around lower parts of embryo sacs and in the presence of a large empty chamber between the tapetum and the embryo sac. A thorough study of mature embryo sac stages of *Hirpicium* could not be done due to lack of material. The embryological differences between *Gazania* and *Berkheya* can possibly be used to separate these genera from each other. Since only a few species are embryologically investigated, however, the validity of such characters for this purpose is very unsafe for the present. Besides no less than eight series have been recognized in *Berkheya* (Roessler 1959) and the species up to now embryologically investigated belong to the same series. In accordance with great variations of the pollen grains in *Berkheya*, a wider array of characteristics should be expected in a more far-reaching embryological investigation of this genus. Nevertheless the embryological results confirm the palynological and cytotaxonomical differences between *Berkheya* and *Gazania*.

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Embryology of Arctotideae-Gundeliinae (Compositae)

Lennart Ahlstrand

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The embryology of *Platycarpha carlinoides* Oliv. & Hiern and *Gundelia tournefortii* L. has been studied. Microspore formation is simultaneous and the microspores are tetrahedrically arranged; in some cases isobilateral tetrads were found in *Gundelia*. *Platycarpha* develops a secretory microsporangial tapetum, *Gundelia* a tapetal periplasmodium. Both species have the monosporic 8-nucleate Polygonum type of embryo sac development. *Platycarpha* has long synergids; possibly one of them can form a haustorium. The synergids in *Gundelia* are short. *Platycarpha* and *Gundelia* never develop antipodal haustoria.

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The monotypic genus *Gundelia* L. is distributed from Asia Minor to Iran. *Platycarpha* Less. with a few species only is restricted to S Africa and Namibia (Norlindh 1977).

In the system by Hoffmann (1894) *Platycarpha* and *Gundelia* are the only genera in the subtribe Gundeliinae of the tribe Arctotideae. This subtribe has dense clusters of homogamous, paleaceous flower-heads, a difference from the other two subtribes (Arctotidinae and Gorteriinae).

Hoffmann regarded the relationship between *Platycarpha* and *Gundelia* as uncertain, and pointed out that *Platycarpha* has much in common with the tribe Mutisieae. Based on pollen similarities Stix (1960) transferred *Platycarpha* to the tribe Mutisieae and *Gundelia* to the Cynareae. Evidence from morphological microcharacters caused Robinson & Brettell (1973) to move *Platycarpha* to the tribe Cynareae. Norlindh (1977) also placed *Platycarpha* in the Cynareae but retained *Gundelia* in the Arctotideae. Dittrich (1977) accepted neither *Platycarpha* nor *Gundelia* in the Cynareae; he found they were best placed in the Arctotideae.

The present investigation deals with the microsporogenesis, the macrosporogenesis and the embryo sac development of *Platycarpha carlinoides* Oliv. & Hiern and *Gundelia tournefortii* L.

Material and methods

The material of *Platycarpha* was fixed in the field by Dr L. E. Kers, Stockholm, during his visit to SW Africa in 1963. The *Gundelia* material was gathered in Jerusalem in the beginning of May in 1968 by Miss Bilha Nachman. Part of the material she fixed in the field, the other part she sent in fresh condition to Göteborg for fixation.

The cytological technique used is that described by Ahlstrand (1978). In addition staining with Heidenhain's Iron-Haematoxylin was successfully used in *Gundelia*.

The voucher specimens of *Platycarpha carlinoides* (Kers 1616) are kept at S. All the slides studied, as well as the voucher specimens of *Gundelia tournefortii,* are at GB.

Results

Platycarpha carlinoides. In early pollen mother cell stages the microsporangium wall consists of four cell-layers: epidermis, endothecium, middle layer and tapetum (Fig. 1 A). At the time when separate pollen mother cells are differentiated, the middle layer is degenerated; the nuclei of the tapetal cells are very often divided and the cells

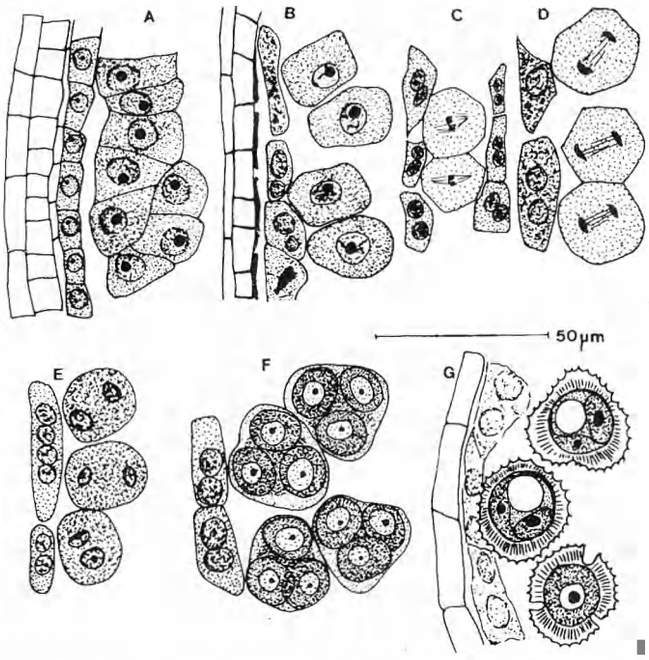

Fig. 1. *Platycarpha carlinoides*. Microsporogenesis (anthers in longitudinal sections). – A: Microsporangial wall and sporogenous tissue. – B: Middle layer degenerating; tapetal cells 2-nucleate; microspore mother cells. – C: Microspore mother cells in metaphase of the heterotypic division. – D: Anaphase. – E: Telophase; tapetal cells 2- or 4-nucleate. – F: Microspore tetrads; tapetal cells still in situ, unchanged. – G: Pollen grains; tapetal cells poor of plasma; endothecial cells.

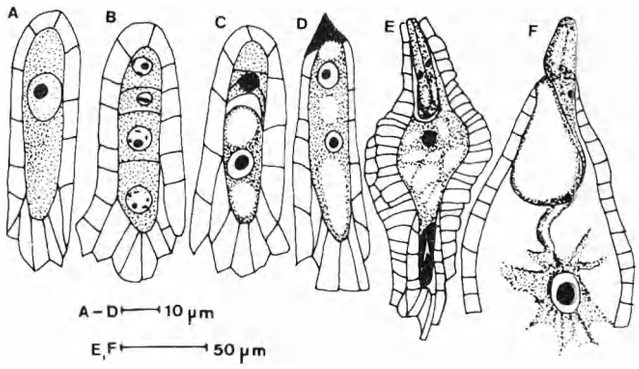

Fig. 2. *Platycarpha carlinoides*. Megasporogenesis and embryo sac development. – A: Megaspore mother cell. – B: Tetrad. – C: Old tetrad; 1-nucleate embryo sac. – D: 2-nucleate embryo sac. – E: Mature embryo sac. – F: Upper part of an embryo sac after fertilization.

have become 2-nucleate (Fig. 1 B). During the meiotic divisions the tapetal cells remain in situ and sometimes they become 4-nucleate (Fig. 1 C–E). Microspore formation is simultaneous, resulting in tetrahedral tetrads (Fig. 1 F). The tapetal cells gradually disappear during gametogenesis, and their staining gets much less conspicuous. The contours of the tapetal cell walls and nuclear membranes can, however, be observed even when the pollen grains are in an advanced stage of development. When the pollen is ripe, the tapetal cells have disappeared. The tapetum may be classified as Secretory (Fig. 1 G).

The single archespore cell functions directly as the megaspore mother cell. Below this cell are some slender cells (Fig. 2 A) with a rather dark staining (not marked on the figure). These cells persist unchanged during the entire embryo sac development (Fig. 2 A–E). Meiosis gives rise to a linear tetrad (Fig. 2 B). The chalazal megaspore develops into the embryo sac (Fig. 2 C). The nucellar epidermis begins to degenerate in 2-nucleate embryo sac stages (Fig. 2 D). The embryo sac development is monosporic, of the Polygonum type (Fig. 2 C–E). The organized embryo sac is widened in its middle part and tapers from there in the micropylar and chalazal directions (Fig. 2 E). The synergids are rather elongated (Fig. 2 E). The three antipods begin to degenerate already before endosperm formation has started (Fig. 2 E). The integumentary tapetum consists of one layer of cells (Fig. 2 E, F), which have a tendency to divide (Fig. 2 E). The egg cell is not very prominent before fertilization (Fig. 2 E). An embryo sac stage with the double fertilization process accomplished is seen in Fig. 2 F; the passage of the pollen tube into the egg cell and to the primary endosperm nucleus can be followed; the fertilized egg cell has increased considerably in volume and is very poor of plasma; in the micropylar region a haustorium, probably originating from a synergid, is developing. Due to lack of material it is impossible to decide if such haustoria are frequent.

Gundelia tournefortii. The microsporangial wall at the microspore mother cell stage consists of the same four layers as in *Platycarpha* (Fig. 3 A). Microsporogenesis is simultaneous (Fig. 3 B, C) and the tetrads are tetrahedral (Fig. 3 D); sometimes, however, there are also isobilateral tetrads. The tapetal cells often become 2-nucleate already during the first meiotic division (Fig. 3 B). A tapetal periplasmodium develops when the primordial pollen grains appear (Fig. 3 E). The middle layer of the microsporangial wall is ephemeral (Fig. 3 C).

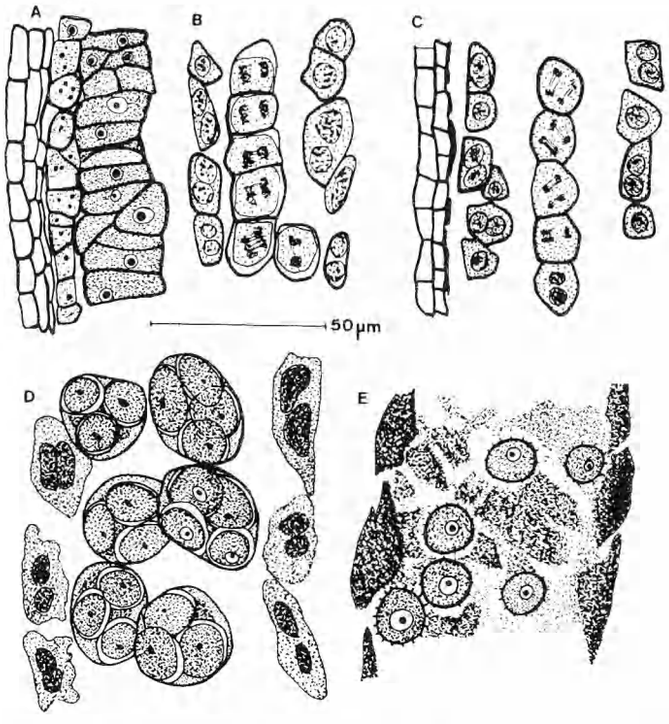

Fig. 3. *Gundelia tournefortii.* Microsporogenesis. – A: Microsporangial wall and sporogenous tissue. – B: Sporogenous cells in anaphase of the heterotypic division; tapetal cells 1- or 2-nucleate. – C: Anaphase of the homotypic division; the middle layer degenerating. – D: Microspore tetrads. – E: Tapetal periplasmodium; young pollen grains.

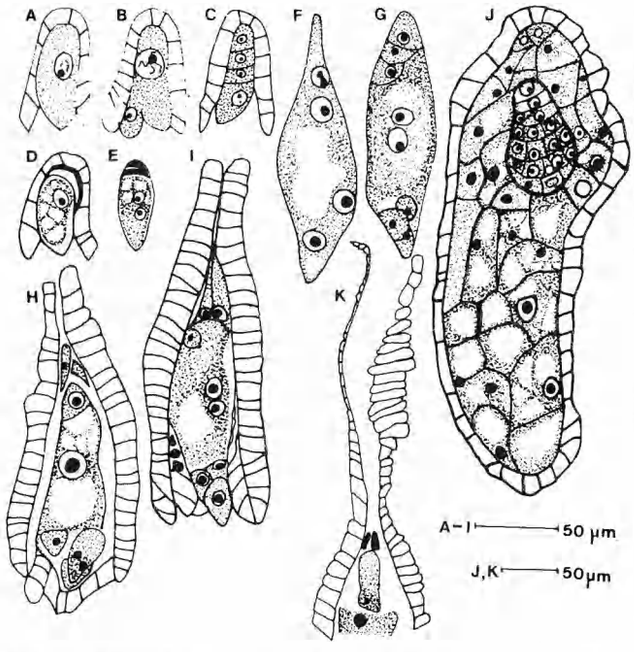

Fig. 4. *Gundelia tournefortii.* Megasporogenesis and embryo sac development. – A, B: Megaspore mother cells. – C: Tetrad. – D: 1-nucleate embryo sac. – E: 2-nucleate embryo sac. Nucellar epidermis wholly used up. – F: 4-nucleate embryo sac. – G: Early 8-nucleate embryo sac. – H, I: Organized embryo sacs. – J: Embryo sac with proembryo and endosperm. – K: Upper part of an embryo sac with broad micropylar canal and hair cells.

The archespore of the megasporangium is usually 1- or 2-celled (Fig. 4 A, B). Some potential archesporial cells are sometimes present at the base of the functional embryo sac mother cell. The tetrad is linear. The chalazal megaspore develops into an embryo sac (Fig. 4 C). The remainders of the other megaspores are still visible in 2-nucleate embryo sac stages. The nucellar epidermis has then disappeared (Fig. 4 E). The embryo sac development is of the Polygonum type (Fig. 4 D–G). The synergids of the organized embryo sac are not particularly long; their tips are not extended into the micropylar canal (Fig. 4 H, I). There are always three antipodes (Fig. 4 G–I) which remain 1-nucleate and do not divide. The integumentary tapetum is one-layered (Fig. 4 H–K); this embryo sac envelope widens from the micropylar region in chalazal direction (Fig. 4 H, I). Endosperm cells fill up the embryo sac totally already in early endosperm stages (Fig. 4 J); endosperm formation is probably Cellular.

Discussion

The species investigated show some important embryological differences.

Platycarpha has a secretory tapetum while *Gundelia* has an amoeboid one. The first mentioned condition is regarded to be more primitive (Schnarf 1931 p. 3). The number of cell-layers in the primary microsporangial wall of the two species is the same which hints a not too distant relationship. An amoeboid tapetum is prevailing in the Compositae (Schnarf 1931 p. 216).

The megasporangial archespore is 1-celled in *Platycarpha,* while conditions are more varied in *Gundelia.* Even though a 1-celled archespore is very common in Compositae, this condition is not necessarily original (Schnarf 1931 p. 8).

The slender, dark-staining cells below the nucellus in *Platycarpha* are not a hypostase for they do not prevent the embryo sac to extend chalazally. They probably have a secretory function.

The integumentary tapetum widens in chalazal direction in *Gundelia* but tapers in *Platycarpha,*

causing different shapes of the growing embryo sacs. In endosperm stages, however, chalazal parts of the embryo sacs become enlarged in both genera.

In *Gundelia* the synergids are not very prominent and they degenerate in late organized embryo sac stages. The synergids of *Platycarpha* are rather tall; sometimes at least they seem to develop into haustoria.

The micropylar canal is broad and bordered with hair cells at one side in *Gundelia*. In *Platycarpha* the corresponding cells are not enlarged, but they turn towards the embryo sac in the same way as in *Gundelia*.

The embryological differences between *Platycarpha* and *Gundelia* support the view that they have no close relationships. *Platycarpha* seems to be slightly more original due to the presence of a secretory tapetum and an invariably 1-celled archespore.

The embryology of Gundeliinae is in many respects similar to that of the Cynareae (studied by Poddubnaja-Arnoldi 1931), especially with the subtribes Centaureinae and Carlininae. However, there are also many important differences and the relationships do not seem certain. The same is true for the proposed relationship of *Platycarpha* to the Mutisieae; in the latter tribe only one species has been studied embryologically, viz. "*Mutisia candolleana*" (Dahlgren 1924).

Acknowledgements. My sincere thanks are due to Miss Bilha Nachman, Jerusalem, Dr Lars E. Kers, Stockholm, and Professor Gunnar Harling, Göteborg, who made it possible for me to undertake this study.

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New combinations in the African genera Chauliodon and Solenangis (Orchidaceae)

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Within the two related genera *Chauliodon* Summerh. and *Solenangis* Schltr. the following new combinations are published: *C. deflexicalcaratum* (De Wild.) L. Jonsson and *S. conica* (Schltr.) L. Jonsson. Selected reference material for *S. conica* is cited, and the relation of the two genera to *Microcoelia* Lindl. is briefly discussed.

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During revisional work on the aphyllous orchid genus *Microcoelia* Lindl. it has been found necessary to transfer *M. deflexicalcarata* (De Wild.) Summerh. and *M. conica* (Schltr.) Summerh. to the genera *Chauliodon* Summerh. and *Solenangis* Schltr., respectively. The relationships between these genera and *Microcoelia* are briefly discussed.

Chauliodon Summerh.

In its vegetative characters the monotypic genus *Chauliodon* very much resembles *Microcoelia,* but differs markedly in floral morphology. The unique, fleshy process of the lip and the type of attachment of the pollinia make *Chauliodon* quite distinct. In *Chauliodon* the pollinia are almost enclosed by the cup-shaped apical part of the stipes, i.e. the side facing the anther-cap (Fig. 1), whereas the pollinia in *Microcoelia* are always attached above the ± convex or curved apical part of the stipes. This difference seems basic and points to an isolated position of *Chauliodon.* The only other aphyllous orchid in Africa with the pollinia attached in a similar way is the monotypic genus *Taeniorrhiza* Summerh., which is, however, well separated in many other characters. With the present material there is no justification for including *Chauliodon* in *Microcoelia* or in *Taeniorrhiza.*

Chauliodon deflexicalcaratum (De Wild.) L. Jonsson, comb. nov.

Basionym: *Angraecum deflexicalcaratum* De Wildeman 1916: 185 – *Gussonea deflexicalcarata* (De Wild.) Schlechter 1918: 90 – *Microcoelia deflexicalcarata* (De Wild.) Summerhayes 1943: 152 – Orig. coll.: Zaïre, Prov. Equateur, between Indjolo (Injolo) and Eala, VI.1905, M. Laurent 1776 (BR holotype).

Chauliodon buntingii Summerhayes 1943: 163, 1956 T. 3566, 1968: 259 – Orig. coll.: Liberia, Eastern Prov., 'Mt Barclay', VI.1912, R. H. Bunting 9 (BM holotype, BR photo, K drawing and fragments), synon. nov.

When revising *Microcoelia,* Summerhayes (1943) did not have access to the material of aphyllous orchids in BR, which had already been treated by De Wildeman (1916). He consequently transferred *Angraecum deflexicalcaratum* De Wild. to *Microcoelia.* However, comparison of the type material of this species and that of *Chauliodon buntingii* Summerh. shows that these taxa are conspecific.

Solenangis Schltr.

The genus *Solenangis,* as circumscribed today, comprises 5 species. Two species are aphyllous, *S. aphylla* (Thou.) Summerh. and *S. cornuta* (Ridl.) Summerh. In vegetative characters, especially the long climbing stem and the diminutive leaves, *S. angustifolia* Summerh. (=*S. conica* (Schltr.) L. Jonsson) forms a natural link to the

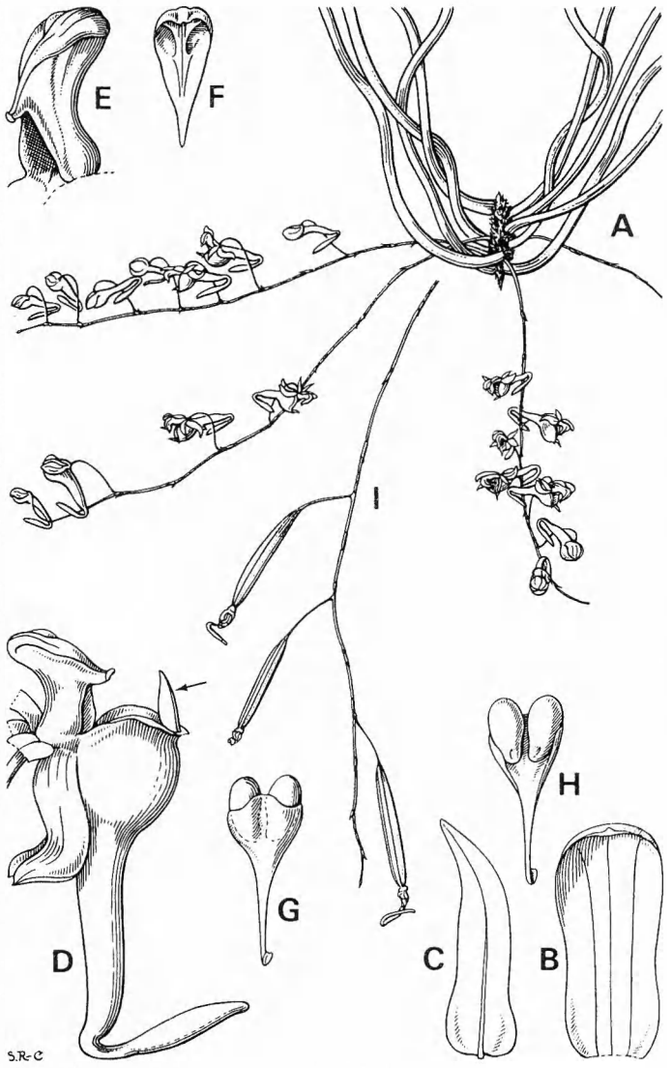

Fig. 1. *Chauliodon deflexicalcaratum.* – A: Habit. – B: Dorsal sepal. – C: Petal. – D: Opened flower in side view, showing column and labellum with apical process (arrow). – E: Column. – F: Anther-cap from behind. – G; Pollinarium, back view. – H: Pollinarium, front view; note the enclosed pollinia. – I: Infrutescence. – Magnifications: A, I ×0.6, B, C, G, H ×7.2, D ×3.5, E, F ×4.7. – Drawing from Hook., Ic. Pl. T. 3566 by permission of Bentham-Moxon Trustees.

other leaf-bearing species, *S. clavata* (Rolfe) Schltr. and *S. scandens* (Schltr.) Schltr. The similarity in general floral morphology, e.g. in the type of column and pollinarium, also indicate that these taxa form a reasonably homogeneous unit. All these long-stemmed angraecoid orchids have at some time been placed in the genus *Angraecum* Bory s.lat. The genus *Gussonea* was established by A. Richard (1828 p. 67) for the long-stemmed *A. aphyllum* Thou., which was then the first African leafless orchid in a distinct genus. This view was supported by Ridley (1885 p. 490), who also included a few short-stemmed aphyllous taxa. Schlechter (1918 pp. 89–94) adopted the name *Gussonea* A. Rich. for all the aphyllous orchids in Africa known at that time, but arranged the long-stemmed and short-stemmed species in separate sections. However, as pointed out by Summerhayes (1943 p. 138) *Gussonea* A. Rich. is a later homonym for a genus of Euphorbiaceae established by Sprengel (1821) under the alternative spelling *Gussonia*. Summerhayes (1943) placed the long-stemmed and most of the short-stemmed aphyllous taxa mentioned above in the genera *Solenangis* Schltr. and *Microcoelia* Lindl., respectively. This is fully justified when vegetative as well as floral characters are taken into consideration.

Therefore, with the facts mentioned above taken into consideration there are indications of a more remote relationship between *Solenangis* and *Microcoelia* than between *Chauliodon* and *Microcoelia.*

Solenangis conica (Schltr.) L. Jonsson, comb. nov.

Basionym: *Angraecum conicum* Schlechter 1906: 160 – *Gussonea conica* (Schltr.) Schlechter 1918: 91, 1932 T. 96, no. 382 – *Microcoelia conica* (Schltr.) Summerhayes 1943: 142 – Orig. coll.: Moçambique, Prov. Manica e Sofala, surroundings (unweit) of Beira, IV. 1895 (non 1885), R. Schlechter s.n. (B holotype †).

Solenangis angustifolia Summerhayes 1958: 280, 1967 T. 3640 – Orig. coll.: Rhodesia, Umtali distr., Engwa, III.1954, H. Wild 4536 (K holotype, BR, P, SRGH (not seen), isotypes), synon. nov.

On his way back from South Africa in 1895, Schlechter made a short stop in Moçambique at the coastal town of Beira, where he collected an apparently aphyllous orchid. In his publication of this taxon Schlechter (1906 p. 160) reported the collecting year as 1885, which must be a misprint, since according to Loesener (1926 p. 924) his journey began in 1891.

In his description of *Angraecum conicum* Schlechter (1906) stressed its general affinities to *Angraecum cyclochilum* Schltr. (=*Solenangis cornuta* (Ridl.) Summerh.), which is a distinct aphyllous long-stemmed species. When Summerhayes (1943), without seeing Schlechter's material, transferred *A. conicum* Schltr. to the genus *Microcoelia* Lindl., he argued that Schlechter (1918) had placed it among the short-stemmed species. However, Schlechter had also placed the distinctly long-stemmed *A. cyclochilum* in

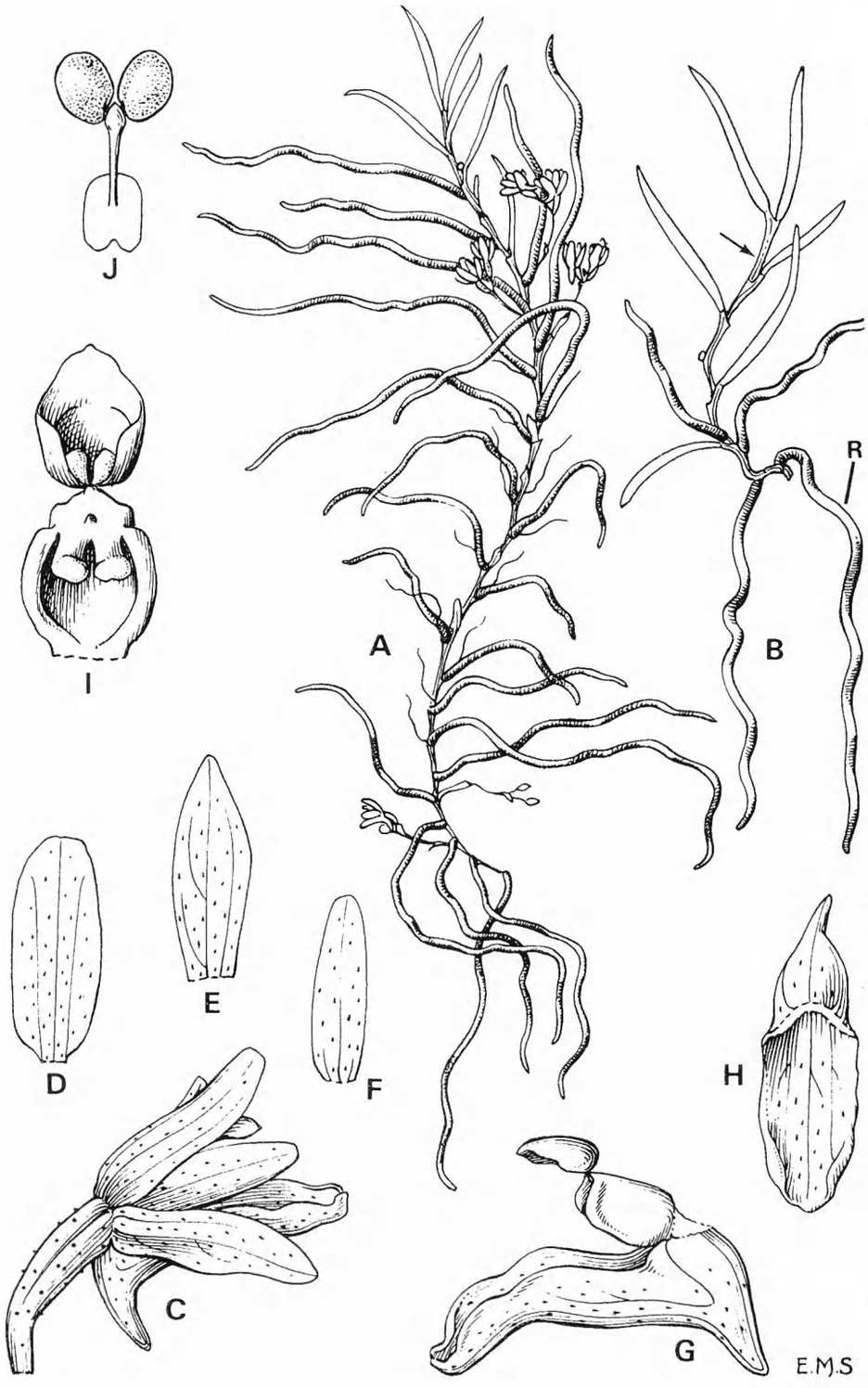

Fig. 2. *Solenangis conica*. – A: Habit. – B: Sterile stem (arrow), showing leaves and aerial roots (R). – C: Flower, side view. – D: Dorsal sepal. – E: Lateral sepal. – F: Petal. – G: Opened flower, showing labellum with spur, column and anther-cap. – H: Labellum from above. – I: Column from below, anther-cap lifted up, pollinarium removed. – J: Pollinarium. All from Drummond & Hemsley 2548 (K). – Magnifications: A × 0.8, B × 1.3, C–H × 8.3, I, J × 16.7. – Drawing from Hook., Ic. Pl. T. 3640 by permission of Bentham-Moxon Trustees.

the same section. Therefore, when examining Schlechter's work I get the impression that he emphasized the floral characters more than the vegetative ones when he arranged the species into groups. It may sometimes be very easy to interpret the thin elongated stem as one of the branched roots. *A. conicum* can be temporarily without leaves, as for example *Angraecopsis breviloba* Summerh. and *Mystacidium gracile* (Rchb. f.) Harv., and when present, the diminutive leaves are easily overlooked, especially in an early stage. The plant then makes the impression of a tiny *Microcoelia*. However, careful examination reveals the abscission layer on the thickened blunt apex of the remaining leaf sheaths; the scale-leaves in the truly aphyllous species always have a thin ± pointed apex. In his original description Schlechter (1906) stres-

sed the conical form of the spur. This character was also emphasized by Summerhayes (1958) for his *S. angustifolia,* and when comparing the drawings by Schlechter (1932 T. 96, no. 382) and in Summerhayes (1967 T. 3640) a very close resemblance is found, justifying the opinion that these taxa are conspecific.

The material examined shows that the spur varies from only a small protrusion to a well developed, although short, spur. The spur in Schlechter's (1932) illustration is somewhat larger than that shown in Summerhayes' figure (Fig. 2). It also seems as if the Schlechter material represents a disjunction from the main highland distribution, where all material seen has been collected. Similar disjunctions in the distribution have been recorded for other orchid species, e.g. *Microcoelia guyoniana* (Rchb. f.) Summerh. and *Habenaria welwitschii* Rchb. f. However, the inconspicuousness of the plant, the inaccessibility of suitable habitats and the human activity in lower, more easily cultivated areas, may explain the apparent discontinuity. Therefore, pending new material from the surroundings of Beira for neotypification, I have preferred only to select representative material from the known disjunct distribution areas:

Tanzania. Lushoto distr., W Usambara Mts, Shagayu Mt, 15.V.1953, Drummond & Hemsley 2548 (K) – *Rhodesia.* E Prov., Umtali distr., Vumba Mts, Nyamheni Farm, 24.VI.1960, Chase 7357 (K, SRGH not seen).

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Nomenclatural notes on Thouars' works on orchids

Finn N. Rasmussen

Rasmussen, F. N. 1979 09 30: Nomenclatural notes on Thouars' works on orchids. *Bot. Notiser 132:* 385–392. Stockholm. ISSN 0006-8195.

A. Richard lectotypified the genus *Amphorkis* Thouars, and the type is included in the later genus *Arnottia* A. Rich. as presently circumscribed. *Habenaria citrata* Thouars is the correct name for *H. citrina* Thouars. The following author citations are shown to be correct: *Bulbophyllum nutans* (Thouars) Thouars, *Hederorkis scandens* (Thouars) Bosser and *Liparis cespitosum* (Lam.) Lindl. The name *Graphorkis scripta* (L.) O. Kuntze, usually attributed to Thouars, is based on an Asiatic plant. Thouars' taxon is here described as a new variety, *Graphorkis concolor* (Thouars) O. Kuntze var. *alphabetica*. *Stichorkis* Thouars has priority over *Liparis* L. C. Richard and is the correct name of the combined genus unless *Liparis* is conserved against *Stichorkis*.

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L.-M. A. A. Du Petit-Thouars may be considered the founder of African orchidology. He was one of the first to collect and work scientifically on orchids, being chiefly concerned with Madagascar and the Mascarene Islands. His orchid collections are treated in three works: (1) Thouars 1809, in which he proposed 21 new genera, all ending in *-orkis* (in later works changed to *-orchis*), and 24 species of *Angorkis* (≡*Angraecum* Bory); (2) Thouars 1804–19, a "cahier" of six coloured plates in grand folio, depicting six species of different genera. Probably, all Thouars' orchids were planned to appear illustrated in this manner; (3) Thouars 1822, in which the remainder of Thouars' new species of orchids was proposed. The numbering of the plates in this work vary. In the present paper the plates of Thouars (1822) are referred to by their letter-and-number code (see Friis & Rasmussen 1974); the numbers given in brackets refer to the numbering in the copy seen at Kew.

Except for the genera published in 1809, Thouars employed two sets of names throughout his works on orchids: one set according to his own new principles of coining names, which he hoped would be generally accepted; and another set, conforming to traditional principles. Thouars' works on orchids and his nomenclatural ideas are reviewed in Friis & Rasmussen (1974). The specific names in both systems are binary combinations, and both alternatives must be considered validly published (being published before 1953, Art. 34). Thouars' epithets formed in the new way are always ending in the first syllable of the generic name *+is*, e.g. *Leptorkis flavoleptis* and *Epidorkis volucrepis*, alternatively *Malaxis flavescens* and *Epidendrum volucrum*. The peculiar form of the "new kind" epithets, and Thouars' way of arranging them on the plates of Thouars (1822) have caused several misinterpretations of his names. Lindley (1830–40) took the epithets for generic names, and Kuntze (1891) regarded them as uninomials and combined Thouars' "new kind" generic names with the "traditional" epithets, e.g. *Leptorkis flavescens* "Thouars". This interpretation has been widely followed, and Thouars' 91 "new kind" names are not listed in the Index Kewensis. Ironically, Kuntze (1894 p. 458) eventually perceived the correct interpretation of Thouars' names, and admitted that his former combinations should not be ascribed to Thouars; but this

admission was overlooked or ignored in the controversies over Kuntze's nomenclatural efforts, and sunk into oblivion.

The Code does not indicate the status of two different epithets published simultaneously for the same taxon, but merely mentions that they should be considered validly published if being before 1953. The Code does state, however, that in the reverse case – the same name published simultaneously for two different taxa – the first subsequent author is authorized to accept one of the two alternative applications and reject the other. It seems a reasonable and sound analogy to suggest that this principle should work also the other way round, so that the first author who adopts one of two alternative names is to be followed. This procedure will preserve current usage of Thouars' names, although it is not explicitly prescribed in the Code.

The status of the rejected alternative names is not clear from the Code, but they can be treated as superfluous names based on the same types as the accepted ones.

As the "new kind" specific epithets of Thouars (1804–19, 1822) were not accepted by any subsequent authors, they should be regarded as synonyms to the accepted "traditional" ones. They are, however, in agreement with the usage for proper superfluous names, available in case the "traditional" epithet in a new combination should become a later homonym (in analogy with Art. 63).

Most of the new generic names published in Thouars (1809) have later names conserved against them, or are considered as taxonomic synonyms of earlier genera. However, a few of Thouars' generic names are left to be taken into consideration, and it may be argued that Thouars' alternative "new kind" epithets should be accepted in combination with these as this is how they appear on Thouars' plates. E.g., *Gastorkis tuberogastris* Thouars is the correct name for *Phajus tuberculosus* (Thouars) Blume (based on *Limodorum tuberculosum* Thouars) if *Gastorkis* is considered a genus distinct from *Phajus*. However, if the once rejected epithets are treated as superfluous as suggested above, the correct name will be the "new kind" generic name in combination with the "traditional" epithet, e.g. *Gastorkis tuberculosa* (Thouars) Schltr. The advantage of this procedure will again be to preserve most of the current usage.

The combinations of Thouars' "new kind" generic names with his "traditional" epithets are often ascribed to Thouars, but must be regarded as combinations made by the authors who first used them.

One such case and seven other nomenclatural observations referring to Thouars' works on orchids are reported on in the present paper.

Amphorkis Thouars emend. A. Rich.

Thouars 1809 p. 516 – Type: *Amphorkis inermis* Thouars; lectotype, selected by A. Richard (1828 p. 24).

Arnottia A. Richard 1828 p. 33 – Type: *A. mauritiana* A. Rich.; holotype.

When Thouars (1809) described *Amphorkis,* he chose the generic name to signify the rather great difference between the two species included. One of the species is provided with a spur, the other is not. The species were established in 1822 as *A. calcarata* (alternatively *A. calcaramphis*) and *A. inermis* (alternatively *A. inermamphis*). Thouars created no alternative "traditional" generic name, but indicated in his "Premier tableau des espèces" that the two species were related to *Orchis* L. and *Ophrys* L., respectively.

Sprengel (1826) treated *Amphorkis calcarata* as a *Habenaria* (*H. amphorchis* Spr., 1826 p. 689) and *Amphorkis inermis* as a *Rodriguezia* (*R. mascarenensis* Spr., 1826 p. 719). A. Richard (1828 p. 24) stated that *Amphorkis calcarata* Thouars was conspecific with *Orchis squamosa* Poiret (1798 p. 601), and proposed the combination *Gymnadenia squamosa* (Poir.) A. Rich. (as *G. squamata,* orth. mut.), citing *Amphorkis calcarata* Thouars in synonymy. In the same work A. Richard proposed the genus *Arnottia* (1828 p. 33), containing one species, *A. mauritiana* A. Rich. Richard admitted that this species was closely related to *Amphorkis inermis* Thouars, but found that it was distinguished by broader leaves and a different labellum. He did not, however, transfer Thouars' species to *Arnottia*.

It seems inescapable that A. Richard by excluding one of Thouars' two species of *Amphorkis* indirectly lectotypified the genus in the sense of the "Guide for determination of types" published in the Code, and that his choice should be respected according to Art. 8.

Unfortunately, this was not realized by later authors. Lindley (1835 p. 332–333) cited (with a ?) *Amphorkis calcarata* in synonymy of *Cynorkis squamosa* (Poir.) Lindl., and *Amphorkis inermis* under *Arnottia mauritiana* A. Rich. (with a ?), stating that "It is as well to suppress the former name [*Amphorkis*] altogether." Blume (1856 p. 190) reestablished *Amphorkis* Thouars, citing *A. calcarata* and a new species, *A. laxiflora* Blume. He further stated that *Amphorkis inermis* Thouars should neither belong to *Amphorkis* nor to *Arnottia*. Lindley (1862 p. 139) adopted Blume's taxonomic view and typification of *Amphorkis*, but Moore (1877 p. 318) transferred *A. inermis* to *Arnottia* as *A. inermis* (Thouars) S. Moore. Post & Kuntze (1903 p. 26) cited correctly *Amphorkis inermis* as type of *Amphorkis*, and *Arnottia* as a synonym, but they did not comment the case and their statement was ignored. Schlechter (1915 p. 402) reduced *Amphorkis* Thouars emend. Blume to a synonym of *Cynorkis* Thouars (a view still held by modern authors), but retained *Arnottia* A. Rich. to include *A. inermis* (Thouars) S. Moore.

Arnottia A. Rich. contains about four species, all endemic to Mauritius (Senghas 1974 p. 264). It would appear from the above that the correct name for that genus should be *Amphorkis* Thouars emend. A. Rich., but I suggest that the necessary new combinations – or the conservation of *Arnottia* A. Rich. – should be left to a monographer of the genus.

Bulbophyllum nutans (Thouars) Thouars

Thouars 1822 Trois. tabl. des espèc. & Plate u13 (107) – *Phyllorkis* ("*Phyllorchis*") *nutans* ("*ncctans*", typographic error) Thouars 1804–19 Plate IV.

Phyllorkis ("*Phyllorchis*") *nuphyllis* Thouars 1804–19 Plate IV; alternative name based on the same type as *P. nutans*.

Thouars was well aware that his new principles of nomenclature were liable to rejection. The "traditional" alternative names were meant to be used if that should become the fate of his reformatory suggestions. When coining the "traditional" names Thouars tried in most cases to place his new species in already existing genera. He was, however, convinced that his genus *Phyllorkis* (Thouars 1809 p. 319) was very distinct from all other genera known at his time. He therefore used the generic name *Phyllorkis* (as "*Phyllorchis*") in both alternative combinations when he published *P. nuphyllis* ≡*P. nutans* in Thouars (1804–19).

It appears that he later considered the possibility of eventual rejection not only of the peculiar "new kind" epithets, but also of the generic names ending in *-orkis* (or *-orchis*). They were criticized by, among others, Desfontaines (Friis & Rasmussen 1974 p. 309). The name *Bulbophyllum* was thus created as traditional alternative to *Phyllorkis*, and published in Thouars (1822), in which also *Bulbophyllum nutans* appeared. Although this species usually is cited as published in 1822, *Bulbophyllum nutans* (Thouars) Thouars must be considered a new combination, based on *Phyllorkis nutans* Thouars (1804–19). *Bulbophyllum* is conserved against the earlier *Phyllorkis*, and *Bulbophyllum nutans* (Thouars) Thouars was designated as lectotype of the genus by Green (1929 p. 100).

Graphorkis concolor (Thouars) O. Kuntze

Kuntze 1891 p. 662.

Graphorkis concolor var. **concolor**

Limodorum concolor Thouars 1822, Sec. tabl. des espèc. & Plate n4 (45) – *Eulophia concolor* (Thouars) Lindley 1833 p. 181 – *Eulophiopsis concolor* (Thouars) Schlechter 1915 p. 422 – *Eulophia scripta* (L.) Lindley var. *concolor* (Thouars) S. Moore 1877 p. 360 – *Graphorkis* ("*Graphorchis*") *scripta* (L.) O. Kuntze var. *concolor* (Thouars) Senghas 1964 p. 65 – Orig. coll.: Thouars s.n., Réunion (P holotype).

Graphorkis ("*Graphorchis*") *monographis* Thouars 1822 Sec. tabl. des espèc. & Plate n4 (45), alternative name based on the same type as *Limodorum concolor*.

Graphorkis concolor var. **alphabetica** F. Rasm., var. nov.

Orig. coll.: Thouars s.n., Réunion or Madagascar (P holotype).

Graphorkis ("*Graphorchis*") *aiolographis* Thouars 1804–19 Plate III, nom. illeg. (Art. 63).

Epidendrum scriptum auct. non L.; Thouars 1804–19 Plate III (as alternative name for *Graphorkis aiolographis*). – *Limodorum scriptum* (L.) Thouars sensu Thouars 1822 Sec. tabl. des espèc. & Plate n5–n5bis (46–47), excl. the Linnean taxon – *Eulophia scripta* (L.) Pfitzer sensu Pfitzer 1889 p. 183, excl. the Linnean taxon – *Lissochilus scriptus* (L.) Perrier de la Bâthie sensu Perrier de la Bâthie 1941 p. 37, excl. the Linnean taxon. – *Graphorkis scripta* (L.) O. Kuntze var. *scripta*, sensu Senghas 1964 p. 65, excl. the Linnean taxon.

A Latin diagnosis of the taxon here called *G.*

concolor var. *alphabetica* is provided in Sprengel (1826 p. 703) under the name "*Limodorum scriptum* Thouars". Sprengel (1826) was the first author to exclude the Linnean taxon (cited as *Vanda scripta* on p. 719) from the circumscription of the Thouarsian taxon.

Thouars (1809 p. 318) did not propose any species of *Graphorkis* when he described the genus, and designated thus no type. He stated, however, that one of the species of his new genus was illustrated and described by Rumphius (1750 p. 95–98, Plate 42) and named *Epidendrum scriptum* by Linneaus (1763 p. 1351). This specific name was by Thouars (1804–19) used as "traditional" alternative name for his *Graphorkis aiolographis* (Fig. 1), but the Mascarene plant depicted is not an *Epidendrum scriptum* L. (an Asiatic species now known as *Grammatophyllum scriptum* (L.) Blume). One of the distinct characters of *Graphorkis* is the short spur of the labellum (Thouars 1809 p. 318), which is absent in *Grammatophyllum*. The spur is well illustrated on Thouars' plate (Fig. 1). Thouars' name *Graphorkis aiolographis* is illegitimate, as the epithet *scriptum* should have been adopted (Art. 63).

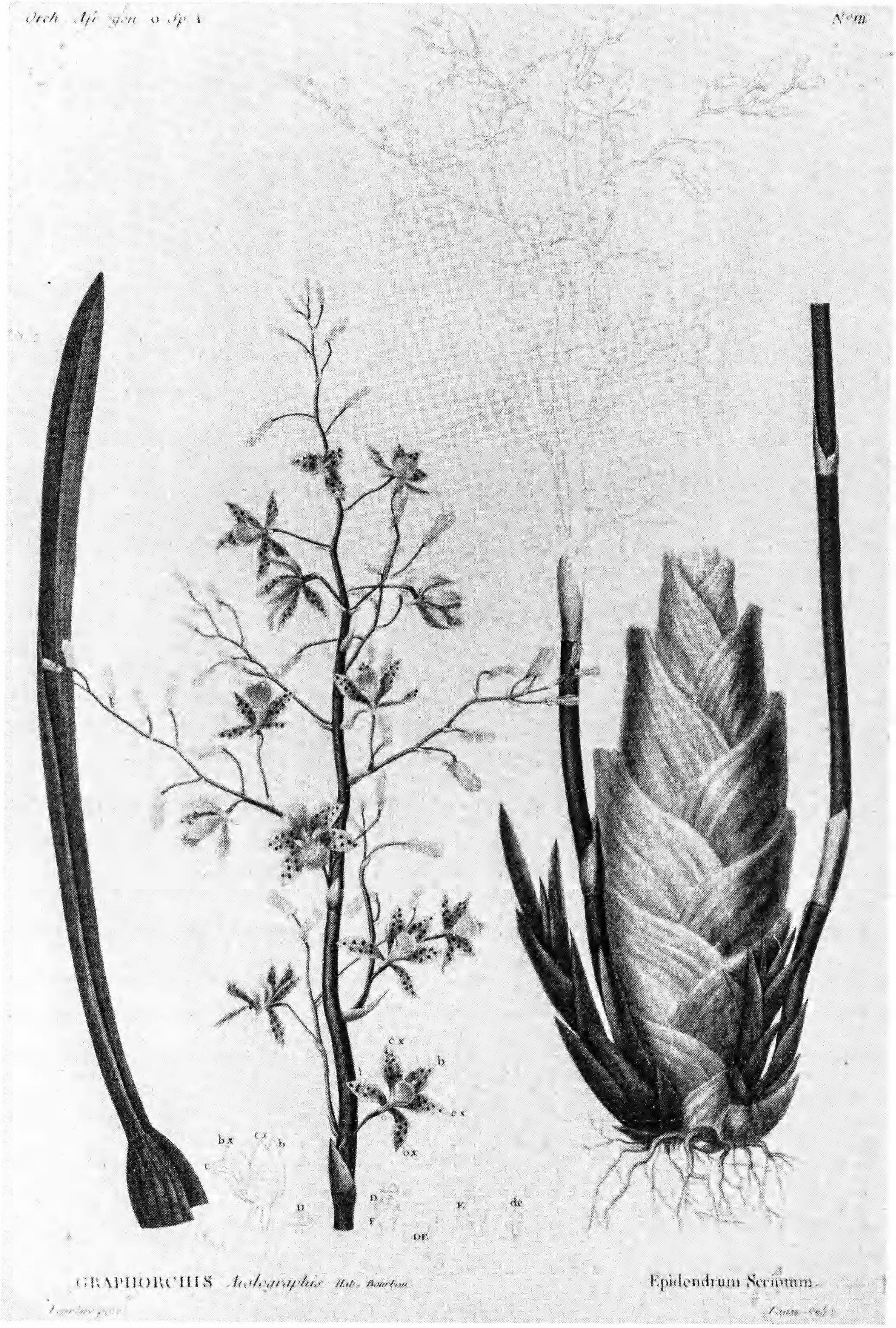
Three nomenclatural elements are presented in connection with the publication of the "Letter-Graphorkis": (1) the specimen collected by Thouars; (2) the plate illustrating this plant; and (3) the citation of a Linnean taxon. Thouars (1809 p. 315, 1822 title page) stated explicitly that all his illustrations, descriptions and "new kind" names of his orchids were based on his own collections, in fact prepared already during his stay on the localities. As only one specimen is possible in the case of *G. aiolographis*, it must be regarded as the type of this name (Art. 7.11 & Guide-types).

Thouars (1822) changed the traditionally formed name to *Limodorum scriptum*, but indicated with an asterisk that this epithet was not of his own. He repeated the direct reference to *Epidendrum scriptum* L. in the descriptive part of the work (Thouars 1822 p. 19). It is thus evident that the name *Limodorum scriptum* in Thouars (1822) is based on *Epidendrum scriptum* L., and to be regarded as a synonym of *Grammatophyllum scriptum* (L.) Blume. This also applies to all the combinations based on "*Limodorum scriptum* Thouars". Actually, they are correct names in hypothetical cases, e.g. when *Epidendrum scriptum* L. is regarded as a *Eulophia*.

It follows from the above statements that there is no legitimate name available for Thouars' Mascarene "Letter-Graphorkis". If it is considered a distinct species, as in Schlechter (1915) and Summerhayes (1953), it must be provided with a new name. But if it is regarded as a taxon conspecific with *Graphorkis concolor* (Thouars) O. Kuntze (=*Limodorum concolor* Thouars), the latter name is available for the combined species. This taxonomic view has been expressed by Moore (1877 p. 360), Ridley (1885 p. 468) and Senghas (1964 p. 64). Moore (1877) and especially Senghas (1964) discussed the question and reduced eventually *G. concolor* to a variety of respectively *Eulophia scripta* and *Graphorkis scripta*. After having studied herbarium material I can confirm Senghas' observation that there appears to be only one clearcut difference between the two taxa, namely the colouring of the perianth. This difference is, on the other hand, very remarkable, and the uniformly coloured form is apparently endemic to Réunion, while the Letter-Graphorkis has a wider distribution (Mascarenes, Madagascar, Comores). I agree with the above cited authors that this is not enough to justify specific rank, but the geographical evidence, combined with the one clearcut distinctive character, makes it worth to recognize the taxon as a variety. I therefore propose a new name for the Letter-Graphorkis in this rank, treating it as a new taxon (Art. 72,1 option b). As it would be unfortunate to use the very descriptive, but so often misapplied epithet '*scripta*', I have preferred to coin a new one with the same meaning, namely '*alphabetica*'.

The Graphorkis depicted in Thouars (1804–19) is the first taxon referred to the genus, and it was thus considered the type of *Graphorkis* by Kuntze (1891 p. 662), a view adopted by Summerhayes (1953 p. 160). When cited as type

Fig. 1. Plate III of Thouars (1804–1819). Note the alternative names: *Graphorchis aiolographis* and *Epidendrum scriptum*. Only two copies are known of this work. One is in the Library of the Conservatoire de Botanique, Geneve, the other is in the Library of the Royal Botanic Gardens, Kew. – Reproduced with the permission of the Controller of Her Majesty's Stationary Office and the Director of The Royal Botanic Gardens, Kew.


GRAPHORCHIS
Epidendrum Scriptum.

species the designation *Graphorkis aiolographis* Thouars nom. illeg. = *Graphorkis concolor* (Thouars) O. Kuntze var. *alphabetica* F. Rasm. should be used instead of the misapplied *Limodorum scriptum* (L.) Thouars. I must emphasize that the illegitimacy of the name *Graphorkis aiolographis* does not affect the status of the Letter-Graphorkis as the type of the genus *Graphorkis*, even if my conclusion concerning the type of Thouars' illegitimate epithet should be doubted (Art. 7.11), since it is a species as a taxon, and not its name, which typifies the name of a genus. This has been definitely stated by the nomenclatural authorities on several occasions, latest in Stafleu & Voss (1975 p. 207) and Voss (1976 p. 170).

Habenaria citrata Thouars

Thouars 1804–19 Plate V.
Habenorkis ("Habenorchis") citrabenis Thouars 1804–19 Plate V.
Habenaria citrina Thouars 1822 Prem. tabl. des espèc. & Plate e1 (16).

This species is usually cited as *Habenaria citrina* Thouars, but as it has been shown (Friis & Rasmussen 1974) that the six grand folio plates of Thouars (1804–19) were published before his "Histoire particulière (Thouars 1822), the first published epithet *citrata* must be reinstated for this species. "Citrata", a word used e.g. by Pliny, means "steeped in *Citrus* juice", and is hardly to be regarded as a printing error.

Hederorkis Thouars

Thouars 1809 p. 319.
Scandederis Lindley 1847 p. 183 ("*Scaredederis*").

Lindley (1847) cited "*Scaredederis*" as a generic name and ascribed it to Thouars. However, *scandederis* is the epithet of the specific name *Hederorkis scandederis* Thouars (alternatively *Neottia scandens*). Although Lindley (1847) gave no description of the genus, the reference to Thouars validates this monotypic genus. A similar case is *Corymbis* Lindl. (Rasmussen 1977).

The spelling "*Scaredederis*" is a typographic error occuring under Plate s (91) of Thouars (1822), and the spelling in Lindley (1847) is thus to be corrected as an orthographic error (Art. 73.1).

In Lindley (1830 p. 537) "*Scaredederis*" (indeed more correctly) is assigned specific rank.

Hederorkis scandens (Thouars) Bosser

Bosser 1976 p. 226 – *Neottia scandens* Thouars 1822 Trois. tabl. des espec. & Plate s (91).
Hederorkis ("Hederorchis") scandederis Thouars loc. cit., alternative name based on the same type as *Neottia scandens*.
Bulbophyllum mauritianum Hunt 1968 p. 491, nom. illeg. (Art. 63).

Bosser (1976 p. 226) believed that the name *Hederorkis scandens* was published by Thouars. However, Thouars' alternative names are *H. scandederis* and *Neottia scandens*. As stated in the introductory discussion of this paper, the combination *Hederorkis scandens* may be ascribed to Bosser, who is the first chosing one out of two available epithets.

Hunt (1968 p. 491) regarded this species as a *Bulbophyllum* and proposed *Bulbophyllum mauritianum* nom. nov. because of *B. scandens* Rolfe. As the epithet *scandederis* was available, *B. mauritianum* is superfluous.

As demonstrated by Bosser (1976), *Bulbophyllum scandens* Rolfe is actually a *Hederorkis*, but a species different from Thouars'! After having reserved the epithet *scandens* for Thouars' species, Bosser (1976) proposed *Hederorkis seychellensis* for Rolfe's species.

Hederorkis is, as pointed out by Bosser, a very distinct genus and probably not related to *Bulbophyllum*.

Stichorkis Thouars

Thouars 1809 p. 318; Thouars 1822 ("*Stichorchis*") Trois. tabl. des espèc. & Plate r1 (89) – Type: *Stichorkis disticha* (Thouars) Pfitz. (*Stichorkis distichis* Thouars, alternatively *Malaxis disticha* Thouars); lectotype, selected here.
Leptorkis Thouars 1809 p. 317, nom. rej. in favour of *Liparis* L. C. Richard.
Liparis L. C. Richard 1817 p. 43 & 52, nom. cons. against *Leptorkis* Thouars – Type: *Liparis loeselii* (L.) L. C. Richard (*Ophrys loeselii* L.); holotype.
Cestichis Lindl. ex Pfitz.; Lindley 1824 Plate 832 nom. nud.; Pfitzer 1888 p. 130 – Type: *Cestichis cespitosa* (Lam.) Ames (*Epidendrum cespitosum* Lam.); holotype.
Distichis Lindley 1847 p. 181, nom. nud.

Thouars (1809) published two genera as segregates of *Malaxis* Sw., viz. *Leptorkis* Thouars and *Stichorkis* Thouars. He was well aware that his genus *Stichorkis* was closely related to

Leptorkis, but he preferred to keep the two species of *Stichorkis* in a separate genus because he found only one pollinium in each locule of the anther, and because of the general habit of the plants.

Although the observation of the numbers of pollinia was faulty, Thouars' taxonomic arrangement of his sparse material of the large generic entity now known as *Liparis* had a surprising predictive value. *Leptorkis* and *Stichorkis* correspond to the major subdivisions of *Liparis*, viz. the thin-leaved terrestrials and the coriaceous-leaved epiphytes. In *Stichorkis*, the species named *S. distichis* by Thouars represents the well-defined group of species with a distichous, compressed inflorescence. As Thouars stressed that peculiarity when he described *Stichorkis*, I chose this species as type of the genus. This choice may also preserve current use of some subdivisional names as stated below.

L. C. Richard (1817) proposed the genus *Liparis* based on *Malaxis loeselii* (L.) Willd. – a species actually mentioned as a member of *Leptorkis* by Thouars (1809). As Thouars (1809) never became widely known in the botanical establishment, *Liparis* became the accepted name until Kuntze (1891) reinstated *Leptorkis* and transferred more than 100 species of *Liparis*. Eventually, *Liparis* L. C. Rich. was conserved against *Leptorkis* Thouars.

Stichorkis Thouars was included in *Liparis* L. C. Rich. by Lindley (1825 Plate 882, 1830 p. 29) but recognized on sectional level. Unfortunately, Lindley misunderstood Thouars' naming and believed that the generic name given by Thouars was *Cestichis*, actually the epithet of the specific name *Stichorkis cestichis* Thouars (nom. illeg., ≡*Malaxis cespitosa* (Lam.) Thouars). *Cestichis* as a generic name was mentioned by Lindley in an enumeration of the genera forming *Epidendreae* sect. [sic] *Ecalcaratae* (Lindley 1824 Plate 832). However, *Cestichis* as generic name can not be ascribed to Lindley, as Thouars, to whom Lindley refers, does not provide a description of the taxon in the rank of genus or subdivision of a genus (Art. 41.1).

Lindley (1847 p. 181) seems to have changed his mind later and cited *Cestichis* in synonymy of *Liparis*, but recognized *Distichis* as a genus, likewise ascribed to Thouars.

The taxonomic view of Lindley (1830) was followed in the monograph by Ridley (1886 p. 252), who referred the epiphytic species with coriaceous leaves to the "Division" *Coriifoliae*, including both Thouars' species of *Stichorkis*. *Coriifoliae* was subdivided in four sections. *Liparis cespitosa* (Lam.) Lindl. (≡*Stichorkis cestichis* Thouars) was included in the main section, not named by Ridley, and *Liparis disticha* (Thouars) Lindley (≡*Stichorkis distichis* Thouars) in sect. *Distichae*.

Pfitzer (1888 p. 130) adopted *Stichorkis* on generic level, using the erroneous name "*Cestichis*". *Cestichis* Pfitz. was apparently identical with the "Division" *Coriifoliae* of Ridley (1886), and divided into the same four sections. Later Pfitzer (1897 p. 103) corrected *Cestichis* to *Stichorchis* [sic], and proposed four combinations with that name.

Notwithstanding Pfitzer's correction several authors continued to use *Cestichis*, and about 38 combinations have been made with this name.

Schlechter (1911) intended a thorough revision of the infrageneric taxonomy of *Liparis*. He recognized *Cestichis* as a subgenus and cited *Liparis cespitosa* under subgenus *Cestichis* Schltr. sect. *Hologlossum* Schltr. *Liparis disticha* was cited under subgenus *Cestichis* sect. "*Distichion*".

Modern authors (e.g. Seidenfaden 1976) unanimously agree with Lindley and Schlechter in referring Thouars' species of *Stichorkis* to *Liparis*. The correct name for the combined genus is the earlier *Stichorkis* Thouars, unless it is added to the list of names rejected in favour of *Liparis* L. C. Rich. In *Stichorkis* only four combinations have been made, whereas hundreds are made in the already once conserved *Liparis*. I see no reason why *Liparis* should not be conserved against *Stichorkis* as well as against *Leptorkis* and are taking the necessary formal steps to propose the conservation.

It appears that *Liparis* sect. *Cestichis* Lindley (1830 p. 29) has to be accepted, and also *Liparis* subgenus *Cestichis* Schlechter (1911 p. 199), if these taxa are not circumscribed to include types of earlier, validly published sections or subgenera. The name *Liparis* sect. *Distichae* Ridley (1886 p. 291) is based on *Liparis disticha* (Thouars) Lindl., and may be used if that species is excluded from sect. *Cestichis* Lindl., as the latter section must be based on *Liparis cespitosa* (Lam.) Lindl. (≡*Stichorkis cestichis* (Lam.) Thouars).

The infrataxonomy of *Liparis* is, however, highly complex and badly in need of an exhaustive modern treatment.

Liparis cespitosum (Lam.) Lindl.

Lindley 1825 Plate 882 – *Epidendrum cespitosum* Lamarck 1783 p. 187 – *Malaxis caespitosa* (Lam.) Thouars 1822 Trois. tabl. des espèc. & Plate r2 (90).

Stichorkis ("Stichorchis") cestichis Thouars loc. cit. See Seidenfaden (1976 p. 61) for a full synonymy.

Malaxis caespitosa Thouars is usually cited as basionym of the name for this species, but when Thouars (1809 p. 518 ff.) described the genus *Stichorkis* he stated: "L'une d'elles [i.e. the two species Thouars intended to establish in *Stichorkis*] a été décrite par M. Lamarck, sous le nom d'*Angraecum cespitosum*." Thouars was evidently referring to Lamarck's (1783) "*Angrec en gazon*", *Epidendrum cespitosum*. Lamarck's orthography is to be retained (Art. 73).

Acknowledgements. I wish to thank Dr I. Friis for many valuable discussions and suggestions during the work with the problems treated here, and Dr G. Seidenfaden for reading the manuscript. The responsibility for the decisions made is, however, entirely mine.

The herbaria P and BM have put material at my disposal, and the Royal Botanic Gardens, Kew, has kindly provided the negative reproduced as Fig. 1.

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Acacia amythethophylla, the correct name of a widespread African tree

Asfaw Hunde

Hunde, A. 1979 09 30: Acacia amythethophylla, the correct name of a widespread African tree. *Bot. Notiser 132:* 393–395. Stockholm. ISSN 0006-8195.

Acacia amythethophylla Steud. ex A. Rich. is shown to be the correct name of the widespread tropical African tree generally known as *A. macrothyrsa* Harms. The latter name is reduced to synonymy and a distribution map is presented. A lectotype is selected for *A. amythethophylla*.

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Acacia amythethophylla Steud. ex A. Rich. was described on material collected from the Tekkeze Valley (Richard 1847), most probably N of the Tekkeze River, in Tigre Region, Ethiopia. Since then, *A. amythethophylla* has been re-collected a few times in the Tekkeze Valley and a single collection has also been reported from the Mereb Valley in the neighbouring Eritrea Region (Fiori 1911 p. 286). Besides, this name has been used also for material from Angola (Baker 1928, 1930, Torre 1956).

While working on the Mimosoideae of Ethiopia, my attention was turned to the striking similarity between *A. amythethophylla* and *A. macrothyrsa* Harms, a widespread species in tropical Africa although never recorded from Ethiopia.

Both are medium-sized trees with glabrous branches and relatively small stipular spines. The leaves are outstanding among African acacias by their large size and the great number of their pinnae and leaflets. The inflorescence is a loose panicle of orange-yellow flower-heads and the pods are coriaceous.

A comparison of morphological variation of important characters in the Ethiopian material of *A. amythethophylla* and in *A. macrothyrsa* is summarized in Table 1. From this comparison it is evident that the Ethiopian *A. amythethophylla* in every respect falls within the variation range of *A. macrothyrsa* and that the two taxa are conspecific. *A. amythethophylla,* being the earlier specific epithet, has priority and *A. macrothyrsa* is reduced to synonymy.

Acacia amythethophylla Steud. ex A. Rich.

Richard 1847 p. 245; Oliver 1871 p. 346; Baker 1928 p. 157, 1930 p. 852; Cufodontis 1954 p. 187; Torre 1956 p. 286 – *Types:* Ethiopia, Tekkeze Valley, Quartin Dillon & Petit s.n. (P lectotype!), Schimper 887, 20.V.1840 (P syntype!).

A. macrothyrsa Harms 1900 p. 396, syn. nov.; Andrews 1952 p. 148; Gilbert & Boutique 1952 p. 157; Hutchinson & Dalziel 1958 p. 501; Brenan 1959 p. 101, 1970 p. 85 – *Type:* Tanzania, Iringa, Goetze 635 (K isotype, not seen).

Other synonyms: *A. buchananii* Harms et *A. prorsispinula* Stapf, fide Brenan 1959 p. 101; *A. dalzielii* Craib, fide Hutchinson & Dalziel 1958 p. 501.

Distribution and habitat

A distribution map of *A. amythethophylla* (Fig. 1) has been prepared on the basis of material received on loan from some herbaria (see under specimens examined) and mainly through compilation from reliable literature sources. *A. amythethophylla* has a typical Sudano-Zambezian distribution (White 1965 p. 658) and occurs between 30 and 1650 m in different types of woodlands.

Table 1. Comparison of important characters in Ethiopian *A. amythethophylla* and *A. macrothyrsa*. Dimensions in cm.

Characters	*A. amythethophylla*	*A. macrothyrsa*
Stipular spines		
Length	0–0.7	0–0.8
Leaves		
Petiole length	2–2.6	1.5–5
Petiole gland	large, basal	large, basal
Rhachis length	9.5–26	10–24
Pinna length	5.5–9.5	4–11.5
Pinna number	7–22	7–35
Leaflet length	0.7–0.9	0.6–1.1
Leaflet number	33–45	33–45
Flowers		
Peduncle length	2.6–3.5	1.2–3.6
Involucel position on peduncle	c. in the middle	c. in the middle
Calyx length	0.1	0.1
Calyx lobes, vestiture	ciliolate	ciliolate
Corolla length	0.4–0.5	0.3–0.5
Corolla lobes, number	4–5	4–5
Pods		
Length	14.5	9.8–20.5
Width	1.8	1.7–3

The geographical isolation of the Ethiopian population apparently is the reason why the name *A. amythethophylla* has been overlooked in previous works dealing with this species. However, more or less isolated occurrences in N Ethiopia of otherwise widespread tropical African species is not unique for *A. amythethophylla*. Some other examples are *Strychnos inocua* Del. and *S. spinosa* Lam. (Leeuwenberg 1969 Maps 21, 23), *Cussonia arborea* Hochst. ex A. Rich. (Wickens 1976 Map 96), *Hypericum roeperanum* Schimp. ex A. Rich. (Bamps 1971 Map 75, Bamps et al. 1978 p. 29). It is noteworthy that in most of these cases the species were first described on material from N Ethiopia owing to the early botanical exploration of that part of Africa.

Specimens examined

Ethiopia Tigre/Beghemder, Tekkeze Valley, Quartin Dillon et Petit s.n., Schimper 849, 25.12.1839 (P), Schimper 887, 20.5.1840 (P, S), J. J. F. E. De Wilde 7135 (WAG) – *Uganda* N Prov., Eggeling 1918 (LISC) – *Tanzania* E Prov., Schlieben 3618 (LISC) – S Prov., Schlieben 6420 (LISC) – *Zaïre* Katanga (Shaba), Schmitz 5264 (LISC) – *Zambia* C Prov., Duff A35/32 (LISC) – *Malawi* C Prov., Jeke 81, Townsend 112 (LISC) – *Mozambique* N Prov., Barbosa 1962, Pedro & Pedrogão 3224, Torre 1324, 1352, 5400, Torre & Paiva 10403, 10842, 10982, 11522 (LISC) – Zambezia Prov., Andrada 1482, Torre 4891, Torre s.n. (LISC) – Manica e Sofala Prov., Andrada 1091, Barbosa 1320 Simão 100/48, 336/48 (LISC) – *Zimbabwe* E Prov., Chase 5963, Leach 9818 (LISC) – *Angola* Cuanza Sul, Gossweiler 9932, Mendes dos Santos 1285, Teixeira & All 7383 (COI), Teixeira & All 7381 (LISC) – Moxico, Gossweiler 12339 (LISC) – Benguela, Gossweiler 11940 (COI).

Acknowledgements. I wish to thank Professor O. Hedberg and Dr M. Thulin who read through the manuscript and made helpful suggestions. The Directors of the Herbaria in Coimbra (COI), Lisbon (LISC), Paris (P), Stockholm (S) and Wageningen (WAG) kindly placed material at my disposal.

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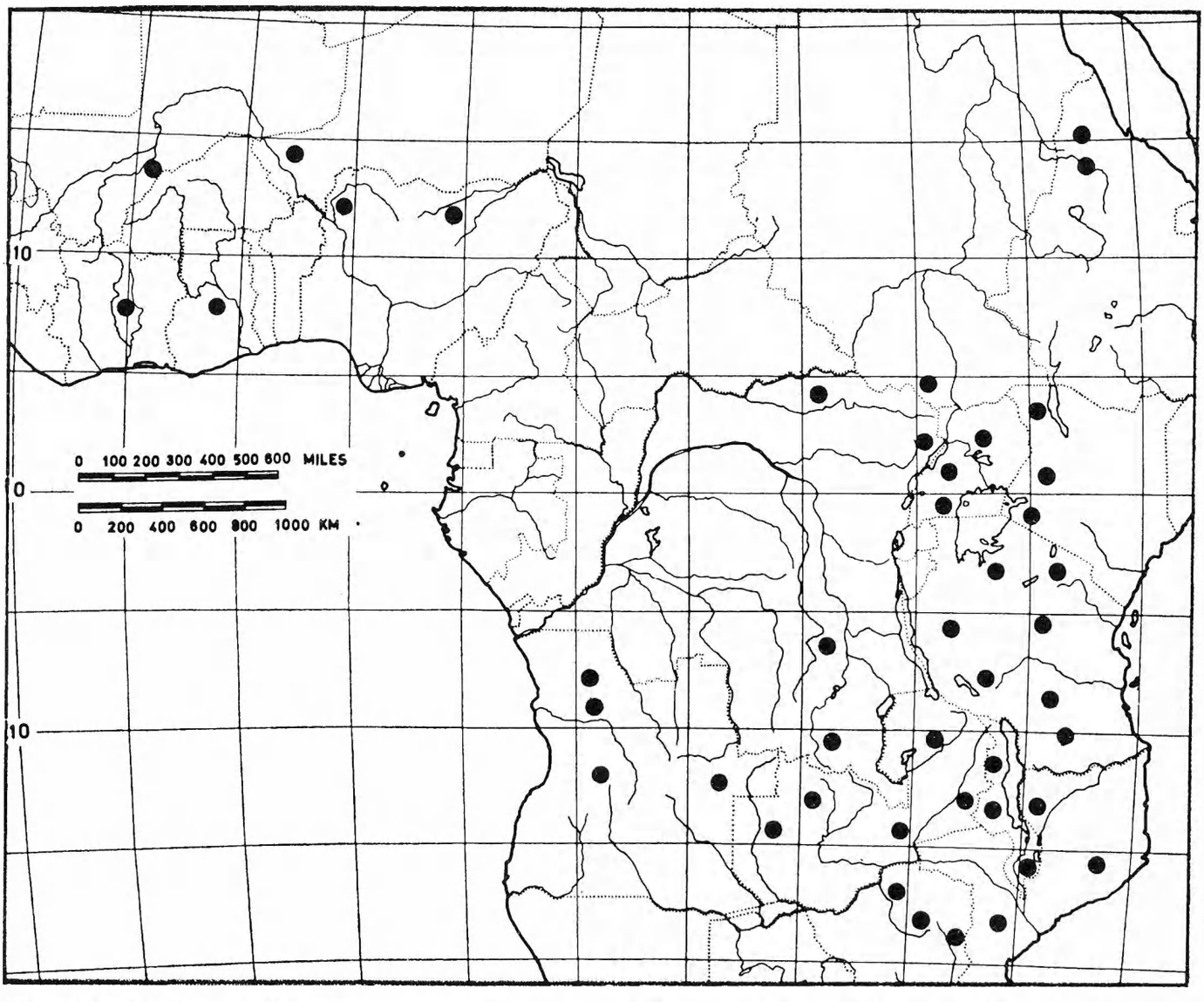

Fig. 1. Distribution map for *Acacia amythethophylla,* based on material seen by the author (from COI, LISC, P, S and WAG) and on information from the literature.

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Botanical literature

Stafleu, F. A. et al. (eds.) 1978: *International code of botanical nomenclature*. Adopted by the Twelfth International Botanical Congress, Leningrad, July 1975. Regnum vegetabile 97. 457 pp. Bohn, Scheltema & Holkema, Utrecht. ISBN 90 313 0332 1. Price HFl 70:– (cloth).

The Leningrad Code appears in a bright red cloth-binding in contrast to the dusky black covers well-known from its three nearest predecessors. However, the keenly expectant reader anticipating revolutionary new trends in botanical nomenclature will surely come away disappointed. Only 41 of the 152 proposals concerning changes in the Code were accepted at Leningrad and these involved only small amendments. The proposals were summarized in *Taxon 24* p. 201 and the decisions in *Taxon 25* p. 169. A full report of the proceedings and decisions of the Nomenclature Section is in press at Leningrad.

Since the Stockholm Congress in 1950 the question of retaining certain well-established species names which have proved to be invalid under the Code has been under permanent discussion. This proposal was defeated again at Leningrad although the gap between "no" and "yes" has narrowed considerably. An ultimate yes is perhaps in sight at the next Congress (at Sydney, 1981).

However, the Code now allows "nomina specifica rejicienda" in some rather special cases. The previous Art. 69 "A name is to be rejected if it is used in different senses and so has become a long-persistent source of error" left much room for arbitrary decisions. Following a proposal by Faegri (see *Taxon* 23 (1974) p. 824) a new wording was accepted. "A name is to be rejected if it has been widely and persistently used for a taxon not including its type. Names thus rejected shall be placed in a list of *nomina rejicienda*." The present Code recommends that all proposals for rejection of names under Art. 69 should be referred to the General Committee of Nomenclature for transmittal to the special committees.

The Congress also decided to delete Articles 70 (dealing with type material consisting of discordant elements) and 71 (dealing with names based on monstrosities). The main contents of Art. 70 are covered by Art. 9.2 (lectotypification of a mixed type material). As to Art. 71, it has proved impossible to define the concept "monstrosity" ("deriving from idealistic morphology") adequately.

Otherwise, we find few major changes. For easier reference, individual articles and recommendations are numbered in a decimal-like system. Paleobotanists should note that the concept of "organ-genus" is eliminated (Art. 3), whereas "form-genus" has been retained. The Code explicitly makes clear that it does not deal with bacteria. The section on orthography (Articles 73–75) has been thoroughly rewritten. The "Guide to the citation of botanical literature" has been omitted. The recommendations previously given there are now repeated in detail in Stafleu & Cowan, *Taxonomic literature, ed. 2* (1976).

The Code is still rather inaccessible for people lacking the historical background. A fuller set of examples and more references to the discussion on nomenclatural rules and practice would have made this volume far more useful.

Ove Almborn

Dombeya torrida, the correct name for James Bruce's 'Walkuffa'

F. N. Hepper & I. Friis

Hepper, F. N. & Friis, I. 1979 09 30: Dombeya torrida, the correct name for James Bruce's 'Walkuffa'. *Bot. Notiser 132:* 397–398. Stockholm. ISSN 0006-8195.

Dombeya torrida (J. F. Gmel.) Hepper & Friis, comb. nov., is the correct name for the species previously known as *D. bruceana* A. Rich. (Sterculiaceae). The species appears to be endemic to Ethiopia. Its closest relative seems to be *D. schimperana* A. Rich.

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When working on the identification of the botanical material from James Bruce's famous journey to Ethiopia 1768–73 we realized that J. F. Gmelin (1792) had published a valid name for the 'Walkuffa' which Bruce had described and illustrated from Sakalla near the source of the Blue Nile (Bruce 1790, 1805). Gmelin's name, *Walkuffa torrida,* is based entirely on Bruce's printed information as Bruce objected to herbaria (Bruce 1790 p. 67–68), and no specimen has been preserved.

A. Richard (1847) later described the collections of Quartin-Dillon and Petit, together with the early collections of Schimper from Ethiopia. Apparently unaware of Gmelin's name, Richard identified three collections of a species of *Dombeya* from N Ethiopia with the Bruce illustration, and proposed the name *Dombeya bruceana* for the species. In the protologue Richard quotes the three collections and refers both to the vernacular name 'Walkuffa' mentioned on Bruce's plate, and to 'PENTAPETES Bruce, Voy. v. 84, t. xx'. It is likely that this refers to the quarto edition in six volumes of Bruce's 'Travels', translated into French by M. Castera (Bruce 1790–92), but we have been unable to confirm this. A similar reference is made on the printed label of the Schimper exsiccate Iter Abyssinicum I no. 378 and in Hochstetter (1841 p. 29). *Pentapetes,* which is a Linnaean genus of Sterculiaceae now considered to be restricted to SE Asia, is not mentioned in any of the English editions of the 'Travels' seen by us. However, there is no doubt to which plant Richard refers. He quotes the name 'Walkuffa' and refers to a 'plate 20', which is the number of the plate showing the 'Walkuffa' in the second English edition (Bruce 1805).

As Richard's protologue of *Dombeya bruceana* includes a reference to the type of J. F. Gmelin's *Walkuffa torrida,* the former name was nomenclaturally superfluous when published (Art. 63) and a new combination based on Gmelin's name is necessary.

It is unfortunate that this name change also causes the replacement of good type specimens with a plate which does not show the most reliable diagnostic features. However, the ICBN, states 'If he (the original author) included only one element, that one must be considered the holotype.' The designation of a specimen neotype would therefore be illegitimate, and the usage of the name *Dombeya torrida* has to rely on Richard's interpretation.

Dombeya torrida (J. F. Gmel.) Hepper & Friis, comb. nov.

Basionym: *Walkuffa torrida* J. F. Gmelin 1792 p. 1029 – Original material: Bruce's plate and description from Sakalla (Gojjam, Ethiopia); holotype.

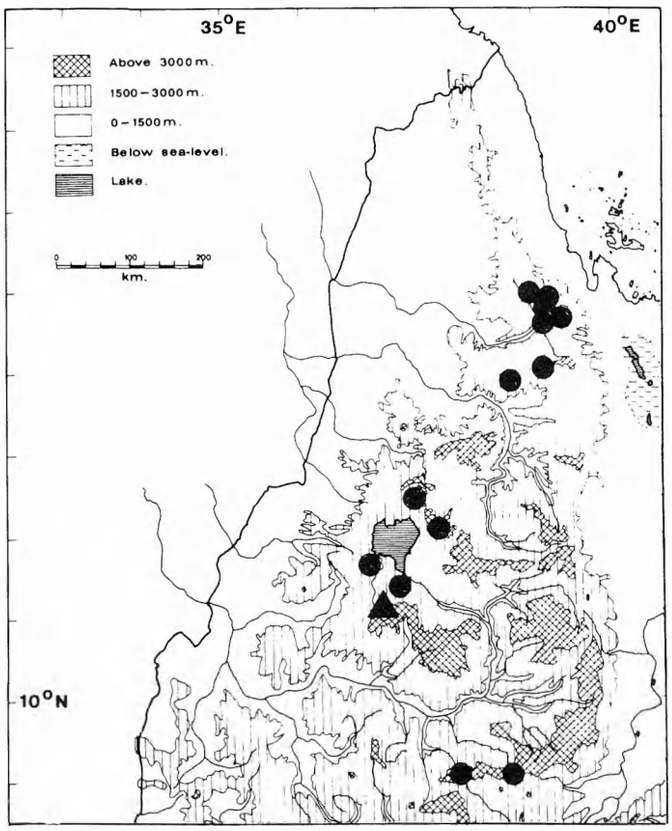

Fig. 1. Map of the N Ethiopian uplands, showing the distribution of *Dombeya torrida*. The dots represent localized specimens, the triangle the locality where Bruce's drawing of the 'Walkuffa' was made. – Based on specimens at BM, FI and K.

Dombeya bruceana A. Richard 1847 p. 77, nom. illeg. – Original material: Schimper, Iter Abyss. I no. 378, Tigré, Antitschoa at Mt Semjata (P, BM, K); Quartin-Dillon s.n., Tigré, Selleuda near Adua (P); Petit s.n., Shoa (P); Bruce's plate and description; syntypes.

Xeropetalum brucei Hochst., on the printed label of Schimper's exsiccate Iter Abyss. I no. 378 and Hochstetter 1841 p. 29; nom. nud.

['Walkuffa', Bruce 1790 p. 67 and plate opposite p. 67; Bruce 1805 Vol. 7, p. 176, and Vol. 8, Plate 20.]

Ecology and distribution. A small tree, 3–5(–8) m, growing in *Juniperus procera* forest or in evergreen scrub derived from juniper forest, at 1800–2500 m. Seems to be common in Eritrea, from where we have seen a number of specimens at FI (see Fiori 1912 p. 262), but also recorded from Tigré, Begemder, Gojjam and Shoa (Fig. 1). Apparently endemic to Ethiopia.

Taxonomy. The genus *Dombeya* urgently needs a revision on a continental scale, and the following taxonomic remarks can only be tentative. *Dombeya torrida* and *D. schimperana* A. Rich. (*'schimperiana'*) seem to be closely related, and are part of a complex of species which also involves C African species such as *D. goetzenii* Engl.; *D. torrida* is the oldest available epithet in the group. It represents the northernmost populations of the complex. The peduncles of *D. torrida* are as long as or longer than the petiole of the supporting leaf, a character which is seen on Bruce's plate, whereas *D. schimperana* usually has shorter peduncles. The peduncles and petioles of *Dombeya torrida* are puberulous or almost glabrous, and the leaf blades have scattered stellate hairs, whereas the peduncles and petioles of *D. schimperana* are tomentose at least when young, and the leaf blades have long, brittle hairs on the lower side and often long, brown hairs on the terminal part of the petiole. The two species are usually readily distinguishable.

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The genus Neurocalyx (Rubiaceae-Argostemmateae) in Ceylon

Birgitta Bremer

Bremer, B. 1979 09 30: The genus Neurocalyx (Rubiaceae-Argostemmateae) in Ceylon. *Bot. Notiser 132:* 399–407. Stockholm. ISSN 0006-8195.

Neurocalyx is a genus of the tribe Argostemmateae (Rubiaceae). Three of the species are endemic to Ceylon, while the fourth also occurs in S India. The nomenclature, morphology, phytogeography, phylogeny, and systematic position of the genus are discussed.

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A revision of the genus *Neurocalyx* is presented here. The genus belongs to the Argostemmateae, a homogeneous, mostly herbaceous tribe of the Rubiaceae consisting of c. 200 species and having a wide Old World distribution from W Africa to SE Asia. This paper is part of an investigation regarding the phylogeny and phytogeography of this tribe.

I have studied all the species of *Neurocalyx* in the field, and examined all cited collections from BM, K, PDA, and S.

Morphological aspects

Habit. The species of *Neurocalyx* are suffruticose, unbranched or rarely sparsely branched. In *N. calycinus* the leaves are separated by distinct internodes, but in the other species they form apical rosettes. In *N. zeylanicus* the rosette is borne on a short stem, but in *N. championii* and *N. gardneri* the stem is very reduced and the rosettes are pressed densely against the ground, obviously a derived condition.

Hairs and papillae. All the species have monoseriate hairs (Fig. 1 A–D) on the peduncle, the ovule, the calyx, the pedicel, and on the leaf veins, especially underneath. The hairs of *N. zeylanicus* and *N. calycinus* are stiff, erect and spreading, and few-celled; the hairs of *N. championii* and *N. gardneri* are thin-walled and many-celled, a derived condition. The two former species have papillae (Fig. 5 B, 6 B) mainly near the margin of the leaves. *N. championii* (Fig. 7 B) has similar papillae, spread densely over the entire leaf surface. *N. gardneri* has long, many-celled hairs with a distinct foot cell (Fig. 8 B) on the lamina between the veins. These hairs are probably homologous with the papillae; they are different from the hairs on the nerves, which lack a foot cell.

Glandular hairs, similar to those of other Rubiaceae, illustrated by Solereder (1899 p. 503), are found, three to five at a time, laterally at the base of the bracts and calyx lobes.

Leaves. The lamina is flat (*N. zeylanicus* and *N. calycinus*) or bullate with the areas between the veins convex (*N. championii* and less distinct in *N. gardneri*). The latter condition is obviously derived, and is not known elsewhere in the tribe.

Flowers. The calyx and the bracts are pink to white and showy. The corolla is white. The staminal cone is bright yellow and very obvious. The corolla with the inserted stamens drops easily. Many collections of *Neurocalyx* have no flowers at anthesis, probably because the collectors have been attracted by the calyx and the bracts.

Pollen. Acetolysed pollen has been studied. There are apparently no differences in pollen morphology between the species. The pollen is described as follows.

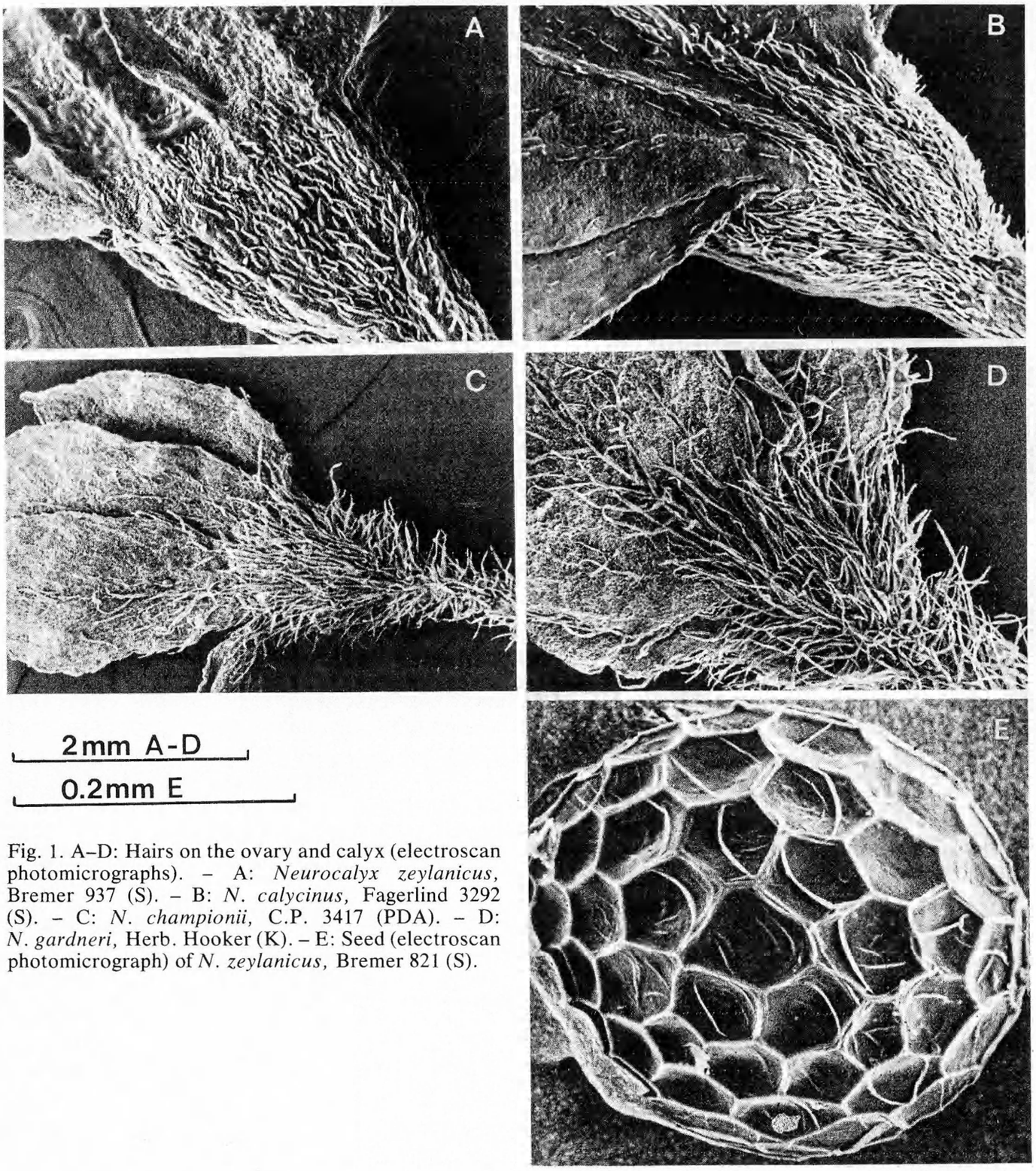

Fig. 1. A–D: Hairs on the ovary and calyx (electroscan photomicrographs). – A: *Neurocalyx zeylanicus*, Bremer 937 (S). – B: *N. calycinus*, Fagerlind 3292 (S). – C: *N. championii*, C.P. 3417 (PDA). – D: *N. gardneri*, Herb. Hooker (K). – E: Seed (electroscan photomicrograph) of *N. zeylanicus*, Bremer 821 (S).

Pollen grains 3-colporate, spheroidal to prolate-spheroidal (9.5 μm). Apocolpium c. 3 μm. Colpi relatively wide. Ora lalongate, narrow. Exine 1–1.3 μm thick. Sexine $\pm$ smooth, not clearly differentiated from the nexine.

Phytogeography

Three species of *Neurocalyx* are endemic to Ceylon (Fig. 2, 3) but the fourth, *N. calycinus*, is also to be found in S India. The species have vicariant, albeit partly overlapping, rather limited distributions and are strictly bound to the

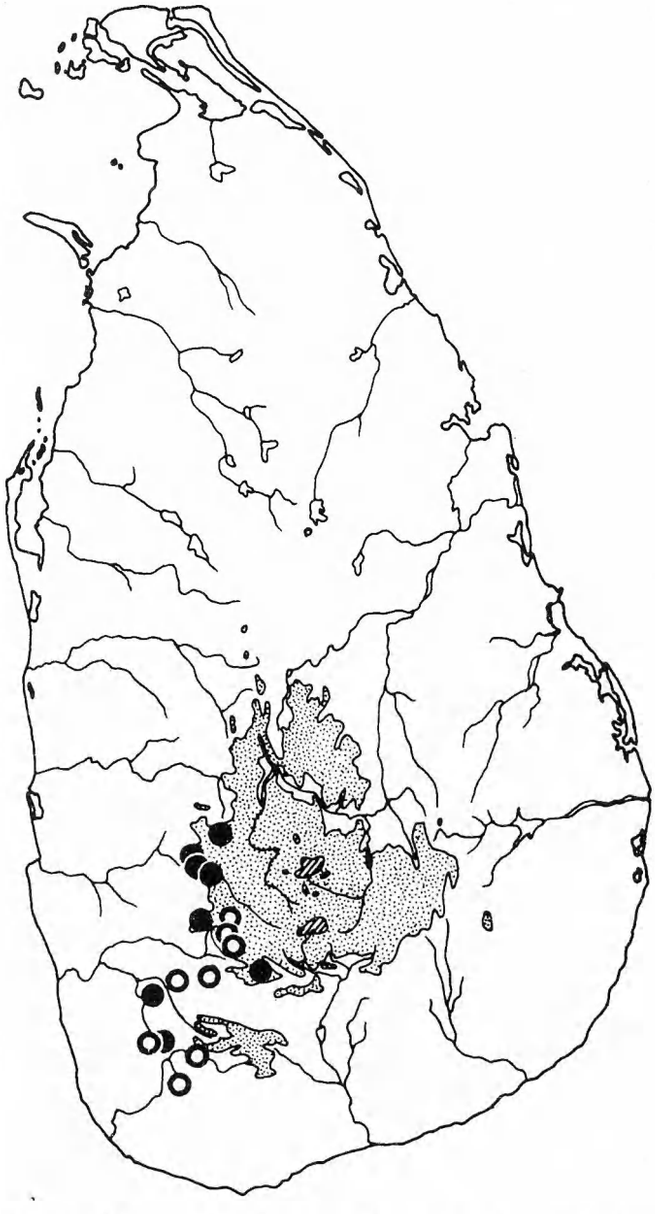

Fig. 2. Known distribution of *Neurocalyx calycinus* (●) and *N. zeylanicus* (○).

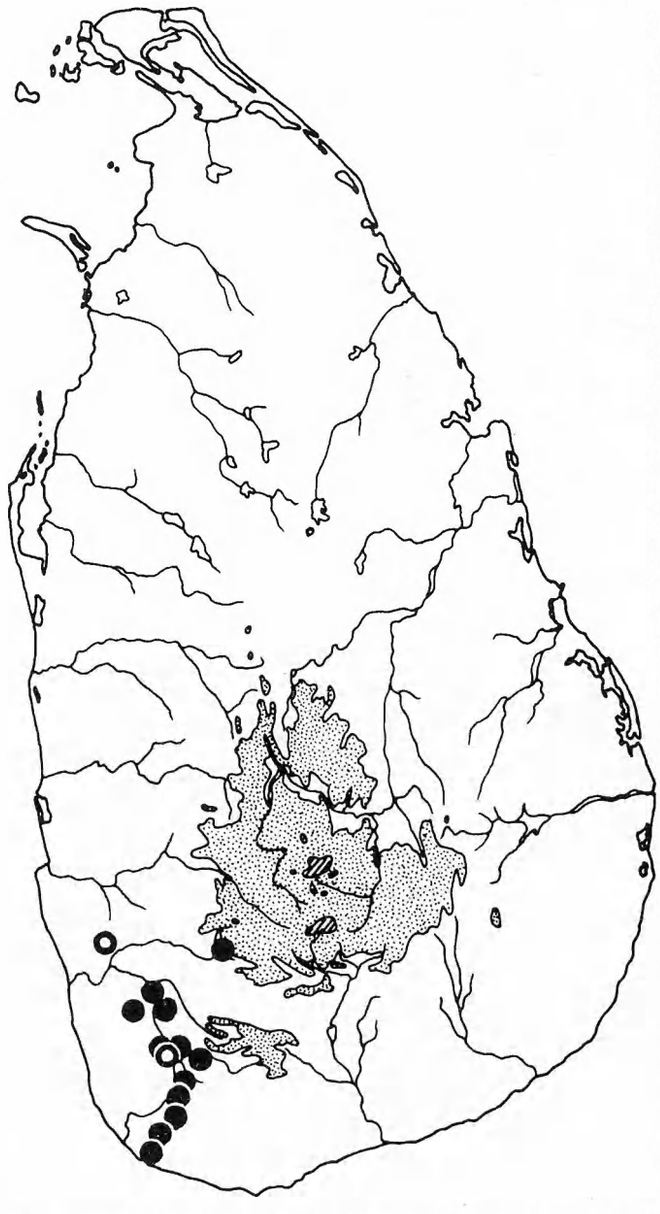

Fig. 3. Known distribution of *Neurocalyx championii* (●) and *N. gardneri* (○).

lowland rain forest with a mean annual rainfall over 2000 mm and no dry season. There is little of this rain forest vegetation left today and that which remains is threatened by logging and cultivation. This habitat destruction may partly explain the present limited distribution of the species. All the species are uncommon; *N. gardneri* now probably only occurs in one locality, which may soon be destroyed by cultivation.

Another possible reason for the restricted distribution is the mode of seed dispersal. The species have long peduncles (except for *N. calycinus*) and after anthesis these bend to the ground. The fruit does not open until animals or fungi destroy the walls and liberate the seeds close to the mother plant.

Taxonomy

Phylogeny of the genus. In order to present a possible interpretation of the phylogeny in a group (a cladogram, Fig. 4) it is necessary to identify derived (apomorph) and primitive (plesiomorph) character conditions. Joint possessions of apomorphies (synapomorphies) indicate sister groups and monophyletic groups (a monophyletic group is a group derived from a common ancestor and comprising all species descended from this ancestor). This method of

phylogenetic reconstruction was developed by Hennig (1950, 1966) and its application to botany is discussed by Bremer & Wanntorp (1978).

Within the Argostemmateae there are some traits which are only to be found in *Neurocalyx*, such as a large corolla-like calyx (a, indicated in Fig. 4) and long racemose inflorescences (b), which after anthesis are bent towards the ground. There is no reason to assume that these traits have evolved several times in the tribe, as they are possessed by a small group of species with a limited distribution, vicariant to the distribution of the remaining major part of the tribe. I consider them synapomorphies, defining the genus *Neurocalyx* as a monophyletic unit.

N. zeylanicus, *N. championii*, and *N. gardneri* form a monophyletic group defined by leaves in a dense rosette (c) and inflorescences reaching the ground (d). In this group of three species, *N. championii* and *N. gardneri* are sister species both with several-celled hairs (e) and bullate leaves (f).

Position of the genus. Within the tribe Argostemmateae *Neurocalyx* is related both to *Argostemma* and *Steenisia* and I believe that the sister group is one of these genera or perhaps a group of species in one of them. The dry indehiscent fruit of *Neurocalyx* is very much like the capsule of *Argostemma*. Furthermore, the two genera have similar pollen, very small and 3-colporate but *Argostemma* has elliptic or round ora and *Neurocalyx* has lalongate ora. *Steenisia* and *Neurocalyx* have similarities in testa structure, whereas *Argostemma* is quite different with a large distinct mamilla in each testa cell.

The tribe Argostemmateae is placed in the subfamily Rubioideae near the tribe Hedyotideae (Verdcourt 1958, Bremekamp 1954, 1966), where it was earlier included. Argostemmateae differs from Hedyotideae by the adnate anthers.

Argostemmateae possesses the features of the subfamily Rubioideae, raphides and valvate corolla aestivation. Its affinity to the Hedyotideae is supported by the similarities in the pluri-ovular ovary cells, the testa structure, and the pollen morphology. The synapomorphy or complex of synapomorphies, which defines the Argostemmateae, and separates it from the Hedyotideae, is the special arrangement of the stamens, which is similar to that of *Solanum* flowers. The adnate anthers form a cone, but the short filaments are free and inserted at the base of the corolla. Stamens with adnate anthers occur in only one other genus of the Rubiaceae, *Strumpfia*, a genus with uncertain position. In this genus both filaments and anthers are adnate to each other, and form a tube. *Strumpfia* has imbricate aestivation and uni-ovular ovary cells, and these characteristics do not indicate relationship to Rubioideae.

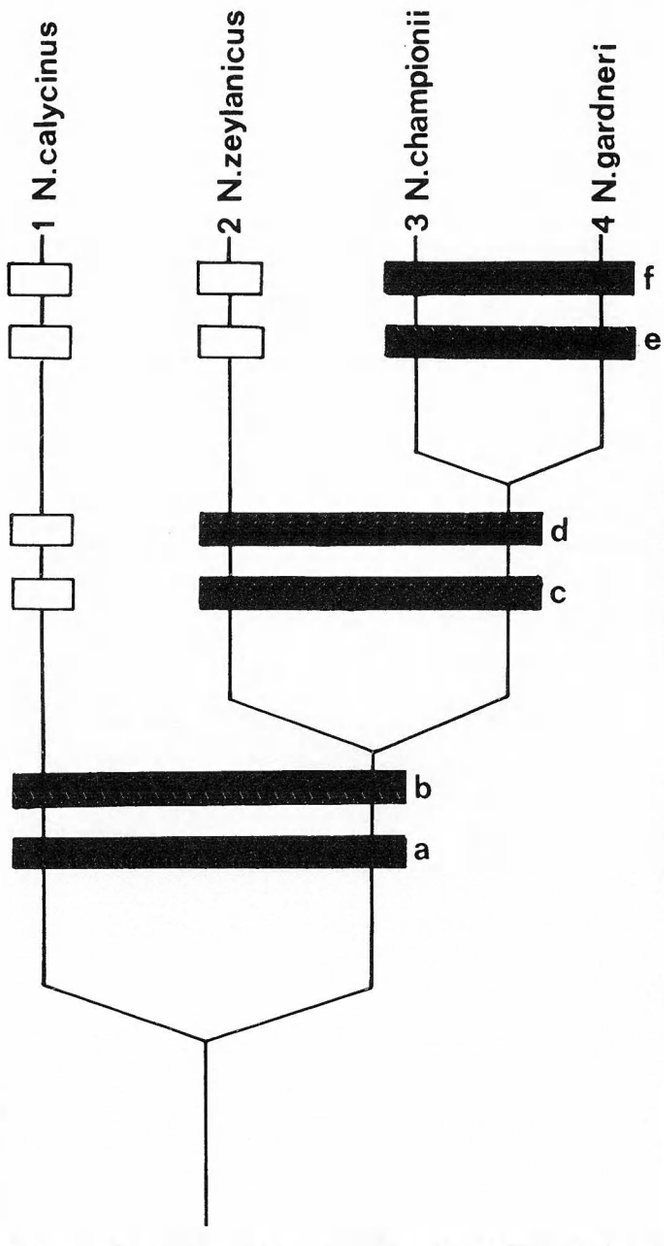

Fig. 4. Cladogram of *Neurocalyx*. Black bars indicate synapomorphies, white bars indicate corresponding symplesiomorphies. Letters correspond to derived conditions mentioned in text.

Bremekamp (1966) doubted the position of *Neurocalyx* within Rubioideae–Argostemmateae, and suggested a transfer to the Cinchonoideae. He had studied seeds from an undescribed

species of *Neurocalyx* sect. *Thyrsoideae* (now *Steenisia*), and found that the testa structure was similar to that of species in the Cinchonoideae. I have examined seeds of all *Neurocalyx* species and most *Steenisia* species and none has the large pits characteristic of the Cinchonoideae. The seeds (Fig. 1 E) are similar to those of many other species in the subfamily Rubioideae (e.g. *Oldenlandia* spp.; cf. Bremekamp 1952).

Neurocalyx Hook.

W. J. Hooker 1837 t. 174 – Type species: *N. zeylanicus* Hook.

Perennial and suffruticose, basally woody, ± pubescent plants with leaves opposite or often almost compressed to rosettes. Raphides in most parts of the plant, aggregated to ovoidal bundles which nearly fill the whole cell, white and shiny. Schizogenous cavities filled with a brown substance. *Leaves* oblanceolate to ovate, acuminate or obtuse to acute, pinnate-nerved, dark green above and pale beneath. *Stomata* of rubiaceous type, uniformly spread over the lower surface, with 4–5 alternating subsidiary cells. *Stipules* interpetiolar, undivided or more frequently split. *Inflorescences* axillary, racemose, with up to 30 flowers. *Bracts* pink to white, undivided or cleft. *Calyx* with five free ovate lobes, membranaceous, pink to white, with distinct nerves, shortly pubescent on margins, much broader than the corolla lobes; aestivation open with two opposite lobes unfolded and surrounding the other three, which are conduplicate with the adaxial surface exposed (Fig. 5 C). *Corolla* rotate, easily dropped; lobes five, white, ovate to lanceolate, thick, with recurved tips; aestivation valvate. *Stamens* five, introrse with short free filaments; anthers adnate to a cone and opening in long slits. *Ovary* approximately obconical, with ridges corresponding to the five midribs of the calyx, two-celled with many ovules. *Styles* longer than the stamens; stigma shallowly but distinctly bifid with papillose surface all-round. Fruit dry, thin-walled, indehiscent, with persistent calyx lobes. *Seeds* brown, spheroidal to ovoidal, 0.3–0.4 mm long; surface reticulate-foveate.

Key to the species

1. Calyx 1.5–2 times as long as the corolla. Leaves flat, glabrous between the nerves, acuminate 2
– Calyx as long as the corolla. Leaves bullate, if flat then pubescent on the whole surface, obtuse–acute ... 3
2. Stipules undivided or bifid. Stem up to 45 cm ..... 1. *N. calycinus*
– Stipules split in several subulate parts. Stem < 12 cm ..... 2. *N. zeylanicus*
3. Leaves bullate, glabrous between the nerves, entire–crenate ..... 3. *N. championii*
– Leaves flat–bullate, pubescent, crenate ..... 4. *N. gardneri*

1. **Neurocalyx calycinus** (R. Br. ex Benn.) Robinson – Fig. 5

Robinson 1910 p. 402 – *Argostemma calycinum* R. Br. ex Bennett 1838 p. 97 – Holotype: Wallich 8397 (K-W, Verdcourt pers. comm.).

Neurocalyx hookeriana Wight 1838 t. 52.

Neurocalyx wightii Arnott 1839 p. 22 – Types: Wight 2473 (K).

Neurocalyx capitata Benth. ex J. D. Hooker 1880 p. 47 – Types: Walker (K, PDA).

Nomenclatural note. Two months after Bennett's (1838) description of *Argostemma calycinum N. hookeriana* was published by Wight (1838). No specimens were indicated. Arnott (1839) described *N. wightii* on material collected by Wight (two specimens) and it is probably based on the same collection as *N. hookeriana*.

Stem up to 45 cm, erect, mostly naked with leaf scars, leafy on upper half, with internodes up to 2 cm. *Leaves* 10–35 × 3–9 cm, oblanceolate, rarely obovate, acuminate, entire, membranaceous, flat, glabrous on both sides except for few-celled hairs on the veins. *Petiole* up to 4 cm. *Stipules* undivided or bifid, occasionally irregularly lobed, 1.5–3 cm. *Inflorescences* elongate to compressed with up to 30 flowers. *Peduncle* 2–10 cm, 1/4–1/2 as long as the leaves. *Bracts* entire or 3-lobed; lobes ovate. *Calyx* 1–2 cm diam.; lobes ± broadly ovate. *Corolla* 1/2–2/3 as long as the calyx. *Ovary* shortly pubescent.

Variation. The stipules may be undivided or cleft, even on the same plant. This characteristic was the only one which separated *N. calycinus, N. hookeriana,* and *N. wightii. N. capitata* was distinguished from *N. wightii* by a long stout stem and larger leaves with considerably

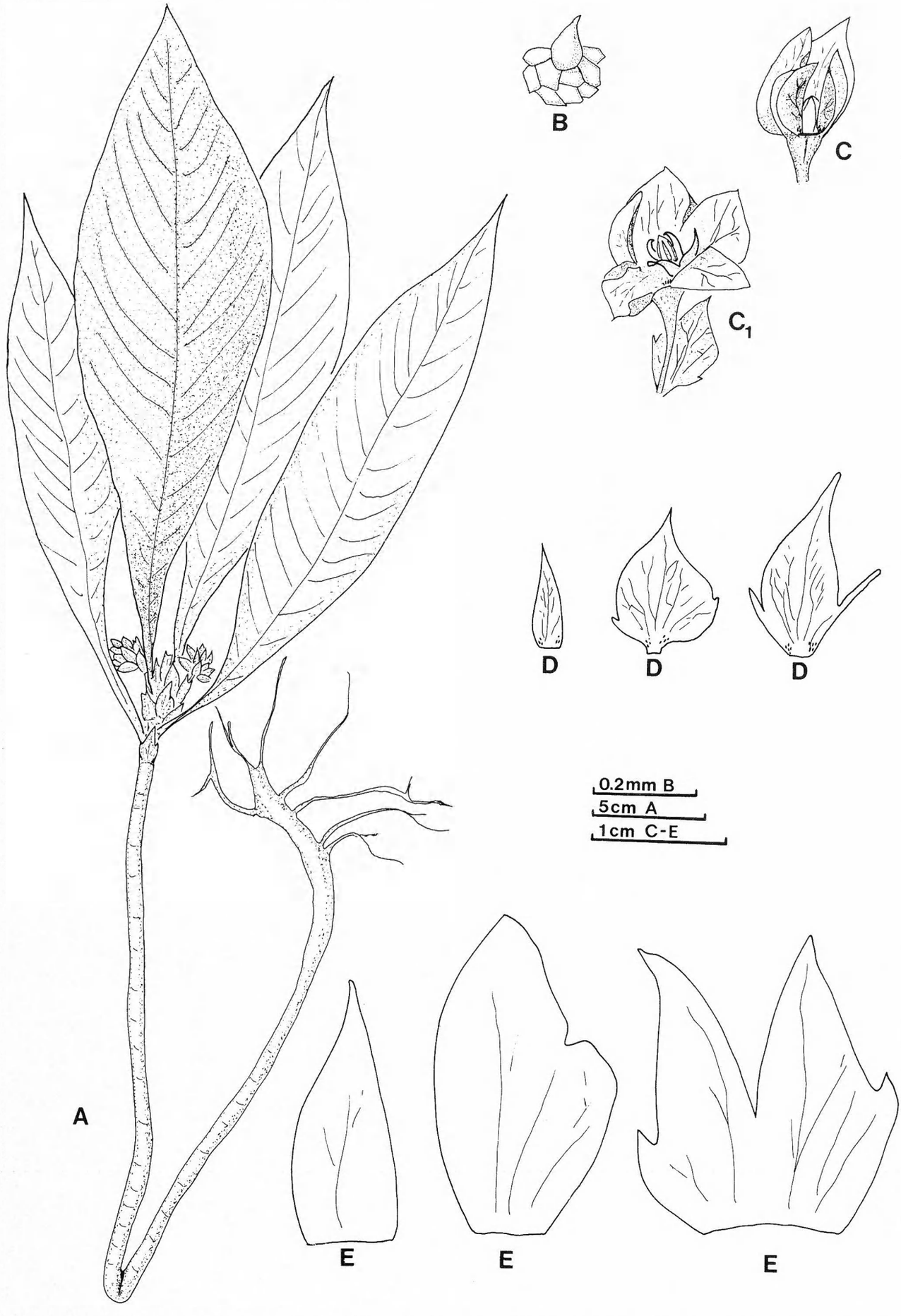

Fig. 5. *Neurocalyx calycinus*. – A: Habit. – B: Leaf papillae. – C, C_1: Flowers, C before anthesis with one calyx-lobe removed. – D: Bracts. – E: Stipules. – A–E, Bremer 868 (S); C_1, Meijer 834 (PDA).

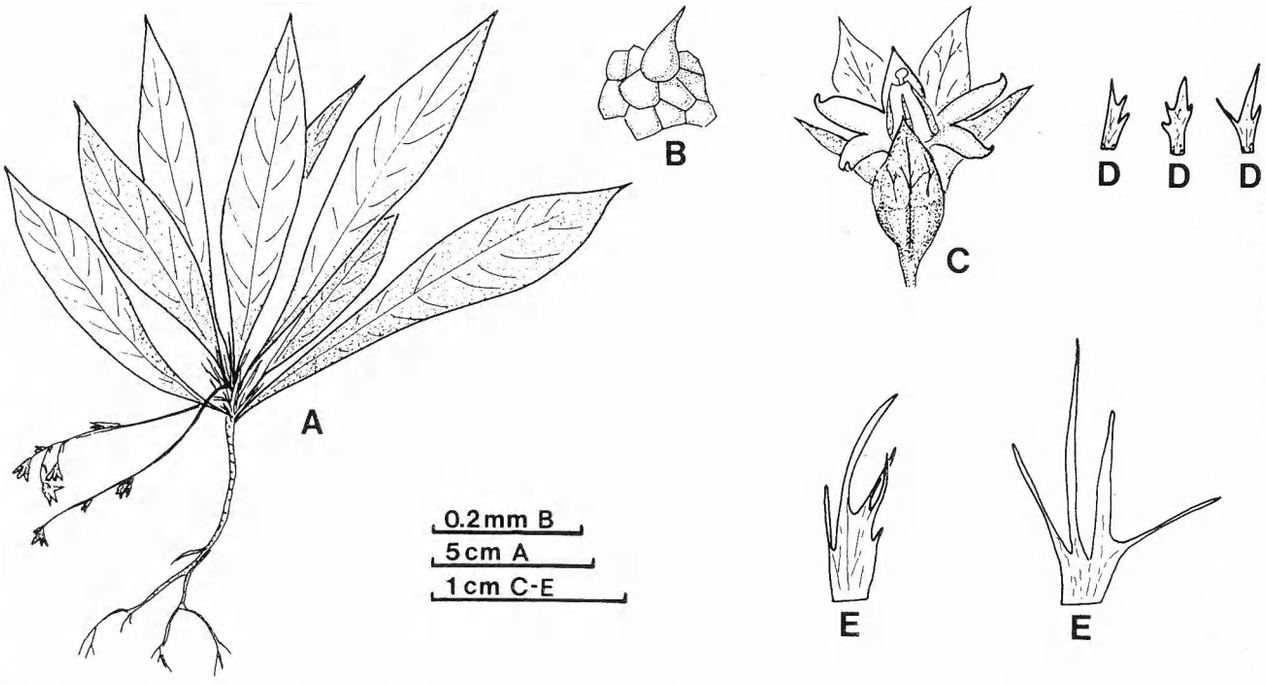

Fig. 6. *Neurocalyx zeylanicus*. – A: Habit. – B: Leaf papillae. – C: Flower. – D: Bracts. – E: Stipules. – Bremer 937 (S).

more nerves as well as allegedly differing capitate inflorescences. These features are modifications and only dependent on the degree of development.

Distribution (Fig. 2). *N. calycinus* grows as undervegetation on flat ground in rain forest from 300 to 900 m (occasionally below 300 m).

Collections. Kandy Distr.: Dolosbage 19th century, unknown coll. (PDA) – Morahenegama 1977, Bremer 1014 (PDA, S, US) – *Kegalle Distr.:* Gonnana 1977, Fagerlind 3491 (S) – Kitulgala 1977, Bremer 938 (PDA, S, US) – *Ratnapura Distr.:* Adawi Kande 1927, Silva (PDA) – Between Balangoda and Rassagala 1971, Meijer 834 (PDA) – Kukul Korale 19th century, unknown coll. (PDA) – *Galle Distr.:* Haycock = Hiniduma Kande 1976, Fagerlind 3292 (K, S); 1977, Bremer 868 (PDA, S, US) – *Unidentified loc.:* Kalugammana 1927, Silva (PDA) – Dotagala Kande 1927, Silva (PDA) – Eratne 19th century, unknown coll. (PDA) – *Without loc.:* C. P. 595 (BM, K, L, PDA) – Macrae 251 (K) – Herb. Hookerianum (PDA) – Walker (K) – Wight (K) – unknown coll. (K).

India: Mysore State, several localities (BM, K) – *Tamil Nadu State,* several localities (BM, K) – *Kerala State,* several localities (BM, K).

2. **Neurocalyx zeylanicus** Hook. – Fig. 6

W. J. Hooker 1837 t. 174 – Holotype: Walker (K).

Stem up to 12 cm, erect, mostly naked with leaf scars, densely leafy at top. *Leaves* 4–22 × 1–4 cm, oblanceolate, acuminate, entire, membranaceous, flat, glabrous above except for few-celled hairs on the basal part of the midrib, beneath with few-celled hairs on the veins. *Petiole* up to 4 cm. *Stipules* split in several subulate parts, 0.5–2.5 cm. *Inflorescences* with up to 10 flowers. *Peduncle* 1–9 cm, 1/3–2/3 as long as the leaves. *Bracts* undivided or more often 3–4-lobed; lobes lanceolate or subulate. *Calyx* 1–1.5 cm diam.; lobes ovate. *Corolla* 1/2–2/3 as long as the calyx. *Ovary* sparsely and shortly pubescent.

Distribution (Fig. 2). *N. zeylanicus* grows on sloping wet ground along streams in rain forest at an elevation of 50 to 600 m. Most collections are from c. 100 m.

Collections. Kegalle Distr.: Kitulgala 1975, Fagerlind 3314 (K, S, US); 1977, Bremer 937 (PDA, S, US); 1977, Fagerlind 4016 (S) – *Ratnapura Distr.:* Adams Peak 19th century, C. P. 286, 362 (K) – Bambarabotuwa 1969, Hoogland 11588 (K, PDA); 1971, Jayasuriya 249 (PDA); 1971, Meijer 870 (PDA) – Paragala along Pokonodole stream 1977, Bremer 793 (PDA, S, US) – *Kalutara Distr.:* Ihala Hewessa 1977, Bremer 821 (PDA, S, US) – *Galle Distr.:* Neluwa 1970, Balakrishnan NBK 232 (PDA) – Kanneliya Forest 1974, Wanntorp 2998 (S); 1977, Bremer 859 (PDA, S, US); 1977, Fagerlind 3166 (S); 1978, Thor 602 (S) – Opatte, unknown coll. (PDA) – *Without loc.:* Finlayson (BM) – Walker (K) – C.P. 286 (BM, K, PDA) – unknown coll. (K).

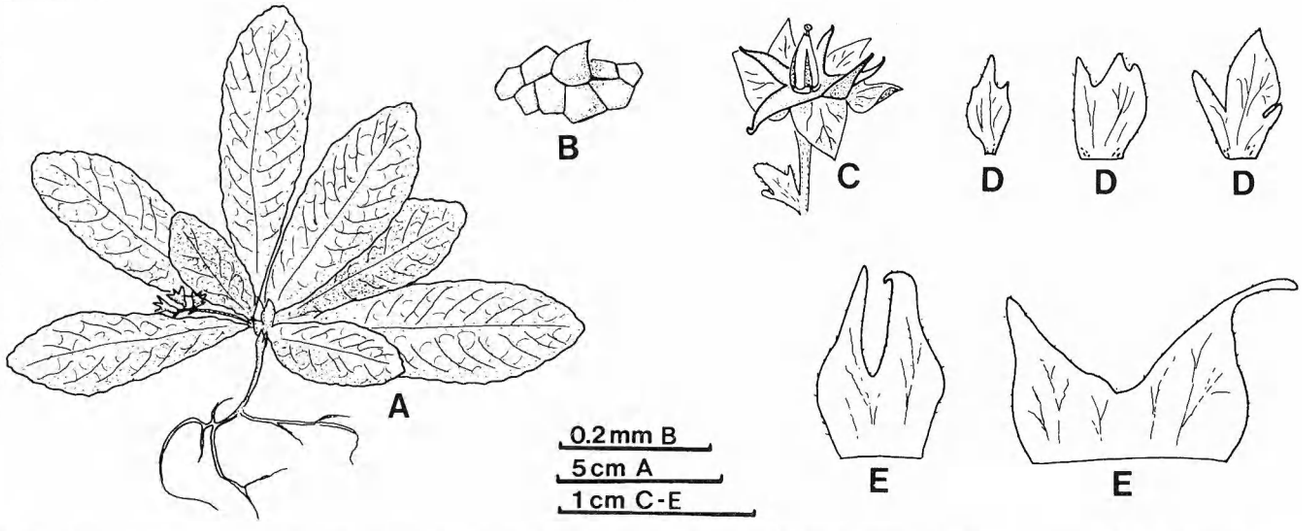

Fig. 7. *Neurocalyx championii*. – A: Habit. – B: Leaf papillae. – C: Flower. – D: Bracts. – E: Stipules. – Bremer, Kers & Thoran 133 (S).

3. **Neurocalyx championii** Benth. ex Thw. – Fig. 7

Thwaites 1859 p. 139 – Lectotype (selected here): C.P. 3480 (PDA).

Stem up to 4 cm; leaves crowded. *Leaves* 4–15 × 1.5–4 cm, oblanceolate–obovate, obtuse–acute, entire–crenate, slightly coriaceous, bullate like toadskin, glabrous on both sides except for many-celled hairs on the veins. *Petiole* up to 1 cm. *Stipules* bifid, 0.5–1.5 cm. *Inflorescences* with up to 8 flowers. *Peduncle* 3–9 cm, 1/3–2/3 as long as the leaves. *Bracts* undivided or 3-lobed. *Calyx* 1–1.5 cm diam.; lobes ± broadly ovate. *Corolla* white, as long as the calyx. *Ovary* pubescent, with long hairs.

Distribution (Fig. 3). *N. championii* grows on open soil in small depressions and road cuttings in rain forest on low elevation up to 300 m.

Collections. Ratnapura Distr.: Kukul Korale 19th century, C.P. 3480 (PDA) – Bambarabotuwa 19th century, unknown coll. (PDA) – *Kalutara Distr.:* Denihena 1974, Wanntorp 2928 (S) – *Galle Distr.:* Neluwa Kande 19th century, unknown coll. (PDA) – Hiniduma 1972, Cramer 3693 (PDA) – NW of Hiniduma 1928, Alston 2343 (K, PDA) – Kanneliya Forest 1971, Meijer 977 (PDA); 1973, Fagerlind 165 (S); 1976, Fagerlind 3285 (K, S, US); 1978, Thor 558, 562, 601 (S) – Udugama 1972, Cramer 3701 (PDA) – Talgampola Arboretum 1969, Kostermans 23642 (PDA) – Kottawa 1970, Balakrishnan NBK 273 (PDA); 1970, Cramer 3016 (PDA); 1973, Bremer, Kers & Thoran 133 (S); 1973, Wanntorp 2555 (S); 1977, Bremer 829 (PDA, S, US) – Akmimana 19th century, de Poli (K) – *Unidentified loc.:* Tilta Weraluwa Kotha 1919, unknown coll. (PDA) – *Without loc.:* C. P. 3417 (BM, K, PDA) – unknown coll. (K).

4. **Neurocalyx gardneri** Thw. – Fig. 8

Thwaites 1859 p. 139 – Lectotype (selected here): C.P. 1671, the specimen with the annotation 'Pasdun Korale Gardner 2/8 1863' (PDA). Isotypes in BM, K, PDA.

Stem up to 6 cm; leaves crowded. *Leaves* 7–22 × 2.5–9 cm, oblanceolate–ovate, obtuse–acute, crenate, membranaceous, slightly bullate, when dried flat, covered with hairs on both sides. *Petiole* up to 1 cm. *Stipules* bifid, occasionally irregularly lobed, 1–2 cm. *Inflorescences* with up to 8 flowers. *Peduncle* 3–8 cm, 1/3–2/3 as long as the leaves. *Bracts* undivided or 3-lobed; lobes ovate. *Calyx* 1–1.5 cm diam.; lobes ovate. *Corolla* as long as the calyx. *Ovary* pubescent with long hairs.

Note. Trimen (1894) described the corolla of *N. gardneri* as 1/2 as long as the calyx. There is no corolla left on the cited specimen but in all the recently collected specimens the corolla is as long as the calyx.

Distribution (Fig. 3). *N. gardneri* grows on open soil in small depressions in rain forest, probably only in one locality today, Haycock. I have searched in vain at Hewessa, one of the original localities, but it is probably extinct there, as most of the area is cultivated. The other original locality, Pasdun Korale, is very inexact and there is apparently no suitable forest left in this area.

Collections. Kalutara Distr.: Pasdun Korale 19th century, Gardner C.P. 1671 (PDA) – Hewessa 19th

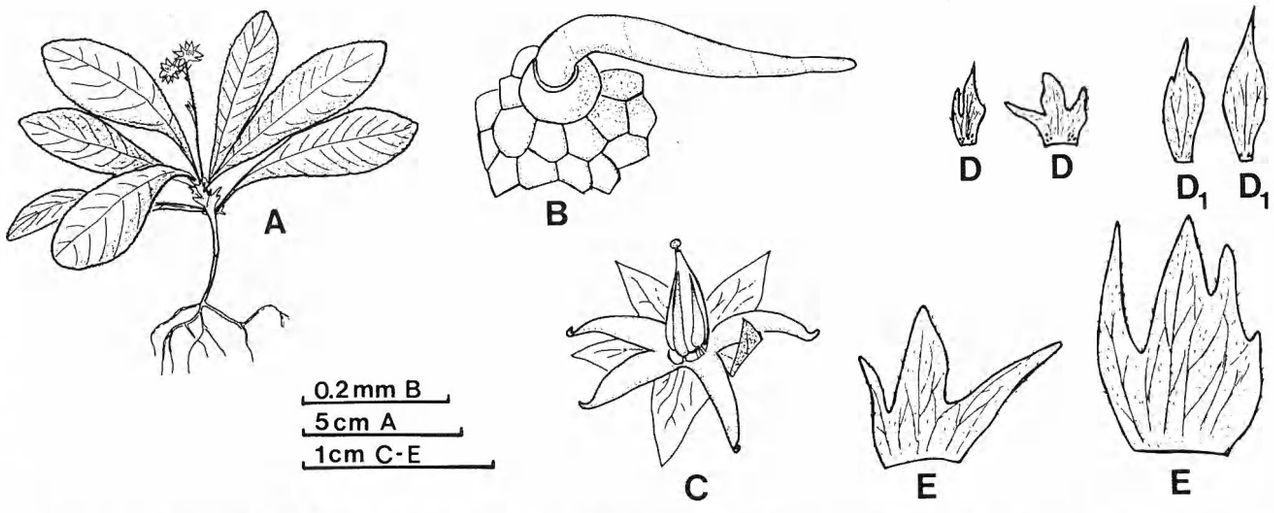

Fig. 8. *Neurocalyx gardneri*. – A: Habit. – B: Leaf hair. – C: Flower. – D, D_1: Bracts. – E: Stipules. – A–E, Bremer 865 (S); D_1, C.P. 1671 (PDA).

century, C.P. 1671 (K) – *Galle Distr.:* Haycock = Hiniduma Kande 19th century, unknown coll. (K); 1969, Cramer 2687 (PDA); 1976, Fagerlind 2567 (K, S, US); 1977, Bremer 865 (PDA, S, US) – *Without loc.:* C.P. 1671 (BM, K, PDA) – C.P. 3417 p.p. (PDA).

Excluded taxa

Neurocalyx borneënsis Valeton 1913 p. 514 = *Steenisia borneënsis* (Valeton) Bakhuizen 1952 p. 381.

Neurocalyx corollinus Valeton 1913 p. 513 = *Steenisia corollina* (Valeton) Bakhuizen 1952 p. 382.

Neurocalyx elatus Valeton 1913 p. 514 = *Steenisia elata* (Valeton) Bakhuizen 1952 p. 382.

Neurocalyx matangensis W. W. Smith 1915 p. 323 = *Steenisia borneënsis* (Valeton) Bakhuizen, cf. Airy-Shaw 1937 p. 288.

Neurocalyx pleurocarpus Airy-Shaw 1937 p. 286 = *Steenisia pleurocarpa* (Airy-Shaw) Bakhuizen 1952 p. 382.

Neurocalyx pterosepalus Airy-Shaw 1937 p. 283 = *Steenisia pterosepala* (Airy-Shaw) Bakhuizen 1952 p. 382.

Acknowledgements. I wish to thank H.-E. Wanntorp for criticism of the manuscript. I am also grateful to the curators of BM, K, PDA, and S, especially B. Verdcourt at K, and A. H. M. Jayasuriya at PDA, and to S. Nilsson at the Palynological laboratory in Stockholm for help with preparation and diagnosis of pollen.

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Two new taxa of Mallomonas (Chrysophyceae)

Berit Asmund and Gertrud Cronberg

Asmund, B. & Cronberg, G. 1979 09 30: Two new taxa of Mallomonas (Chrysophyceae). *Bot. Notiser 132:* 409–418. Stockholm. ISSN 0006-8195.

Mallomonas torquata Asmund & Cronberg, sp. nov. (from Sweden, Denmark and Alaska) and *M. doignonii* Bourrelly var. *tenuicostis* Asmund & Cronberg, var. nov. (from Denmark) are described and illustrated with SEM and TEM pictures. Related species are also illustrated.

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This paper describes two new taxa, *Mallomonas torquata* and *M. doignonii* var. *tenuicostis*, both belonging to section *Torquatae* (Peterfi & Momeu 1976; series *Torquatae* Harris & Bradley 1960). They resemble *M. coronifera* Matvienko, *M. lefeuvrei* Villeret and *M. doignonii* Bourrelly. Description of these three species are also given. But as type material of *M. coronifera* and *M. lefeuvrei* are missing and their ultrastructure is unknown, these species cannot be evaluated.

Methods

Phytoplankton was collected with a Ruttner sampler or plankton net (45 μm). Samples were fixed with Lugol's solution or formalin. For qualitative examination, a drop of the sample was dried on a coverslip which was mounted on a slide with a drop of canada balsam in each corner. The dried sample was examined in phase contrast microscope at 1000×. Samples that contained scaled Chrysophyceae were prepared for TEM and SEM investigations as follows:

Fresh samples were prepared directly for EM, but fixed samples were carefully rinsed with distilled water. For TEM investigations a drop of the samples was put on the formvar-coated grid and air dried. Material for SEM investigations was dropped on a round coverslip that was glued to a specimen stub and dried. The stub was then coated with gold (60%) and palladium (40%) under vacuum. The sample was studied in a Cambridge Stereoscan microscope at 30 kV for optimal resolution. The micrographs were taken with the following electron microscopes: Philips EM 300 (Fig. 4 A–C), Institute of Microbiology, and Cambridge Stereoscan Mark IIA (Fig. 3), Institute of Zoology, University of Lund, Sweden; JEM-T-7 (Fig. 2 C–E, 4 D–E, 5), Institute of Plant Anatomy and Cytology, University of Copenhagen, Denmark.

The descriptions of *Mallomonas torquata* and *M. doignonii* var. *tenuicostis* are based on electron microscopic investigations.

Localities

Lake Trummen is situated in the southern Swedish uplands at the town of Växjö. The lake was heavily polluted up to 1970, when the lake was restored by suction dredging of 0.5 m nutrient-rich sediment. Before restoration the lake was characterized by algal blooms during the summer and rich diatom development during spring and autumn. After restoration a rich development of Chrysophyceae, mainly of the genera *Mallomonas* and *Synura*, appeared in the spring. The blue-green algae became less dominant during the summer. Phosphorus and nitrogen concentrations were reduced through the restoration (Bengtsson et al. 1975).

Lake Vaxsjön is situated in the middle of the province of Skåne, S Sweden. It is a humic lake, originally oligotrophic. A large tourist centre and a zoological garden have been built close to the lake, which is now being increasingly eutrophicated.

The temporary pond was situated on seasonally flooded grass fields W of Sønderskoven, Als, S Jylland, Denmark (Nygaard 1949).

Kobberdam is a eutrophic woodland pond situated in Hellebæk, near Helsingør, N Sjælland, Denmark (Asmund 1955).

Table 1. Chemical and physical data from the lakes.

Parameter	Trummen	Vaxsjön	Temporary pond	Kobberdam	Pond IV
Max. depth, m	2.2	.	.	3	2.5
Date	1974 02 28	1978 03 25	1945 03 13	1955 02 08	1957 12 05
Temperature, °C	4.1	1.0	7.5	.	0.3
pH	6.40	6.98	8.5	6.0	6.4
Conductivity, μS/cm, 20°C	217	116	.	.	95
Colour, mg Pt/l	35	30	.	.	.
P-total, μg/l	32	22	.	.	0
P-PO_4, μg/l	7	6	.	.	0
N-total, mg/l	1.16	1.15	.	.	.
N-NO_3, mg/l	.	0.54	.	.	1.4

Pond IV is situated near Anchorage, Alaska (Asmund & Hilliard 1961).

Further data are given in Table 1.

General description

Members of the section *Torquatae* are characterized by a cell armour composed of three groups of scales; (1) numerous domeless rhomboidal body scales arranged in spiral rows with their longitudinal axes across the cell and overlapping each other; (2) a small number of apical forward-pointing dome-bearing collar scales with bristles; (3) a group of small rounded rhomboidal or ovate rear scales with backward directed spine-bearing distal ends. According to the length of these spines the section *Torquatae* can be divided into two groups, one with very short spines (1–3 μm), and one with spines up to 16 μm. The new taxa belong to the latter group. Seen in light microscope they are difficult to separate from each other or from *M. doignonii;* these three taxa have the following ultrastructural features in common:

Body scales rhomboidal, becoming smaller and more ovate towards the rear. The outer surface of body scales marked with a submarginal rib running parallel to the outline of the scale and dividing it into shield and flange. Anterior half of submarginal rib broad, posterior half narrower, slightly hooded. Shield with closely spaced minute pores. Anterior half of flange with a slightly thickened edge and regularly spaced short ribs radiating from the submarginal rib, often in prolongation of ribs on the shield. *Collar scales* oblong, asymmetric with a convex 'dorsal' side and a concave 'ventral' side, with broad rounded proximal ends and narrower, dome-bearing distal ends. Dome with an anteriorly directed, triangular, pointed projection. Dorsal side of flange with a folded edge; ventral one largely obscured by the rhomboidal rib (or possibly missing); lower ventral corner with a group of regularly spaced, short, transverse ribs with pits between them. Bristles smooth, tapering, slightly curved. *Rear scales* ovate, bearing smooth, tapering, straight or curved spines of various lengths, projecting from the distal angle of the submarginal rib; usually lacking ornamentation other than the submarginal rib and the minute pores of the shield.

M. coronifera Matvienko

Matvienko 1941, 1954, 1965, Perman & Vinnikova 1955, Fott & Ettl 1959, Fott & Ludvig 1961, Glenk & Fott 1971.

According to Matvienko's diagnosis and drawings (Fig. 1 A) the cells of *Mallomonas coronifera* are oval to thick fusiform with 1–7 straight rear spines, radiating in somewhat different directions. There is no detailed description of the five collar scales, but it appears from the drawings that they are rather short and broad and have a relatively large, pointed dome. The collar scales bear straight tapering bristles. In addition to the rhomboidal body scales, Matvienko's figure shows some tripartite scales, probably originating from another *Mallomonas* species. The cyst is ellipsoidal and smooth.

Dimensions: Cells 12–41 × 6–16 μm; body

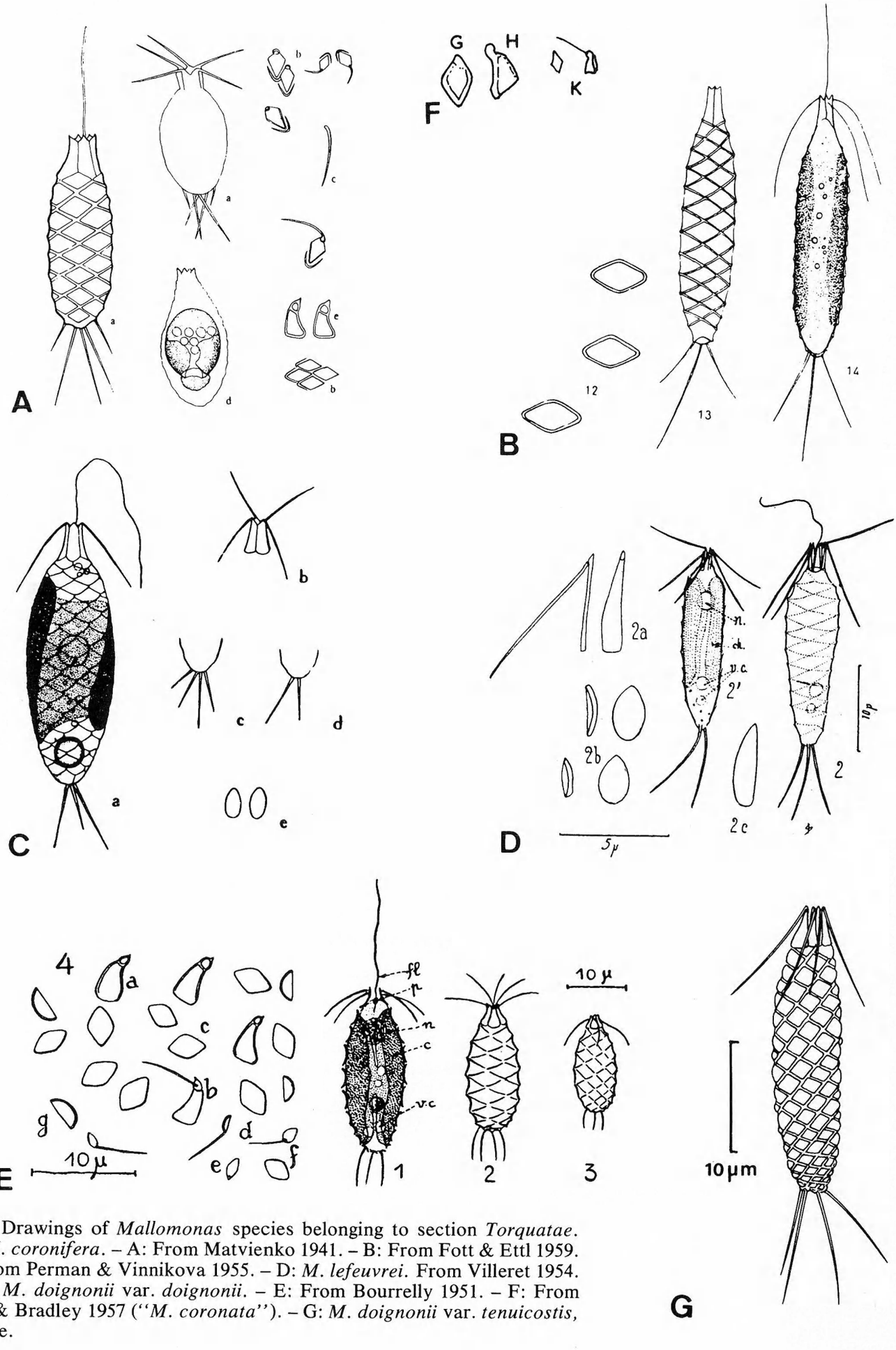


Fig. 1. Drawings of *Mallomonas* species belonging to section *Torquatae*. A–C: *M. coronifera*. – A: From Matvienko 1941. – B: From Fott & Ettl 1959. – C: From Perman & Vinnikova 1955. – D: *M. lefeuvrei*. From Villeret 1954. – E, F: *M. doignonii* var. *doignonii*. – E: From Bourrelly 1951. – F: From Harris & Bradley 1957 (*"M. coronata"*). – G: *M. doignonii* var. *tenuicostis*, holotype.

scales 3–6 × 1.5–3 μm; spines 3–7.5 μm; cysts 10–12 μm long.

Matvienko's material was collected in the vicinity of Kharkov, Ukraine. Fott & Ettl (1959) reported *M. coronifera* from Bohemia. Their specimens (Fig. 1 B) were elongate cylindrical, slightly more slender than those from Ukraine and with some of the spines slightly curved. It is uncertain whether it was the same species as that described by Matvienko. The same is true of the specimens recorded by Perman & Vinnikova (1955) from Bohemia. They noted a thick ellipsoidal cell and straight rear spines (Fig. 1 C). Glenk & Fott (1971) refer to the carbon replica of *M. coronifera* published by Harris & Bradley 1957 (erroneously called *M. coronata* Perman & Vinnikova). However, later Harris & Bradley (1960) and Harris (1970) declared that their species was *M. doignonii*. Thus the ultrastructure of *M. coronifera* is unknown and as no type material exists, the information about this species is not adequate for a diagnosis.

M. lefeuvrei Villeret

Villeret 1954

This species (Fig. 1 D) is often considered to be a synonym of *M. coronifera* (Perman & Vinnikova 1955, Fott & Ettl 1959, Glenk & Fott 1971). It has the main characters of sect. *Torquatae* with long rear spines, but the 5–6 pointed collar scales and the posterior scales with three curved spines are remarkably long and narrow. This peculiarity may be due to difficulties in interpretation of small objects in the light microscope or it might be of taxonomic significance. As no micrographs of this species exist and type material is not available, its identity cannot be proved.

Dimensions: Cells 6–8 × 30–40 μm; collar scales 4.5–5 × 1 μm at the base; middle body scales 2–3 μm; rear scales 1–1.2 × 3.5–4 μm.

M. doignonii Bourrelly var. **doignonii**

Bourrelly 1951, 1957, Harris & Bradley 1957 (*"M. coronata"*), 1960, Harris 1970, Marquis 1977.

The electron micrographs of the carbon replicas by Harris & Bradley (1957) as *M. coronata* represent in reality *M. doignonii* (Harris & Bradley 1960). We chose their carbon replica of the whole cell as neotype of *M. doignonii* (Fig. 2 A). The scanning micrographs of the material from Texas (Marquis 1977) completely agree with those of Harris & Bradley.

Bourrelly gave a careful description and drawings of *M. doignonii* (Fig. 1 E) as seen in the light microscope. The cells are ellipsoid or ovoid. The 5–6 triangular collar scales have pointed domes. The body scales are rhomboidal with rounded sides and shaped like watch-glasses, without ornamentation. The five very small rear scales have a slightly thickened corner from which straight or slightly curved spines project almost axially. The bristles are smooth and slightly curved.

The distinctive character of *M. doignonii* var. *doignonii* is the appearance of the rib systems on the shield of the scales. It consists of transverse, coarse, straight or more or less curved, sometimes forked ribs. Cysts are still unknown.

Dimensions: Cells 6.5–15 × 15–30 μm; collar scales 2.5 × 5 μm; body scales 1.7–2.5 × 3–4 μm; rear scales 0.7–1 × 2–2.5 μm; spines 2–10 μm.

M. doignonii var. *doignonii* is recorded from S England, France and Texas (USA).

M. doignonii var. **tenuicostis** Asmund & Cronberg, var. nov.

Holotype: Fig. 1 G, 2 B–D (Denmark, Sjælland, Helsingør, Lake Kobberdam).

A var. *doignonii* differt costis transversis squamae pluribus, tenuioribus, margine undulatis. Cysta ignota. Cellula 4–6.5 × 19–34 μm. Squama collaris 3–4 × 5–6 μm, media 2–4 × 3–6 μm; seta 10–12, spina ad 12 μm longa.

M. doignonii var. *tenuicostis* differs from var. *doignonii* in having more numerous and more delicate, wavy-edged ribs across the shields of the scales. The rear spines project in various directions. This feature gives the live cell a very characteristic appearance.

Dimensions: Cells 4–6.5 × 19–34 μm; collar scales 3–4 × 5–6 μm; body scales 2–4 × 3–6 μm; bristles 10–12 μm; spines up to 12 μm.

M. doignonii var. *tenuicostis* was found in Kobberdam between February and May in 1948–1957. It was most frequent in the early spring shortly after the breaking-up of the ice.

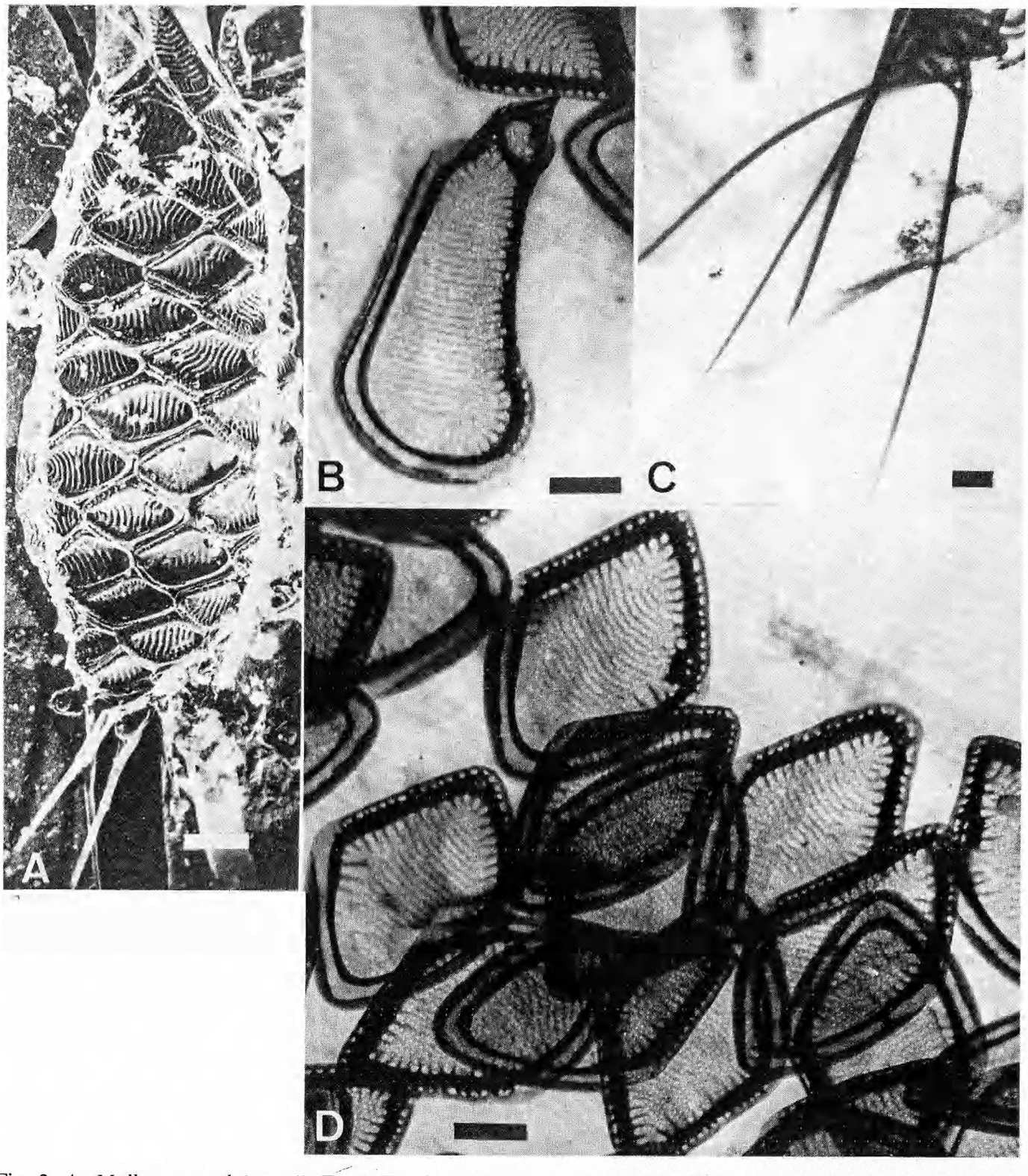


Fig. 2. A: *Mallomonas doignonii*. From Harris & Bradley 1957. – B–D: *M. doignonii* var. *tenuicostis*. – B: A collar scale showing numerous delicate, wavy-edged ribs. – C: Rear part of the cell with four scales extended to spines. – D: Rhomboidal body scales. – Scale 1 μm.

At this time of the year the pond contained a diatom–flagellate association dominated by *Melosira* spp., *Cyclotella* spp., *Chrysosphaerella brevispina, Dinobryon cylindricum, D. divergens, Mallomonas akrokomos, M. heterospina, M. reginae* and *M. teilingii*.

The epithet *tenuicostis* alludes to the delicate ribs on the shields.

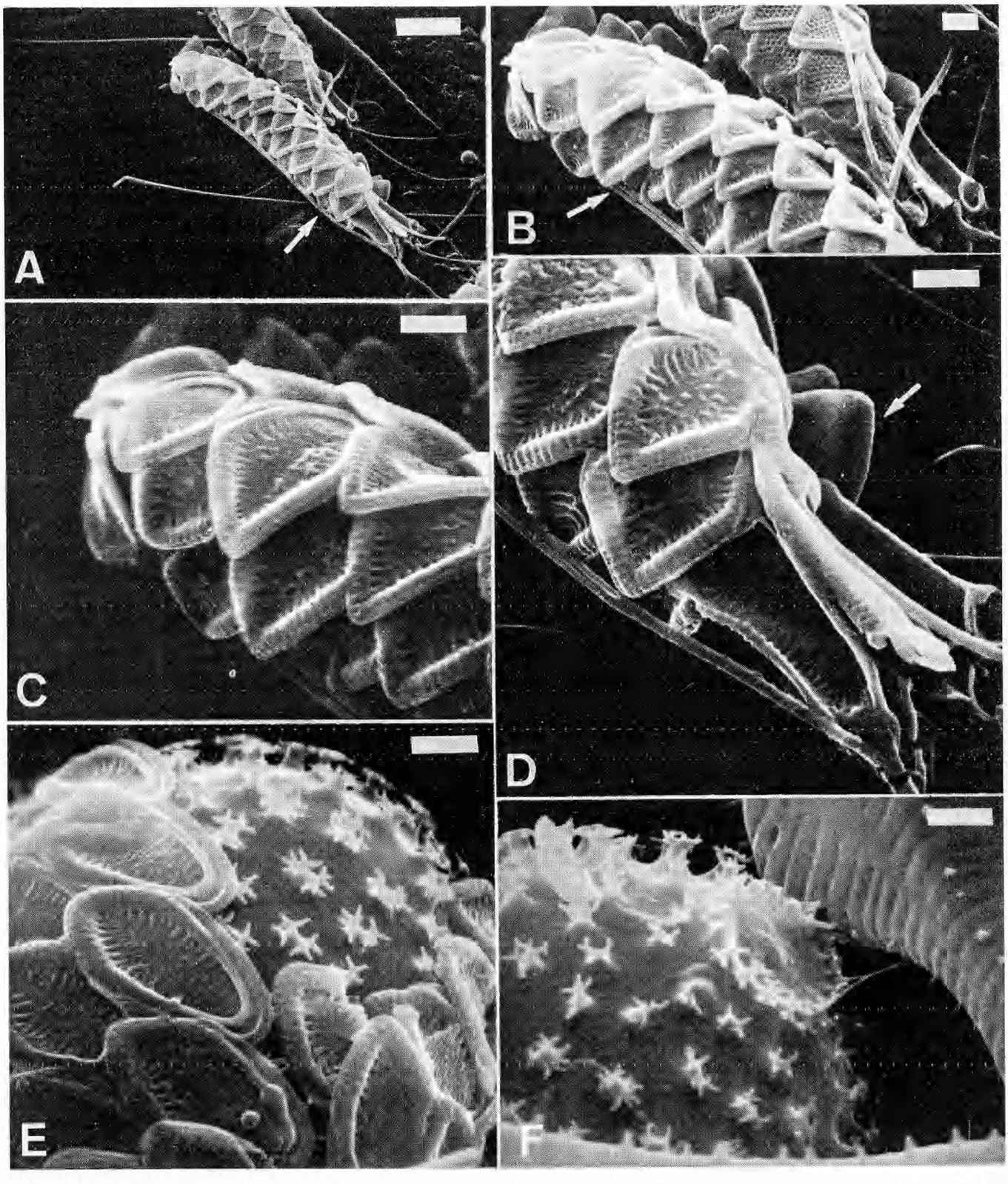
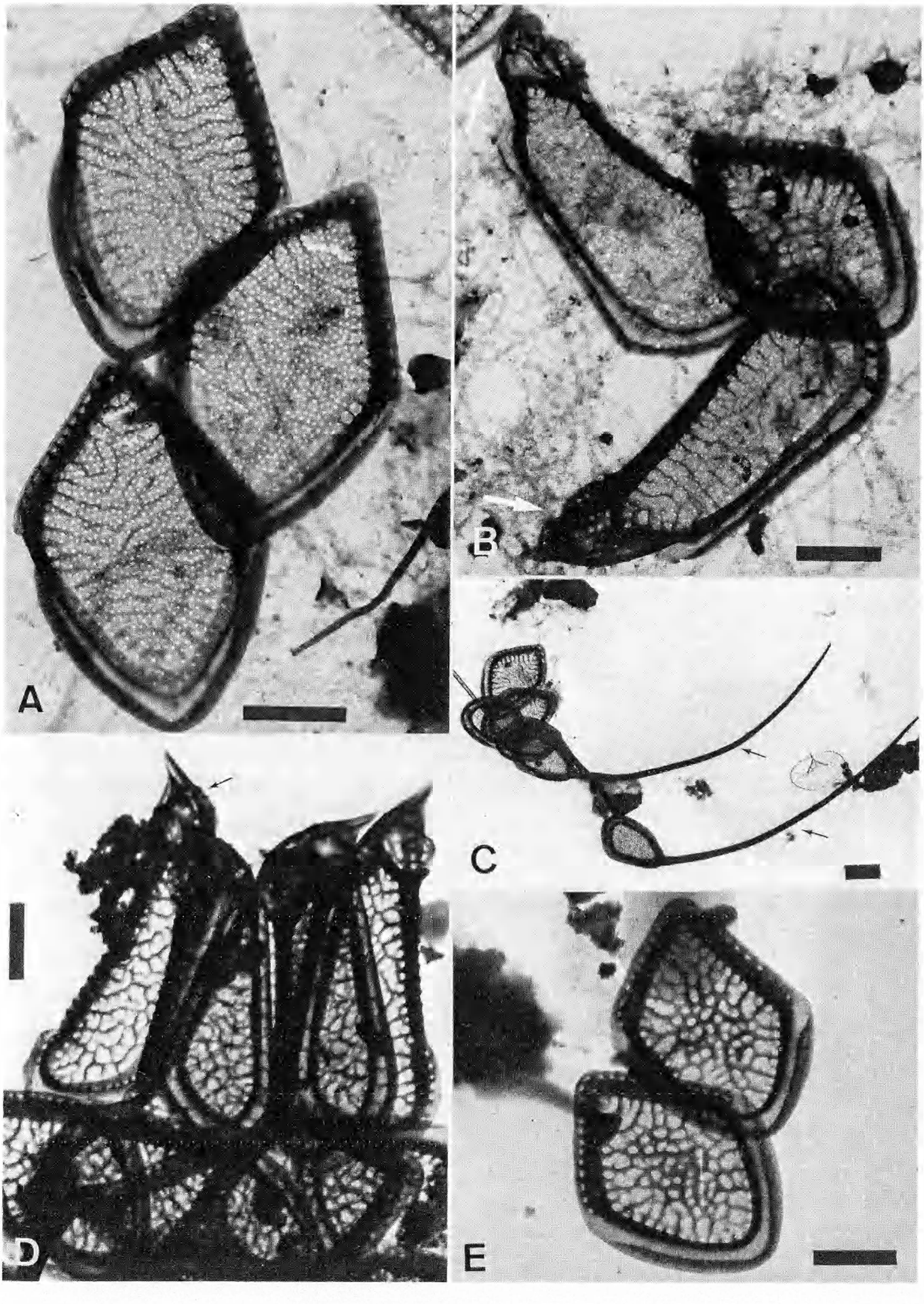


Fig. 3. A: *Mallomonas torquata,* holotype (arrow) and *M. eoa* Takahashi from Lake Trummen. – B: *M. torquata* (arrow) and *M. eoa* showing the different structure, but identical arrangement, of the scales. – C–F: *M. torquata*. – C: Rear part; the spines are missing. – D: Apical part. The inner side of the scales (arrow) is quite smooth. – E: Cyst still covered by some body scales. – F: Cyst showing the plugged pore. Around the pore the protrusions coalesce to form a fringe. – Scale in A 10 μm, in B–F 1 μm.

Fig. 4. *Mallomonas torquata*. – A: Body scales with ribs and pores. – B: Two collar scales and a body scale. Arrows indicate the domes where bristles were inserted. – C: Two rear scales (lacking ribs) extended into spines (arrows). – D: Collar scales with dome and (below) body scales. – E: Two body scales. – A–C from Lake Trummen; D–E from Anchorage. Scale 1 μm.


A
B
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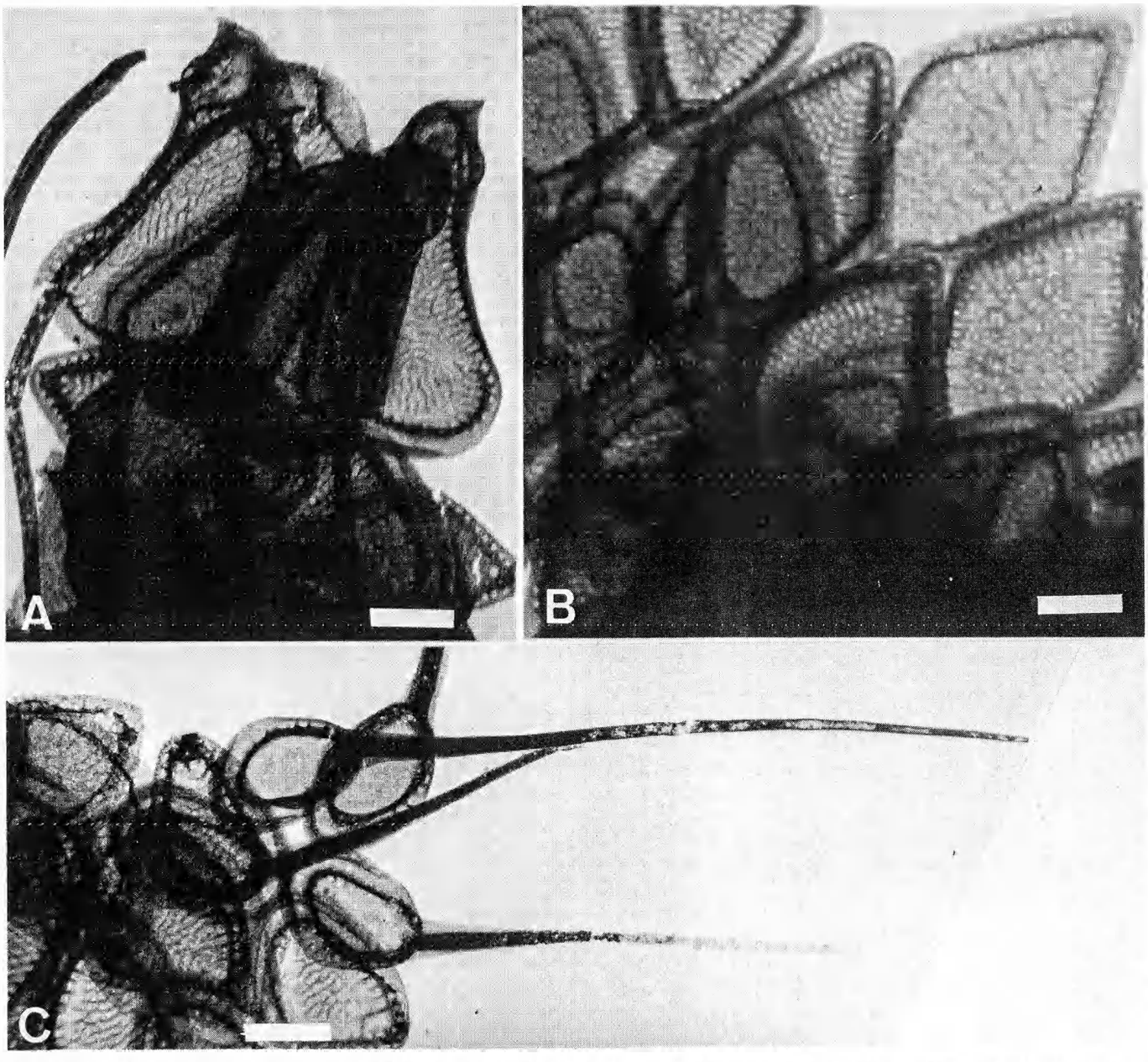

Fig. 5. *Mallomonas torquata*. – A: Collar scales with bristles and (below) some body scales. – B: Body scales. – C: Rear scales with spines. Material from the temporary pond, Jylland. – Scale 1 μm.

Mallomonas torquata Asmund & Cronberg, sp. nov.

Holotype: Fig. 3 (Sweden, Småland, Lake Trummen).

Cellula elongata, ellipsoides. Squamae trimorphae, collares setigerae, mediae rhombicae appendicibus nullis, posticae spinigerae. Squama media costis transversis ornata rectis vel subcurvis, interdum furcatis, costae submarginali crassae conjunctis, prope illam aeque distantibus, saepe costulis inter se connexis, ad medium versus magis irregularibus, in ipso medio saepe in reticulum irregulare contextis aut paene vel plane evanescentibus. Squama collaris cupulam praebens satis parvam, in spinam crassam terminatam, praeterea foraminibus circularibus cribrosam, interdum denticulis in lateribus congregatis armatam: costae mediae partis extra marginem in denticulos ventrales prolongatae. Squamae posticae spinigerae 5–7. Cysta sphaerica appendiculis stellatis ornata circum ostium in coronam congestis, praeterea apertius sparsis. Cellula 4–5 × 23–25 μm. Squama collaris 1.1–3.0 × 4.0–7.7 μm, media 1.8–2.2 × 2.2–4.5 μm, postica 0.4–1.4 × 2.0–2.2 μm; spina 2–10 μm, seta 8–15 μm longa. Cysta 9–12 μm diam.

Body scales with straight or slightly curved, sometimes forked, ribs radiating from the submarginal rib. Close to the submarginal rib they are evenly spaced, often joined with short cross-ribs. In the middle area they form a more or less elaborate, irregular meshwork, but may

be indistinct or absent. *Collar scales* with rather small, strongly pointed domes covered with a more or less well developed reticulum with circular meshes. Groups of minute teeth can be present on the sides of the dome. Distal ends of the ribs on the shields prolonged into minute teeth along the ventral side of the scale. Rear spines 5–7. *Cyst* spherical with a pore; cell wall covered with evenly spread, starlike protrusions. Around the pore the protrusions coalesce to form a ring.

Dimensions: Cells 4–5 × 23–25 μm; collar scales 1.1–3.0 × 4.0–7.7 μm; body scales 1.8–2.2 × 2.2–4.5 μm; rear scales 0.4–1.4 × 2.0–2.2 μm; spines 2–10 μm; bristles 8–15 μm; cyst 9–12 μm diam.

The epithet *torquata* means furnished with a necklace. We have chosen this name because the species is very characteristic of sect. *Torquatae*.

M. torquata differs from *M. doignonii* in having a more irregular and less marked rib system on the shields of the body scales and the collar scales.

M. torquata is known from Lake Trummen and Lake Vaxsjön (Sweden), a seasonally flooded grassfield in S Jylland (Denmark) and Anchorage (Alaska).

In Lake Trummen *M. torquata* was present from February to May. It was found together with *M. eoa, M. trummensis, Synura petersenii, S. spinosa* and *S. echinulata* (Cronberg 1973, 1975).

M. torquata was collected in Lake Vaxsjön on 3 April 1976. The lake was partly ice-covered. The most important associates were *Dinobryon cylindricum* and *Chrysosphaerella brevispina*. The appearance of the specimens from Lake Vaxsjön is identical with that of the specimens from Lake Trummen.

The samples from the temporary pond in S Jylland were taken on 13 March 1945. The association was dominated by *M. lychenensis, M. annulata, M. insignis, Synura spinosa* and *S. petersenii*. The specimens from this locality differ from those of Lake Trummen in having somewhat broader and shorter collar scales (2.5–3.5 × 4–4.5 μm) and less pointed domes (Fig. 5).

The Alaskan specimens (Fig. 4 D–E) were collected on 5 December 1957. The most important associates were *Dinobryon* spp., *M. crassisquama, Synura spinosa* and *S. echinulata*. These specimens have a more marked pattern on the scales, but are otherwise like *M. torquata* from Lake Trummen. Asmund & Hilliard (1961) published a TEM micrograph from this material as *M. pumilio* Harris & Bradley. Asmund & Takahashi (1969) stated that the name should be *M. pumilio* var. *silvicola* Harris & Bradley, but it is now evident that the scale pattern of the Alaskan specimen is identical with that of *M. torquata*, only with somewhat coarser ribs. In 1961 only rear scales with short spines were observed, but reexamination of the material has disclosed the presence of scales with long spines.

The ultrastructure changes somewhat with locality, but all cells have the same general features.

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The effect of centrifugal force on the ontogeny of Eleocharis mamillata pollen

Anita Dunbar

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Spikes of *Eleocharis mamillata* (Cyperaceae) have been centrifuged at different stages of development. Anthers from the spikes were either fixed directly after centrifugation or after varying periods of time, ranging from 35 min to 27 hours, allowing the cells eventually to reorganize. Some of the material developed normally. However, pollen treated in a sensitive stage of metabolism developed abnormally. The abnormality is reflected by, e.g., a fragmentary callose deposition, change in shape and content of the nucleus both at premeiosis and after meiosis, and an atypical pattern of the exine.

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The ontogeny of *Eleocharis* (Cyperaceae) pollen, where only one tetrad cell usually survives to become a viable pollen grain after a normal meiosis, while in most higher angiosperms one pollen mother cell (PMC) produces four pollen grains, has been described by Strandhede (1973) and Dunbar (1973 a, b, 1975). The conclusion arrived at was that the change in cell shape from spherical at premeiosis to pear-shaped after meiosis and the position of the meiotic products in the tapering end of the tetrad, are of decisive significance for the pattern of the ontogeny in *Eleocharis*.

The aim of the present study is to try to displace the meiotic products by centrifugation and in this way influence further development. A preliminary report was published recently (Dunbar 1978).

Material and methods

Spikes together with part of the culms (ca 2 cm) of greenhouse grown plants of *Eleocharis mamillata* collected by Dr L. E. Kers, Stockholm (Uppland, Täby parish, Mörtsjön), were detached from the plant, immediately immersed in pond water and centrifuged for 10 min at 5,000 g. Part of the material was fixed directly after centrifugation. In another part of the material, the culm was after centrifugation inserted through a small hole punched in a sheet of aluminium foil which floated like a raft on the pond water. The spikes were left in the water at + 20°C for varying periods of time, ranging from 35 min to 27 hours before fixation. Control material was fixed without any centrifugation.

The anthers were fixed in 2% glutaraldehyde in 0.1 M phosphate buffer at pH 7.2, followed by 0.2% O_8O_4 in a phosphate buffer. The anthers were dehydrated in an acetone series from 30 to 95% followed by 5 changes in 100% acetone and thereupon embedded in an epoxy medium (Spurr 1969). Ultrathin sections were successively collected on uncoated copper grids and stained with uranyl acetate and 0.2% alkaline lead citrate (Venable & Coggeshall 1965).

Results

Anthers in various stages of development were selected from each spike. Some of the anthers developed further during the different periods of time that the spikes were kept in the pond water before fixation. The stages range from sporogenous tissue to almost mature pollen (Table 1). Some of the anthers fixed at different times after centrifugation reached the same stage of development, and had a similar appearance. While all of them are listed in Table 1, only one from each stage is described below.

Anthers from the same spike, fixed at the

Table 1. Anthers within the spikes of *Eleocharis mamillata* centrifuged at 5.000 g. + normal, − abnormal, brackets: predominant condition, a, b, c anthers from the same spike, treated identically.

No.	Time between centrifugation and fixation	Spike	Developmental stage	Results	
				PMCs tetrad pollen	tapetum
1	27 h	a	sporogenous tissue	(+)	(−)
2	1 h	b	PMC	−	+
3	24 h	.	do.	−	+
4	26 h	c	do.	−	+
5	−	.	tetrad	+	+
6	1 h	b	primexine templ.	+	+
7	27 h	a	exine initiation	+	+
8	1 h	b	pollen, early exine	−	+
9	16 h	.	nexine formation	+	+
10	1 h	.	do.	+	.
11	35 min	.	start of intine formation	+	.
12	3.5 h	.	nexine formation	+	.
13	24 h	.	do.	+	.
14	24 h	.	young Ubish bodies	+	.
15	26 h	c	progressive degeneration of 3 cells	+	.
16	1 h	.	do.	+	.
17	9 h	.	do.	+	.
18	24 h	.	tapetal residue	−	.
19	16 h	.	mature exine, Ubish bodies	−	.

same time after centrifugation may produce normal or abnormal pollen (Table 1).

The cells of the anther wall appear to be quite unaffected after the treatment and so do those of the tapetum (with one exception, Table 1).

Sporogenous tissue. In the earliest stage (1), the sporogenous tissue contains large vacuoles (Fig. 1 A, B). Such a vacuolisation of the young cells was not observed in untreated material. An assembly of irregular vesicles is occasionally found in the vacuoles (Fig. 1 A). In other aspects, however, the sporogenous cells appear to be normal. They are surrounded by thin walls and thin walls separate the sporogenous tissue from the tapetum (Fig. 1 A). A large nucleus is located centrally in the sporogenous cells. RER, mitochondria and proplastids occur. The cytoplasm is richly populated with free ribosomes (Fig. 1 A, B). In the tapetal cells large vacuoles occupy almost the entire volume (Fig. 1 A). In the peripheral cytoplasm, however, RER, mitochondria, proplastids, a few Golgi bodies and a great number of free ribosomes and ribosomes assembled into polysomes can be discerned (Fig. 1 A).

Premeiosis. In the following stage (2), PMCs have developed. They have a fragmentary callose wall and the PMC wall is partly ruptured (Fig. 2 A). The nucleus of the PMCs has a conspicuous appearance. A material of medium electron density and with a finely granular structure is obvious in the karyoplasm, and apparently occupies a considerable part of the nucleus. The cluster of material is easily distinguishable from chromosomes and nucleoli both by its lack of a distinct shape and by the divergent electron density (Fig. 2 B). The tapetum has a normal appearance. Grey bodies seem to pass through the plasma membrane of the tapetal cells both at the abaxial and adaxial surface (Fig. 2 A).

In no. 4 the PMCs have developed abnormally. It is difficult to interpret how far the development has advanced. While the disintegration of the tapetum has started, the ontogeny of the PMCs is apparently delayed.

Fragments of callose surround the PMCs (Fig. 2 C). The nucleus has lost its normal shape and is stretched out widely in the cytoplasm. The content of the karyoplasm shows unmistakeable signs of deterioration (Fig. 2 C).

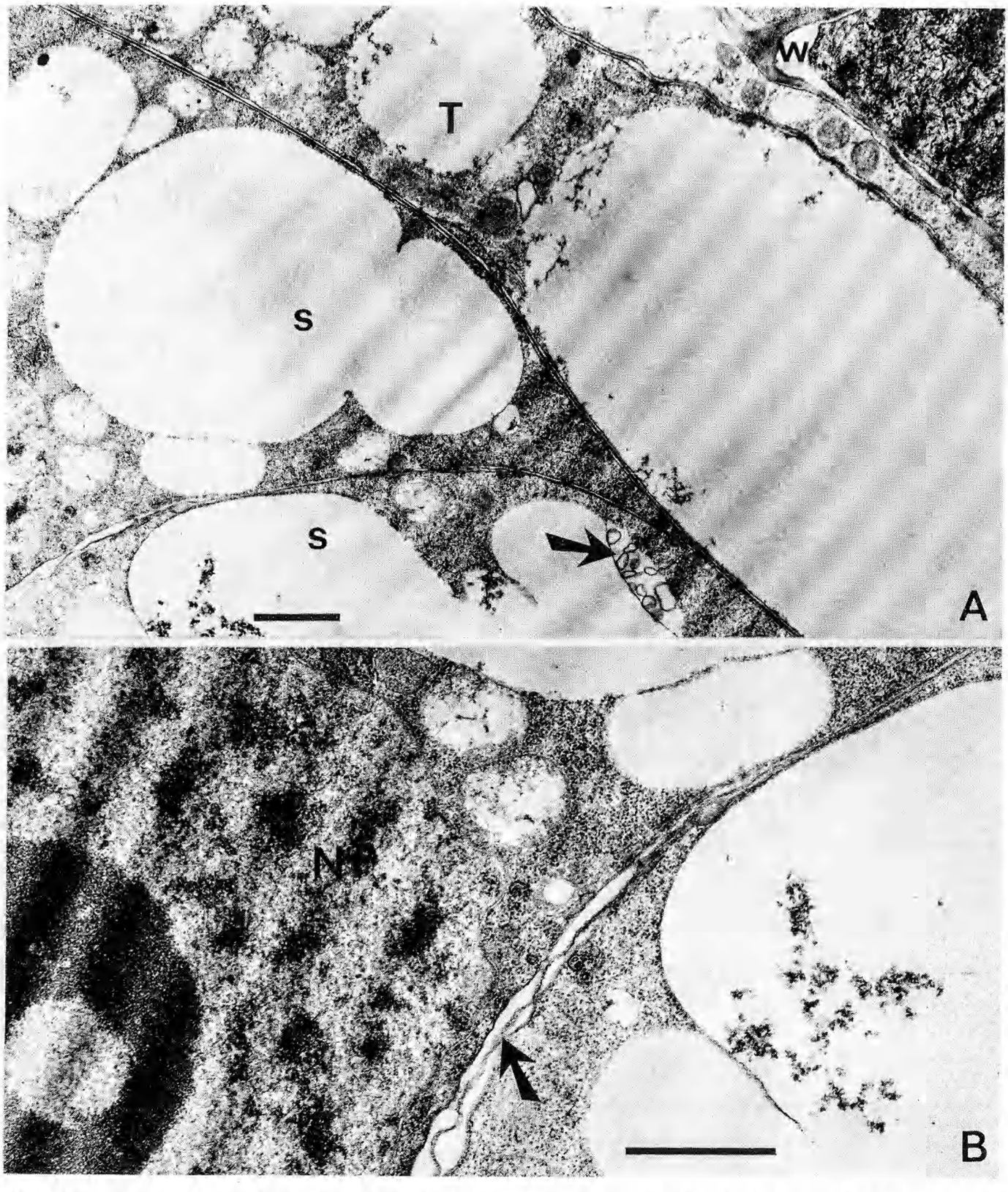

Fig. 1. Sporogenous tissue of centrifuged *Eleocharis mamillata* anthers. No. 1. – A: Anther wall cells (w); tapetal cell (T) with large vacuoles; sporogenous cells (s) with large vacuoles; irregularly shaped vesicles (arrow) in a vacuole. – B: Thin walls separate the sporogenous cells (arrow); large nucleus (N). – Scales 1 μm. Fig. 1B from Dunbar (1978).

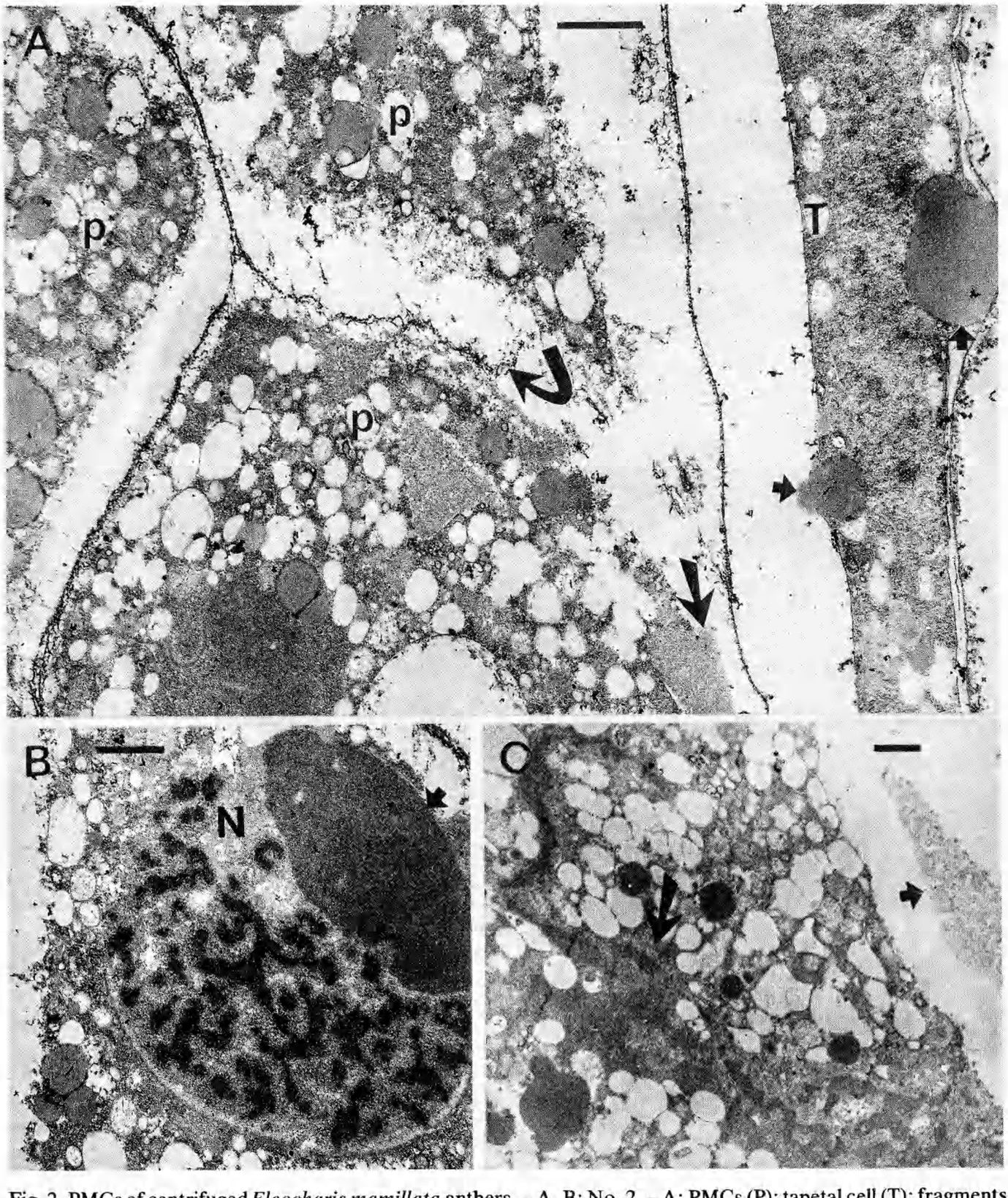

Fig. 2. PMCs of centrifuged *Eleocharis mamillata* anthers. – A, B: No. 2. – A: PMCs (P); tapetal cell (T); fragments of the callose wall (arrow); ruptured PMC wall (bent arrow); grey bodies (short arrows) seem to pass through the plasma membrane of the tapetal cell. – B: Nucleus of PMC (N) with medium dense material (short arrow). – C: No. 4. PMC which has developed abnormally. Fragment of callose (short arrow); nucleus widely stretched in the cytoplasm (arrow). – Scales 1 μm.

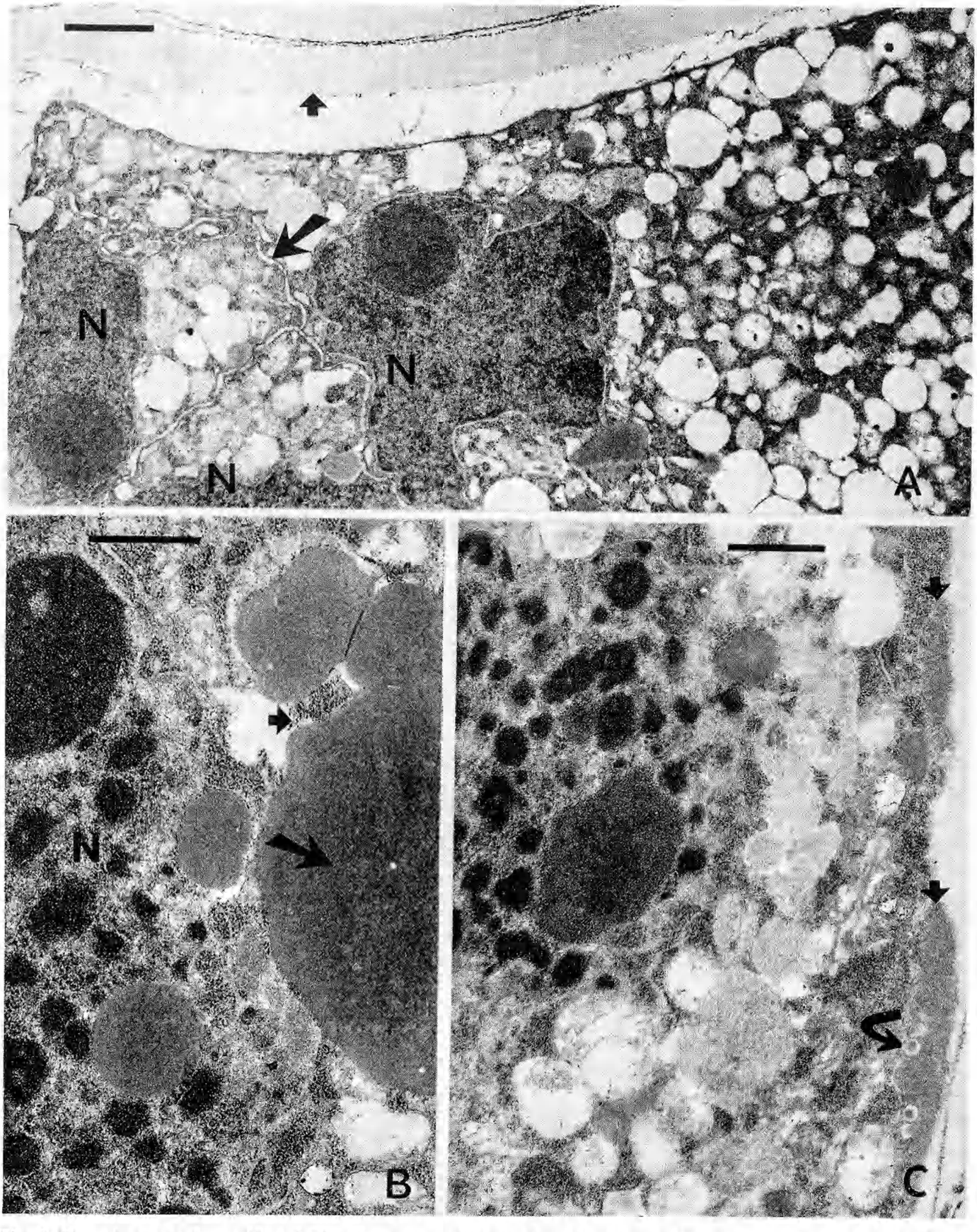

Fig. 3. Tetrad stage of centrifuged *Eleocharis mamillata* pollen. No. 5. – A: Tetrad complex surrounded by a callose wall (short arrow); three nuclei are seen in the abortive cells (N) separated partly by the cell plate (arrow). – B: Tapetal cell with young tapetosome (arrow); ribosomes adjacent to the tapetosome (short arrow); nucleus (N). – C: Fuzzy coat (short arrows) on surface of tapetal cell, enclosing vesicles (bent arrow) with a medium dense content. – Scales 1 μm.

Tapetosomes (Dunbar 1973 a, c) are located in the tapetal residue or free in the anther loculus. In normal material tapetosomes appear in the anther loculus only at a stage of development past microspore mitosis and are formed during pre- and postmeiosis (Dunbar 1973 a).

Postmeiosis. In no. 5 the PMCs have undergone meiosis. A layer of callose encloses the entire complex of microspores. As in untreated material (Dunbar 1973 a, b, 1975) no callose was formed between the individual tetrad cells. The microspore complex is pear-shaped after meiosis. The three abortive nuclei (Fig. 3 A) are located in the tapering, proximal end of the microspore. Cytokinesis has not yet been completed. Microtubules are attached to the cell plate during formation (Fig. 4 A). Apart from having a greater number of vacuoles, the material appears to be similar to the untreated material. In the tapetum large tapetosomes are forming. They are not surrounded by a membrane and are consequently free in the cytoplasm. Ribosomes (Fig. 3 B) and RER occur adjacent to the tapetosomes. At the surface of the tapetal cells there are elongated lumps of a medium electron dense material, which is finely granular in structure, probably a fuzzy coat. The coat contains vesicles including a material (Fig. 3 C).

Tetrad stage. A thin layer of the primexine template appears in association with the internal surface of the callose wall in stage 6. As in untreated material it forms around the entire microspore complex and not between the individual tetrad cells (Dunbar 1973 a, b, 1975). At some points the cytoplasm and plasma membrane extend outwards and fuse with the primexine template (Fig. 4 B). Just outside the plasma membrane a distinct, rather thin layer, consisting of a fibrous material, is situated parallel to the cell surface (Fig. 5 B). Many Golgi bodies occur near the distal nucleus. This nucleus will go through mitosis to produce the viable pollen grain. The Golgi bodies are well developed and appear to be in an active condition, producing vesicles. There are numerous mitochondria near the nuclei, fewer in the peripheral cytoplasm. Vacuoles, mostly with small, electron dense inclusions (Fig. 4 B) are located in the peripheral zone. Parallel cisternae of RER can be seen close beneath the plasma membrane (Fig. 5 B). It is thought that probacula will form in such places (Heslop-Harrison 1963, Skvarla & Larson 1966). No effect of the treatment was observed, although the material was collected from the same spike as no. 2 (premeiosis) and no. 8 (post mitosis) which both developed abnormally.

Exine initiation. In no. 7 the primexine template has become more compact. The first exine seems to be initiated into this layer (Fig. 5 A). Clusters of ribosome-like elements are present in the outer part of the callose wall, attached to the inside of the former PMC wall (Fig. 5 A). Grey bodies occur in the tapetal cells. A great number of RER cisternae appear to be continuous with the grey bodies (Fig. 4 C). No effect of the treatment was observed. This material was collected from the same spike and treated in exactly the same way as no. 1 (sporogenous tissue) with highly vacuolized cells.

Post mitosis. The pollen grains from no. 8 show a strongly abnormal development. While the abortive cells have decreased in size and by now occupy only a small volume of the pollen grain, the exine shows an unexpected immaturity. Furthermore this immature exine differs from the early exine of untreated material. The characteristic pattern of the protectum in *Eleocharis* consists of short units interrupted by spaces filled with fibrous material of the primexine template (Fig. 5 C) while in this materia the protectum is almost continuous (Fig. 6 A) The cytoplasm of the distal cells is mostly normal, but in some of the pollen there is a conspicuous reduction and deterioration of the cell components (Fig. 6 A). Large lumps of chromatine are located peripherally in the karyoplasm of the vegetative nucleus (Fig. 6 B), a feature not observed in untreated material.

Nexine formation. In no. 9 nexine formation is taking place. The bacula of the sexine are still thin as are the lamellae of the nexine (Fig. 7 A, C). In some places the tapetal cells are adjacent to the surface of the tectum (Fig. 7 A). Vesicles are attached to the outside of the plasma membrane and are also present in the space between the nexine and the cell surface of the pollen (Fig. 7 A). A fibrous network is obvious in the baculoid region (Fig. 7 A). In the degenerating cells a prominent structure, 20 nm in width, probably a fibre-protein, stretches

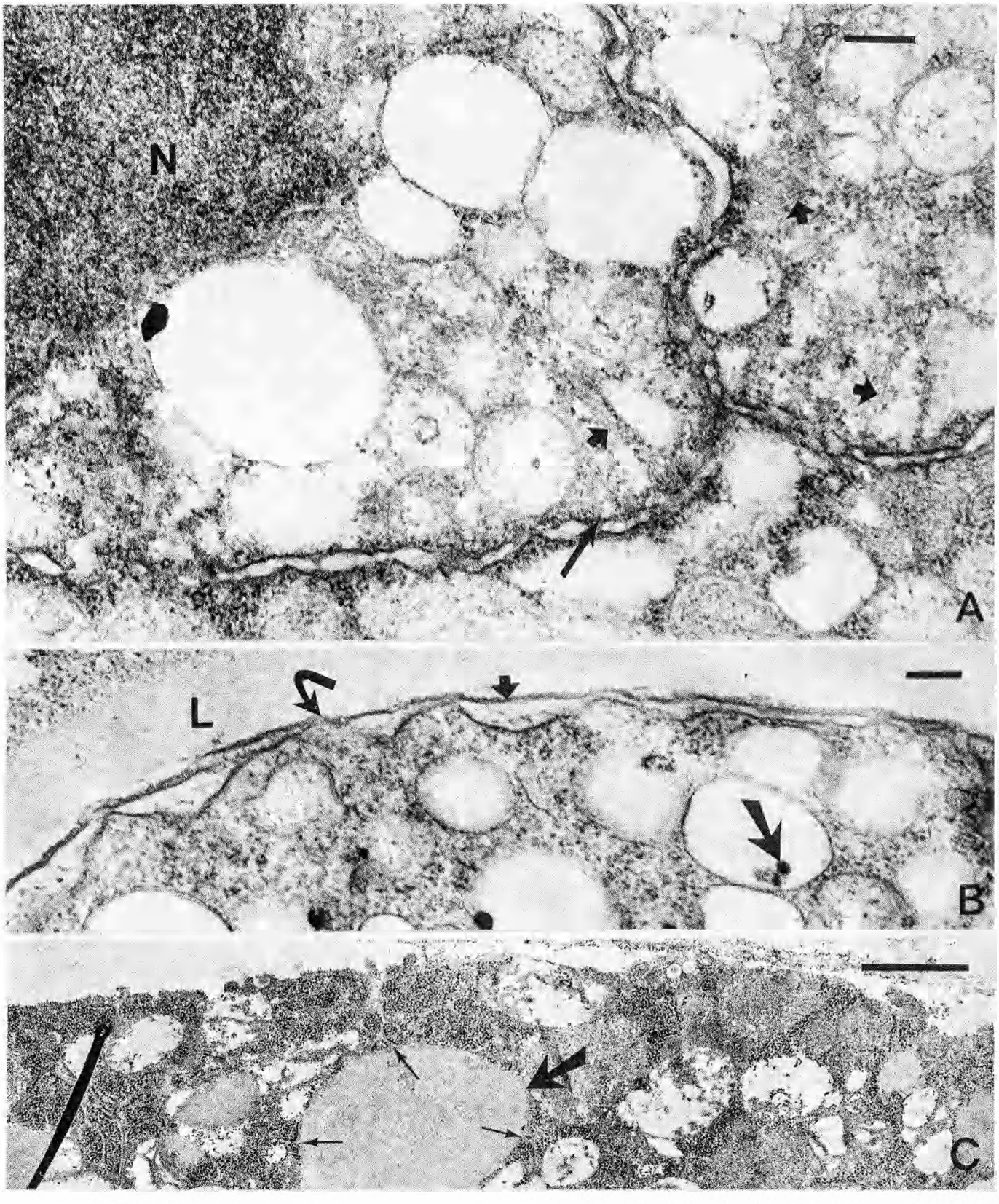

Fig. 4. Tetrad stage of centrifuged *Eleocharis mamillata* pollen. – A: No. 5. Microtubules (short arrows) connected to the cell plate (arrow); nucleus (N) near the cell plate. – B: No. 6. Primexine template (short arrow) beneath the callose wall (L); tips of evaginating plasma membrane in contact with primexine template (bent arrow); vacuole with dense inclusion (arrow). – C: No. 7. Tapetal cell with grey body (arrow) surrounded by cisternae of RER, some of them in connection with the grey body (thin arrows). – Scales in A, B 0.2 μm, in C 1 μm.

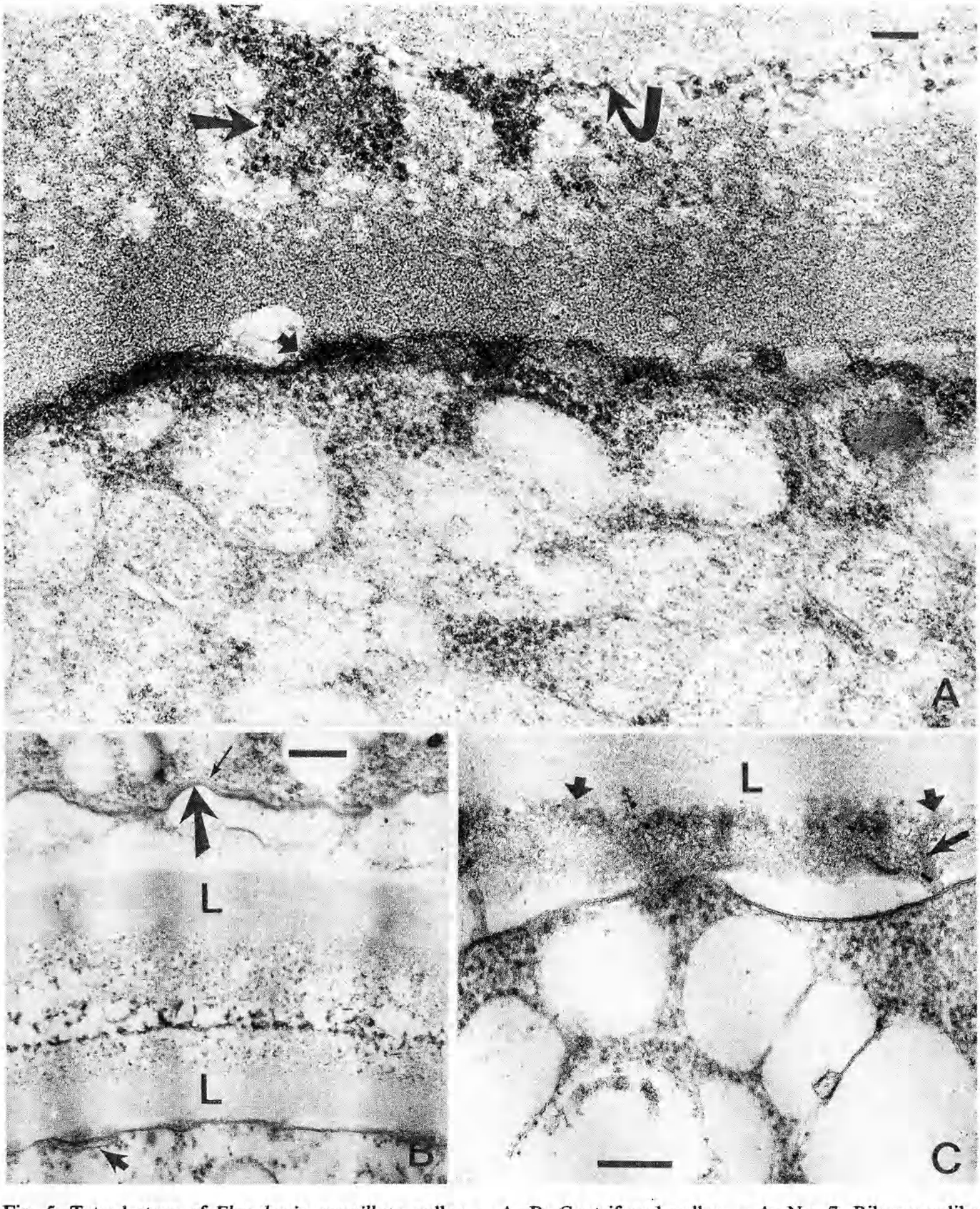

Fig. 5. Tetrad stage of *Eleocharis mamillata* pollen. – A, B: Centrifuged pollen. – A: No. 7. Ribosome-like elements (arrow) in the outer part of the callose wall, adjacent to the former PMC wall (bent arrow); primexine template (short arrow) into which the first exine seems to be initiated. – B: No. 6. Two adjacent tetrads with callose layers (L); cisternae of RER (short arrow) beneath the plasma membrane; distinct thin layer (arrow) outside the plasma membrane (thin arrow). – C: Not centrifuged pollen. Tetrad enclosed in callose (L) while the early sexine is formed. Protectum (short arrows); probacula (arrow). – Scale in A 0.1 μm, in B, C 0.2 μm.

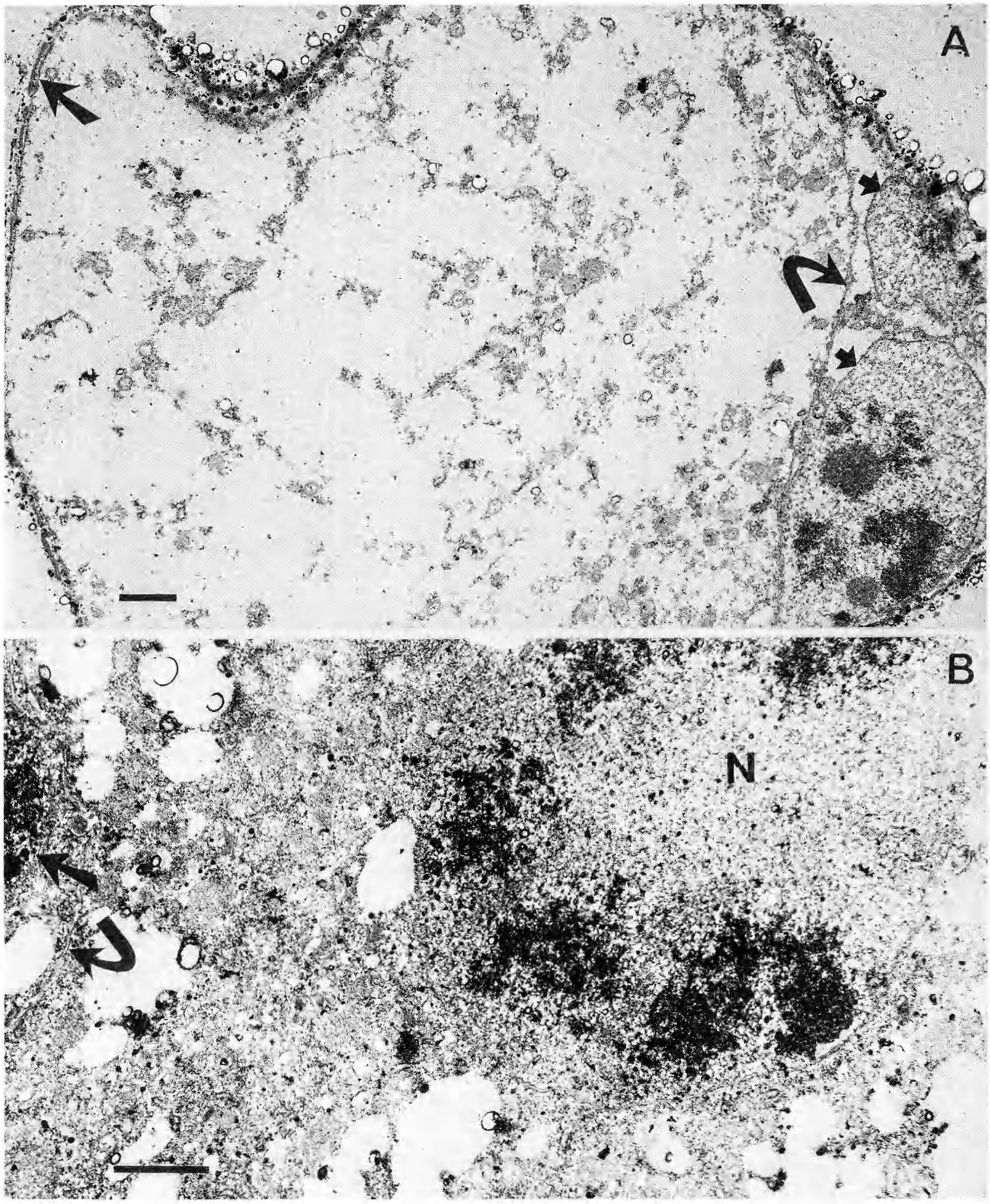

Fig. 6. Postmitotic stage of centrifuged *Eleocharis mamillata* pollen, no. 8. – A: Pollen with an abnormal appearance. Degenerating cells (short arrows); inner wall (bent arrow) separating the degenerating cells from the "viable" one, which shows reduction of cell components; atypical pattern of the early exine (arrow). – B: Vegetative cell with nucleus (N); generative cell with nucleus (arrow) and cell wall (bent arrow); note large assemblage of chromatin peripherally in the vegetative nucleus. – Scale in A 1 μm, in B 0.5 μm.

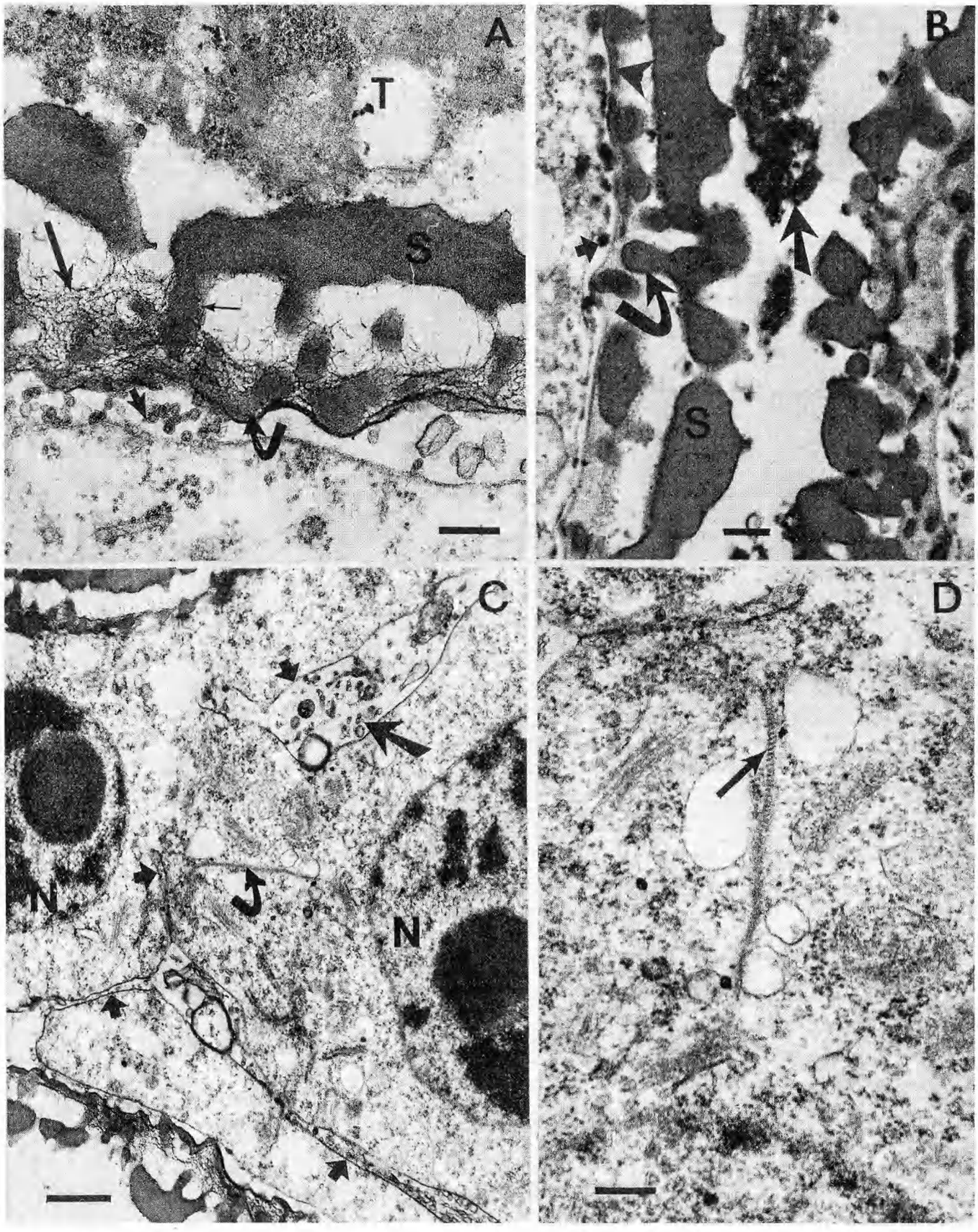

Fig. 7. Stage of nexine formation of centrifuged *Eleocharis mamillata* pollen. – A, C, D: No. 9. – A: Tapetum (T) adjacent to the surface of the tectum (S); bacula (thin arrow); fibrous network (arrow) in the baculoid region; nexine (bent arrow); vesicles (short arrow) between nexine and plasma membrane in the space where the intine soon will form. – B: No. 15. Disintegrating tapetum (arrow) between two pollen grains; small, electron dense bodies (short arrow) at the border of the plasma membrane; tectum (S); bacula (bent arrow); nexine (arrowhead). – C: Proximal part of pollen. Two of the three abortive nuclei (N); the inner wall partly separating the abortive

between the inner wall separating the abortive cells and one of the nuclei (Fig. 7 C). Transverse elements can be traced in the structure (Fig. 7 D). These elements consist of transverse subunits about 2nm in width. Segments of RER and Golgi bodies occur frequently near the nuclei and the inner wall (Fig. 7 C) and also peripherally beneath the plasma membrane of the distal cell. The cytoplasm is rich in free ribosomes and ribosomes assembled into polysome configurations (Fig. 7 C, D). In the inner wall, separating the abortive cells, there are multiformed vesicles revealing structural irregularities (Fig. 7 C). No effect of the treatment was observed.

Intine formation. In no. 11 round bodies with a fine structure similar to that of the sporopollenin of the exine, although slightly more electron dense, are located in the nexine region (Fig. 8 A). The inner wall is continuous with the space where, at this stage, intine formation has started (Fig. 8 A).

Degeneration of abortive cells. In no. 15 the tapetum is disintegrating and the remainder of the tapetal cells are located between pollen grains (Fig. 7 B). Young Ubish bodies occur in the anther loculus, either adjacent to the former tapetal wall, or to the surface of the pollen grains. The degeneration of the abortive cells has started (Fig. 8 B) and at this stage their nuclei lack an envelope. No effect of the treatment was observed. This material came from the same spike as no. 4, which developed abnormally.

Towards maturity. How far the development has advanced in the following material, no. 18, is a matter of conjecture, as the pollen grains have developed abnormally to a degree where it becomes hard to draw any conclusions about their stage of ontogeny. However, the condition of the tapetal residue and the appearance of Ubish bodies point towards an advanced stage.

In the pollen wall a type of border made up of a fibrous material separates multiformed lumps of varying size, attached both to the outside and the interior of the border (Figs. 8 C, 9 A). The material forming these lumps resembles sporopollenin of a stage near maturity, when the sporopollenin has lost most of its stainability towards heavy metals (Fig. 9 A). This wall has no similarity to the specific pattern typical of the pollen sporoderm of *Eleocharis*. The nucleus is also affected. It is fusiform in shape. Spherical, electron dense bodies are located in the karyoplasm together with a medium electron dense material, similar to that which occurred in the premeiotic nucleus, no. 2. The other cell components are difficult to identify. It is of significance that young Ubish bodies with a normal appearance are found in the anther loculus near the pollen grains (Fig. 9 A).

Mature exine. The exine is almost mature in no. 19. It has lost most of its stainability towards heavy metals. This is also the case where the sporopollenin layer on the Ubish bodies is concerned. They have reached their final shape with the "wing structure" characteristic for *Eleocharis* (Fig. 9 C). The bacula of the sexine and the lamellae of the nexine have become thicker. While the development has advanced normally so far, the degeneration of the abortive cells is delayed. There is no obvious decrease in the size of these cells (Fig. 9 B), which in untreated material at this stage of development have altered beyond recognition, and are extruded into the layer of intine.

Discussion

Centrifugation generally causes a displacement of cell organelles, which, however, varies considerably with force and time of centrifugation. Pollen grains of *Lilium henryi* were centrifuged at 1,000–1,200 g for about half an hour which undoubtedly provided means for displacing cell organelles during periods likely to be critical for the determination of the wall pattern (Heslop-Harrison 1971). While no displacement of cell components was observed in pollen of *Eleocharis,* there is a possibility that a temporary displacement took place. In roots of *Pisum sativum* most of the cell organelles were re-

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cells (short arrows); multiformed vesicles (arrow) in the inner wall, which may be involved in the degenerating process, which is about to start; fibre-protein configuration (bent arrow). – D: Higher magnification of Fig. 7 C. Transverse elements (arrow) in the fibre-protein. These elements are likewise consisting of transverse subunits. – Scales in A, B, D 0.2 μm, in C 0.5 μm.

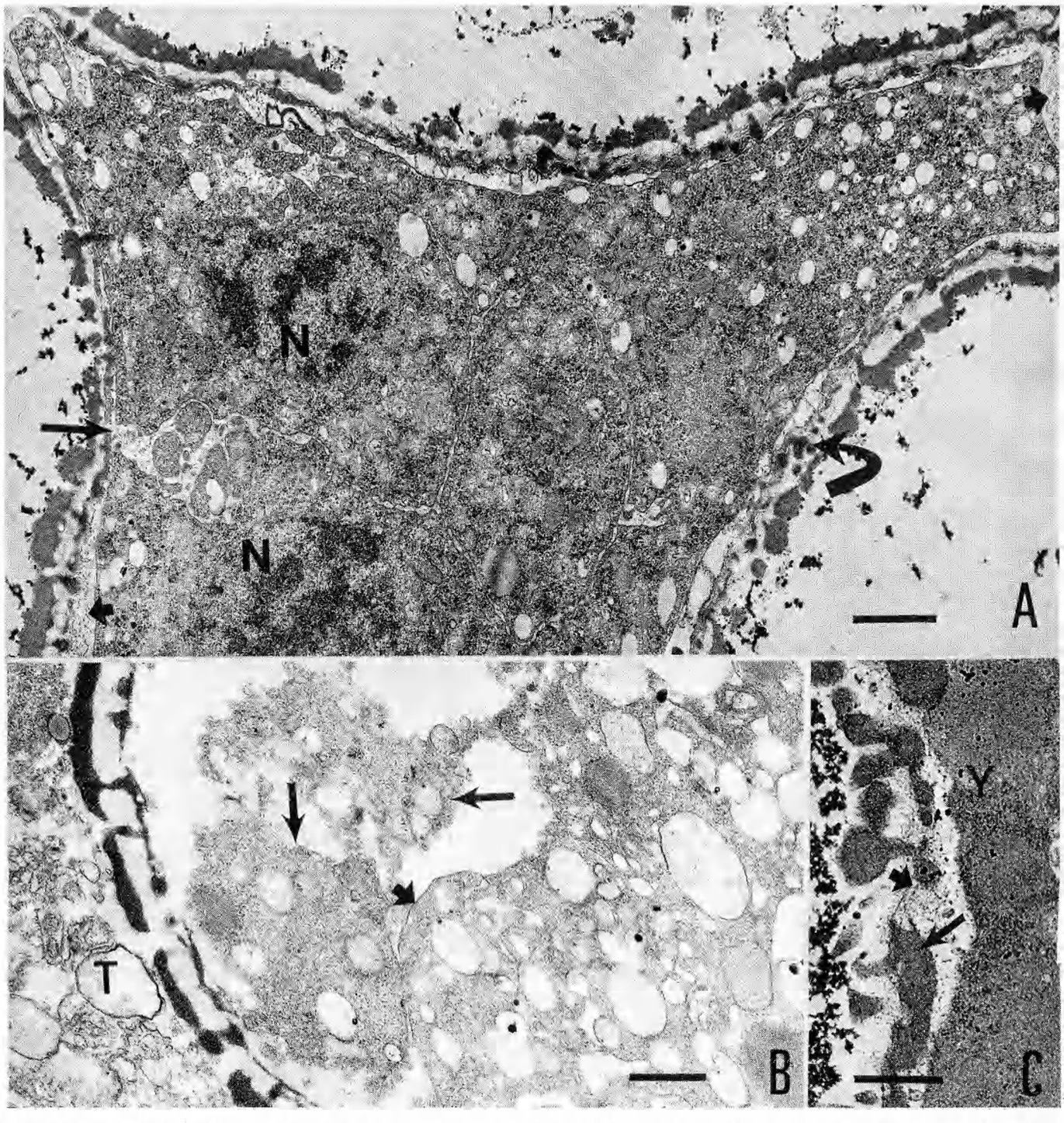
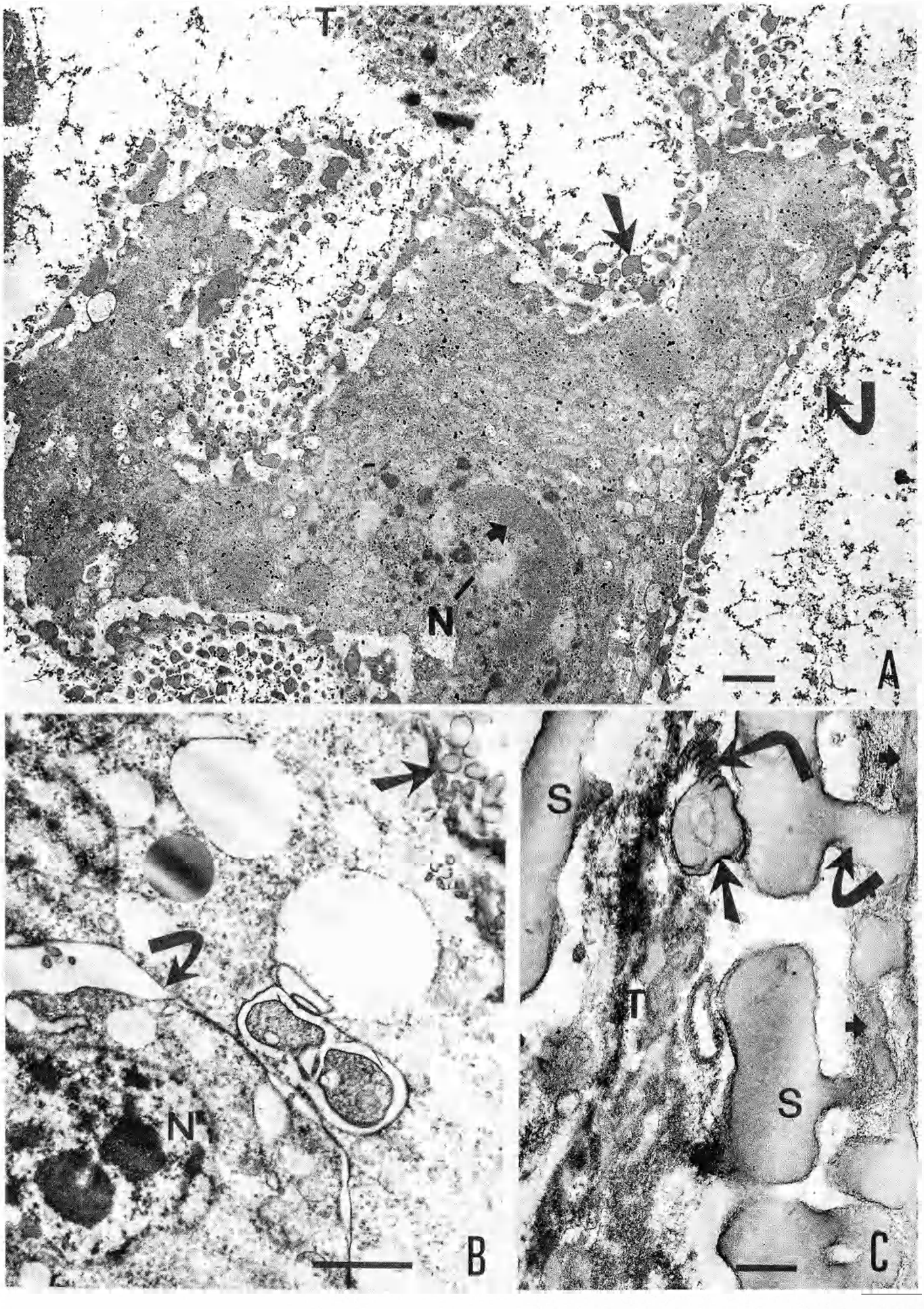


Fig. 8. Centrifuged pollen of *Eleocharis mamillata*. – A: Stage of intine formation, no. 11. Proximal part of pollen. Cytokinesis is completed, the inner wall being continuous with the space (arrow) where early intine formation is seen as fibrillar–granular elements (short arrows); two of the abortive nuclei (N); round bodies (bent arrow) may take part in nexine formation. – B: Degeneration of abortive cells, no. 15. Proximal part of pollen with two of the degenerating cells (arrows), remainder of the inner wall (short arrow) and tapetum (T). – C: No. 18. Detail of Fig. 9 A. Part of pollen wall with atypical pattern of exine; fibrous material (short arrow) forms a border; lumps (arrow), similar to sporopollenin units, attached to the border; cytoplasm (Y) of pollen. – Scales in A, C 1 μm, in B 0.5 μm.

Fig. 9. Centrifuged pollen of *Eleocharis mamillata*. – A: No. 18. Pollen with atypical pattern of exine formed by sporopollenin-like lumps (arrow); nucleus (N) with medium dense material (short arrow); tapetal residue (T); young Ubish body with normal appearance (bent arrow). – B, C: No. 19. – B: Delayed degeneration of abortive cells; inner wall (bent arrow); nucleus (N), cf. degeneration in stage 15, Fig. 8 B; almost mature units of exine (arrow). – C: Almost mature exine with tectum (S); bacula (bent arrow); nexine (short arrows); remainder of tapetum (T); Ubish body (arrow) with "wing structure" (curved arrow). – Scales in A, B, 1 μm, in C 0.2 μm.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distributed after 2 hours after centrifugation at 20,000 g for 24 hours (Bouck 1963).

In *Eleocharis* the nuclei are strongly affected by the treatment. During the prophase of meiosis and towards maturity of the pollen a cluster of material was seen in the karyoplasm. This cluster may represent an assemblage of relatively heavy particles, or it may reflect an alteration of the nucleus components caused by a change in its metabolism. Such changes can be expected to affect further development, especially callose deposition and the formation of the primexine template, which is usually the site of the future sexine, and which, if affected, may in turn alter the normal formation of the specific wall pattern.

The different stages of ontogeny the pollen have reached are difficult to correlate with the varying periods of time which passed between centrifugation and fixation. While no irreversible damage seems to have occurred in the material from nos. 10, 12 and 13 the pollen have reached about the same stage of ontogeny (nexine formation) regardless of whether the spike has been kept in the pond water for 1, 3.5 or 24 hours, respectively.

Hesse (1978) reported that the pollenkitt (tapetosomes) of *Tilia platyphyllos* and *T. tomentosa* is produced by tapetum plastids and hence is primarily enclosed in membranes. No membranes could, however, be seen to enclose the tapetosomes in *Eleocharis* during any stage of development.

Grey bodies are present in the tapetum during premeiosis. Apparently they pass through the plasma membrane of the tapetum both at the abaxial and adaxial surface, viz. towards the anther wall cells or PMCs, respectively. Grey bodies also occur in the tapetum during the tetrad stage. Cisternae of RER are associated with these bodies, suggesting that the RER participates in their synthesis.

The fuzzy coat, which is present on the surface of the tapetal cells at a rather active stage of the tapetum metabolism, encloses vesicles, which may be involved in the transport of material from the cytoplasm. The fuzzy coat may constitute a medium for transportation rather than playing a secretory role.

A distinctive structure occurs in the abortive cells just before their degeneration starts. The structure, consisting of regularly spaced, transverse elements, which in turn are made up of transverse subunits, may represent a fibre-protein. Probably this fibre-protein is involved in the approaching degeneration process.

Anther wall cells and tapetal cells are almost unaffected by the centrifugation. PMCs and pollen, however, are sensitive to centrifugation during some of the ontogenetical stages. This is shown when anthers collected from the same spike, but at various stages of development, were treated identically. It seems that when the treatment was applied at an early stage, before meiosis, abnormal tetrads were produced, while when applied after meiosis, the material produced normal pollen grains.

The sensitivity is reflected by some phenomena which could be, but not necessarily have to be coordinated, viz. (1) change in shape and content of the nucleus; (2) failure of synchronisation of developmental processes such as exine formation contra degeneration of abortive cells; (3) failure of wall deposition and determination of the specific wall pattern of *Eleocharis*.

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Botanical literature

Torrey, J. G. & Clarkson, D. T. (eds.) 1975: *The development and function of roots*. Third Cabot Symposium. X + 618 pp. Academic Press, London. ISBN 012-6957-509.

Few symposia are, like this one, dealing with one organ in an interdisciplinary way. Nearly all aspects of the development and function of roots are covered in the proceedings here reviewed. The main emphasis in all the papers is on the relation between structure and function, and thus the book should be of great value to the modern plant physiologist, with his often somewhat restricted training in plant anatomy and morphology. To him the first part of the book with the chapters on the quiescent centre, the root cap, the formation of vascular tissues and the development of lateral roots may be of special interest. Although the chapter on aerial roots may seem somewhat digressive, it may give some ideas of using these specialized structures for experiments on differentiation. Of primary interest to the plant physiologist is part two, where the emphasis is on the physiological aspects of root function. Here, especially in the chapters on water relations, the endodermis and on the ion transport, the anatomical and cytological background is discussed and the facts integrated in the statements. The third part of the book is of special interest to soil biologists and mycologists.

Although the book is of primary appeal to plant physiologists, ecologically and physiologically orientated plant anatomists can reap richly from the book by getting an idea of all the processes going on in the structures they study.

A common drawback of most meeting proceedings is the uneven quality of the papers, some being reviews by longtime workers in the field, whereas others, in this case a few, report recent research only. Most of the chapters cover their subjects excellently, and due to the many citations they give a firm basis for further work. The list of references discloses how relatively meagre the literature is on such important a subject as the behaviour of roots in the field, e.g. their distribution, longevity and reaction to water stress.

In summary the book is heartily recommended, primarily to plant physiologists using roots in their work, but also to plant anatomists and other students in botany or soil biology.

Steen Allerup

Taxonomic and floristic notes from the Galápagos Islands

Ole Hamann

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Sida veronicaefolia Lam., *S. ciliaris* L. (Malvaceae), *Calceolaria mexicana* Benth. (Scrophulariaceae) and *Galinsoga caracasana* (DC.) Schultz-Bip. (Asteraceae) are reported as new to the archipelago. The taxonomy and distribution of the endemic *Euphorbia equisetiformis* Stewart (Euphorbiaceae) are discussed. Notes are given on the occurrence of *Najas guadalupensis* (Spreng.) Morong (Najadaceae), *Callitriche deflexa* A. Br. ex Hegelm. (Callitrichaceae) and *Triumfetta semitriloba* Jacq. (Tiliaceae).

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Some new taxonomic and floristic records from the Galápagos Islands are reported. They are based on collections made during a 11 months' stay in the archipelago in 1971–72 and shorter stays in 1976 and 1977. The collections are deposited in C. Plant names are in accordance with Wiggins & Porter (1971).

Sida veronicaefolia Lam. (Malvaceae)

Lam., Encycl. 1, p. 5, No. 11 (1783).

Sida veronicaefolia resembles *S. hederifolia* as circumscribed by Bates (1971), but differs in a number of characters (Table 1). Bates (1971) stated that the collections of *Sida hederifolia* from the Galápagos were uniform, with the exception of one specimen (Wiggins & Porter 396, BH, CAS), but he preferred to include this aberrant collection in *S. hederifolia*. Having examined the collections of *Sida* in CAS, I agree with Bates in this. However, one other collection, Stewart 2037, which Bates (1971) included in *S. hederifolia,* belongs in my opinion to *S. veronicaefolia*. The specimen lacks mature fruits, but matches in all available characters (Table 1).

Schumann (1891) reported *S. veronicaefolia* from Brazil and reduced *S. hederifolia* Cav. and *S. humilis* Cav. to varieties. The Galápagos collections, which are here referred to *S. veronicaefolia,* fit the description made by Schumann (1891), but do not conform neither with his descriptions of var. *humilis* or var. *hederifolia,* nor with Bates' (1971) description of *S. hederifolia*. *S. hederifolia* and *S. veronicaefolia* belong to a difficult pantropical complex. As they are well distinguished in the Galápagos, I prefer to recognize them as species, pending a modern taxonomic treatment.

In the Galápagos *Sida veronicaefolia* appears to be restricted to Pinta island, while *S. hederifolia* is widespread (Bates 1971). *S. veronicaefolia* occurs on Pinta at intermediate elevations on the S slope in dry season deciduous steppe forest and forest, and in evergreen steppe forest and forest, often as a dominant member of the communities.

Collections. Pinta, S slope, common above 1000 ft, 21.9.1906, Stewart 2037 – S slope NW of Cabo Ibbetson, 450 m, 22.3.1972, M. & O. Hamann 797 – do., 350 m, 23.3.1972, M. & O. Hamann 835; 18.10. 1977, O. Hamann 2512 – S slope, 430 m, in *Zanthoxylum* forest, 12.11.1974, A. & H. Adsersen 1153.

Table 1. Some characteristics differentiating *Sida hederifolia* and *S. veronicaefolia* in the Galápagos Islands.

Sida hederifolia	*Sida veronicaefolia*
prostrate	± ascending
stem slender, not woody	stem thicker, woody at base
stem minutely or rather sparsely pubescent with mostly few-armed or simple hairs	stem ± densely pubescent with many-armed and simple hairs
leaf blade usually less than 25 mm long	leaf blade c. 30–50 mm long
pedicels thin, 15–30 mm long	pedicels thicker, 20–38 mm long
mericarps 1.8–2 mm long	mericarps 2–2.25 mm long
awns on mericarps 0.75–1.5 mm long	awns on mericarps 1.25–2 mm long

Sida ciliaris L. (Malvaceae)

L., Syst. Nat. ed. 10, 1145 (1759).

Sida ciliaris (a ± woody-based perennial) is easily distinguished from other species of the genus in the archipelago by the mostly 6–15 mm long, serrate, oblong to obovate leaves, by the peduncle being adnate to the petiole of a leaf-like bract, and by the pink to copper-red petals.

Sida ciliaris is new to the Galápagos. We collected it in desert scrub vegetation on the arid, southern plateau of Baltra island, and A. & H. Adsersen found it in Puerto Baquerizo Moreno, San Cristóbal. It is probably a recent introduction; this species is widely distributed in mostly very dry areas of the Americas (Standley & Steyermark 1949).

Collections. Baltra, near the W coast, SW part of the island, 15–20 m, 3.6.1972, M. & O. Hamann 1382 – *San Cristóbal,* Puerto Baquerizo Moreno, 20 m, 24.8.1974, A. & H. Adsersen 705.

Calceolaria mexicana Benth. (Scrophulariaceae)

Benth., Pl. Hartweg. 47 (1840).

Annual, stems brittle, sparsely branched or much branched from the base, 10–40 cm tall, pilose and viscid; leaves petiolate, varying from ovate and dentate to pinnatisect with dentate or serrate lobes (thereby easily distinguished from *Calceolaria meistantha,* the other species of the genus known from the archipelago); flowers sulphur-yellow, solitary or a few together in the leaf axils, long-pedicellate, pedicels villous and viscid; calyx lobes oblong to ovate, acute, c. 4 mm long at anthesis, sparsely glandular-pilose on the outside; corolla c. 1 cm long; capsule ovoid, glandular-pilose, c. 6 mm long.

Calceolaria mexicana is a very variable species, which perhaps includes several taxa (Standley & Williams 1973). It is new to the Galápagos. It was growing as an apparently well-established weed in fields and pastures above Bella Vista, Santa Cruz island. According to A. Kastdalen (pers. comm.), farmer and resident, *Calceolaria mexicana* was introduced to Santa Cruz by seeds sent from Norway to be grown as an ornamental. *C. mexicana* is actually grown as an ornamental summer-flower in European gardens (Bonstedt 1932).

Calceolaria mexicana is known from C America, according to Standley & Williams (1973), who suggested that the proper name for the C American material examined by them perhaps should be *C. tripartita* Ruiz & Pavón. *C. tripartita* is known from Chile and Bolivia through Peru and Ecuador to Colombia (Pennell 1951). The Galápagos collection matches the description and actual material of *C. mexicana* (in C and CAS) better than that of *C. tripartita.*

Collection. Santa Cruz, Kastdalen Farm, above Bella Vista, c. 250 m, 1.9.1972, M. & O. Hamann 2158.

Galinsoga caracasana (DC.) Schultz-Bip. (Asteraceae)

Schultz-Bip., Linnaea 34, 529 (1865–66); Bull. Soc. Bot. Fr. 12, 80 (1865).

Annual, erect, glandular-pilose herb; leaves opposite, shortly petiolate, ovate, acute or acuminate, 1.5–8 cm long, 1.5–5 cm broad; heads 3–5 mm broad with biseriate involucre; recep-

tacle chaffy, paleae narrow, persistent, 2–2.5 mm long; ray florets uniseriate, pistillate, corolla rose to purple, tube c. 1 mm long, ligule 1.5–2 mm long; disc florets perfect, corolla yellow, 1.5–3 mm long; achenes 1–1.5 mm long, glabrous (ray florets) or minutely strigose (disc florets); achenes of both ray and disc florets with pappus composed of 10–15 fringed scales c. 1 mm long.

Galinsoga caracasana resembles *G. urticaefolia* (H.B.K.) Benth., which recently was reported from the Galápagos (van der Werff 1977). However, this taxon lacks a pappus (Bentham 1852).

Galinsoga caracasana is new to the archipelago. It was found along roadsides and in adjacent fields at Occidente, Santa Cruz island. It is a weedy species with a wide distribution in tropical America and the Antilles (Aristeguita 1964).

Collection. Santa Cruz, Occidente, SW part of the island, c. 200 m, 12.9.1972, M. & O. Hamann 2200.

Euphorbia equisetiformis Stewart
(Euphorbiaceae)

The endemic *Euphorbia equisetiformis* (Fig. 1) is the only member of the genus in the archipelago. The species is only known from two localities, both on Isabella: the type locality on the floor of the caldera of Volcan Sierra Negra (Stewart 1911), and the lower SE slope of Volcan Cerro Azul (Weber 1973). The type specimen has neither leaves nor mature fruits, and so the taxonomic position within the genus was uncertain (Burch 1971).

During our stay in 1971–72 *Euphorbia equisetiformis* was collected on the SE slope of Volcan Cerro Azul, some 25 km W of the type locality. A fruiting specimen was secured and seeds later germinated in greenhouse in the Botanical Garden, Copenhagen (Figs. 2, 3). Based on this collection some additions to the descriptions can be made.

Leaves caducous, opposite, linear, c. 0.2×7 cm, leaving persistent gland-like bases; midvein rather prominent; stipules almost obsolete, membranaceous, interpetiolate; cyathia solitary, subtended by two keeled, caducous bracts (rarely two abortive cyathia in the axils of the bracts); lobes of cyathium ending in 5 fimbriate, membranaceous scales, between which 5 elliptical, entire glands are situated; male flowers subtended by filiform, fimbriate, membranaceous bracteoles of about the same length as the cyathia; capsule obtusely angulate, deeply trisulcate, irregularly rugulose, dark grey-brown, c. 5 mm long and 6–7 mm wide; seeds puncticulate, dark grey-brown, c. 2.4×2.1 mm, carunculate, the caruncle yellowish white, c. $0.6 \times 0.7 \times 0.3$ mm.

It is suggested that *E. equisetiformis* should be placed in sect. *Euphorbia* ("*Euphorbium* Benth."), as the glands are entire and exappendiculate, and in subsect. *Arthrothamnus* (Klotsch & Garcke) Boiss. on the opposite, caducous leaves, the minute stipules, the fimbriate bracteoles between the male flowers, the bifid style and the carunculate seeds (cf. Pax & Hoffman 1931). Its position here should be regarded as preliminary, as a modern treatment of the American euphorbias is lacking.

The closest relatives of *Euphorbia equisetiformis* seem to be *E. alata* Hook. from Jamaica and *E. cassythoides* Boiss. from Cuba; Boissier (1862) placed these two species in the group *Americanae* within subsect. *Arthrothamnus*. *E. equisetiformis* differs from both e.g. in having terete branches and solitary cyathia.

The vegetation in the area on Volcan Cerro Azul, where our collection was made, is described in Weber (1973). Apparently *Euphorbia equisetiformis* is restricted to a certain type of heavily weathered lava. The locality on Volcan Cerro Azul had a unique vegetation growing on this substrate; terrestric lichens, bryophytes and ferns were abundant. Eliasson visited the type locality on the floor of the caldera of Volcan Sierra Negra during his stay in 1966–67, and reported a similar habitat there, although the vegetation was more open (Eliasson, pers. comm.).

Collection. Isabela, SE slope of Volcan Cerro Azul, 610 m, 28.9.1972, M. & O. Hamann 2413.

Najas guadalupensis (Spreng.) Morong
(Najadaceae)

Najas guadalupensis was collected in 1972 on Santa Cruz island in the tortoise reserve in the SW part of the island. It was growing in a large pool near El Chato, together with *Azolla micro-*

Fig. 1. *Euphorbia equisetiformis* on the SE slope of Volcan Cerro Azul, Isabela (c. 610 m). Photo D. Weber, No. 68/14, 31.10.1969.

phylla. In 1976 *Najas guadalupensis* was found to be very abundant in the pool, this time together with *Ceratophyllum llerenae* (cf. Hamann 1974a). The one previous report of *Najas guadalupensis* from the Galápagos was from Santa Maria island (Wiggins & Porter 1971).

Mature fruits of the Santa Cruz specimens were compared with authentical material of *N. guadalupensis* and *N. flexilis* (Willd.) Rost. & Schmidt; the Galápagos plants matched material of *N. guadalupensis* from S America. Especially seed characters distinguish *N. guadalupensis* from *N. flexilis:* the seeds of *N. guadalupensis* are reticulated with 16–20 rows of areolae which are visible under a hand-lens, while those of *N. flexilis* are more obscurely reticulated with 30–40 rows of areolae.

Aquatic species like *Najas guadalupensis* and *Ceratophyllum llerenae* may be more common in the archipelago than indicated by the sparse collections, and should be sought for in the temporary pools found in the evergreen forests on the larger islands.

Collections. *Santa Cruz,* pool near El Chato, SW part of the island, 4.4.1972, M. & O. Hamann 1013; 31.8.1972, M. Hamann, O. Hamann & B. Toro 2167.

Callitriche deflexa A. Br. ex Hegelm. (Callitrichaceae)

This species was first reported from the Galápagos by Eliasson (1972), who collected it in 3 localities on 3 islands, viz. Isabela (Volcan Alcedo), San Salvador (summit area) and Santa Cruz (S slope). In 1972 we collected *Callitriche deflexa* on Volcan Sierra Negra (Isabela) and on the E slope of San Salvador. Both our localities were influenced by feral mammals. This supports Eliasson's opinion that *C. deflexa* is a recent introduction, which prefers habitats disturbed by goats and pigs.

Collections. *San Salvador,* E slope below central highland, c. 530 m, 19.8.1972, M. & O. Hamann 2099 – *Isabela,* Sierra Negra, at Corazon Verde, 400 m, 1.10.1972, M. & O. Hamann 2494.

Triumfetta semitriloba Jacq. (Tiliaceae)

Until the 1970s, the small shrub *Triumfetta semitriloba* had apparently not been collected in the Galápagos since the turn of the century, when it was recorded from Volcan Cerro Azul, Isabela (Wiggins & Porter 1971). However, the species is now widespread in the archipelago. We collected it in three localities on Isabela, and in one on Santa Maria. A. & H. Adsersen also found the species on Isabela and, in addition, on Santa Cruz.

In most of these localities *Triumfetta semitriloba* was abundant. As it has spiny fruits, its apparently recent spread may be associated with the continuing disturbance of the natural vegetation caused by feral mammals.

Collections. *Santa Maria,* lower N slope of Cerro Pajas, c. 325 m, 6.6.1972, M. & O. Hamann 1538 – *Santa Cruz,* between Bella Vista and Puerto Ayora (old trail), 70 m, 5.6.1974, A. & H. Adsersen 359 – *Isabela,* Volcan Alcedo, W slope, at the rim of the caldera, 1000 m, 14.7.1972, M. & O. Hamann 1784 – Cerro Azul, SW slope, 200 m, 25.9.1972, M. & O. Hamann 2264 – Sierra Negra, at the S rim of the caldera, 1000 m, 30.9.1972, M. & O. Hamann 2473 – Sierra Negra, at the sulphur mine, inside slope of the caldera, 900 m, 30.7.1977, A. & H. Adsersen 2338.

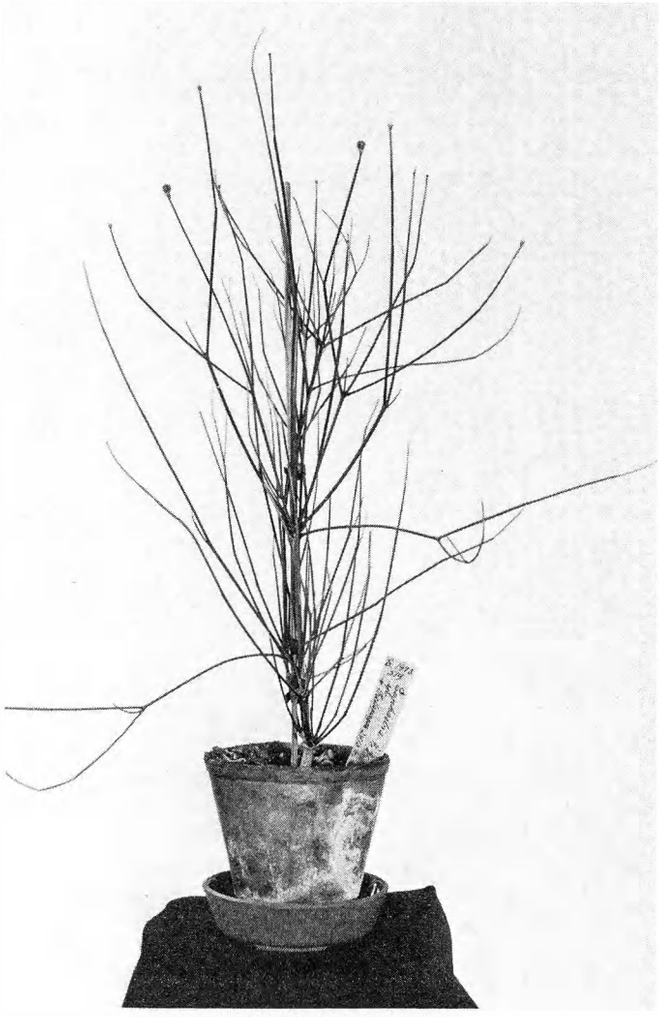

Fig. 2. Two and a half year old specimen of *Euphorbia equisetiformis*, grown in greenhouse. Almost all leaves have been shed.

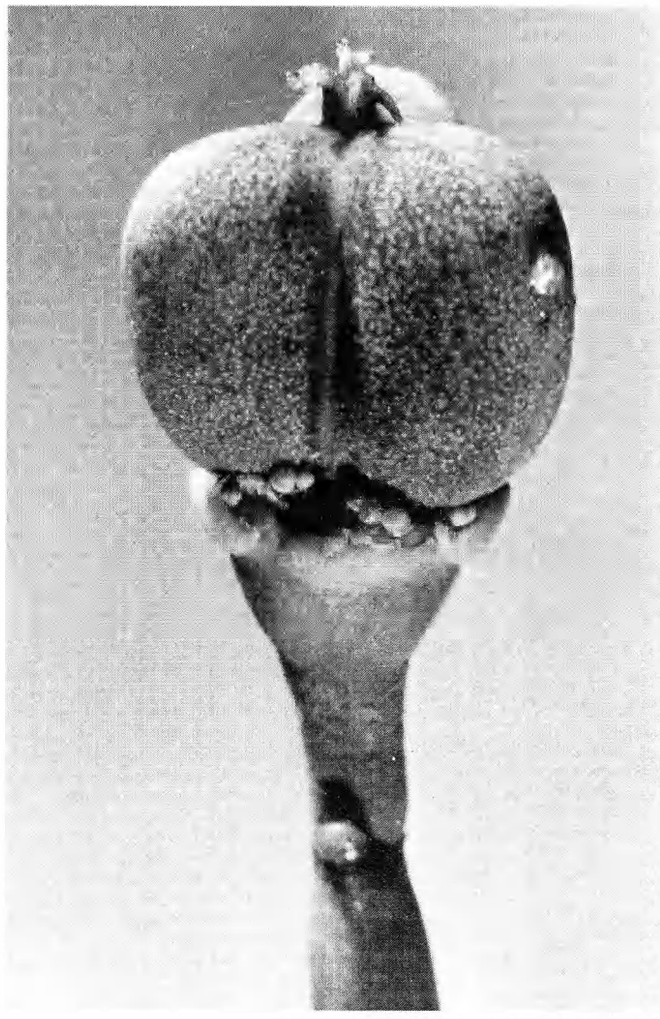

Fig. 3. Mature capsule of *Euphorbia equisetiformis*. Note gland-like structure formed below the cup where one of the caducous bracts have been shed. Same specimen as in Fig. 2.

Concluding remarks

Black (1974) listed 132 introduced species from the Galápagos; of these, 101 were additions to those 77 species treated as recently introduced by Wiggins & Porter (1971). However, Black did not elaborate which species were considered as being naturalized (he also included crop plants, ornamentals, kitchen herbs, etc.). I can add some species which were planted in various places, e.g. *Guazuma ulmifolia* Lam. (Sierra Negra, Isabela), *Phyllanthus acidus* (L.) Skeels (Puerto Ayora, Santa Cruz), *Byrsonima* sp. (farm region, Santa Maria) and *Sambucus* sp. (Bella Vista, Santa Cruz).

29 well-established exotic species (both woody and non-woody) have been reported from the archipelago since the publication of the Flora in 1971 (Eliasson 1972, Hamann 1974 a, b, van der Werff 1977). *Sida veronicaefolia, Sida ciliaris, Calceolaria mexicana* and *Galinsoga caracasana* present further additions. The spread of such species as *Callitriche deflexa* and *Triumfetta semitriloba* may be symptomatic for the alterations in the ecosystems which are caused by feral mammals, and which may favour the exotic species at the expense of the indigenous ones.

The continuously growing number of exotic species that become established in the archipelago deserves serious attention. Some introduced species already cause great conservational problems ("pangola" grasses, which include *Digitaria decumbens* Stent (van der Werff 1977) and species of *Paspalum; Psidium guajava* and *Eugenia jambos* (Hoeck, pers. comm.); *Cinchona succirubra* Pavón ex Klotzsch (Ha-

mann 1975); and some others). So far the efforts of the Servicio Parque Nacional Galápagos to control the aggressive exotic species have been rather unsuccessful. The transfer of plants from other regions of the world to the Galápagos Islands also presents a risk of concomitant transfer of plant parasites and pathogens. Special programs for conservation planning on a long-term scale should be implemented to cope with these problems.

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Resumen

Se anuncian por primera vez como habitantes del archipiélago *Sida veronicaefolia* Lam., *S. ciliaris* L. (Malvaceae), *Calceolaria mexicana* Benth. (Scrophulariaceae) y *Galinsoga caracasana* (DC.) Schultz-Bip. (Asteraceae). Se discuten la taxonomía y la distribución de la endémica *Euphorbia equisetiformis* Stewart (Euphorbiaceae). Se presentan notas sobre la forma en que se encuentran *Najas guadalupensis* (Spreng.) Morong (Najadaceae), *Callitriche deflexa* A. Br. ex Hegelm. (Callitrichaceae) y *Triumfetta semitriloba* Jacq. (Tiliaceae).

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