Chromosome numbers of Scandinavian Odontites species

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The chromosome number has been determined for 29 populations. Aneuploidy and aneusomaty have been observed. Karyotypes are given for *Odontites verna* (Bell.) Dum. (2n = 40), *O. rubra* (Baumg.) Opiz (2n = 18) and *O. litoralis* Fr. (2n = 18). Both mitosis and meiosis were studied. Two theories of previous possible misinterpretation of the chromosome number of the diploids are given.

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Within Scandinavia the following taxa of *Odontites* have been recognized by different authors:

Odontites verna (Bell.) Dum.
Odontites rubra (Baumg.) Opiz (*O. serotina* Dum.)
  ssp. *rubra*
  ssp. *rubra* var. *pallida* Lange
  ssp. *rubra* f. *tescaria* K. Joh.
  ssp. *pumila* (Nordst.) U. Schneider
Odontites litoralis Fr.
  ssp. *litoralis*
  ssp. *litoralis* var. *baltica* Eklund ex Markl.
  ssp. *fennica* Markl.

O. verna is known only as a weed. It is distinguished from *O. rubra* in being few-branched, the branches (mostly in the upper part of the stem) making an acute angle with the stem. *O. rubra* is much-branched, the branches arising from the base of the stem at an obtuse angle. *O. rubra* is the commonest species, occurring in grassland, salt marshes and as a weed. The epithet ssp. *pumila* has been given to an extremely low-growing salt-marsh ecotype (Pedersen 1963). The epithets *verna* and *rubra* have both been used in a collective sense.

O. litoralis grows in salt marshes and on the brackish shores of the Baltic and is distinguished from *O. rubra* in having the first flower at the 5th–7th node, leaves shorter than the internodes and the style shorter than the upper lip of the flower. The epithets ssp. *fennica* and var. *baltica* were given to local races from the brackish shores of the Gulf of Finland and of the Åland Islands respectively (Marklund 1955).

Material and methods

The seeds of *Odontites* do not germinate unless exposed to low winter temperatures and moisture for 12–18 weeks (Vallance 1951). Seeds were sown in pots in December and placed in open frames at the Botanical Gardens, Lund, for 18 weeks and then moved to a greenhouse (15°C). Within a week the seeds had germinated. Seedlings were pretreated with a saturated solution of 1,4-dichlorobenzene for 1 1/2–2 hours (Lepper 1968), fixed in absolute alcohol:acetic acid (3:1) overnight, stained with Feulgen (hydrolysis 10 mins.) according to Lepper (1968) and then treated with a 5% aqueous solution of pectinase for 2–3 hours. The squash technique described by Östergren & Heneen (1962) was used on meristematic tissues of the plumule and lateral root-initials. Cell division had ceased in the radicle. If the Feulgen staining proved too weak aceto-carmine was added to the preparation. To prevent bleaching the slides were left in acetone only till the astralon coverslip loosened.

Slides for investigating meiosis were made from flower buds fixed overnight in absolute alcohol, chloroform and glacial acetic acid (6:3:1) and stained overnight in HCl-carmine at 60°C (Snow 1963). Excess stain was removed in 70% alcohol. Anthers were crushed in 45% HAc and squashed in a drop of Hoyer's medium under a glass coverslip (Beeks 1955). PMCs, pollen mitoses and dividing somatic tissues were studied. Well spread-out chromosomes were found in terminal cells of some anther hairs.

Table 1. Previously published chromosome numbers of *Odontites*.

Species	2n	Counted by
O. rubra	20	Witsch 1932 as *O. serotina*, Rottgardt 1956, Sorsa 1962, Schneider 1964
O. rubra	18	Greilhuber 1971
O. litoralis	20	Sorsa 1963, Schneider 1964
O. verna	40	Witsch 1932, Rottgardt 1956, Schneider 1964

Other methods for preparing slides for chromosome counts were less successful. Pretreatment with colchicine and hydroxychinoline gave rise to overcontraction. Stickiness occurred in such preparations as well as in sections fixed in Navashin-Karpechenko.

Voucher specimens are deposited at LD.

Chromosome numbers and karyotypes

The previously published chromosome numbers in *Odontites* are cited in Table 1. The number 2n = 20 for *O. litoralis* published by Rottgardt in Tischler (1950) and in Rottgardt (1956) refer to erroneously determined material of *O. rubra* (Pedersen 1963). In Fedorov (1969) the number 2n = 20 for *O. rubra* is also cited from Rohweder (1937) and Tischler (1937) and 2n = 40 for *O. rubra* from Tischler (1934) and Soó (1959), but no counts of their own are given in these works. In the same work 2n = 20 is cited for *O. verna* from Fagerlind (1937), which must be a misprint for Fagerlind (1936). Fagerlind discusses chromosome numbers but no counts of his own for *Odontites* are given. Greilhuber (1971) presumes that previous reports of 2n = 20 are the result of misinterpretation. The chromosomes of *Odontites* are small and often show stickiness.

My investigations confirm the diploid number found by Greilhuber. In both mitosis and meiosis I have found 2n = 18 for *O. rubra* and *O. litoralis*. In each of 4 populations out of 20 I have found 1 aneuploid plant (Table 2). Three of them had 2n = 20 and the fourth 2n = 22. This plant showed abnormal meiosis with the metaphase configurations 6^{I}, 5^{II}, 2^{III} or 6^{I}, 8^{II}. Laggards occurred at anaphase. Meiosis was not studied in the other 3 aneuploids.

The normal diploid chromosome complement consists of 18 metacentric to submetacentric chromosomes (Fig. 1 A–C). The chromosomes show a gradual decrease in size from 3.5 μm to

Table 2. Chromosome number of Scandinavian *Odontites* species. N = number of plants investigated. – 1 = Pollen mitosis. – 2 = Material corresponding to Marklund's ssp. *fennica*. – 3 = Material corresponding to Marklund's ssp. *litoralis* var. *baltica*. – 4 = Material corresponding to K. Johansson's ssp. *rubra* f. *tescaria*.

Locality	n	2n	N
O. rubra			
Sweden, Skåne, Klagshamn, BS 14	9		3
Sweden, Skåne, Sjötorp, BS 117	9		1
Sweden, Skåne, Ljunghusen, BS 118	9	18	3
Sweden, Skåne, Skanör, BS 119	9	18	5
		20	1
Sweden, Öland, L. Vickleby, Widén 030119		18	1
Sweden, Öland, Ventlinge, Widén 030115		18	1
Sweden, Gotland, Bälsalvret, T. Karlsson 030203[4]		18	1
Finland, Regio aboënsis, Nauvo, Lillandet, BS 97	9		1
	11		1
O. litoralis			
Sweden, Gotland, Klintehamn, BS 33		18	1
Sweden, Sörmland, Dalbyö, Breviken, BS 18		18	2
Finland, Karelia australis, Vilniemi, BS 66[2]		18	1
		20	1
Finland, Karelia australis, Hämeenkylä, BS 69[2]		18	1
Finland, Karelia australis, Pyötsaari, BS 74[2]	9	18	5
Finland, Regio aboënsis, Korppoo, BS 87[3]		18	1
Finland, Regio aboënsis, Korppoo, Korpoström, BS 91[3]		18	1
Finland, Regio aboënsis, Väättäinen, Vohlo, BS 100	9	18	3
Finland, Regio aboënsis, Lepäinen, BS 104		18	1
		20	1
Finland, Regio aboënsis, Kittamaa, Pitkäluota, BS 101		18	1
Finland, Regio aboënsis, Kustavi, Hannula, BS 108		18	1
Finland, Regio aboënsis, Röölä, BS 115		18	1
O. verna			
Sweden, Skåne, Kiaby, BS 120	20[1]		1
		38	1
Sweden, Gotland, Ardre, BS 22		40	1
Sweden, Gotland, Faludden, BS 47		40	1
		39	2
Sweden, Gotland, Vägumeviken, BS 53		40	1
Sweden, Gotland, Tingstäde, BS 60	20[1]	40	4
		38	1
Sweden, Gotland, Othem, BS 63		40	1
		38	1
Sweden, Gotland, Martebo, BS 61	20[1]		2
Sweden, Gotland, Friggars, BS 64		40	1
		39	1
Sweden, Gotland, Fide, BS 45		40	1

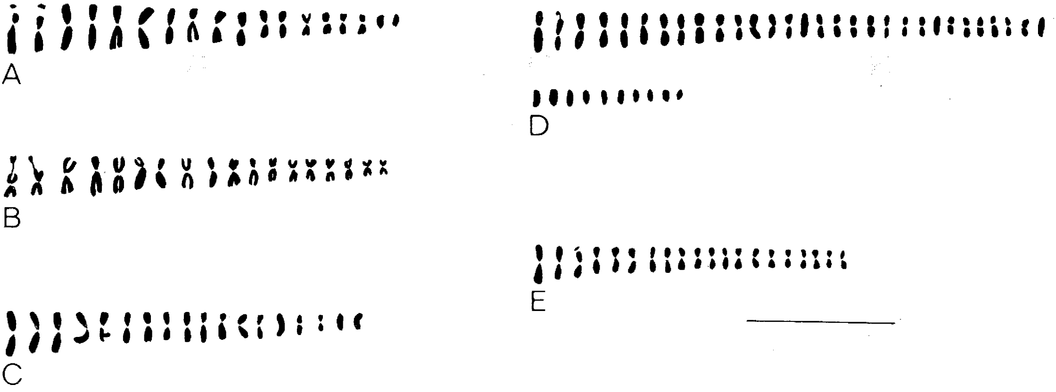

Fig. 1. Karyotypes of *Odontites*. – A: *O. rubra* (BS 119). 2n = 18. – B: *O. litoralis* (BS 33). 2n = 18. – C: *O. litoralis* (BS 74), material corresponding to Marklund's ssp. *fennica*. 2n = 18. – D: *O. verna* (BS 60). 2n = 40. – E: *O. verna* (BS 60). n = 20, pollen mitosis. – Scale 10 μm.

1 μm. A satellite is often visible on one of the longest pairs.

For *O. verna* I have found the numbers 2n = 38, 39, 40 (Table 2). The euploid number of *O. verna* is 2n = 40, which is confirmed in the pollen mitosis (Fig. 1 E). I have also found aneusomaty in some individuals where the numbers 36, 38, 39 and 42 are found together with the euploid number.

The chromosomes are metacentric to submetacentric. They range from 3 μm to 1 μm with a gradual decrease in size from the largest to the smallest. One of the longest pairs has a satellite (Fig. 1D).

In PMCs of *O. rubra* and *O. litoralis* one bivalent usually divides precociously giving the impression of 10 bivalents instead of 9 (Fig. 2B). At pachytene, diplotene and diakinesis a strongly staining aggregation can be seen on the nucleolus. It is probably heterochromatin belonging to the satellite chromosomes. The nucleolus is visible until late diakinesis. In counts made at diakinesis this aggregation could possibly be interpreted as a separate bivalent (Fig. 2C). Meiosis was normal in nearly all cells investigated.

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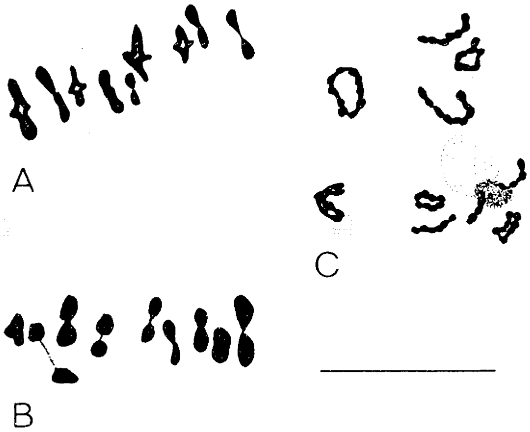

Fig. 2. PMCs of *Odontites*. – A: Metaphase I, *O. rubra* (BS 119). – B: Metaphase I, *O. litoralis* (BS 74), material corresponding to Marklund's ssp. *fennica*. One bivalent is in the process of dividing. – C: Diplotene–diakinesis, *O. rubra* (BS 14). A darkly staining aggregation is visible on the satellite chromosome and the nucleolus. – Scale 10 μm.

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Three new species of brown fruticose Cetraria

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C. arenaria Kärnef. sp. nov., an American lowland species growing on sand and distributed from New England to the Great Plains of western Canada, with a disjunct occurrence in Colombia and *C. australiensis* W. Weber ex Kärnef. sp. nov., an alpine species from Australia, New South Wales, Snowy Mountains, are described and illustrated. *C. fastigiata* (Del. ex Nyl. in Norrl.) Kärnef. stat. nov., based on an infraspecific taxon of *C. delisei*, is redescribed, illustrated and one table is presented comparing it with *C. delisei*.

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When working with the brown fruticose *Cetrariae* I first noticed *C. arenaria* and *C. fastigiata* on herbarium specimens under other names. Only after having studied the plants in the field (*C. arenaria* in Maryland, Wisconsin, Massachusetts and Michigan and *C. fastigiata* in Alaska) did I become convinced of their status.

C. australiensis has been distributed in Lich. Exs. COLO 454 as *Coelocaulon australiense*, unpublished. For morphological, anatomical and chemical reasons the species is better accommodated among the brown *Cetrariae*.

A more extensive presentation of these species is to appear in a monograph (Kärnefelt in prep.).

I have examined all collections of *C. arenaria* and *C. fastigiata* in ABSL, CANL, COLO, FH, H, LE, LD, MICH, MIN, MSC, NEBC, S, UPS, US, WIS. Thin layer chromatography was carried out according to the method described by Culberson (1972).

C. arenaria Kärnef. sp. nov.

Holotypus: Michigan, on sandy soil, 35 miles west of St. Ignace on U.S. 2, 5.9 miles west of junction of M117 to Newberry, Mackinaw Co., 1949 Imshaug 5449 (LD).

Thallus fruticosus (1–)3–4(–7) cm longus, pars proximalis plerumque longe indivisa, partes distales pluries divisae. *Laciniae* (0.5–)1–4(–12) mm latae, leviter canaliculatae, partibus planis, marginibus hic inde pontibus connectis, dichotome divisae. *Superficies inferior* cinereo-brunnea vel pallide cinerea, raro obscure brunnea, laevis vel longitudinaliter porcata, opaca vel nitida. *Superficies superior* concolor vel saepe obscurior, laevis sed saepe rugis transversalibus distantibus munita, nitida, interdum opaca. Partes basales raro rubentes. *Pseudocyphellae marginales* plerumque praecipue partibus distalibus perspicuae. *Pseudocyphellae laminales* plerumque paucae, minutissimae, sed aliquando in partibus thalli expansis numerosae. *Margines laciniarum* prominentiis acicularibus, 0.5–1 mm longis munitae. *Apothecia* rarissima, marginalia ad apices laciniarum posita, discus 0.5–3 mm, obscure brunneus. *Sporae* octonae, hyalinae, ellipsoideae, 3.5–4 × 5.5–6 µm. *Pycnidia* rara terminalia in prominentiis maginalibus posita, microconidia bacillaria, circa 1 × 5 µm. Medulla K−, C−, KC−, PD−.

Thallus fruticose (1–)3–4(–7) cm large, proximally with usually long undivided portions and distally more densely branched. *Lobes* (0.5–)1–4(–12) mm broad, weakly channelled and with plane parts, lobe margins here and there folded together and connected with thallus bridges, dichotomously branched. *Lower surface* greyish brown to pale greyish, rarely dark brown, smooth or weakly ridged along the lobes, dull or glossy. *Upper surface* concolorous or often darker, smooth but with sparse transverse wrinkles, usually glossy, sometimes dull. Basal parts only rarely reddish. *Marginal pseudocyphellae*

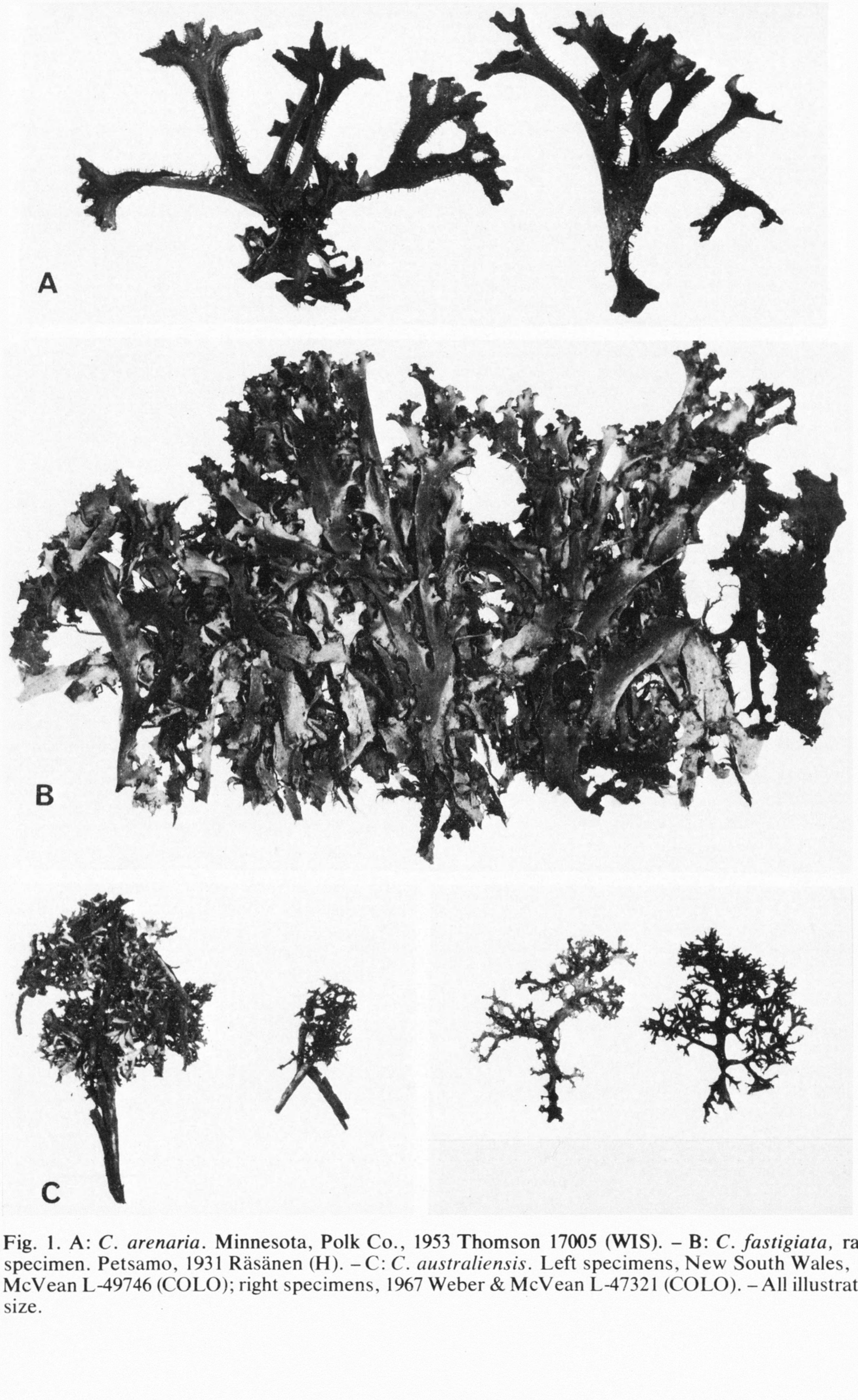

Fig. 1. A: *C. arenaria*. Minnesota, Polk Co., 1953 Thomson 17005 (WIS). – B: *C. fastigiata*, rather luxuriant specimen. Petsamo, 1931 Räsänen (H). – C: *C. australiensis*. Left specimens, New South Wales, 1968 Weber & McVean L-49746 (COLO); right specimens, 1967 Weber & McVean L-47321 (COLO). – All illustrations in natural size.

usually distinct, especially on the upper parts of the thallus. *Laminal pseudocyphellae* usually uncommon and very small, but occasionally numerous on expanded thallus parts and then larger. *Marginal projections* 0.5–1 mm long, acicular. *Apothecia* marginal on the lobe ends, very rare, disc 0.5–3 mm, dark brown. *Spores* 8 per ascus, hyaline, ellipsoidal, 3.5–4 × 5.5–6 μm. *Pycnidia* on top of the marginal projections, very rare; microconidia rod-shaped, about 1 × 5 μm. Medulla K–, C–, KC–, PD–.

C. arenaria (Fig. 1 A) differs from *C. islandica* mainly in the acicular marginal projections and in the absence of distinct laminal pseudocyphellae. Otherwise the taxon has usually been referred to as *C. islandica* subsp. *crispa* (Brodo 1968) or as *C. ericetorum* (Taylor 1968) because of the PD negative medulla. *C. arenaria* also differs from *C. ericetorum* in the acicular marginal projections and the less channelled and flatter lobes. Chemically *C. arenaria* differs from *C. islandica* in the absence of fumarprotocetraric acid. However, the two species contain the same aliphatic compounds (lichesterinic and protolichesterinic acids). *C. arenaria* and *ericetorum* prove to have different aliphatic compounds when tested in the B-system (Culberson 1972) for the identification of lichen products.

C. arenaria is mainly a North American lowland species preferring sandy environments. The species is fairly common on the Atlantic seaboard from Maine, Massachusetts, Rhode Island, Connecticut to New York (Long Island). Inland it is found in Vermont, Pennsylvania, Maryland, Virginia, West Virginia and Ohio. However, the best-known localities are along the shores of Lake Michigan and Lake Huron. There has been a general agreement among American lichenologists that these plants merit nomenclatural recognition (Imshaug 1957). *C. arenaria* is also found on the eastern shore of Lake Superior and on the northern shore of Lake Ontario. The species occurs only scattered in Wisconsin, Minnesota, Manitoba, Saskatchewan and Alberta. *C. arenaria* also occurs in an isolated locality in Colombia, South America.

The species is named because of its preference for sandy situations.

Cetraria australiensis W. Weber ex Kärnef. sp. nov.

Holotypus: Australia, New South Wales, Snowy Mountains, Kosciusko State Park, summit of Mount Stilwell, Kangaroo Range, 1981 m.s.m., above Charlottes Pass, abundant locally on windswept heath of *Epacris petrophila–Baeckia gunniana*, occurring locally entangled in broom-like masses on dead twigs, 1968 Weber & McVean (Lich. Exs. COLO 454) (COLO).

Thallus fruticosus aliquantum *C. delisei* minutae similis, 1–2(–3) cm longus, pars basalis ad circa 0.5 cm, indivisa, partes distales densissime divisae, partes basales et laciniae principales 1.5–2 mm latae, saepe porcis longitudinalibus praeditae. *Laciniae* irregulariter vel dichotome divisae, 0.5–1 mm latae, fere planae vel laevissime canaliculate. Margines medio crassiores. *Superficies inferior* flaveo-brunnea vel obscure brunnea, laevis et opaca. *Superficies superior* concolor vel plerumque inferiore obscurior, laevis et opaca. Pars basalis laeviter rubens. *Pseudocyphellae marginales* punctiformes in superficie inferiore positae. *Margines laciniarum* prominentiis dispersis, circa 0.5 mm longis et cilis paucis, aliquanto divisis, 1–2 mm longis munitae. *Apothecia* ignota. *Pycnidia* rara terminalia prominentiis marginalibus praedita, microconidia bacillaria circa 1 × 6 μm. Medulla K–, C–, KC–, PD–.

Thallus fruticose somewhat resembling a tiny *C. delisei*, 1–2(–3) cm large, with an unbranched basal portion, about 0.5 cm, and distally more densely branched, basal part and main lobes 1.5–2 mm broad, often with longitudinal ridges. *Lobes* irregularly or dichotomously branched, 0.5–1 mm broad, almost plane or very weakly channelled. The margins usually thicker than the central parts. *Lower surface* yellowish-brown to dark brown, smooth and dull. *Upper surface* concolorous or usually darker, smooth and dull. Basal parts pale reddish. *Marginal pseudocyphellae* dot-like. *Marginal projections* about 0.5 mm, scattered. On the edges also a few branched cilia c. 1–2 mm long. *Apothecia* not known. *Pycnidia* rare, on top of the marginal projections; microconidia rod-shaped about 1 × 6 μm. Medulla K–, C–, KC–, PD–.

The species is accommodated in the group of brown *Cetrariae* because of the lobe form, the marginal pseudocyphellae on the lower surface and the marginal projections with terminal parmeliaceous pycnidia (Fig. 1 C).

The cortical layers, 30–70 μm thick, consist of pachydermatous paraplectenchyma overlying a prosoplectenchymatous tissue. The medulla, 140–190 μm thick, is composed of loosely interwoven hyphae 3–6 μm thick. The algae of *Trebouxia* type, each 10–15 μm in diameter, are

Table 1. Comparison of *C. delisei* and *C. fastigiata*.

Species	Lobes	Lobe tips	Lower surface	Pseudocyphellae
C. delisei	weakly channelled to plane	acute or at least partly acute on wider lobes	smooth or wrinkled	marginal and laminal usually distinct
C. fastigiata	subtubular and cucullate	more obtuse	smooth and pitted	marginal almost indiscernible, laminal few, poorly developed

spread through the medulla or concentrated near the upper cortex.

The species produces lichesterinic and protolichesterinic acids, common in this group of lichens.

C. australiensis is only known from the Snowy Mountains in Australia, where it grows unattached but intertangled amidst twigs of small alpine shrubs or on the ground in protected depressions.

Cetraria fastigiata (Del. ex Nyl. in Norrl.) Kärnef. stat. nov.

Cetraria delisei (Bory ex Schaer.) Nyl. var. *fastigiata* Del. ex Nyl., Flora 52 p. 444 (1869), nomen nudum. – *Cetraria delisei* (Bory ex Schaer.) Nyl. ssp. *fastigiata* ("**C. fastigiata*") Del. ex Nyl. in Norrl., Not. Sällsk. Fauna Fl. Fenn. Förh. 13 p. 323 (1873). – *Cetraria hiascens* (Fr.) Th. Fr. var. *fastigiata* (Del. ex Nyl. in Norrl.) Wainio, Meddel. Soc. Fauna Fl. Fenn. 6 p. 119 (1881) and Ark. Bot. 8 (4) p. 23 (1909). – *Lectotype* (selected here): Finland, Enontekis, Hetta, 1867 Norrlin det. Nylander (H).

Thallus fruticose (1–)3–4(–6) cm large. *Lobes* 2–5 mm broad, canaliculate or almost tubular, dichotomously branched and the margins cucullate with short branchlets, lobe tips obtuse, basal parts more weakly channelled or plane up to 15 mm wide. *Lower surface* dark brown, grey-brown, yellow-brown or pale brown, smooth and pitted, usually glossy. *Upper surface* concolorous, more pitted, dull or glossy. *Marginal pseudocyphellae* very narrow and almost indiscernible. *Laminal pseudocyphellae* sparse and poorly developed. *Marginal projections* 0.1–1 mm, sparse or absent, rarely on the lobe tips. *Apothecia* marginal on the lobe ends, disc 2–10 mm, usually with a slightly wavy margin, dark brown or brown. *Spores* 8 per ascus, hyaline, ellipsoidal, 2.4–3.6 × 6–8.4 μm. *Pycnidia* on top of the marginal projections, dark brown; microconidia rod-shaped, about 0.5 × 5 μm. Medulla K–, C+, KC–, PD–. Contains gyrophoric and hiascinic acids.

The epithet, taken from a Delise herbarium name, was first mentioned by Nylander (1869), but without an acceptable description. A valid description was published a few years later by Nylander in Norrlin (1873). In this work Norrlin adopted Nylander's habit of marking infraspecific units above variety with an asterisk, as in the case of *C. fastigiata*.

C. fastigiata is readily distinguished from its closest relative *C. delisei* on the structure of the lobes and pseudocyphellae (Table 1). The lobes of *C. fastigiata* (Fig. 1 B) resemble more closely those of *C. cucullata* or *C. kamczatica* than the more finely divided lobes of *C. delisei*.

C. fastigiata is a poor competitor on the arctic tundra and occurs chiefly where minor depressions and bare spots form niches. It is also found in depressions in northern boreal bogs. Only rarely is *C. fastigiata* found in other habitats. The same kind of habitats are exploited by other brown *Cetrariae*, e.g. *C. andrejevii*, *C. delisei* and *C. nigricascens*. However, these species all have a much wider ecological amplitude and *C. fastigiata* consequently is the least successful.

C. fastigiata is found on Newfoundland, scattered in the Canadian Arctic and in Alaska. On the Eurasian continent *C. fastigiata* is distributed in the easternmost part of Siberia and from the Urals to northern Scandinavia.

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Galenia secunda (Aizoaceae) new to Europe

Lars Arvidsson and Magnus Lidén

Arvidsson, L. & Lidén, M. 1977 06 30: Galenia secunda (Aizoaceae) new to Europe. *Bot. Notiser 130:* 130. Stockholm. ISSN 0006-8195.

Galenia secunda (L. fil.) Sonder is reported from the province of Cadiz, S Spain. The species is native to S Africa. It probably came to Europe by human activity.

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In 1968 a specimen of *Galenia secunda* (L. fil.) Sonder was collected in S Spain. As far as we know, no *Galenia* has been collected in Europe before. The Spanish plant agrees well with the description given by Adamson (1956) except that the leaves are alternate only in the upper parts of the stems. Some specimens in S, determined by Adamson, also have opposite leaves, however, and Sonder (1862) states that the young leaves are often opposite. Our plant is rather robust with large flowers (perianth lobes 3.0–3.2 mm long), red anthers and a gynoecium with five styles. It agrees well with the type in herb. Thunberg (UPS). *Galenia secunda* is evidently very close to *G. pubescens* (E. & Z.) Druce, which is said to be green and less hairy and with perianth segments 2.0–2.5 mm. Both species are very polymorphic and many subspecific taxa have been described. However, the somewhat larger flowers and the dense hairiness of our specimen seem to justify our determination.

The Spanish specimen (prov. Cadiz, 2 km N Chiclana de la Frontera, 21.4. 1968, Strandhede et al. 826 (GB)) was found on saline soil near the Atlantic Ocean in company with *Arthrocnemum glaucum, A. perenne, Beta macrocarpa, Limoniastrum monopetalum, Mesembryanthemum nodiflorum, Salsola soda* and *Suaeda vera.*

Galenia secunda probably came to Europe by human activity. The plant is indigenous to South Africa (Adamson 1956) and southern Namibia (Friedrich 1972). It has also been collected in Florida, USA (Curtis 6869 (S) "the seeds evidently brought in ballast") and in Adelaide, S Australia (Kaspiew 35 (S)).

The occurrence of *Galenia secunda* in Europe is not very remarkable since several other species of the Aizoaceae have been naturalized here. At least seven of the eleven species of Aizoaceae mentioned in Flora Europaea (Tutin 1964) originate from S Africa.

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Moesziomyces, a new genus of Ustilaginales

Kálmán Vánky

Vánky, K. 1977 06 30: Moesziomyces, a new genus of Ustilaginales. *Bot. Notiser 130:* 131–135. Stockholm. ISSN 0006-8195.

A new genus of Ustilaginales, *Moesziomyces,* is described. The genus is characterized by many-spored, permanent spore balls in which the spores are bound together by surface ornaments appearing as meshes, or at the margins as thin irregular wings, when the spores are separated. There is no columella in the sori. The following new combinations are made: *Moesziomyces bullatus* (Schröt.) Vánky (type species of *Moesziomyces*), *M. evernius* (H. Syd.) Vánky, *M. globuligerus* (Berk. & Br.) Vánky and *M. penicillariae* (Bref.) Vánky.

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The genus *Tolyposporium* was erected by Woronin (1882) for *Sorosporium junci* Schröter. A description of *T. junci* is provided for comparison with the species segregated here in the new genus *Moesziomyces.*

Tolyposporium junci (Schröt.) Woronin

Sori small, tumor-like (Fig. 1 A, B) in the flowers (often involving only part of the inflorescence, the capsule or only the base of the inflorescence and spreading to the adjacent bracts and rachis), less often in the stems, forming a naked, black, granular agglutinated spore mass, composed of spore balls. *Spore balls* (Figs. 1 C, 2 A–C) variable in form and size, globose, subglobose, elongated or irregular, 16–50(–80) µm long, opaque, dark chestnut-brown to black-brown, composed of 3–40 or more spores. *Spores* (Figs. 1 D, 2 D) subglobose to more or less angular, often rounded cuneiform and irregular, (6.4–)8–13.6(–16) µm in diameter, chestnut-brown to black-brown, smooth on the contact surface and provided with irregular warts on the free, slightly convex surface. The wall is unequally thick and may vary from 0.5–4 µm within the same spore. *Type* on *Juncus bufonius* L., Silesia, Carlowitz near Breslau (at present Wroclaw, Poland), coll. J. Schröter.

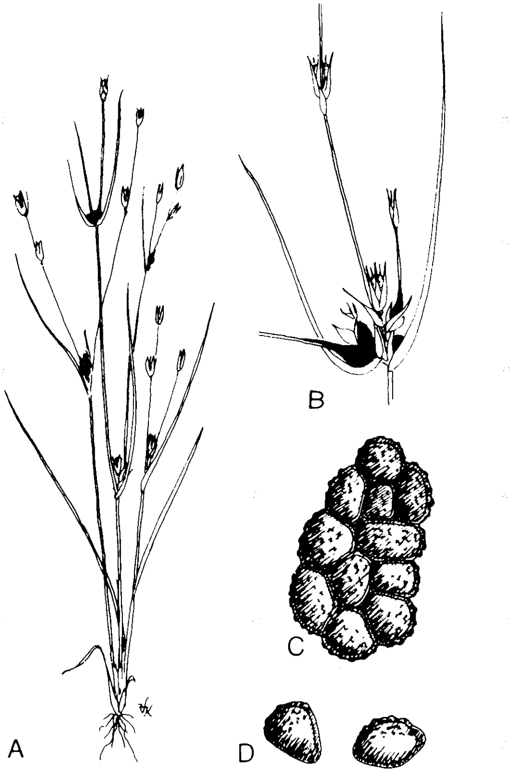

Fig. 1. *Tolyposporium junci* on *Juncus bufonius.* – A: The host plant with the fungus sori, × 0.6. – B: The sori, × 3. – C: Spore ball, × 625. – D: Spores, × 625.

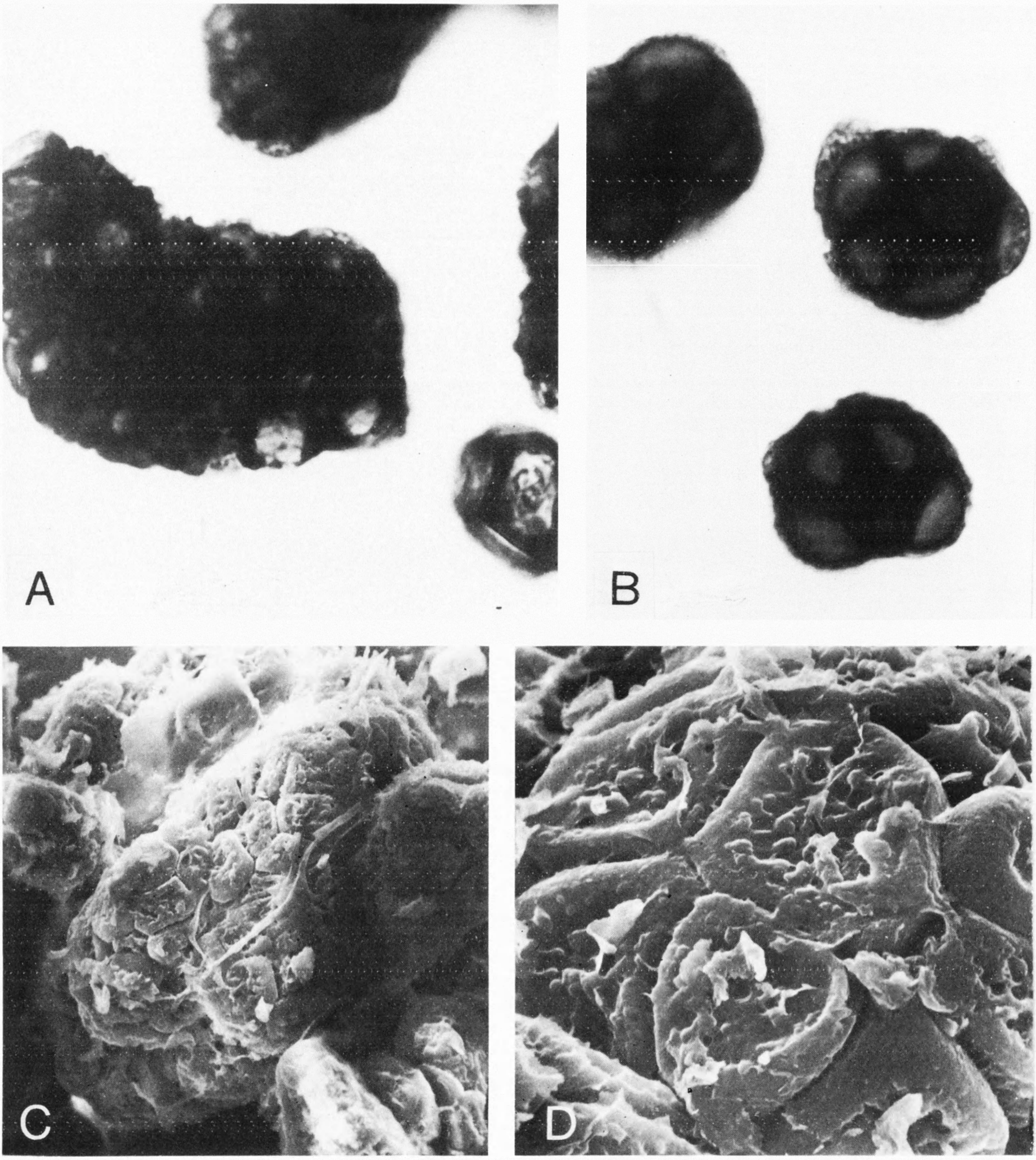

Fig. 2. *Tolyposporium junci*. – A, B: Spore balls, LM × 1100. – C: Spore balls, SEM × 630. – D: Spores in a spore-ball, SEM × 2420.

Distribution: on *Juncus bufonius* L.: Europe, N. America; on *J. capitatus* Weig.: Europe (Poland, Sweden).

The heterogeneity of Tolyposporium

Over the years numerous species of fungi with spore balls and an uncertain systematic position have been included in the genus *Tolyposporium*. Consequently this genus became heterogeneous containing species with widely different morphology and biology. So far about 40 species have been referred to this genus. Some of them belong to the genus *Thecaphora,* e.g. *Tolyposporium davidsonii* Dietel & Holway which in fact is conspecific with *Thecaphora pilulaeformis* Berkeley & Curtis, on *Isocoma veneta* (Compositae), or *Tolyposporium iresine* Elliot which is *Thecaphora iresine* (Elliot) H. S. Jackson on *Iresine celosina* (Amaranthaceae). Several species of *Tolyposporium* turned out to belong to the genus *Sorosporium,* e.g. *T. anthistiriae* P. Henn., *T. cenchri* Bref., *T. christensenii* Ragunath, *T. everhartii* (Ellis & Galloway) Dietel, *T. filiferum* Bussee, *T. tristachidis* (Sydow) Zundel. *Tolyposporium cocconii* Morini on the leaves of *Carex* spp. belongs to the genus *Schizonella* with all the characteristics of this genus, except for one: the spores in pairs are agglutinated in smaller or larger balls. *Tolyposporium crepidis-rubrae* (Jaap) Ciferri is a species of *Entyloma. T. glabrum* Ciferri belongs to the genus *Sphacelotheca; T. bursum* (Berk.) Mc Alpine to the genus *Ustilago; T. junci* Lind (non Woronin) is *Cintractia lidii* Liro and *T. junci* (Schröt.) Woron. *β. johansonii* Blytt on *Juncus bufonius* is *Urocystis johansonii* (Lgh.) Magnus. The genus *Glomosporium* (type: *T. leptideum* Sydow, in the seeds of *Chenopodium album* L.) was separated from the genus *Tolyposporium. Tolyposporium eriocauli* Clinton was recently transferred to the genus *Dermatosorus* (Whitehead & Thirumalachar 1972). Several species of *Tolyposporium* are Fungi Imperfecti e.g. *T. chloridis* P. Henn. (!), *T. pampeanum* Speg., *T. philippinense* H. & P. Sydow, *T. reticulatum* Speg. and *T. volkensii* P. Henn. (!).

Apart from the above-mentioned species, the genus *Tolyposporium* is still rather heterogeneous. However, there is a group of 4 or 5 species with common characteristics which are still quite different from the type of the genus (*T. junci* (Schröt.) Woron.). For this small group of fungi belonging to the family Ustilaginaceae, it proves necessary to set up a separate genus, for which I propose the name *Moesziomyces,* in honour of the Hungarian mycologist Gusztáv Moesz (1873–1946).

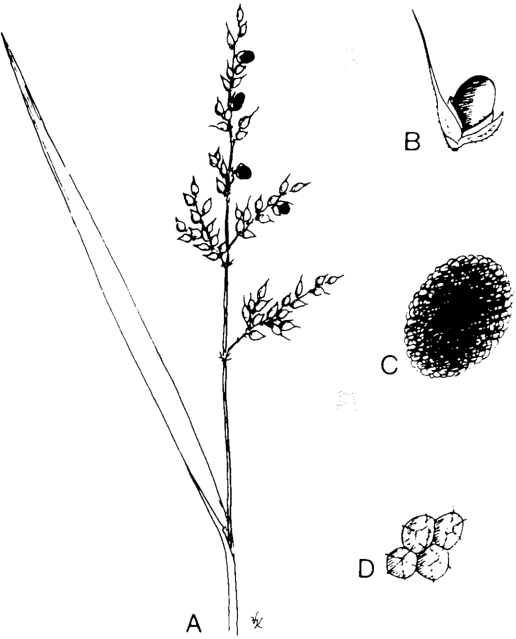

Fig. 3. *Moesziomyces bullatus* on *Echinochloa crus-galli.* – A: The host plant with the fungus sori, × 0.6. – B: One sorus in a spikelet, × 3. – C: Spore ball, × 140. – D: Spores, × 625.

Moesziomyces Vánky gen. nov.

Typus generis: *Moesziomyces bullatus* (Schröter) Vánky.

Sori ovariicoli, sine columella; sporae in glomerulis multisporis ornamentis superficialibus firme conjunctae, haec aspectu macularum irregularium reticuli vel, ad margines sporarum separatarum, alarum irregularium.

Sori in the ovaries, without columella. *Spores* in many-spored spore balls firmly agglutinated by surface ornaments appearing as irregular meshes, or at the margins as thin irregular wings when the spores are separated.

Moesziomyces bullatus (Schröter) Vánky comb. nov.

Sorosporium bullatum Schröt., Abh. Schles. Ges. Vaterl. Cultur, Abth. Naturw. Med. 1869–72: 6, 1869. – *Tolyposporium bullatum* (Schröt.) Schröt., Krypt. Fl. Schles. 3: 276, 1887. – *Type* on *Panicum crus-galli* L. (=*Echinochloa crus-galli* (L.) Beauv.), Germany, Silesia, near Liegnitz (at present Legnica in Poland), Sept. 1869, coll. Schneider, in Rbh. Fgi. eur. 1489 (!).

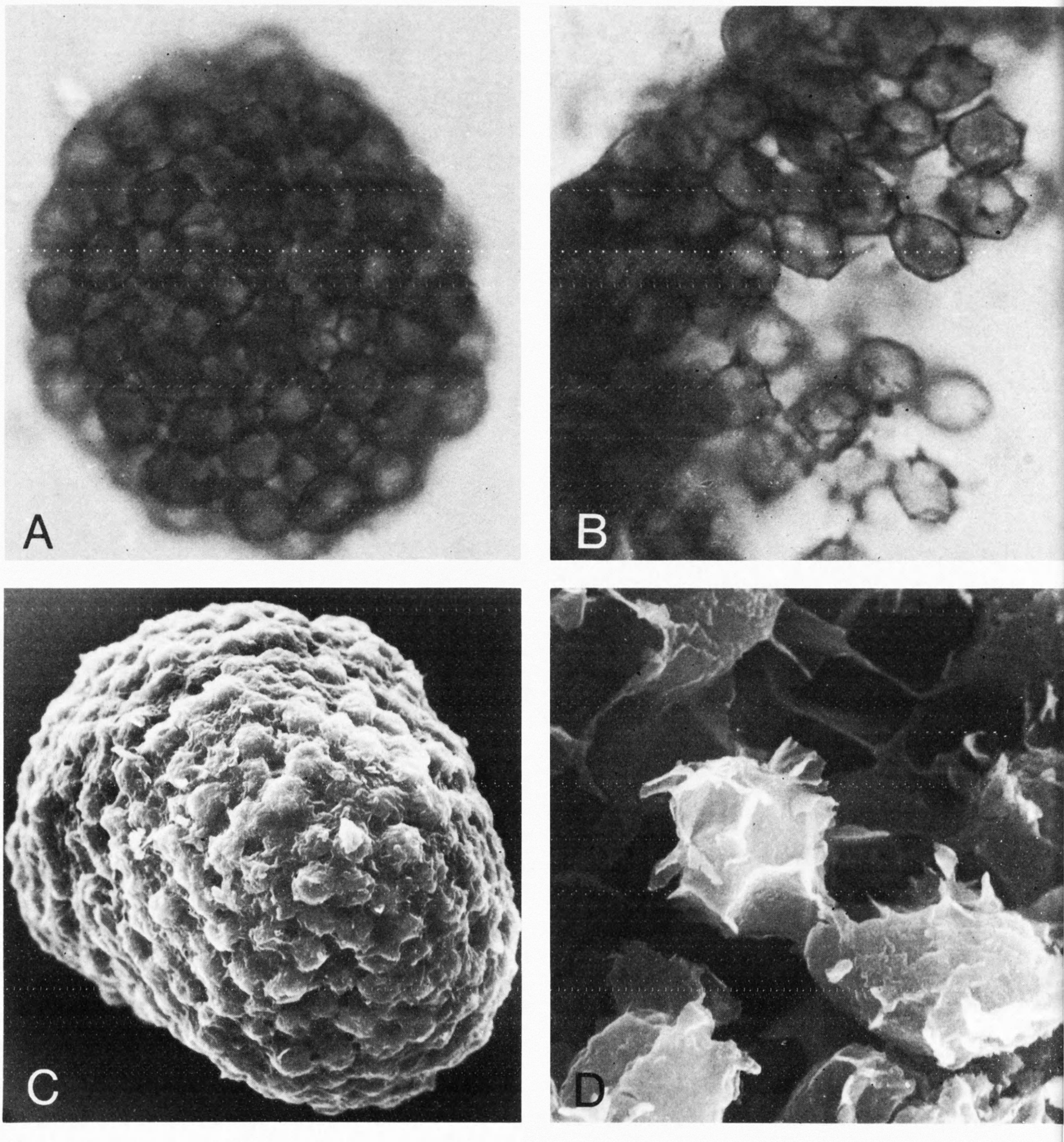

Fig. 4. *Moesziomyces bullatus*. – A: Young spore ball, LM × 1100. – B: Spores, LM × 1100. – C: Spore ball, SEM × 500. – D: Spores, SEM × 2450.

Sori in the ovaries (Fig. 3 A, B), usually infecting occasional ones, globose to ovoidal, 2.5–4 mm in length, covered by a smooth, first green, later brown membrane which ruptures irregularly disclosing a granular, black-brown spore mass composed of spore balls. The sori lack a columella and are often detached entirely. *Spore balls* (Figs. 3 C, 4 A, C) varying in shape and size, globose, subglobose, ovoidal, elongate to irregular, dark brown, opaque, 50–220 × 60–320 μm in diameter, composed of many (often several hundred), firmly agglutinated spores. *Spores* (Figs. 3D, 4B, D) globose, ovoidal to irregular, slightly polyhedral, 6.4–8(–8.8) × 7.2–10.4(–12) µm in diameter, semi-hyaline to light yellowish-brown, bound together by surface ornaments appearing as meshes, or at the margins as thin irregular wings, when the spores are separated (Fig. 4D). The immature spores are round, while the mature spores often become slightly polyhedral as a result of mutual pressure.

Distribution: on different species of *Echinochloa:* Asia, Europe and North America.

Moesziomyces evernius (H. Sydow) Vánky comb. nov.

Tolyposporium evernium H. Syd., Ann. Myc. 37: 443, 1939. – *Type* in the ovaries of *Paspalum distichum* L., Akalgarh, Punjab, W. Pakistan, coll. S. Ahmad (!).

Tolyposporium paspali Langdon, Papers Univ. Queensland, Dept. Biol. 2(9): 4, 1948. – *Type* in the ovaries of *Paspalum distichum* L., Enoggera Creek, Ashgrove, Brisbane, Queensland, Australia, 2.III. 1943, coll. R. F. N. Langdon (!).

Distribution: on *Paspalum distichum* L.: Asia (China, India, W. Pakistan), Australia.

Moesziomyces globuligerus (Berkeley & Broome) Vánky comb. nov.

Thecaphora globuligera Berk. & Br., Trans. Linn. Soc. Lond., Bot. II, 1: 407, 1880. – *Tolyposporium globuligerum* (Berk. & Br.) Ricker, Journ. Myc. 11: 112, 1905. – *Type* in the ovaries of *Leersia hexandra* Swartz, Brisbane River, Queensland, Australia.

Testicularia leersiae Cornu, Ann. Sci. Nat. Bot. VI. 15: 275, 1883. – *Ustilago leersiae* Durieu, in Cornu, Ann. Sci. Nat. Bot. VI. 15: 274, 1883. – *Type* in the ovaries of *Leersia hexandra* Swartz, Algeria, VIII. 1862, coll. M. Letourneaux.

Distribution: on *Leersia hexandra* Swartz: Africa (Algeria, Ivory Coast, Morocco, Nyasaland, Uganda), N. and S. America, Asia (India), Australia; on *L. japonica* Makino: Asia (China).

Moesziomyces penicillariae (Brefeld) Vánky comb. nov.

Tolyposporium penicillariae Bref., Unters. Gesammt. Mycol. 12: 154, 1895. – *Type* in the ovaries of *Penicillaria spicata* Willd., about Febr. 1891, coll. A. Barclay.

Tolyposporium senegalense Spegazzini, Ann. Museo Nac. Hist. Nat. 26: 118, 1914. – *Type* in the ovaries of *Penicillaria typhoidea* Fig. & De Not., W. Africa: Senegal, Dakar, XII. 1913, coll. C. Spegazzini.

Distribution: on *Pennisetum glaucum* (L.) R. Br. (= *P. americanum* (L.) Schum., = *P. typhoideum* L., = *Penicillaria typhoidea* Fig. & De Not., = *P. spicata* (L.) Willd.): Africa (common), S. Asia (India).

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Miscellaneous notes on algal taxonomy and nomenclature IV

Peter S. Dixon and Linda M. Irvine

Dixon, P. S. & Irvine, L. M. 1977 06 30: Miscellaneous notes on algal taxonomy and nomenclature IV. *Bot. Notiser 130:* 137–141. Stockholm. ISSN 0006-8195.

(1) The correct name for the North Atlantic species of *Furcellaria* is *F. lumbricalis* (Huds.) Lamour. (2) *Petrocelis cruenta* J. Ag. must be typified by material at LD, in Herb. Alg. Agardh. 27581. (3) *Rhodophyllis divaricata* (Stackh.) Papenf. must be typified by the original description of *Fucus bifidus* Huds., in the absence of material. (4) With regard to names applying to species of *Gelidium* it is shown that *G. corneum* var. *latifolium* must by typified by material collected at Sidmouth, now at E; that *Fucus pusillus* Stackh. must be typified, provisionally, by material at BM; that *Fucus crinalis* Turn. must be typified by material in BM-K; and that *Fucus corneus* var. *sesquipedalis* Clem. must be typified by material at LD, in Herb. Alg. Agardh. 32975. (5) *Scinaia turgida* Chemin must be typified by material at LD, in Herb. Alg. Agardh. 32180.

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The following notes refer to further taxonomic and nomenclatural problems detected during preliminary work for the first volume (Rhodophyta) of the forthcoming *Seaweeds of the British Isles* (Dixon & Irvine 1977).

The correct name for the North Atlantic species of Furcellaria

The genus *Furcellaria* was described by Lamouroux (1813 p. 45, reprint p. 25) and at the time he included two species, *F. lumbricalis* (based upon *Fucus lumbricalis* var. α Turn.) and *F. fastigiatus* (based upon *Fucus lumbricalis* var. β Turn.). The former species was selected as the lectotype of the genus *Furcellaria* by La Pylaie (1829 p. 66).

Lamouroux's reference is to Turner (1802 p. 317–320) where the latter distinguishes varieties α and β of *Fucus lumbricalis* having either 'lineari-lanceolate cylindrical binate pods, often an inch long' or 'apices very short, diaphanous, of an ovate, or ovato-lanceolate form, compressed, and of a pale-pink colour'. Later, Turner (1808 p. 11) calls these varieties α *lumbricalis* and β *fastigiatus*. From the accompanying illustrations, it is clear that the former represents tetrasporangial plants and the latter spermatangial plants of the species currently but erroneously known as *Furcellaria fastigiata* (L.) Lamour. Turner gives a number of references under his *F. lumbricalis* var. β but *Fucus fastigiatus* L. (1753 p. 1162) is not among them. In fact, in both 1802 (p. 309, p. 315) and 1808 (p. 9) Turner gives *F. fastigiatus* L. as the basionym of *Fucus rotundus* var. γ *fastigiatus* (L.) Turn. Although Linnaeus's plant was shown by Drew (1958 p. 750) also to be representative of the taxon under discussion, she comments that "those familiar only with the usual form found on the Atlantic shores might well be excused for being uncertain of its identity ... Waern ... considers the specimen now selected as the type (Pl. 62 a) to be 'like an old piece of *Furcellaria fastigiata*, which may be found dropped on the roads of Gotland', i.e. what is known in those parts as Kräkel. Comparison of the specimen of Pl. 62

and photographs of Baltic specimens of *F. fastigiata* given by Waern certainly support this statement." A combination based upon *Fucus fastigiatus* L. would however be a later homonym of *Furcellaria fastigiata* Lamour. Drew also investigated the application of the binomial *Fucus lumbricalis* Huds. (1762 p. 471). There is a specimen bearing this name in the Herbarium of the British Museum (Natural History) (BM) which appears to have belonged to Hudson and since Hudson changed the name later (1778 p. 589, *Fucus furcellatus*) it must be an early specimen if not the type. It is proposed to accept this specimen provisionally as having lectotype status. As shown by Drew, it is a typical plant of the species under consideration. Under *Fucus lumbricalis* var. α, Turner (1802) quotes a number of references including '*Fucus lumbricalis*' in Gmelin (1768 p. 108, t.6, f.2) and Goodenough & Woodward (1797 p. 204). Both of these works attribute the binomial to Hudson (1762 p. 471), so the combination becomes *F. lumbricalis* (Huds.) Lamour., the correct name for the taxon in the genus *Furcellaria*.

The typification of Petrocelis cruenta J. Agardh

The species *Petrocelis cruenta* was described by J. Agardh (1851 p. 490) without citing any specimens, but giving the habitat as 'ad oras Hiberniae, Angliae et Galliae'. The Irish record is evidently based on Harvey (1847 pl. 117, as '*Cruoria pellita*') and the English one upon Berkeley (1833 pl. 1, fig. 3, as '*Chaetophora pellita*'), both of which are quoted by J. Agardh, the latter with a query. In the Agardh Herbarium at Lund (LD) are two specimens, nos. 27580 and 27581, sent by the brothers Crouan from Brest, collected on 8th December 1849, which presumably provide the record for France. There is also a pencil sketch by J. Agardh apparently made from no. 27581, a mica preparation. This sketch shows the intercalary tetrasporangia with cruciately arranged tetraspores typical of the genus *Petrocelis* (first described by J. Agardh in the same publication) but not actually mentioned in the species description. Harvey, in his illustration, shows only undivided tetrasporangia and therefore it seems appropriate to select the Crouan specimen preserved on mica, Herb. Alg. Agardh. no. 27581, as the lectotype of *Petrocelis cruenta* J. Ag.

The typification of Fucus bifidus Huds.

Bifida divaricata Stackhouse (1809 p. 95, 97) is derived from *Fucus bifidus* Huds. (1778 p. 581) and shares the same type, as does *Rhodophyllis divaricata* (Stackh.) Papenf. (1950 p. 190) (*Rhodophyllis* Kützing (1847) has been conserved against *Bifida* Stackh.). Hudson's *Fucus bifidus* is a later homonym of *F. bifidus* S. G. Gmelin (1768 p. 201); the combination *Rhodophyllis bifida* must therefore be treated as a new name and attributed to Kützing (1847 p. 23). Papenfuss discussed the interpretation of the binomial *Fucus bifidus* Huds. and concluded that it is synonymous with *Rhodymenia palmetta* sensu Grev. (=*R. pseudopalmata* (Lamour.) Silva). The evidence for this assumption appears to be based on a statement by Turner (1809 p. 5) that Sir Thomas Frankland had sent him an original specimen of Hudson's, which Turner illustrates on Plate 73 (Fig. g). It is known, however, that Hudson's interpretations of his own 'species' changed a great deal over the years. In view of the information given by Frankland in an unpublished paper presented to the Linnean Society in June 1806 that his first correspondence with Hudson took place in 1782, when he sent specimens from Scarborough for identification, it seems likely that any specimens and comments passed to Frankland by Hudson represented the latter's later views. In fact, the wording of Hudson's original description: 'Fronds 1–1 1/2 inches, translucent, once and then immediately twice bifid, cuneiform or dilated towards the apex, flat, veinless, purple, diaphanous' would seem more closely to describe *Rhodophyllis divaricata* than *Rhodymenia pseudopalmata*. Further, the former species occurs not infrequently on the Hampshire coast (e.g. Southsea Castle), whilst the latter appears to be rare in the area. It seems reasonable, therefore, to accept Hudson's original description as the lectotype of *Fucus bifidus* and that it refers to the plant currently known as *Rhodophyllis divaricata*.

The typification of names applying to species of Gelidium

Identification of specimens of *Gelidium* has always been notoriously difficult, so much so that Bornet referred to it as "genre diabolique". The difficulties have been caused by the very great morphological plasticity shown by all entities growing under different environmental conditions and by uncertainties in the application of names caused by improper typification.

Sequential observations of marked plants have indicated that there are only three species in the British Isles – *G. latifolium* (Grev.) Born. & Thur., *G. pusillum* (Stackh.) Le Jol., and *G. sesquipedale* (Clem.)Thur. This represents a marked reduction from the number of species accepted in the most recent revision in Europe (Feldmann & Hamel 1936). The attribution of species, sensu Feldmann & Hamel, is as follows:

Present treatment	Feldmann & Hamel
Gelidium latifolium	*G. attenuatum* *G. latifolium*
Gelidium pusillum	*G. crinale* *G. pulchellum* *G. pusillum*
Gelidium sesquipedale	*G. sesquipedale*

In general, the axes of the *G. pusillum* aggregate are cylindrical although the tips may become somewhat spathulate during the winter months while those of the *G. latifolium* aggregate are predominantly flattened but becoming more terete during the winter months. Both *G. latifolium* and *G. pusillum* occur on the Atlantic coast of Europe from southern Norway to Gibraltar (although of limited occurrence in the North Sea) and also in the Mediterranean. *G. sesquipedale,* in comparison, is one of the few species of the genus with little variation of external form other than in size. It is of rare occurrence in Devon and Cornwall, extending to Mauritania and into the Mediterranean.

Despite the need for accurate typification in a genus where the taxonomy has become so confused, little has been achieved. Dawson (1953) made a few comments on those entities which occurred on the Pacific coast of North America while Segi (1963) attempted to typify many epithets in the genus. The work of Dawson is somewhat unreliable while the supposed typifications of Segi are largely meaningless.

The following comments are offered on the typification of entities relevant to the British flora.

Gelidium corneum var. **latifolium**

This variety was described by Greville (1830 p. 143) on the basis of material from 'Trevone Bay, Cornwall, and Waldon rocks, Torbay, Mrs. Griffiths. Sidmouth and Torquay'. The Greville collection in the herbarium of the Royal Botanic Garden, Edinburgh (E), contains one sheet apparently with material from both Waldon Rocks and Trevone Bay, a second sheet with several specimens from Trevone Bay and a further sheet with a single specimen from Sidmouth. Of these, the single specimen from Sidmouth best shows the characteristics of the taxon, as now understood, and this has been selected as lectotype. The variety was given specific status by Bornet & Thuret (1876).

Fucus pusillus Stackh.

The original treatment of *Fucus pusillus* by Stackhouse (1795 p. 16) was based on material collected at Sidmouth. Attempts at typification were made by Dawson and Segi: Dawson (1953 p. 62) states 'the whereabouts of the original material unknown to the writer'; the comments by Segi (1963) refer to specimens of no relevance to the typification of *F. pusillus* Stackh.

Material possibly relevant to the typification has been found in two herbaria.

(1) The British Museum (Natural History), London (BM), possesses one sheet apparently received directly from Stackhouse himself. This sheet, with two small clumps of material, is annotated '*Fucus pusillus* Ner. Brit.' in Stackhouse's hand and 'J. Stackhouse' on the reverse in the same hand. A second specimen received through the Skrimshire herbarium is annotated '*Fucus pusillus*. Stackh. Ner. Brit. 6. This was sent to me by D. Turner, who had it from Mr. Stackhouse – 1797', in Skrimshire's hand.

(2) The Lamouroux herbarium at the Laboratoire de Botanique, Caen (CN) contains a specimen annotated '*Fucus pusillus* Ner. Brit.', in Stackhouse's hand, filed in carton 19, folder 153.

The first specimen listed above has been accepted provisionally as lectotype of *F. pusillus* Stackh.

Fucus crinalis Turn.

The description of *Fucus crinalis* given by Turner (1819 p. 4) is based on various collections, which are cited as follows: 'On the English and Irish coasts. – Rocks in the sea at Sheringham in Norfolk. – At Sidmouth, growing on *F. abrotanifolius*. Mrs. Griffiths. – Near Ilfracombe. Mr. Hare. – Rocks at Kilmouth in Cornwall. Mr. Rashleigh. – At Brighton, forming large patches on the flat chalk-rocks about low water mark. Mr. Borrer. – Sides of Belfast Lough. Mr. Templeton'. In addition, Turner describes *β tricuspidatus*, based on material received from Mertens, originating on the French coast, to which Thore had applied the manuscript name '*Fucus tricuspidatus*'.

Turner was obviously uncertain as to the attribution of various entities now referable to the genus *Gelidium* since most specimens of that genus in his herbarium are inadequately labelled. This is in marked contrast to other genera, where specimens are fully labelled and, when used as the basis for an illustration, this is clearly stated.

The Kew algal collection, now at the British Museum (Natural History) contains the following material.

(1) A specimen labelled 'Sidmouth Nov 1807 Mrs. Griffiths', in Turner's hand.

(2) Several small clumps of material, associated with two labels, one annotated in Borrer's hand 'Fucus crinalis fr. Brighton July 1812'.

(3) Five specimens mounted on three small pieces of paper, two annotated 'Turner's Herb.', in Hooker's hand, and 'Gelidium crinale J. Ag.', in A. D. Cotton's hand. In addition, one is annotated in A. D. Cotton's hand: 'This is Turner's idea of *G. crinale* and may be taken as type f.[ide] WAS[etchell]'.

(4) Several specimens on small pieces of paper, associated with a label annotated 'From the sandpool Sidmouth around every side. The same as Mr. Stackhouse found small black tubercles scattered on the stem & leaves', in Mrs Griffiths's hand, with two other annotations, 'F. pusillus' and 'corneus var young', in unknown hands. In view of the statement by Turner that Mrs Griffiths's material was collected as an epiphyte on *F. abrotanifolius* and the uncertainty that the label refers to the material with which it is now associated, it would seem best to reject this material from consideration in the typification.

There have been various attempts to typify *Fucus crinalis*. Most accept the material from the Kew Herbarium which Setchell regarded as 'Turner's idea of *G. crinale*'. Setchell apparently removed a portion of this, as Gardner (1927 p. 277) refers to having 'examined a sterile fragment of the assumed type of *G. crinale* Turn., obtained from the Herbarium at Kew, England, by W. A. Setchell'. Dawson (1953 p. 64) comments that the type 'may be considered to be a specimen without locality data from the Turner Herbarium, now in Kew, England. It is annotated 'This is Turner's idea of *G. crinale* and may be taken as type. f. W.A.S.'; he also removed a fragment, now preserved in the Herbarium of the Allan Hancock Foundation, University of Southern California, Los Angeles (HAHF), as specimen 55234. The material Setchell, Gardner and Dawson were dealing with had at least passed through Turner's hands, even if it is of uncertain type status. Of the specimens Segi (1963 p. 514) comments on, however, none can be considered as type material of *Fucus crinalis* Turn.

Selection of the type locality has also posed problems. Turner states that his illustration was based on a specimen collected by Hare: 'to him I am indebted for the specimen here figured, as well as for the name now given to it'. Dawson uses this statement as an indication of the typification but then gives the type locality (Dawson 1953 p. 64) as 'rocks at Kilmouth, Cornwall, England'. This choice results from a misreading of the data presented by Turner due to the curious punctuation used by the latter. The Hare locality is, in fact, 'near Ilfracombe', the collection from Kilmouth, Cornwall having been made by 'Mr. Rashleigh'.

The specimen annotated by Setchell is probably the best choice which can be made at the present time, although the specimen should not be regarded as of higher status than provisional lectotype.

Fucus corneus var. **sesquipedalis** Clem.

This varietal epithet, the basionym of *Gelidium sesquipedale*, was applied by Clemente (1807 p. 317) to plants from Algeciras (Spain). The present location of Clemente's herbarium is unknown and there is every indication that it has been destroyed. There is material sent by Clemente to C. Agardh in the Agardh Herbarium at Lund (LD); a fragment sent by Clemente to Turner, which was present in the Kew Herbarium in 1958, cannot now be located in the material transferred to the British Museum (Natural History) (BM-K).

It would seem best to accept one of the Clemente specimens at Lund as being of provisional lectotype status; the most appropriate is Herb. Alg. Agardh. 32975.

The typification of Scinaia turgida Chemin

Setchell (1914) suggested that there were several species confused in Europe under the name *S. furcellata* (Turn.) J. Ag., now known as *S. forcellata* Biv. (see Dixon & Irvine 1977). Setchell's suggestion was taken up by Chemin (1926) who demonstrated that the entity known as *S. furcellata* var. *subcostata* J. Agardh differed markedly from *S. furcellata* var. *furcellata* in terms of structure, reproduction and spore germination. Chemin proposed that this variety be given specific status but used the epithet *turgida* on the grounds that it is more appropriate than *subcostata*. The later suggestion by Hamel (1930) that the epithet *subcostata* should be used is incorrect, since an epithet has no priority outside its rank.

S. turgida Chemin and *S. furcellata* var. *subcostata* J. Agardh share the same type i.e., the material collected in Tangier and now filed in the Agardh Herbarium, Lund (LD), as Herb. Alg. Agardh. 32180.

Acknowledgements. We are indebted to the Directors of the Botanical Museum, Lund, and the British Museum (Natural History) for permission to examine material; to Dr P. C. Silva and Mr R. Ross for assistance in the preparation of this paper and helpful comments.

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A new species of Crepis from Mt Olympus, Greece

Arne Strid

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Crepis pawlowskii sp. nov. is described from beech forest on Mt Olympus. It is related to *C. geracioides* Hausskn. and *C. viscidula* Froel.

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Crepis pawlowskii Strid sp. nov. – Fig. 1

Herba perennis, 50–70 cm alta, e rhizomate obliquo surgens. *Folia* caudicalia 7–17 × 2–4 cm magna, oblanceolata, petiolis brevibus, profunde runcinate pinnatifida vel lyrata. *Caulis* a basi unicus, erectus, in media planta et supra ramificatus, 3–15 capitulis terminatus, folio caulino unico deminuto ramum infimum fulgente, foliolis ad ramificationes superiores bracteaceis. *Pedunculi* tenues, 3–8 cm longi, ad apices versus non incrassati. *Capitula* erecta circiter 40-flora. *Involucrum* cylindricum, 11–13 × 5–8 mm magnum, glabrum, minute nigro-papillatum. Foveolae receptaculi plerumque ciliis marginatae. *Corolla* 16–20 mm longa, saturate flava; tubus pilis crispis praesertim supra vestitus. *Achenium* glabrum, ad apicem versus attenuatum, nullum tamen rostrum manifestum formans, 8–10 carinis crassis aliisque tenuioribus costatum. *Pappus* albus, 6–8 mm longus, biserialis, pilis basi 30 μm crassis.

Perennial, 50–70 cm high. *Rhizome* oblique, 15–30 × c. 8 mm, bearing many long, fleshy fibres c. 1 mm in diameter. *Caudical leaves* 6–8, ascending, 7–17 × 2–4 cm, oblanceolate, acute to subobtuse, gradually attenuate into a narrow winged petiole c. 1/5 as long as the blade; deeply runcinate-pinnatifid to lyrate, the terminal lobe large, hastate, the lateral lobes narrow, distinctly retrorse; pubescent below, especially on the mid-vein, with white, eglandular, rather short and coarse hairs, glabrescent above. *Stem* single, erect, terete, fistulose, striate, branched at the middle and above, 3–15-headed; sparsely pubescent below, glabrescent above; with a single, 3–7 cm long, linear, entire cauline leaf at the lowest branching, and very small, bract-like leaves at the upper branchings. *Peduncles* suberect, slender, 3–8 cm long, not thickened towards the apex, without or with 1–2 minute bracts, nearly glabrous except for a tuft of crispate hairs just below the head. *Heads* erect, rather large, about 40-flowered; involucre cylindrical, 11–13 × 5–8 mm. *Outer bracts* 6–8, 1/4–2/5 as long as the inner, ovate-lanceolate, acute, margin somewhat scarious and often finely lacerate towards the apex. *Inner bracts* 12–16, linear-lanceolate, acuminate, ciliate in the apical 2–3 mm. Both outer and inner bracts glabrous on both sides, but especially the inner densely covered with minute black papillae on the upper surface, and with a dorsal crest near the apex. *Receptacle* flat, alveolate; the pits without rim, usually fringed with thin, white, 0.5–0.8 mm long cilia. *Corolla* 16–20 mm long, bright yellow; ligule 2–3 mm wide, teeth c. 0.4 mm long, subacute, with a crest of papillae. Corolla-tube 5–7 mm long, crispate-hairy, especially above. *Anther* tube c. 4.5 × 0.8 mm; appendages very small, oblong, obtuse; filaments c. 2 mm long. *Style* branches c. 2 mm long, uniformly thick, obtuse, greenish, with erecto-patent scabridity. Mature *achenes* not seen; half-mature ones medium brown, glabrous, 5–6 mm long, attenuate towards the apex but not distinctly beaked, with 8–10 coarse and some finer ribs, calloused at base, with a slightly expanded pappus disk at

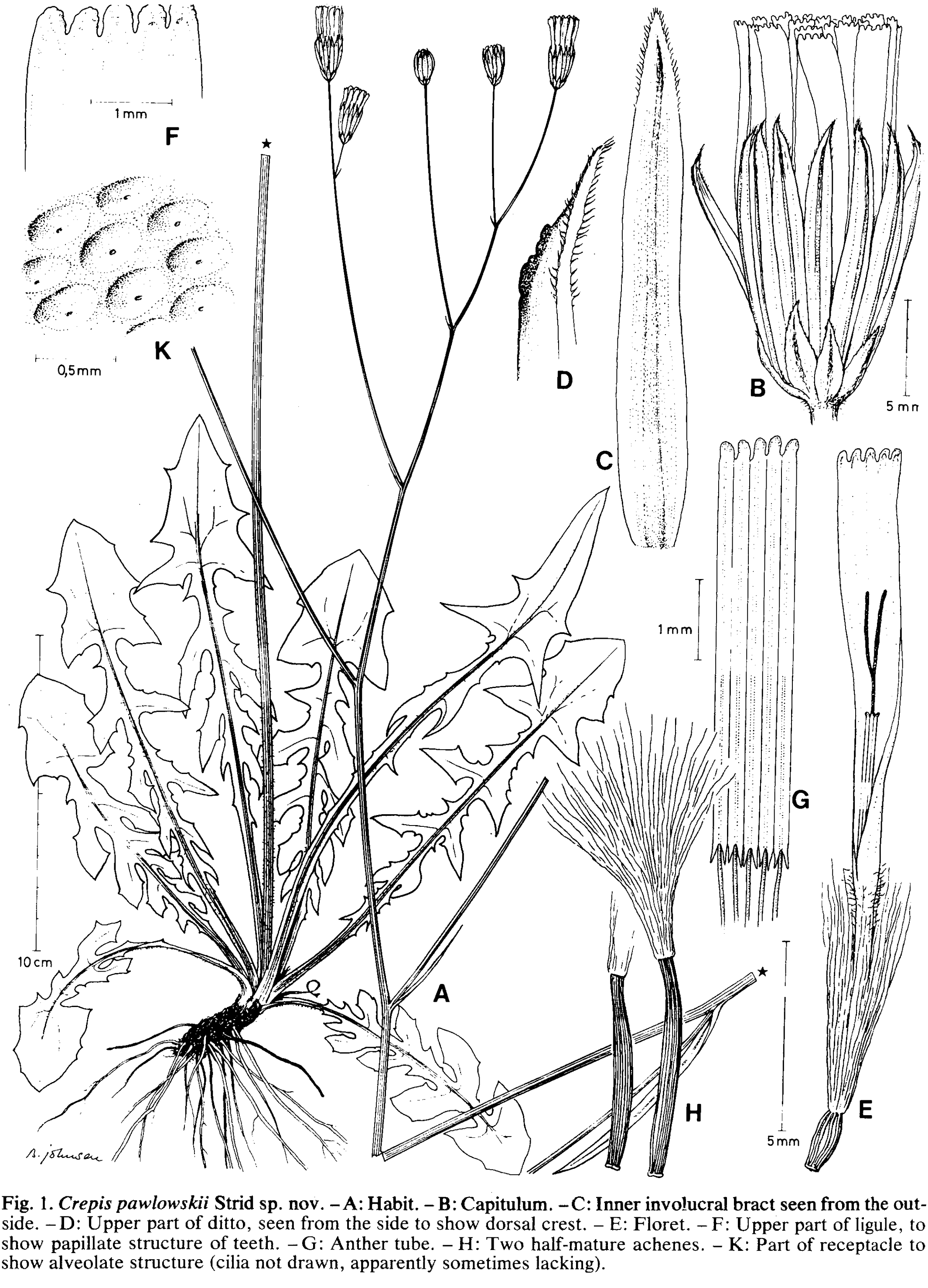

Fig. 1. ***Crepis pawlowskii*** **Strid sp. nov. – A: Habit. – B: Capitulum. – C: Inner involucral bract seen from the outside.** – D: Upper part of ditto, seen from the side to show dorsal crest. – E: Floret. – F: Upper part of ligule, to show papillate structure of teeth. – G: Anther tube. – H: Two half-mature achenes. – K: Part of receptacle to show alveolate structure (cilia not drawn, apparently sometimes lacking).

apex. *Pappus* white, 6–8 mm long, 2-seriate; pappus hairs c. 30 μm wide at the base.

Belonging to sect. *Desiphylion,* and apparently related to *C. geracioides* Hausskn. and *C. viscidula* Froel. (cf. Babcock, Univ. Calif. Publ. Bot. 22: 226–232, 1947), but distinct on account of its very reduced cauline leaves, slender peduncles which are not thickened towards the apex, glabrous involucre, often ciliate receptacular pits, and thinner pappus hairs.

The specific epithet commemorates the distinguished Polish botanist Professor B. Pawlowski who lost his life in a climbing accident on Mt Olympus in 1971.

Orig. coll. Greece, Thessaly, Mt Olympus: NW part, 8.2 km from the village of Petra along forest road to Kokkinoplos, 860 m, at the point where the road crosses lower part of Xerolakki Rema. *Fagus* forest in ravine. Strid & Kjellsson 11161, 4.6. 1976 (ATH holotype, C, LD isotypes). The species is only known from this gathering.

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Chrysochromulina pyramidosa sp. nov. (Prymnesiophyceae) from Danish coastal waters

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Thomsen, H. A. 1977 06 30: Chrysochromulina pyramidosa sp. nov. (Prymnesiophyceae) from Danish coastal waters. *Bot. Notiser 130:* 147–153. Stockholm. ISSN 0006-8195.

Chrysochromulina pyramidosa sp. nov. is described on the basis of electron microscopy of shadowcast whole mounts, prepared from water samples collected in October 1975 at two localities in the Storebælt (Denmark). The saddle-shaped cell possesses two smooth flagella and a short haptonema. The cell surface is covered with scales of two types. The underlying scales are circular, flat, wide-meshed plates, whereas the outer scales have a pyramidal superstructure on an otherwise similar base-plate.

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The genus *Chrysochromulina* was established by Lackey (1939) to comprise a "three-flagellated", golden-brown organism observed in the Scioto river system of Ohio, U.S.A. Lackey (1939) stated that one flagellum was directed forwards; this one was heavier than the two others and was held rigid when the organism was at rest. The two other flagella were posteriorly directed and thinner, and when the cell rested, they were often kept undulating. The locomotory difference noted by Lackey was later ultrastructurally substantiated. Parke et al. (1955, 1962) showed that the anterior flagellum (haptonema in Parke et al. 1955) had a fine structure different from that of usual flagella. Christensen (1962) established a separate class – Haptophyceae – for this and related genera previously placed in the Chrysophyceae. Because of recent recommendations in the International Code of Botanical Nomenclature, Hibberd (1976) proposed that the name Haptophyceae should be replaced by the name Prymnesiophyceae.

Including the new taxon to be described below, there are now 29 named species of *Chrysochromulina,* 28 of which are brackish/marine. Only the generic type species *C. parva* Lackey thrives in freshwater. Leadbeater (1972) listed 22 species; the increase in number is due to the following species: *C. pontica* Rouchijainen (1966), *C. orbiculata* Rouchijainen (1972), *C. campanulifera* Manton & Leadbeater (1974), *C. adriatica* Leadbeater (1974), *C. birgeri* Hällfors & Niemi (1974), *C. spinifera* (Fournier) Pienaar & Norris (1976), and *C. pyramidosa* sp. nov.

Records of *Chrysochromulina* species from Danish waters are rather sparse, at least regarding the number of localities involved. *C. parva* has been recorded from the freshwater lake Haarupsande (Kristiansen 1971) and from the oligohaline lake Selsø (Wøldike 1973). Manton & Leadbeater (1974) reported 19 marine *Chrysochromulina* species from the east coast of North Jutland, five of them also from the west coast. Apart from these findings, a previously unpublished find of *C. ericina* Parke & Manton from the Kattegat bay Isefjorden (District Ks) is included in the check-list of Danish marine algae by Christensen & Thomsen (1974).

Investigations on marine nanoplankton flagellates from the Baltic, the Danish Sounds, and the Kattegat carried out during 1975/76 have provided new information on the occurrence of known *Chrysochromulina* species, and in addition have uncovered some apparently undescribed species.

The present paper deals with the description of *C. pyramidosa* sp. nov.

Chrysochromulina pyramidosa Thomsen sp. nov.

Cellula ephippioides, 3 μm longa, 4 μm lata; flagella bina 10–13 μm longa, haptonema 5–6 μm longum. Squamae dimorphae, aliis e laminis solum constitutis, aliis e laminis et machinis superimpositis. Squama prioris gregis orbicularis, circiter 0.7 μm diam., 24 costis radiantibus et 7–8 anularibus concentricis fere aequidistantibus ornata, costa anulari marginali aliis crassiore. Squama alterius gregis e lamina illius satis simili, 0.8–0.9 μm diam., 27–28 costis radiantibus et 8–9 anularibus ornata, anularibus interioribus aequidistantibus, marginali crassiore a vicina distantiore, et quattuor trabeculis crassis e margine laminae surgentibus machinam pyramidiformem super illam formantibus constituta.

In aqua subsalsa lecta salinitatis 14 ‰ temperaturae 11.5 graduum Celsii die 21 Oct. anni 1975 prope Asnæs e freto danico Storebælt hausta, figura 1 A typifica monstrata.

Cell saddle-shaped, 3 μm long × 4 μm wide; two flagella 10–13 μm long, and a haptonema 5–6 μm long. Scales of two types. Some are plate-like, circular, approximately 0.7 μm in diameter, with a pattern of radiating ridges (24 in number), and 7–8 nearly equidistant concentric rings, the ring at the edge being thicker than the others. The second type of scales have a plate-like base which is constructed in a similar way with a diameter 0.8–0.9 μm, 27–28 radiating ridges, and 8–9 concentric rings. The innermost rings are equidistant, the distance between the outermost thicker ring and the next ring somewhat greater. From the margin of the plate four thick struts branch off creating a pyramidal superstructure.

Found on October 21st 1975, in sea water samples from Asnæs, the Storebælt, Denmark. Salinity 14‰, temperature 11.5°C. Holotype Fig. 1 A.

Material and methods

The sub-surface water samples used for this investigation were collected in October 1975, at two localities in the Storebælt (Asnæs (55° 38.5′ N, 10° 46.5′ E) and Spodsbjerg (54° 56′ N, 10° 53′ E)), Denmark. The preparation of the whole mounts for electron microscopy took place on board the oceanographic vessel "Martin Knudsen".

The water samples were collected by means of a 5 l water bottle and immediately filtered through a 20 μm net in order to remove the larger organisms. The resulting nanoplankton suspension was concentrated by gentle centrifugation. Whole mounts were prepared by transferring small drops of the resuspended pellet of material onto carbon/formvar coated grids. Fixation was made in osmic vapour. After complete drying, the grids were washed for c. 10 min. in redistilled water in order to remove salt crystals. When completely dry, the grids were stored in gelatine capsules. The subsequent handling of the grids took place at the Institut for Sporeplanter, University of Copenhagen. Grids were shadowcasted with gold/palladium, and examined in a JEM-T8 electron microscope at the Institut for Sporeplanter.

Observations

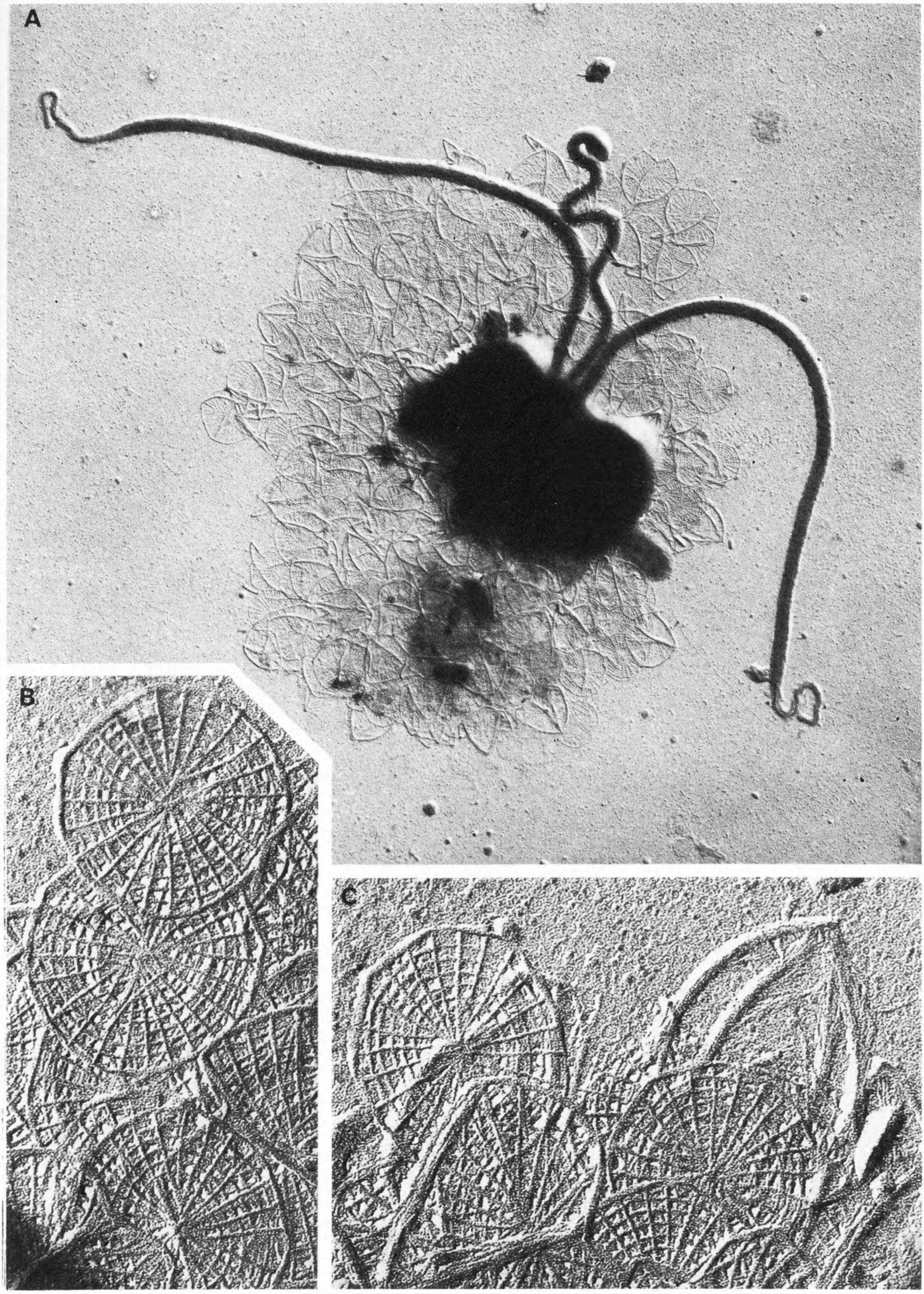
Chrysochromulina pyramidosa occurred in small numbers in the samples. The description of the external morphology is based on electron microscopical evidence only. Light microscopical information is not an absolute necessity for the description of a *Chrysochromulina* species. This is due to the fact that the by far most important specific characteristic within this genus is the scale structure, which can only be clarified by means of the electron microscope. In considering measurements of body size as well as length of flagella and haptonema, allowance must be made for shrinkage during processing of the cells for whole mounts.

The haptonema of *C. pyramidosa* measures 5–6 μm, which is about twice the body length and approximately half the length of the flagella (Fig. 1 A). The two flagella, which both end in a hairpoint (Fig. 1 A), differ slightly in length. The cell proper is saddle-shaped, with the flagella and the haptonema inserted in the apical depression (Fig. 1 A).

Two types of scales cover the cell body. The inner layer consists of circular, plate-like scales, approximately 0.7 μm in diameter (Fig. 1 B, C). These scales show a loosely woven pattern of radiating ridges (24) and 7–8 approximately equidistant concentric rings. The dorsal and ventral surfaces of these scales are virtually indistinguishable. All the ridges that form the scale are of equal thickness, with the exception of the outermost ring which is conspicuously thicker (Fig. 1 B).

The outer layer consists of more elaborate

Fig. 1. *Chrysochromulina pyramidosa* from Denmark. – A: Whole cell showing scales, a haptonema, and two flagella. Micrograph T 1075, × 9000. – B: Plate-like inner scales. Note thickened margins. Micrograph T 1530, × 50000. – C: Mixture of scale types. Inner plate-like scale to the left. Pyramidal superstructure of scale from the outer layer to the right. Micrograph T 1530, × 50000.


A
B
C

scales, made up of a subtending circular flat base plate, and a superstructure composed of four converging struts (Fig. 2A–C). The plate-like base, which in many respects is similar to the inner scale type described above, is 0.8–0.9 μm in diameter, and is formed by 27–28 radiating ridges and 8–9 concentric rings. The innermost rings are equidistant, whereas the distance between the outermost two rings is considerably greater (Fig. 2B, arrows). The outermost ring as well as the four struts that form a pyramidal structure (Figs. 1C, 2C) are thicker than the remainder of the meshwork.

Fig. 2A, C (arrowheads) shows some additional scale material between the four struts, apparently running from one strut to a point above the centre of the scale and back again to the neighbouring strut. A transverse section of the pyramidal superstructure thus presents itself as two right triangles joined together to form a cross. From Fig. 2B it appears, however, that this extra material is not always present.

Fig. 2D, E was kindly supplied by Professor I. Manton. They show some very similar scales from a water sample collected off the South African coast (November 13, 1972; 4 miles NW of Hout Bay Neck near Cape Town; 33° 57.6 S, 18° 16.9 E; 33 ft. depth, water temperature 12°C). The differences between the Danish and the African material are marginal. The simple plate-like inner scales of the latter are slightly larger (approximately 0.8 μm versus 0.7 μm) and have 9–11 concentric rings versus 7–8; otherwise they appear identical. The pyramidal scales seem to agree completely with those found in the Danish material. The interconnecting material between the four struts found on some of the pyramidal scales from the Danish material is apparently lacking in the equivalent South African scales.

In spite of minor differences the Danish and the South African material seem to represent the same species, suggesting that *C. pyramidosa* has a worldwide distribution.

Discussion

The presence of a haptonema and two flagella, the dimorphism of scales, and the structure of the apparently unmineralised scales together justify the inclusion of *C. pyramidosa* in the genus *Chrysochromulina*.

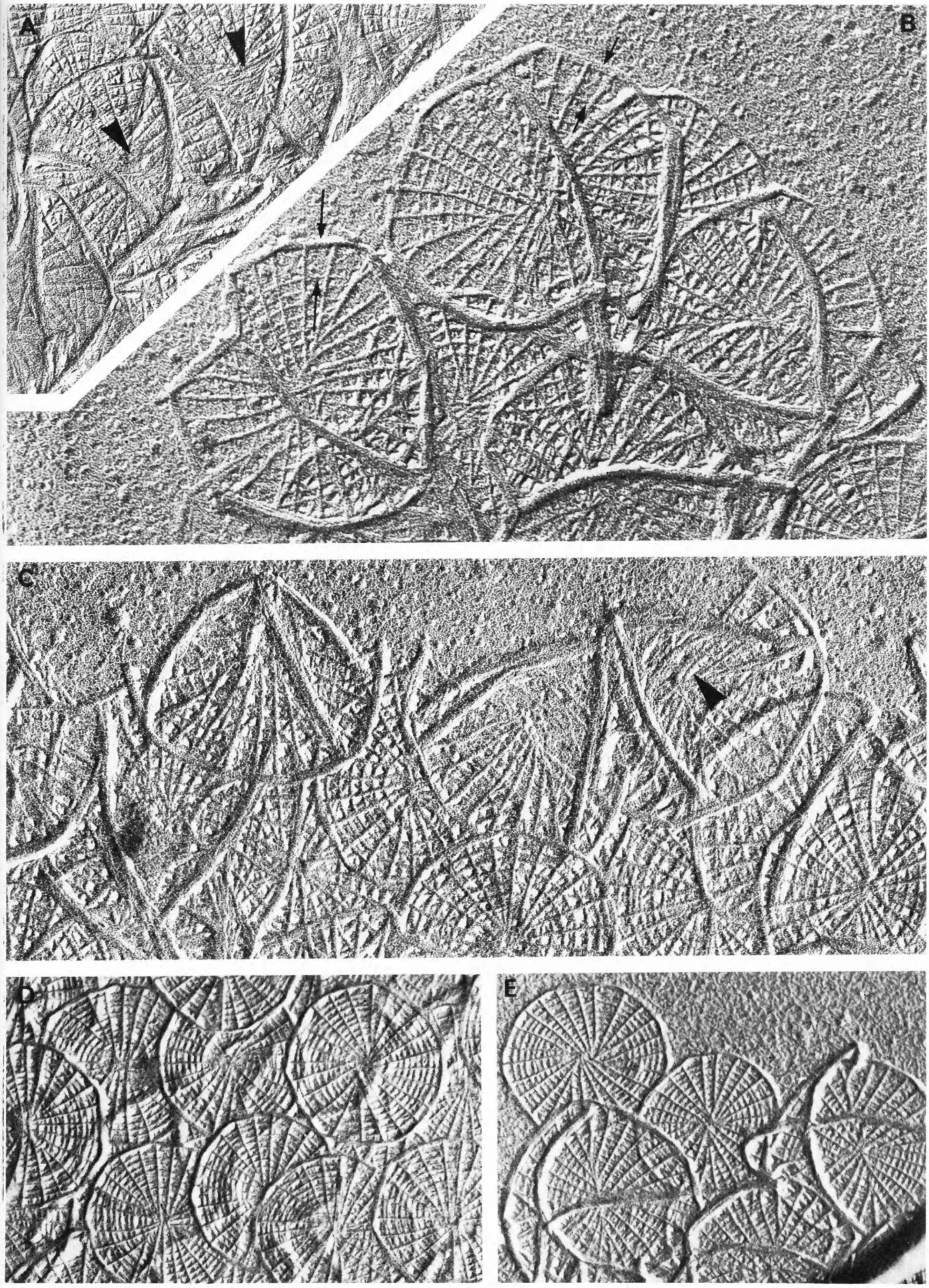
Scale structure alone is sufficient to distinguish *C. pyramidosa* from other species of the genus when observed in the electron microscope. The shape and size of the cell body and the length of the haptonema relative to the length of the flagella can be used for preliminary light microscopical determination. With regard to these characters, however, *C. pyramidosa* resembles *C. fragilis* Leadbeater (1972), *C. minor* Parke & Manton in Parke et al. (1955), and in particular *C. adriatica* Leadbeater (1974).

The pattern of ridges on the plate-like inner scales as well as on the subtending plates of the outer pyramidal scales is similar to that of *C. acantha* Leadbeater & Manton (1971), *C. parva* Lackey (1939) (Parke, Lund & Manton 1962), and *C. adriatica* Leadbeater (1974). The common feature is the sparse woven pattern dominated by delicate radiating ridges equally visible on both surfaces. The entire construction of the outer scales of *C. pyramidosa* also has a certain resemblance to that of *C. acantha*, the superstructure in both cases consisting of four struts. In *C. acantha* the struts support a central spine, whereas in *C. pyramidosa* they make up a pyramidal structure. A central spine supported by four struts is known from several other species of *Chrysochromulina*. In these species, however, the pattern on the lower part of the scale differs substantially from that found in *C. pyramidosa*.

The scale structures of *C. pontica* Rouchijainen (1966), *C. orbiculata* Rouchijainen (1972) and *C. birgeri* Hällfors & Niemi (1974) remain to be characterized on the basis of electron microscopy.

The haptonema of *C. pontica* measures up to

Fig. 2 A–C: *Chrysochromulina pyramidosa* from Denmark. – A: Scales from the outer layer. Arrowheads indicate the connecting scale material between struts. Micrograph T 1536, × 40000. – B: Scales from the outer layer. The arrows demarcate the gap between the two outer rings. Note the thickness of the outer ring and the struts as opposed to the remainder of the meshwork. Micrograph T 1534, × 50000. – C: Scatter of scales from both layers. The three scales from the outer layer at the top of the figure clearly show the pyramidal form. Arrowhead indicates scale material between struts. Micrograph T 1532, × 50000. – D, E: *Chrysochromulina pyramidosa* from the coast of South Africa (courtesy of Prof. I. Manton). – D: Scales from the inner layer. × 30000. – E: Pyramidal scales from the outer layer. × 30000.


A
B
C
D
E

70 μm, which definitely rules out any possibility of conspecificity between this species and *C. pyramidosa*.

C. birgeri has not only a quite different shape, but is also considerably larger than *C. pyramidosa*. A forthcoming paper will demonstrate important differences also on the electron microscopical level.

C. orbiculata may be conspecific with *C. minor* Parke & Manton in Parke et al. (1955), *C. fragilis* Leadbeater (1972), *C. adriatica* Leadbeater (1974), or *C. pyramidosa* sp. nov., the description by Rouchijainen (1972) being too little detailed to ensure positive identification. If future investigations demonstrate the presence of *C. pyramidosa* in the Black Sea, which is the type locality of *C. orbiculata*, one may claim that *C. pyramidosa* (described on the basis of electron microscopy only) and *C. orbiculata* (described on the basis of light microscopy only) are conspecific. With regard to *C. adriatica* the situation is the same. From a biogeographical point of view it seems probable that at any rate this latter species may well occur in the Black Sea (type locality: Kastel Bay, Adriatic Sea (Leadbeater 1974); also found in the Gulf of Elat, Red Sea (Thomsen 1977)). In both cases the specific epithet *orbiculata* takes priority.

If either *C. minor* or *C. fragilis* occurs in the Black Sea, *C. orbiculata* may be quoted as synonym to one of these (the specific epithets *minor* and *fragilis* take priority).

As pointed out by Black (1968) a significant parallelism exists between calcified and uncalcified members of the Prymnesiophyceae. A comparison of the scale structure in *Chrysochromulina* with that of a number of coccolithophorid genera clearly demonstrates that the calcified and the uncalcified genera do not represent two separate evolutionary lines (see Manton et al. 1975, 1976, 1977). The new species here described provides a remarkable example to this general observation. The pattern on the inner and the outer scales of *C. pyramidosa* shows obvious similarities with that on the scales and unmineralized coccoliths of the coccolithophorid *Wigwamma arctica* Manton in Manton et al. (1977), the main difference being a matter of degrees of symmetry. In both species four struts attach themselves to the thickened rim of the basal plate of some of the scales, converging above the plate to form a pyramidal, or tent-like, superstructure.

On account of the obvious similarities between *C. pyramidosa* and *W. arctica* it is quite likely that these two species are phylogenetically more closely related than e. g. *C. pyramidosa* and *C. campanulifera* Manton & Leadbeater (1974).

Continued investigations of marine nanoplankton will undoubtedly result in the demonstration of many more examples of evolutionary affinity between coccolithophorids and species of *Chrysochromulina*. Pending such observations and cultural experiments on some of the organisms, however, it is probably most convenient to maintain the traditional classificatory principle of keeping mineralized and unmineralized genera in separate families.

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A new genus of the Compositae from North Africa

Christopher John Humphries

Humphries, C. J. 1977 06 30: A new genus of the Compositae from North Africa. *Bot. Notiser 130:* 155–161. Stockholm. ISSN 0006-8195.

The new, monotypic North African genus *Heliocauta* is formally published and its relationship to other genera of the *Anthemis* complex is discussed.

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On the basis of a detailed morphological and anatomical study it is possible to show that *Anacyclus*, like several other currently recognised genera of the *Anthemis* complex is a paraphyletic assemblage. The affinities of the curious mat-forming alpine species named by Litardière & Maire (1924) as *Anacyclus atlanticus* were brought into question in a revision of the genus (Humphries in prep.) as the capitulum, floret and cypsela differ in most respects from those of the type species and its close allies. In this species there are also several character states which are not shared by other genera of the Anthemideae. Thus, it is placed into a new genus, *Heliocauta*, described below, and the reasons for its separation from *Anacyclus* are discussed.

Heliocauta Humphries gen. nov. – Figs. 1, 2

Herbae perennes humiles; caudex brevis, praemorsus. *Folia* basalia, rosulata, triternatisecta, segmentis ultimis brevibus linearibus. *Pedunculi* simplices, monocephali ex axillis foliorum orti. *Capitula* hemisphaerica, parva (7–11 mm diametro) homogama, discoidea, flosculis hermaphroditis fertilibus; receptaculum conicum paleaceum. *Anthodii phyllaria* (involucri bracteae seu squamae) triangularia vel oblongo-lanceolata, dorso viridia, margine scariosa fusco apice versus plusminusve erosa. *Receptaculi phyllaria* (paleae) oblongo-linearia, carinata hyalina, scariosa apicibus obtusis serrulatis. *Flosculi* regulares hypocrateriformes; minuti (2.5–3.2 mm longi) lobis limbi parvis patentibus triangularibus apicibus fere cucullatis. *Antherae* basi obtusae; filamenta infra antherum tumida. *Stylus* teres, glaber, nectario conspicue lobato basi cinctus, ramis 2 brevibus divaricatis anguste oblongis apice paulo penicillatis. *Cypselae* anguste obcuneatae, leviter dorsoventraliter compressae, costis lateralibus 2, costis intermediis utrinque 1–3 obscuris apice truncatae; pappus coroniformis, minutus.

Typus: *Heliocauta atlantica* (Litard. & Maire) Humphries. Nomen ex *ηελιοκαυτεω* oritur, ob capitulorum aspectum adustum.

Perennial creeping herb; stems short, reduced to a praemorse caudex. *Leaves* in a basal rosette, tripinnatisect, with tiny, linear, ultimate lobes; primary lobes in 3–6 opposite or subopposite pairs; rhachis flat or slightly canaliculate, narrowly triangular in outline, with a broad, hyaline, winged, sheathing base and 4–6 distinct veins. *Peduncles* simple, monocephalous, emerging from the leaf axils. *Capitulum* hemispherical, small (7–11 mm in diameter), homogamous, discoid with fertile, hermaphrodite florets; receptacle conical, paleaceous. *Phyllaries* in 3 rows, triangular to oblong-lanceolate, green on the dorsal surface, the margins scarious, brown at the apex, ± erose. *Receptacular scales* oblong-linear, carinate, hyaline scarious, the apex obtuse, serrulate. *Florets* regular, hypocrateriform, minute (2.5–3.2 mm long), the lobes patent, triangular in shape, with a somewhat cucullate apex. *Anthers* obtuse at the base, the filaments distinctly enlarged at the collar. *Style* terete, slightly swollen at the base, set in a conspicuous lobed nectary; style branches short, about the same thickness or slightly thicker than the shaft, truncate-penicillate at the tips. *Cypselas* narrowly obcuneate, terete to slightly dorsally-ventrally compressed with 2 distinct, vascularized lateral ribs and 1–3 obscure dorsiventral ribs; truncate, dark-brown or grey-black due to a dense tannin layer in the testa; the scalariform, thickened epicarp is invested, here and there, with linear series of dark-brown resin cells; pappus a minute, erose corona. *Cotyledons* anteriorly-dorsally orientated.

Heliocauta atlantica (Litard. & Maire) Humphries comb. nov.

Basionym: *Anacyclus atlanticus* Litard. & Maire, Mem. Soc. Sci. Nat. Maroc 4 (1): 13 (1924).

Caudex 2–4 mm crassus, interdum stolones emittens. *Folia* ambitu oblongo-lanceolata, 3–8 × 1–2.5 cm, plusminusve glabra ad villosa. *Pedunculi* decumbentes, 3.5–15 cm longi, apicem versus parce villosi sed sub capitulo dense pubescentes. *Capitula* 7–11 mm diametro. *Anthodii phyllaria* circa 2 mm longa. *Flosculi* primo pallide flavis demum brunnescentibus, tubo 2.5–3.2 mm longi, lobis 0.1–0.3 mm longi. *Antherae* 1–1.5 mm longae. *Cypselae* 1.5–2 mm longae, fere 1 mm latae.

Stems 2–4 mm thick, occasionally producing stolons. *Leaves* oblong-lanceolate in outline, 3–8 × 1–2.5 cm, ± glabrous to densely villous. *Peduncles* decumbent, 3.5–15 cm long, sparsely to densely pubescent below the capitulum. *Capitula* 7–11 mm in diameter. *Phyllaries* c. 2 mm long. *Floret tubes* 2.5–3.2 mm long, lobes 0.1–0.3 mm long. *Anthers* 1–1.5 mm long at anthesis. *Cypselas* 1.5–2 mm long and up to 1 mm wide.

var. **atlantica**

Anacyclus atlanticus var. *eu-atlanticus* Maire in Jahandiez & Maire, Cat. Pl. Maroc 3: 767 (1934).

A variety from the Atlas mountains occurring on granitic or porphyritic rocks between 2900 and 3600 m.

Specimens seen: Grand Atlas, Reraya: rocailles porphyriques terreuses au Tizi-n-Tagherat 3300–3600 m, 22.7.1922, Maire (MPU holotype, P, LD, S isotypes) – Great Atlas mountains, Refuge Neltner, Djebel Toubkal, 3200 m, Polunin 2155 (BM); same locality, granite gravel and scree nr. stream, Newbould 490 (BM); same locality, 9600 ft., pastureland on granite bedrock, 9.7.1966, Lambert 119 (BM); same locality, 22.7.1976, C. J. & A. R. Humphries 101 (BM); same locality, 3500 m, 20.8.1951 Rauh 299 (M); same locality, 3600 m, 2.8.1951, Schoffer (M); same locality, 1933, Stodieck (M); Jbel Toubkal, nr. stream, 11,000 ft., 14.9.1955, Newbould 403 (BM) – Refuge d'Hangaye, vers 3000 m, Grand Atlas Central, 31.7.1938 in herb. Maire (MPU).

var. **dasyphylla** Humphries

Anacyclus atlanticus var. *vestitus* Humbert ex Jahandiez & Maire, Cat. Pl. Maroc 3: 768 (1934), nom. nud.

Varietas rara maroccana in montibus Grand Atlas (in parte orientali) et Moyen Atlas inter 2800 et 3500 m supra mare crescens, a var. *atlantica* indumento foliorum pilis densis simplicibus distinguenda.

An extremely rare variety from the eastern High Atlas and the Middle Atlas mountains occurring between 2800 and 3500 metres, distinguished from the type variety by its dense indumentum of simple hairs on the leaves.

Specimens seen: Grand Atlas, Ari Ayachi, Humbert (AL holotype, RAB); same locality, Sindsiert, 3600 m, Schmittfluren, 17.9.1953, Rauh 754 (M) – Middle Atlas, Chaine du Bou Iblane, 2800–3200 m, Emberger & Maire (AL, RAB) – Mont Bou Nacer, 3000 m, Emberger (AL, RAB).

Distribution and habitat

H. atlantica is known exclusively from wet, cold montane pastures in the Middle and High Atlas mountains, where it has only been found in 4 locations (Fig. 2), all of which are over 2900 m.

Cytology

Twenty-two plants of var. *atlantica* collected during August 1976 (C. J. & A. R. Humphries 101) from Jbel Toubkal (High Atlas) were cultivated at the Chelsea Physic Garden. After pre-treatment overnight in a saturated solution of paradichlorobenzene root-tips were stained in Feulgen and squashed in 45% acetic acid. Fresh buds were squashed directly in aceto-orcein.

The chromosome number, reported here for the first time, was found to be $2n = 18$, the most common number for diploids in the Anthemideae. There are nine pairs of meta- and submetacentric chromosomes, two pairs of which have satellites on their shorter arms. Meiosis was normal with 9 pairs of bivalents at metaphase I.

Taxonomic remarks

This interesting taxon was originally described by Litardière & Maire (1924) from material col-

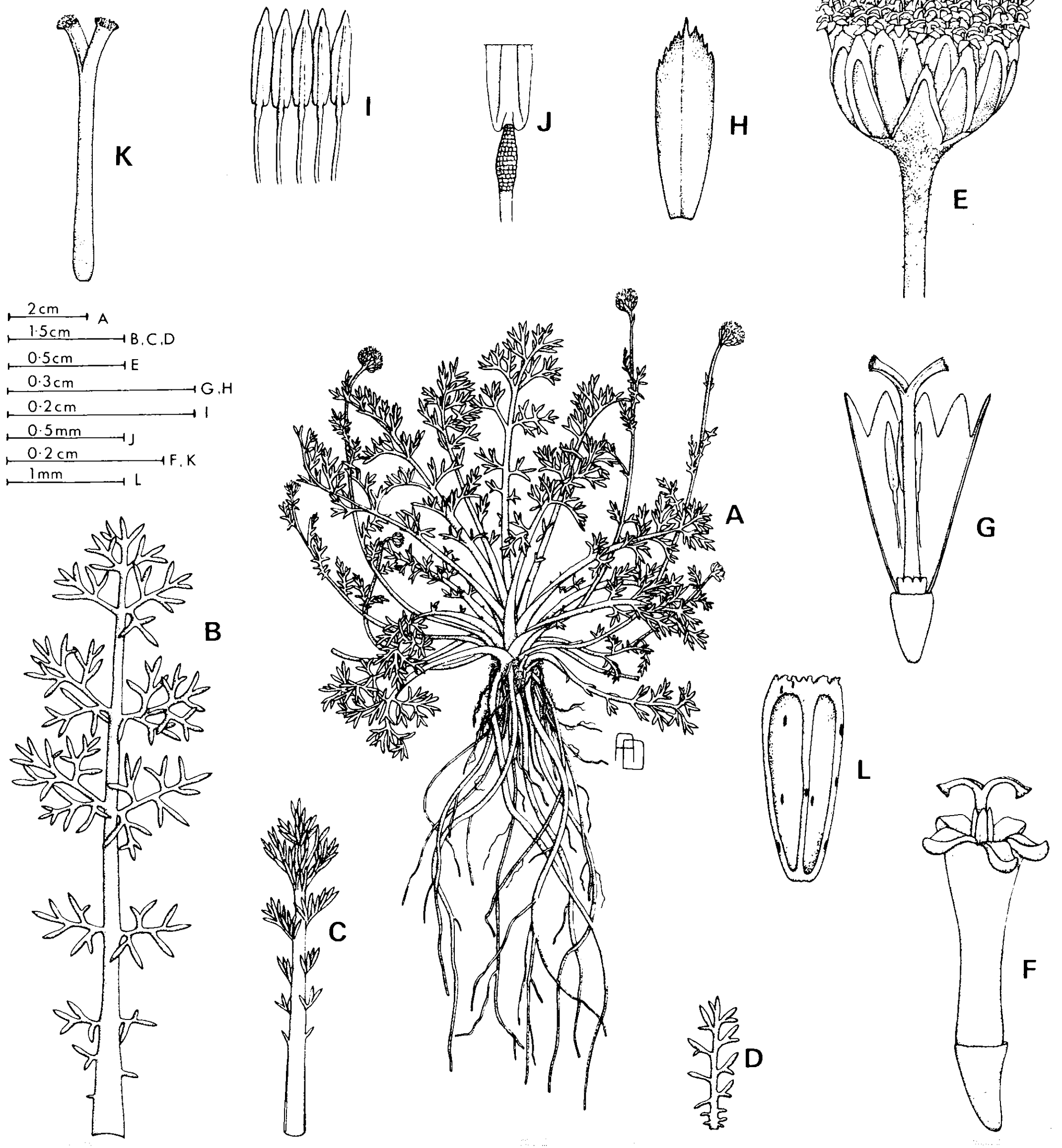

Fig. 1. *Heliocauta atlantica.* Based on live material (C. J. & A. R. Humphries 101). – A: Habit. – B: Mature leaf. – C: Young leaf. – D: Stem bract. – E: Flowering capitulum. – F: Floret at anthesis. – G: Dissected floret at anthesis. – H: Receptacular scale. – I: Anthers. – J: Filament collar and anther base. – K: Stigma. – L: Mature cypsela, anterior view.

lected in the High Atlas mountains: "In ditionis Ourika jugo Tachdirt (Maire 1921. nondum florens, Maire and Litardière, 1922) et in valle amnis Ouelga (Litardière, 1923); in ditionis Reraya valle amnis Ouenkrim (Litardière, 1923)."

Because *Heliocauta atlantica* resembles the two perennial varieties of *Anacyclus pyrethrum*

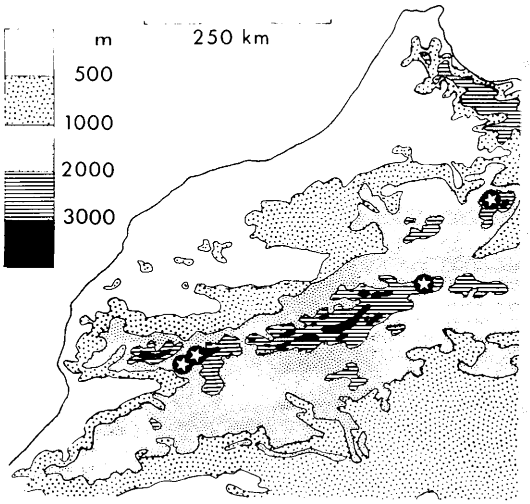

Fig. 2. Known range of *Heliocauta atlantica*.

(Humphries in prep.) in gross morphology Maire placed it in the same genus with the comment, "Affinis *A. pyrethro* L. et *A. depresso* Ball, a quibus valde differt caudice brevi praemorso radices fasciculates edenti (nec in radicem crassam palarem abeunti, capitulis minoribus homogamis, florescentia valde serotina etc. Sectioni Pyrethrariae DC etsi eligulatus, ob perennitatem, flosculos regulares, tubum compresseum et vegetationis modum adscribendus." This is clearly a classification mainly based on an overall resemblance in convergent characters, i.e. similar adaptations to the alpine environment in which both species occur. A more detailed examination shows that the two species are very different from each other.

Mature individuals of *A. pyrethrum* are characterised by the presence of a solitary, woody rootstock which can be up to four or five years old. The premorse stem of *H. atlantica,* on the other hand, produces at least three fasciculate roots (Fig. 1 A). Transverse sections show that these roots rarely survive for longer than two years. Instead perenniality is achieved by the development of stolons, capable of reaching lengths of up to 12 cm. Transverse sections of the protracted stem show that it can survive for two or three years. Both species produce an annual rosette of leaves which emerges from the centre of the perennating stocks. The flowering shoots in *A. pyrethrum,* homologous to the lateral branches of cauline corymbose cymes in other genera of the Anthemideae (Humphries in prep.), emerge during the month of February to form a rosette of procumbent shoots which flower at the tips from March until June. The decumbent flowering shoots of *H. atlantica* do not form flat rosettes but develop from the axils of the leaves and flower from August until October or November.

The flowers and fruits of *H. atlantica* differ in many respects from those of *Anacyclus.* The receptacular scales of the former are extremely narrow, delicate, carinate and chartaceous with an acuminate, brown-tipped apex and somewhat erose at maturity. By comparison the scales of *Anacyclus* are tough, mucronate and barely keeled but distinctly herbaceous at the base and centre, particularly in those from the outer parts of the capitulum. The heads of *Heliocauta* are homogamous consisting only of disc florets with regular corolla lobes. Homogamous heads are found in annual species of *Anacyclus* (*A. monanthos* and *A. valentinus*) but these frequently have zygomorphic corollas with two of the apical lobes longer than the other three. The cypselas of *Heliocauta* are also very different from anything to be found in *Anacyclus*, especially by the thin pericarp, the small ribs and the overall size (Figs. 1 L, 3). The epicarp consists of colourless, horizontally thickened cells and is invested with tanniniferous sphacelae which appear to be 4–7-celled resin glands (Fig. 1 L). The pappus is a tiny, marginal, toothed corona. In a transverse section of the pericarp a one-celled, scalariform epicarp (Fig. 3 C), a narrow 1–2-celled mesocarp and 3–5 sclerenchymatous ribs are shown. The deep brown colour is brought about by a very thick tanniniferous substance in the inner layers of the testa (Fig. 3 B).

The cypselas of *Anacyclus,* as in so many other genera of the Anthemideae, provide the unambiguous diagnostic features of the genus (Humphries in prep.). They are flattened in an anterior-dorsal plane with 2 lateral wings. The pericarp consists of a basal layer of sclerenchyma, some 2–3 cells thick covered by a 1–2-celled layer of parenchyma. The wings contain radially elongated parenchymatous tissue surrounding 2 laterally placed vascular bundles. The epicarp is covered with slime cells in linear series, as in *Heliocauta,* but they contain colourless mucilage. The pappus varies in different species from a marginal rim to an anterior appendage.

Relationship to other genera

The representatives of the *Anthemis* and *Achillea* complexes in the Northern Hemisphere form a group of 11 related genera (Table 1). Although each possesses many differential features the individual taxa can be delimited on a few diagnostic character states of unique status, as these help to define monophyletic groups, an essential requirement for natural classifications (Hennig 1966). The most important features of this kind are obtained from the morphology of the cypselas and the capitulum. Other possibly useful character states are found in the type of embryo-sac development (Harling 1950, 1951) and in the distribution of secondary metabolites (Greger 1975, 1977, Harborne et al. 1970). A summary of useful morphological features of genera in the *Anthemis* complex together with *Achillea, Heliocauta* and *Sclerorhachis* is given in Table 1.

A detailed examination of the fruits in the genera of the *Anthemis* complex reveals a number of parallel morphological trends which tend to obscure actual relationships. Such features include the anteriorly-dorsally compressed cypselas of *Anthemis* section *Cota* which have 7–22 ribs and a similar number of vascular bundles in the pericarp (Wagenitz 1968, Kynčlova 1970, Reitbrecht 1974); the weakly monosymmetric shape, the barely visible ribs and the thin pericarp of the cypselas in *Chamomilla;* and the thick tanniniferous layers of the testa in the dark coloured cypselas of *Matricaria*. The presence of myxogenic cells on the pericarp represent a plesiomorphous condition as they are common to all of the main generic complexes in the Anthemideae. However, the resin-filled glands of the type found in *Heliocauta* have only been observed elsewhere in *Sclerorhachis*.

Heliocauta can immediately be distinguished together with *Anacyclus, Leucocyclus* and *Achillea,* from the remainder of the complex on the basis of slightly or completely anteriorly compressed cypselas with 2 distinct lateral ribs or wings containing only 2 vascular bundles in the pericarp wall. The remaining genera have more or less terete, angled, monomorphic, laterally compressed or even occasionally anteriorly-dorsally compressed cypselas but with at least 3, usually

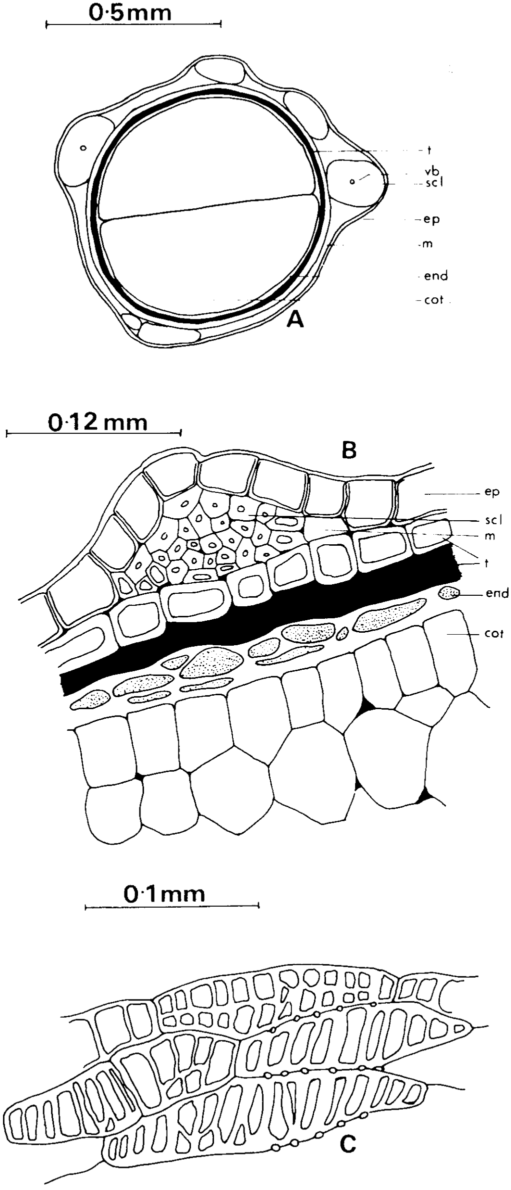

Fig. 3. Cypsela anatomy of *Heliocauta atlantica*. – A: T.s. across the median region. – B: T.s. in the region of a rib. – C: Surface view of the epicarp to show scalariform thickening of the cell walls. – cot cotyledon, end endosperm, ep epicarp, m mesocarp, scl sclerenchyma, t testa, vb vascular bundle.

Table 1. Morphological features of *Heliocauta, Achillea* and related genera. The characters are as follows:

1 Habit: a annual, b biennial, c perennial
2 Perennial habit: a rhizomes, b stolons
3 Receptacular scales: + present, − absent
4 Receptacular hairs: + present, − absent
5 Cypselas: + heteromorphic, − homomorphic
6 Cypsela symmetry: a terete/actinomorphic, b laterally compressed, c anteriorly/dorsally compressed, d zygomorphic
7 Number of vascular bundles in the pericarp
8 Number of cypsela ribs
9 Cypsela wings: + 2 wings, − absent
10 Cypsela parenchyma: a absent, b spongy, c single-layered, d multi-layered
11 Cypsela sclerenchyma: a absent, b hypodermic sclerocarp, c oval braced, d palisade, e multi-stranded, f 1–2-stranded
12 Pericarpic resin ducts and glands: + present, − absent
13 Pericarp lacunae: + present, − absent
14 Slime cells: − absent, a present, b sphacelate, c on ribs, d over whole surface
15 Number of nuclei in embryo-sac
16 Corolla: − not basally enlarged, a basally saccate, b anteriorly-dorsally overlapping fruit, c dorsally overlapping fruit
17 Cotyledons: a anteriorly-dorsally orientated, b laterally orientated

Genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Leucocyclus	c	a	+	−	−	c	2	±	+	c	e	−	−	c		b	
Achillea	c	a	+	−	−	c	2	2	−	b	f	−	−	c	2	−	b
Sclerorhachis	b		+	−	−	a b	4–5	0				+	−	c		−	
Heliocauta	c	b	+	−	−	c	2	3–5	−	b	f	+	−	−		−	a
Anacyclus	a c	(a)	+	−	−	c	2	0	+	b	e	−	−	d	1	(c)	a
Cladanthus	a		+	+	−	b		0	−	a	e	−	−	−	1	−	b
Anthemis sect. *Anthemis*	a–c	a	+	−	−	a	10	8–10	−	c d	e	−	−	(a)	4	−	a b
Anthemis sect. *Cota*	a–c	a	+	−	−	a c	22	22	−	d	c	−	−	−	4	−	b
Anthemis sect. *Ammanthus*	a		(+)	−	−	a		0–10	−			−	−	−		−	
Chamaemelum	a c	(a)	+	−	−	b	5	0	−	d	b d	−	−	−	1	a	b
Chamomilla	a		−	−	−	b	4–5	3	−	b	f	(+)	−	d	1	−	b
Matricaria	a c	(a)	−	−	−	b d	3	4–5	−	d	f	−	(+)	(a)	4	−	a b
Otospermum	a		−	−	+	a	5	5–6	−	d	e	−	−	−		−	

5–10, or even up to 22 vascular bundles in the pericarp wall. *Anacyclus* and *Leucocyclus* together form a monophyletic assemblage characterized by large cypselas with lateral wings and thick, continuously thickened pericarp walls. Grierson (1975) considers *Leucocyclus* to be unique on account of its vermiform leaves, the narrow wings on the cypselas and the dorsiventrally compressed disc corollas divided into 2 overlapping lobes at the base, which clasp the upper part of the cypsela on the anterior and dorsal faces.

By comparison both *Heliocauta* and *Achillea* have relatively tiny cypselas with 2 distinct lateral ribs rather than wings, and extremely thin pericarp walls (cf. Briquet 1916, Reitbrecht 1974, for details of *Achillea*). The relationship between *Heliocauta* and *Achillea* was originally suggested by phytochemical data. Greger (1977) has shown that the flavonoid profile of *Heliocauta* represents a widespread plesiomorphous pattern with compounds similar to those found in *Tanacetum, Artemisia, Anthemis* and *Achillea* although the exact profile is identical only to the one of *Achillea*. Morphologically, *H. atlantica* is closest to the montane species of the *Achillea barrelieri* (Ten.) Schultz Bip. – *A. oxyloba* (DC.) Schultz Bip. group of the European Alps, on the basis of the monocephalous heads, slender, brown-tipped receptacular scales, dark-brown margins on the phyllaries, cypsela size, pinnatisect leaves and its perennial habit.

Although *Achillea* is one of the largest genera in the Anthemideae and comprises a wide variation in many characters, *Heliocauta* cannot be included without a grave distortion of its coherent definition. Features of *Heliocauta* not found in any species of *Achillea* include the actual position of the vascular bundles in the ribs of the cypselas (basal rather than central), the horizontal wall thickenings of the cells in the pericarp, the variable strands of sclerenchyma forming extra ribs and the small, erose coroniform pappus.

Acknowledgements. My sincere thanks go to Dr W. T. Stearn for helping me to write the Latin description and deciding upon an appropriate name for the genus. I would also like to thank Anne Davis for producing Fig. 1 and Dr H. Greger for allowing me access to unpublished information.

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New and noteworthy species of Neottioideae (Orchidaceae) from Ecuador

Bernt Løjtnant

Løjtnant, B. 1977 06 30: New and noteworthy species of Neottioideae (Orchidaceae) from Ecuador. *Bot. Notiser 130:* 163–172. Stockholm. ISSN 0006-8195.

Three species of Ecuadorian orchids are described as new, *Altensteinia fragosa* Løjtnant, *Cranichis pachnodes* Løjtnant and *Sobralia melanothrix* Løjtnant. Two new combinations, *Altensteinia nigrescens* (Schltr.) Løjtnant and *Psilochilus physurifolius* (Rchb. f.) Løjtnant are made. The latter two species and *Cranichis diphylla, Elleanthus amethystinus, E. haematoxanthus, E. sphaerocephalus, Erythrodes arietina, Gomphichis traceyae, Ponthieva keraia,* the genus *Palmorchis, Pterichis barbifrons, P. galeata, P. multiflora, Sobralia candida* and *S. rigidissima* are reported for the first time from Ecuador.

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The taxonomic decisions presented result from determination of a great number of orchids collected during the 1st and 2nd Danish Botanical Expedition to Ecuador (cf. Holm-Nielsen & Jeppesen 1968, Holm-Nielsen et al. 1975, Løjtnant 1977). The research was carried out at the Orchid Herbarium of Oakes Ames, Harvard. Without the comprehensive collections of type-material at AMES and the unique guidance of the curator Dr Leslie A. Garay, this work would not have been practicable.

The flowers and floral parts in Fig. 2 are drawn from material preserved in FAA, those in Figs. 1 and 3 are from dried material.

Altensteinia fragosa Løjtnant sp. nov.

Orig. coll.: Ecuador, prov. Napo, 10 km above Laguna de Papallacta on road Quito–Papallacta, road sides and grass páramo with numerous small lakes, 3800 m (78°07′ W, 0°20′ S), 5.6.1973, Holm-Nielsen, Jeppesen, Løjtnant & Øllgaard 6755 (AAU holotype).

Terrestris, erecta, 40 cm alta. *Radicibus* fasciculatis, crassis, pilosis. *Foliis* rosulatis, 4–5, glabris, lanceolato-ellipticis, lamina 4–6 cm longa, in medio 10–24 mm lata, petiolo c. 2 cm longo. *Scapo* simplici, tereti, vaginis c. 11 scariosis, sub anthesin jam emarcidis, imbricantibus obtecto, supra versus rhachidem parce puberulo. *Spica* dense multiflora, cylindrica, 9 cm longa, 11–14 mm in diametro. *Bracteis* hyalinis, ovato-lanceolatis, acuminatis, flores multo superantibus, sursum decrescentibus, primum erectis, deinde reflexis, margine erosulis, 1.5–2.5 cm longis. *Floribus* albescentibus, parvulis, inversis, glabris. *Sepalo postico* concavo, oblongo-elliptico, obtuso, uninervato, margine valde erosulo, 2.1 mm longo, 1.2 mm lato. *Sepalis lateralibus* valde concavis, oblique obovato-oblongis, uninervatis, margine valde erosulo, 3.2 mm longis, 1.2 mm latis. *Petalis* oblongo-ligulatis, obtusis, uninervatis, margine apicem versus irregulariter eroso-denticulato, 2.5 mm longis, 1 mm latis. *Labello* calceolato, trilobato; lobis incurvis, laceratis, lobis lateralibus expansis semiorbicularibus, lobo medio triangulari; disco praecipue 5-nervato, nervis lateralibus ramosulis; juxta basin glandulis 2 subglobosis ornato; toto labello 2.3 mm longo, 1.6 mm lato. *Columna* brevi, *rostello* emarginato. *Ovario* sessili, cylindrico, apicem versus sparsim pilosulo.

Terrestrial, erect, 35 to 45 cm tall. *Roots* fasciculate, fleshy, pilose. *Leaves* 4–5, rosulate, glabrous, lanceolate-elliptic, basally produced into a 2 cm long petiole, including the petiole 4–6 cm long and 10–24 mm wide in the middle. *Scape* erect, terete, completely enclosed by c. 11 scarious sheaths which are evanescent during anthesis, those close to the rhachis partly pubescent. *Spike* dense, many-flowered, cylindric, 6–10 cm long and 11–14 mm in diameter excl. bracts. *Bracts* hyaline, ovate-lanceolate, acuminate, much longer than the flowers, decreasing in size upwards, first erect, then with age reflexed in middle, with erose margins, 1.5–2.5 cm long. *Flowers* whitish, small, non-resupinate, glabrous. *Dorsal sepal* concave, oblong-elliptic, obtuse, one-nerved, with deeply erose margins, 2.1 mm long and 1.2 mm wide. *Lateral sepals* obliquely ovate-oblong, deeply concave, one-nerved, with prominently erose margins, 3.2 mm long and 1.2 mm wide. *Petals* oblong-ligulate, obtuse, l-nerved with irregularly erose-denticulate margins towards the apex, 2.5 mm long and 1 mm wide. *Lip* calceolate, 3-lobed, lobes incurved, lacerate, lateral lobe when expanded semi-orbicular, the median lobe triangular; disc principally 5-nerved with lateral nerves branched, near the base with 2 subglobose glands, the whole lip up to 2.3 mm long and 1.6 mm wide. *Column* short; *rostellum* emarginate. *Ovary* sessile, cylindric, near the apex sparsely pilose.

This new species (Fig. 1) is distinguished from *A. riobambae* (Schltr.) Hawkes and *A. macra* (Schltr.) Hawkes by the erose sepals, erose-dentate petals, and by the more stalwart appearance and smaller flowers. In addition, it differs from *A. macra* by its long and acuminate bracts. The species is distinguishable from *A. leucantha* Rchb. f. and *A. paleacea* Kth. by the characteristics mentioned above and by the 3-lobed lip.

The specific name is descriptive of the margin of bracts, sepals and petals, *fragosus* meaning broken, rough, uneven.

The following collection is referable to this new species: Ecuador, prov. Imbabura, timber line vegetation on the hacienda Yura Cruz, 10 km N of Ibarra, páramo dominated by grass, 3700–3800 m (78°05′ W, 0°22′ N), 25.5.1973, Holm-Nielsen et al. 6481 (AAU).

Altensteinia nigrescens (Schltr.) Løjtnant comb. nov.

Basionym: *Aa nigrescens* Schltr. in Feddes Rep. Beih. 7: 49, 1920.

This species has formerly only been known from Cauca, Colombia, whence it has been described.

As *Aa* Rchb. f. hardly deserves the rank of a genus (cf. Schweinfurth 1958, Brieger 1974, Dunsterville & Garay 1976) the above new combination has been made.

Ecuador, prov. Imbabura, hacienda Yura Cruz, 10 km N of Ibarra, *Festuca* páramo and scrub (mainly in the quebradas), 3500–3600 m (78°05′ W, 0°22′ N), 25.5.1973, Holm-Nielsen et al. 6376 (AAU).

Cranichis diphylla Sw.

Sw., Prodr. Veg. Ind. Occ. 120, 1788.

This species, ranging from Mexico through C America and the West Indies to Peru (Schweinfurth 1940, 1958, Dunsterville & Garay 1972), has not formerly been reported from Ecuador, although it seems to be widely distributed in that country.

Ecuador, prov. Carchi, Valle de Maldonado, km 60 on road Tulcán-Maldonado, cleared slopes along road and denser cloud forest, 2700 m (78°04′ W, 0°51′ N) 18.5.1973, Holm-Nielsen et al. 5701, 5705 (AAU). – Prov. Loja, road Loja–Zamora, 1 km E of the pass (km 12), dry grass slopes, shrubby mountain slopes and elfin forest, 2725–2750 m (79°09′ W, 4° S), 17.4.1973, Holm-Nielsen et al. 3692 (AAU).

Cranichis pachnodes Løjtnant sp. nov.

Orig. coll.: Ecuador, prov. Carchi, Páramo El Angel, just before the pass on road El Angel-Tulcán, humid páramo vegetation with abundance of *Espeletia hartwegiana*, 3450–3500 m (77°54′ W, 0°41′ N), 14.5.1973, Holm-Nielsen, Jeppesen, Løjtnant & Øllgaard 5245 (AAU holotype).

Terrestris, erecta, gracilis, 50 cm alta, *Radicibus* fasciculatis, fusiformibus. *Foliis* basilaribus, 2, suberectis vel erecto-patentibus, longepetiolatis; lamina elliptica, acuta, usque ad 9 cm longa, 4 cm lata; petiolo 8–10 cm longo. *Scapo* stricto, apicem versus glanduloso-piloso, vaginis 7, acuminatis ornato. *Racemo* cylindrico, subdense multifloro, 3.5 cm longo. *Bracteis* patentibus, lanceolato-ellipticis, acuminatis, quam ovariis pedicellatis brevioribus, margine sparse glanduloso-pilosis. *Floribus* glabris, albidis, extus viridi suffusis. *Sepalo postico* late elliptico, subacuto, 4.2 mm longo, 1.8 mm lato, obscure 3-nervio. *Sepalis lateralibus* ellipticis, subacutis, 4.6 mm longis, 2.5 mm latis, obscure 2-nerviis. *Petalis* uninerviis, spathulatis, obtusis, 4 mm longis, 1.1 mm latis. *Labello* concavo, suborbiculari, obtuso, 4 mm longo, 2.5 mm lato; disco obscure 3-nervio, nervis obscure ramosis. *Rostello* simplici. *Ovario* cylindrico, glabro vel sparse puberulo.

Terrestrial, erect, slender, up to 50 cm tall. *Roots* fasciculate, fusiform. *Leaves* basal, 2–3, suberect to erecto-patent; lamina elliptic, acute, up to 9 cm long and 4 cm wide; petioles 8–13 cm long. *Scape* erect, glandular pilose with 4–7 acuminate sheaths. *Raceme* cylindric, subdensely many-flowered, 3.5–7 cm long. *Bracts* patent, lanceo-

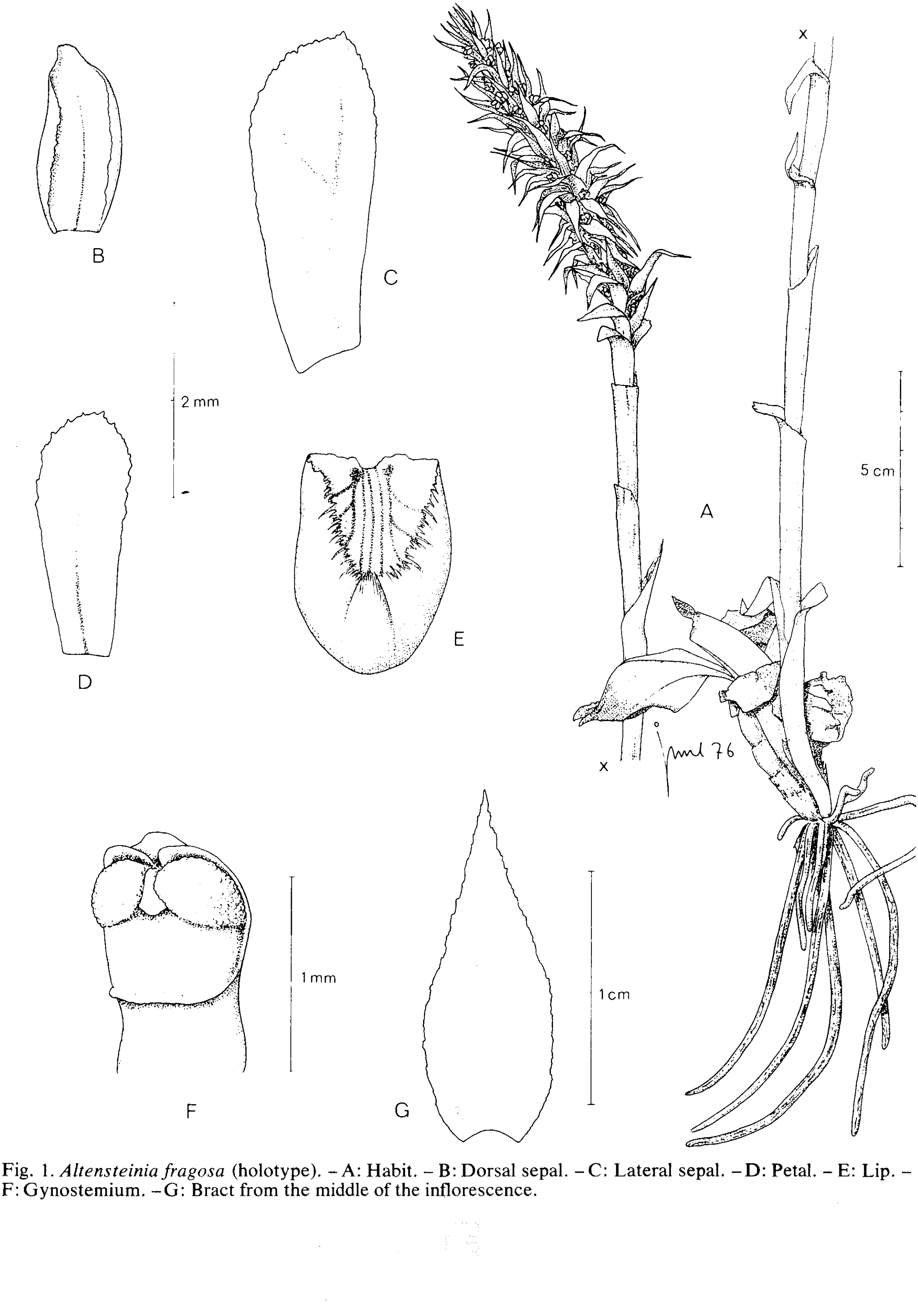


Fig. 1. *Altensteinia fragosa* (holotype). – A: Habit. – B: Dorsal sepal. – C: Lateral sepal. – D: Petal. – E: Lip. – F: Gynostemium. – G: Bract from the middle of the inflorescence.

late to elliptic, acuminate, shorter than the ovary, sparsely glandular pilose along the margins. *Flowers* glabrous, white, faintly greenish tinted, particularly on the outer side. *Dorsal sepal* broadly elliptic, obtusely acute, 4.2 mm long and 1.8 mm wide, inconspicuously 3-nerved. *Lateral sepals* elliptic, bluntly acute, 4.6 mm long and 2.5 mm wide, indistinctly 2-nerved. *Petals* l-nerved, spathulate, blunt, 4 mm long and 1.1 mm wide. *Lip* concave with green dots on the inner side, suborbicular, obtuse, 4 mm long and 2.5 mm wide, with 3 inconspicuous and indistinctly ramose nerves. *Rostellum* simple. *Ovary* cylindric, glabrous or sparsely pubescent at the base when young.

This new species (Fig. 2) is characterized by its spathulate petals and its indistinctly ramose and inconspicuous nerves on the lip. *Cranichis pachnodes* resembles *C. fendleri* Schltr., but is differentiated by a less rounded lip and by the characteristics mentioned above.

The specific name is descriptive of the cold habitat of the species, *pachnodes* meaning chilly or cold.

Elleanthus amethystinus (Rchb. f. & Warsz.) Rchb. f.

Rchb. f. in Walp. Ann. 6: 479, 1862. – Basionym: *Evelyna amethystina* Rchb. f. & Warsz. in Bonpl. 2: 113, 1854.

After comparing a copy at AMES of Reichenbach's drawing of the type of this species, it was obvious that our collection represents this rarely collected species, hitherto reported only from Peru and Colombia (Schweinfurth 1958).

Ecuador, prov. Loja, km 13 on Pan American Highway N of Loja, dry rocky slopes with scattered grass and shrubs, 2050 m (79°14′ W, 3°55′ S), 1.5.1973, Holm-Nielsen et al. 4635 (AAU).

Elleanthus haematoxanthus (Rchb. f. ex Lind.) Rchb. f.

Rchb. f. in Walp. Ann. 6: 485, 1863. – Basionym: *Evelyna haematoxantha* Rchb. f. ex Lind., Illustr. Hortic. 29: 51, 1882.

Hitherto only known from Colombia this species may now be acknowledged as part of the Ecuadorian flora.

Ecuador, prov. Zamora–Chinchipe, road Loja–Zamora, km 37, steep slopes covered with shrubs, 1750 m (79°04′ W, 3°59′ S), 18.4.1973, Holm-Nielsen et al. 3758 (AAU).

Elleanthus sphaerocephalus Schltr.

Schltr. in Feddes Rep. Beih. 27: 17, 1924.

Elleanthus sphaerocephalus, which is closely related to *E. cephalotus* Garay & Sweet and *E. sodiroi* Schltr., is recorded here for the first time from outside Colombia.

Ecuador, prov. Zamora–Chinchipe, road Loja–Zamora, km 54, steep clayey slopes with scattered shrub vegetation and dense herb cover, 1300 m (78°59′ W, 4°02′ S), 18.4.1973, Holm-Nielsen et al. 3784 (AAU).

Erythrodes arietina (Rchb. f. & Warm.) Ames

Ames, Orchidaceae 7: 66, 1922. – Basionym: *Physurus arietinus* Rchb. f. & Warm., Otia Bot. Hamb. 2: 52, 1881.

This inconspicuous but characteristic species, known from Brazil (type), Peru, and Venezuela (Foldats 1969), is reported here for the first time from Ecuador.

Ecuador, prov. Morona–Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34′ W, 3°29′ S), 23.4.1973, Holm-Nielsen et al. 4153 (AAU).

Gomphichis traceyae Rolfe

Rolfe in Kew Bull. 1916: 78.

Gomphichis traceyae has so far only been reported from Colombia, where it is widely distributed (Renz 1948). Although it is apparently common in the southern Ecuadorian dry scrub regions, it has undoubtedly been either overlooked or confused with the allied *G. alba* Lehm. & Kränzl. (cf. Kränzlin 1899, Renz 1948).

Ecuador, prov. Azuay, km 67 S of Cuenca on Pan American Highway, xerophytic scrub, 2–3 m high, intermingled with meadows and drier grass land, 3250 m (79°08′ W, 3°18′ S), 4.5.1973, Holm-Nielsen et al. 4933 (AAU). – Prov. Azuay, km 85 on Pan American Highway N of Loja, dry low scrub vegetation, more humid in small hollows and valleys, 2850–2950 m (79°11′ W, 3°35′ N), 3.5.1973, Holm-Nielsen et al. 4829 (AAU).

Fig. 2. *Cranichis pachnodes* (holotype, B isotype). – A: Habit. – B: Old inflorescence. – C: Dorsal sepal. – D: Lateral sepal. – E: Petal. – F: Flower. – G: Lip. – H: Gynostemium. – I: Anther.

The genus Palmorchis

The genus *Palmorchis*, which has its centre in northern S America and extends to Panama and Trinidad (Schweinfurth & Correll 1940), has not up to the present time been reported from Ecuador. Plants of *Palmorchis* are not rare in the Amazonian lowlands of Ecuador but due to their insignificant appearance they can easily be overlooked.

Despite the immature buds, the cited collection may be referable to *P. lobulata* (Mansf.) C. Schweinf. & Correll, which, according to Schweinfurth & Correll (1940) is known from Peru and Colombia. However, strangely enough, Schweinfurth (1958) excludes any mention of species of *Palmorchis* in his Orchids of Peru.

Ecuador, prov. Morona–Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34′ W, 3°29′ S), 23.4.1973, Holm-Nielsen et al. 4154 (AAU).

Ponthieva keraia Garay & Dunsterv.

Garay & Dunsterv., Venz. Orch. Ill. 6: 382, 1976.

This species, which has recently been described as endemic to Venezuela, seems to be rather widespread. It is distinguished from the closely related Colombian *P. ochreata* Renz by the distinct horn on the lateral petals and by the cordate base of these floral segments.

Ecuador, prov. Azuay, km 91 on Pan American Highway N of Loja, dry scrub, 1–3 m high, 2900 m (79°10′ W, 3°25′ S), 5.5.1973, Holm-Nielsen et al. 5111 (AAU).

Psilochilus physurifolius (Rchb. f.) Løjtnant comb. nov.

Basionym: *Pogonia physurifolia* Rchb. f. in Nederl. Kruidk. Arch. 4: 324, 1858.

The genus *Psilochilus* is new to the flora of Ecuador; in fact the members of this small genus also seem to be rare in the two other northern Andean countries, Colombia and Peru (cf. Schweinfurth 1970, Garay 1974).

Psilochilus physurifolius (type from Guiana) is closely related to *P. macrophyllus* (Lindl.) Ames, which is described from Cuba. *P. physurifolius* is, in fact, often considered conspecific with *P. macrophyllus* (cf. Ames & Correll 1952, Foldats 1969). However, an examination of the types of the two taxa has shown that they are not conspecific. But it is deplorable that the flowers of the type of *P. physurifolius* were in very poor condition even at the time the species was described. In describing *Pogonia macrophylla*, Lindley (1858) writes: "There is one very like it in Schomburgk's collections, but my specimens of it are scarcely sufficient for publication." In the very same year Reichenbach (1858) based *Pogonia physurifolia* on the collection of Schomburgk mentioned above.

Vegetatively *P. physurifolius* and *P. macrophyllus* are differentiated by the following characters:

Character	*P. physurifolius*	*P. macrophyllus*
Leaves	acuminate, tapering	acute
Leaf base	tapering–rounded	cordate
Petiole	more than 1 cm	very short, leaf-base clasping the stem
Bracts	acuminate	acute to blunt

The Colombian *P. maderoi* (Schltr.) Schltr. may be conspecific with *P. physurifolius* (cf. Schlechter 1920). Thus *P. maderoi* resembles *P. physurifolius* in having a long claw to the lip unlike the short claw of *P. macrophyllus*.

Of the collections studied at AAU and AMES, the following are referable to *P. physurifolius:*

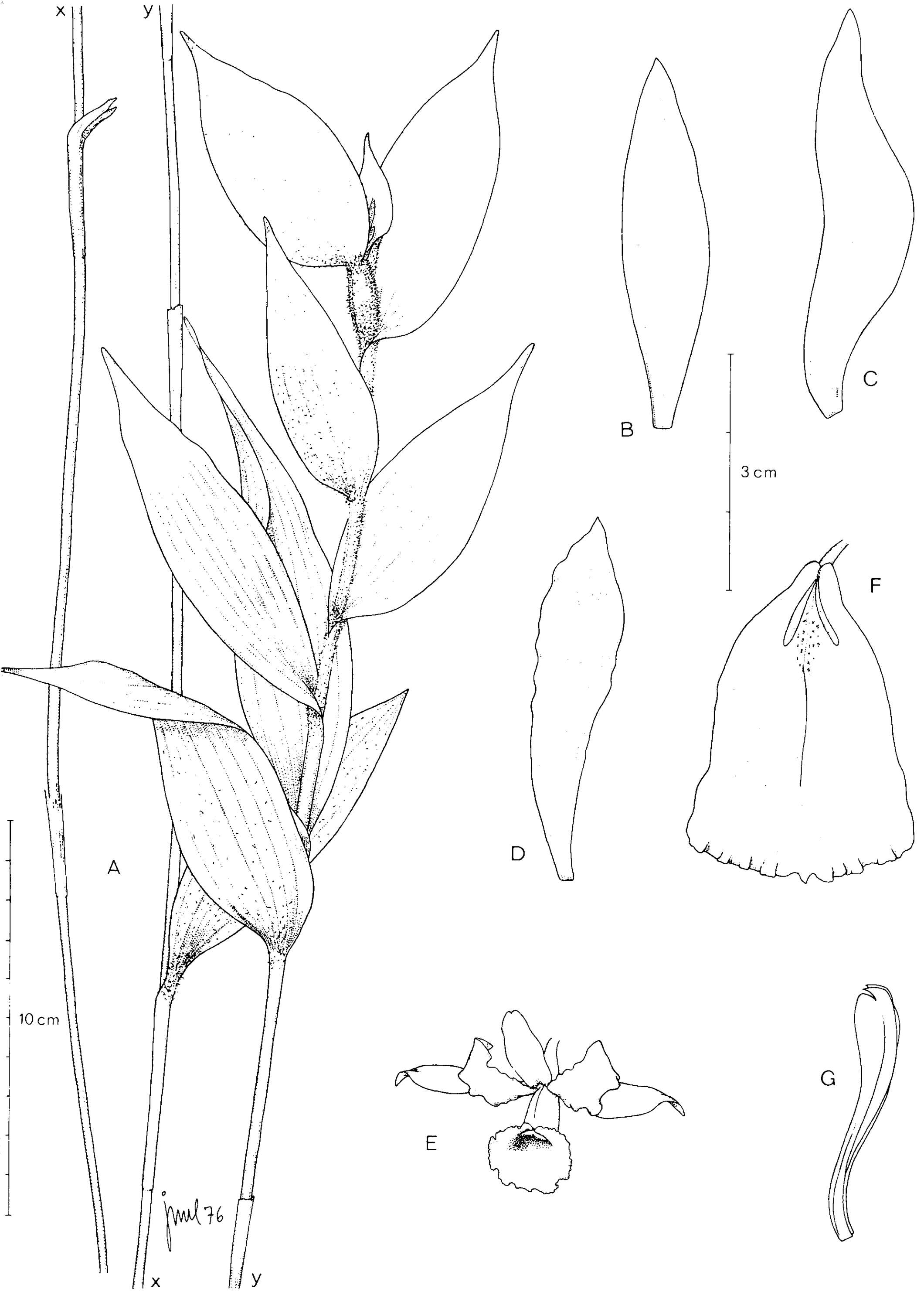
Venezuela, Bolivar, Cerro Venamo (parte Sur-Oeste), cerca de los límites con la Guayana Inglesa, 950–1150 m, 29–30.12.1963, Steyermark, Dunsterville & Dunsterville 92382 (AMES). – Merida, woods above las Cuadras, along Quebrada Molino, N of Torondoy, 1820–2255 m, 27.3.1944, Steyermark 55780 (AMES).

Ecuador, prov. Pastaza, Shell Mera rain forest, 2 km N of Shell Mera, 1050 m (78°03′ W, 1°29′ S), 6.6.1968, Holm-Nielsen & Jeppesen 340 (AAU).

Pterichis barbifrons (Kränzl.) Schltr.

Schltr. in Feddes Rep. Beih. 9: 127, 1921. – Basionym: *Prescottia barbifrons* Kränzl. in Engl. Bot. Jahrb. 54, Beibl. 117: 19, 1916.

Fig. 3. *Sobralia melanothrix* (holotype). – A: Habit. – B: Dorsal sepal. – C: Lateral sepal. – D: Petal. – E: Flower. – F: Lip. – G: Gynostemium.


x
y
A
10 cm
B
C
3 cm
D
E
F
G
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x
y

This species, described from Peru, was regarded as being conspecific with *P. galeata* Lindl. by Schweinfurth (1941); however, comparisons with type material have shown that *P. barbifrons* is most likely a distinct species. It is distinguished from *P. galeata* by its glabrous sepals and bracts and by its linear falcate petals.

Apparently *P. barbifrons* is a rather common species in Ecuador; yet, because it has been considered identical with *P. galeata* up to now, it has only been reported from Peru.

Ecuador, prov. Carchi, Páramo El Angel, in the pass on road El Angel–Tulcán, very humid *Espeletia* páramo, 3750–3850 m (78°54′ W, 0°41′ N), 15.5.1973, Holm-Nielsen et al. 5450 (AAU). – Prov. Azuay, km 50 S of Cuenca on Pan American Highway, páramo, c. 3500 m (79°07′ W, 3°18′ S), 6–10.5.1973, Holm-Nielsen et al. 5128 (AAU). – Prov. Azuay, km 85 on Pan American Highway N of Loja, dry, low scrub vegetation, more humid in small hollows and valleys, 2850–2950 m (79°11′ W, 3°35′ S), 3.5.1973, Holm-Nielsen et al. 4767 (AAU).

Pterichis galeata Lindl.

Lindl., Gen. Sp. Orch. 445, 1840.

This species has been reported from Peru (type), Bolivia, Colombia, and Venezuela and is hereby confirmed as being part of the Ecuadorian flora.

Ecuador, prov. Cotopaxi, Quevedo–Latacunga road, above Pilaló, in cloud forest, mostly steep slopes, c. 3200–3300 m (78°56′ W, 0°58′ S), 8.4.1973, Holm-Nielsen et al. 3279 (AAU).

Pterichis multiflora (Lindl.) Schltr.

Schltr. in Engl. Bot. Jahrb. 45: 389, 1916. – Basionym: *Acrea multiflora* Lindl., Orch. Linden 26, 1846.

During this study the number of *Pterichis* species recognized as native to Ecuador has almost been doubled. Hitherto four species, *P. parviflora* (Lindl.) Schltr., *P. pauciflora* Schltr., *P. seleniglossa* Schltr. and *P. triloba* (Lindl.) Schltr. have been reported from Ecuador. Including the species in discussion, which, up to now, has only been known from Colombia (cf. Dunsterville & Garay 1966, 1976) the number has reached seven.

Ecuador, prov. Carchi, Páramo El Angel, in the pass on the road El Angel-Tulcán, very humid *Espeletia* páramo, 3750–3850 m (78°54′ W, 0°41′ N), 15.5.1973, Holm-Nielsen et al. 5453 (AAU).

Sobralia candida (Poepp. & Endl.) Rchb. f.

Rchb. f., Fl. Serres 8: 247, 1853. – Basionym: *Cyathoglottis candida* Poepp. & Endl., Nov. Gen. Sp. Pl. 1: 56, 1836.

This characteristic species has so far been known from Peru (type), Colombia, and Venezuela (Dunsterville & Garay 1961, Foldats 1969) and is now also reported from Ecuador.

Ecuador, prov. Zamora–Chinchipe, road Loja–Zamora, km 54, steep clayey slopes with scattered shrub vegetation and dense herb cover, 1300 m (78°59′ W, 4°02′ S), 18.4.1973, Holm-Nielsen et al. 3779 (AAU). – Also km 49, c. 1500 m, Holm-Nielsen et al. 3829 (AAU).

Sobralia melanothrix Løjtnant sp. nov.

Orig. coll.: Ecuador, prov. Pichincha, km 40–51 on road Santo Domingo de los Colorados–Quito, forested slopes along Rio Pilatón, 1100–1400 m (78°55′ W, 0°22′ S), 14.6.1973, Holm-Nielsen, Jeppesen, Løjtnant & Øllgaard 7150 (AAU holotype).

Terrestris, usque ad 1 m alta; caulibus erectis, infra vaginis emarcidis obtectis, supra foliosis. *Vaginis* adpressis, plus minusve pubescentibus. *Foliis* ovatis vel ovato–lanceolatis, acutis vel abrupte subacuminatis, sessilibus, cum vaginis articulatis, laminis subtus atropilosis, 7–14 cm longis, 2.3–3.2 cm latis. *Inflorescentiis* terminalibus, sessilibus, unifloris. *Floribus* succedaneis. *Sepalo postico* anguste elliptico, utrinque attenuato, acuto, 42 mm longo, 11 mm lato. *Sepalis lateralibus* oblique falcato–lanceolatis, acutis, vel subobtusis, margine undulatis, revolutis, 51 mm longis, 12 mm latis. *Petalis* obovato–oblanceolatis, acutis, margine undulatis, usque ad 44 mm longis, 10 mm latis. *Labello* e cuneata basi infundibuliformi, in ambitu subquadrato–obovato, antice subtruncato, minute apiculato, margine valde undulato et minute eroso-denticulato; disco in medio incrassato et alte unicarinato, basin versus carinis abbreviatis, oblique insertis ornato, inter carinas minute papilloso; toto labello 4 cm longo, 2.9 cm lato. *Columna* gracili, leviter sinuosa, apicem versus alata, juxta clinandrium falcata, usque ad 3 cm longa. *Ovariis* cylindraceis.

Terrestrial, up to 1 m tall, basal half leafless, provided with distinct evanescent sheaths. *Sheaths* appressed, more or less pubescent. Upper half of the stem leafy. *Leaves* ovate to ovate-lanceolate, acute to abruptly subacuminate, sessile, articulate with leaf sheaths, 7–14 cm long, 2.3–3.2 cm wide, leaf sheaths and the underside of the leaf blades dark pilose. *Inflorescence* terminal, single-flowered, flowers produced in succession from 3 pubescent, imbricating sheaths. *Flowers* with reddish brown sepals and petals and purple lip margined with white and yellow in the throat. *Dorsal sepal* narrowly elliptic, attenuated in both ends, acute, 42 mm long, 11 mm wide. *Lateral sepals* obliquely falcate–lanceolate, acute to subobtuse with revolute, wavy margins, up to 51 mm long and 12 mm wide. *Petals* obovate–oblanceolate, acute, with undulate margins up to 44 mm long and 10 mm wide. *Lip* infundibuliform from a cuneate base, subquadrate–obovate in outline when spread, subtruncate in front, minutely apiculate, the truncate part heavily undulate and minutely erose-denticulate, disc thickened in the middle with a longitudinal, erect keel and with a pair of obliquely inserted short keels at the base, the area between the basal fleshy keels and the median carina minutely papillose, the base of the lip dorsally carinate, the whole lip 4 cm long and 2.9 cm wide at the truncate apex. *Column* sinuous, rather slender, winged towards the apex, terminating in a pair of falcate processes at the clinandrium, up to 3 cm long. *Ovary* cylindric.

This new species (Fig. 3) is distinguished from *S. atropubescens* Ames & C. Schweinf. and *S. lowii* Rolfe by the distinct keels on the lip. In addition, it differs from *S. atropubescens* by its larger flowers and from *S. lowii* by its considerably broader leaves and red-brown, not purple flowers.

Sobralia melanothrix resembles *S. atropubescens* from Costa Rica with its darkly pubescent sheaths and leaves. In fact, *S. melanothrix* and *S. atropubescens* seem to represent another example of the close phytogeographical relationship which exists between Costa Rica and Ecuador, and which Reichenbach (1878) has already pointed out.

It may be noted that the type of *S. atropubescens* does not measure more than 28 cm in height; the height differences between *S. atropubescens* and *S. melanothrix* taken from the diagnoses, however, can hardly be considered to have any significance because only the upper leaf-bearing part of *S. atropubescens* is present on the type sheet of that particular species.

The specific name is descriptive of the darkly pubescent sheaths and leaves, *melanos* meaning black, dark; and *thrix* meaning hair.

Sobralia rigidissima Lind. ex Rchb. f.

Rchb. f. in Bonpl. 2: 278, 1854.

Sobralia rigidissima has so far only been reported from the type locality in Colombia.

Ecuador, prov. Zamora–Chinchipe, road Loja–Zamora, km 24–25. steep rocky slopes with scrub, 1950–2100 m (79°05′ W, 3°59′ S), 15.4.1973, Holm-Nielsen et al. 3455 (AAU).

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Morphological and anatomical variation of Vulpia (Gramineae)

R. Cotton and C. A. Stace

Cotton, R. & Stace, C. A. 1977 06 30: Morphological and anatomical variation of Vulpia (Gramineae). [Taxonomy of the genus Vulpia 2.] *Bot. Notiser 130:* 173–187. Stockholm. ISSN 0006-8195.

The genus *Vulpia* in its widest sense is reviewed. Almost all the 28 or so species in the world have been examined with respect to a wide range of morphological, anatomical and cytological characters, with due emphasis on caryopsis morphology and leaf anatomy, which have been neglected in the past. It is concluded that *Vulpiella* (one species) is a genus quite distinct from *Vulpia* and more properly placed close to *Cutandia,* and that *Ctenopsis* (four species) is also best recognised as a distinct genus, although close to *Vulpia.* Within *Vulpia* four well-defined groups are recognisable; these are given sectional status and their nomenclature and scope are set out in detail. Of the four, section *Monachne* (three species) occupies a key position, as it is intermediate between sections *Loretia* and *Vulpia* and is the section which section *Spirachne* most closely approaches.

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In its widest historical sense the genus *Vulpia* C. C. Gmel. contains some 28 species, among which five major groups have been recognised: *Vulpia, Loretia, Spirachne, Ctenopsis* and *Vulpiella.* These groups have at various times been given different taxonomic ranks, either as distinct genera or as subgenera or sections of *Vulpia.* The species assigned to these five groups are given in Table 1, in which the classification suggested by Maire (1955) and adopted by us in the first paper in this series (Cotton & Stace 1976) is provisionally used. *Vulpia, Loretia* and *Spirachne* are there considered as sections of *Vulpia,* and *Ctenopsis* and *Vulpiella* as distinct genera.

In addition to these five groups, other taxa have from time to time erroneously been included in *Vulpia.* Notable among these are *V. michelii* (Savi) Reichenb. and *V. tenuicula* Boiss. & Reut., for which the sectional name *Koelerioides* Willk. has been used (Willkomm & Lange 1870), but which are nowadays placed in the separate genus *Avellinia* Parl. in the tribe Aveneae. Species such as these are not covered in this account.

The five groups differ cytologically and geographically (Cotton & Stace 1976); on both counts *Vulpia* is the most diverse. In this group diploids ($2n = 14$) (*V. bromoides, V. fontquerana, V. membranacea, V. muralis, V. octoflora*), tetraploids ($2n = 28$) (*V. ambigua, V. ciliata, V. fasciculata*) and hexaploids ($2n = 42$) (*V. hirtiglumis, V. megalura, V. microstachys, V. myuros, V. persica, V. sciurea*) occur, and it has the widest distribution of all the groups, being found throughout Europe as far north as Scotland and S. Scandinavia, and in North Africa, W. and C. Asia, and North and South America. Several species have become naturalized in E. Asia, Australasia and C. and S. Africa. In the other four groups only diploids ($2n = 14$) have been recorded and the species are restricted to the Mediterranean region. Chromosome numbers of *Loretia* and *Spirachne* are given in Cotton & Stace (1976). In *Ctenopsis* and *Vulpiella* we know of only one published chromosome count each: *Ctenopsis delicatula* from Portugal (Fernandes & Queirós 1969) and *Vulpiella tenuis* from Tunisia (Kerguélen 1975).

Table 1. Species of *Vulpia* sensu lato allocated to the genera and sections recognised by Maire (1955).

Vulpia C. C. Gmel. section **Vulpia**

V. ambigua (Le Gall) More
V. antofagastensis Parodi
V. bromoides (L.) S. F. Gray
V. ciliata Dumort.
V. fasciculata (Forsk.) Samp.
  (*V. membranacea* auct.)
V. fontquerana Melderis & Stace
V. hirtiglumis Boiss. & Hausskn.
V. membranacea (L.) Dumort.
  (*V. longiseta* (Brot.) Hackel)
V. microstachys (Nutt.) Benth.
V. muralis (Kunth) Nees (*V. broteri* Boiss. & Reuter)
V. myuros (L.) C. C. Gmel.
  (incl. *V. megalura* (Nutt.) Rydb.)
V. octoflora (Walt.) Rydb.
V. persica (Boiss. & Buhse) Krecz. & Bobr.
V. sciurea (Nutt.) Henr.

Vulpia section **Loretia** (Duval-Jouve) Boiss.

V. alopecuros (Schousboe) Dumort.
V. geniculata (L.) Link
V. ligustica (All.) Link
V. litardiereana (Maire) A. Camus
V. obtusa Trabut
V. pauana (Font Quer) Font Quer
V. setacea Parl.
V. sicula (C. Presl) Link

Vulpia section **Spirachne** (Hackel) Boiss.

V. inops (Del.) Hackel

Ctenopsis De Not.

C. cynosuroides (Desf.) Paunero
C. delicatula (Lag.) Paunero
C. gypsophila (Willk. ex Hackel) Paunero
C. pectinella (Del.) De Not.

Vulpiella (Trabut) Burollet

Vulpiella tenuis (Tineo) Kerguélen
  (*V. incrassata* (Salz. ex Loisel.) Burollet)

Variation in morphology is of obvious importance in taxonomy at all levels, and that in *Vulpia* has been documented in many publications. Anatomical variation in grasses has, however, mostly been applied to the taxonomy of the higher ranks, and only more recently to that of species and genera. Leaf anatomy of *Vulpia* was mentioned by Pée-Laby (1898), Lewton-Brain (1904) and Burr & Turner (1933), but only as uncritical descriptions of one or two species. Later Paunero (1963, 1964) gave detailed descriptions of the leaf epidermal anatomy of many species of *Vulpia* (including *Vulpiella*) and *Ctenopsis*.

Although there are many floristic accounts of parts of the genus *Vulpia*, and other accounts covering specialised aspects such as leaf epidermis, a broad review of the whole genus covering a very wide range of structural aspects, which is essential for the proper understanding of any genus, has not previously been attempted. In this paper we present the results of such a survey of the above five groups and discuss this in relation to their taxonomy. Specific limits are not in general covered here, but it is necessary to adopt four changes from the names used in Cotton & Stace (1976): *Vulpia fasciculata* (Forskål) Samp. for *V. membranacea* (L.) Dumort.; *V. membranacea* (L.) Dumort. for *V. longiseta* (Brot.) Hackel; *V. muralis* (Kunth) Nees for *V. broteri* Boiss. & Reuter; and *V. myuros* f. *megalura* (Nutt.) Stace & Cotton for *V. megalura* (Nutt.) Rydb. Reasons for these changes have been given by Stace & Cotton (1976a, 1976b, 1977).

Material and methods

Material studied consisted of wild collected plants or plants grown from wild collected caryopses (c. 450 collections), and herbarium specimens from BM, K, LISI, LTR and MANCH. Vouchers of all the wild collections subsequently cultivated are preserved in LTR.

Measurements were made on spikelets taken from the middle portion of the inflorescence or of a panicle branch, since these exhibited the least variation. Unless otherwise noted the size range of characters given is the range of means calculated for each specimen, and not the range of extremes.

The second culm leaf below the inflorescence was used for anatomical work. For internal anatomy leaves were variously hand-sectioned, sectioned with a freezing microtome, or wax-embedded and sectioned with a rocking microtome. Preparation of epidermises followed the technique of Clarke (1960), with some modifications. After softening in hot 88 % lactic acid the abaxial epidermis was isolated by laying it on a slide and scraping away the adaxial epidermis and internal tissues from above with a sharp scalpel. In the isolation of the adaxial epidermis it was necessary to cut away the tough abaxial epidermis and its associated sclerenchyma with a scalpel held at a narrow angle to the leaf, before scraping away the soft mesophyll. The terminology used to describe the leaf epidermis follows that of Metcalfe (1960).

We have examined material of all the species named in Table 1 except *V. obtusa*, which is only a doubtfully distinct species. For ease of reference, for the most part in this paper we use the names of the five groups without qualification as to rank. However, the species are referred to as belonging to one of the three genera *Vulpia, Ctenopsis* and *Vulpiella,* although in the case of *Vulpia* their allocation to the sections *Vulpia, Loretia* or *Spirachne* is indicated. The abbreviation *V.* stands for *Vulpia; Vulpiella* is never abbreviated.

Results

The grasses considered here are typically pooid (festucoid) in their major characteristics. Within the five groups under review the morphological and anatomical characters of greatest taxonomic value are as follows.

Growth habit

All species, with the exception of *V. setacea, V. sicula* and *V. litardiereana* (*Loretia*) are annuals. This pattern persists in cultivation, although certain specimens of *V. alopecuros* and *V. geniculata* (*Loretia*) showed a response to warm, humid glasshouse conditions by rooting at the lower nodes of some culms.

Branching of all species, including the perennial ones, is intravaginal only, in contrast to that in the related perennial genus *Festuca,* where both intravaginal and extravaginal branching occurs.

Vivipary, the premature germination of the caryopses while still attached to the inflorescence, has been observed only in one sample of *V. ciliata* (*Vulpia*), from Ardingly, E. Sussex, England.

Inflorescence characters

Exsertion. The degree of exsertion of the inflorescence at and after anthesis is a valuable specific character within certain groups of *Vulpia*. In particular, it is a discriminant between *V. bromoides* and *V. myuros,* and a partial discriminant between *V. membranacea* and *V. fasciculata*. This character is, however, subject to ecophenetic variation, for in very dry conditions the normally exserted inflorescences of *V. bromoides* may become included in the uppermost leaf-sheath and closely resemble those of *V. myuros*. We have observed this condition in material of *V. bromoides* from a wall-top in Ireland and from shingle-banks in England.

Branching. In *Vulpia* and *Loretia* inflorescences range from branched panicles with long pedicels to subspicate racemes. The most extreme examples of the latter occur in *V. alopecuros* (*Loretia*) and *V. persica* (*Vulpia*). All the species of *Ctenopsis* have very sparsely branched inflorescences and in *C. pectinella* they are more or less spicate. In species with racemose or spicate inflorescences the pedicels are borne on only two of the three faces of the triquetrous rhachis, and the inflorescences are therefore secund. This is particularly marked in *C. pectinella. Vulpiella* and *Spirachne* have paniculate inflorescences.

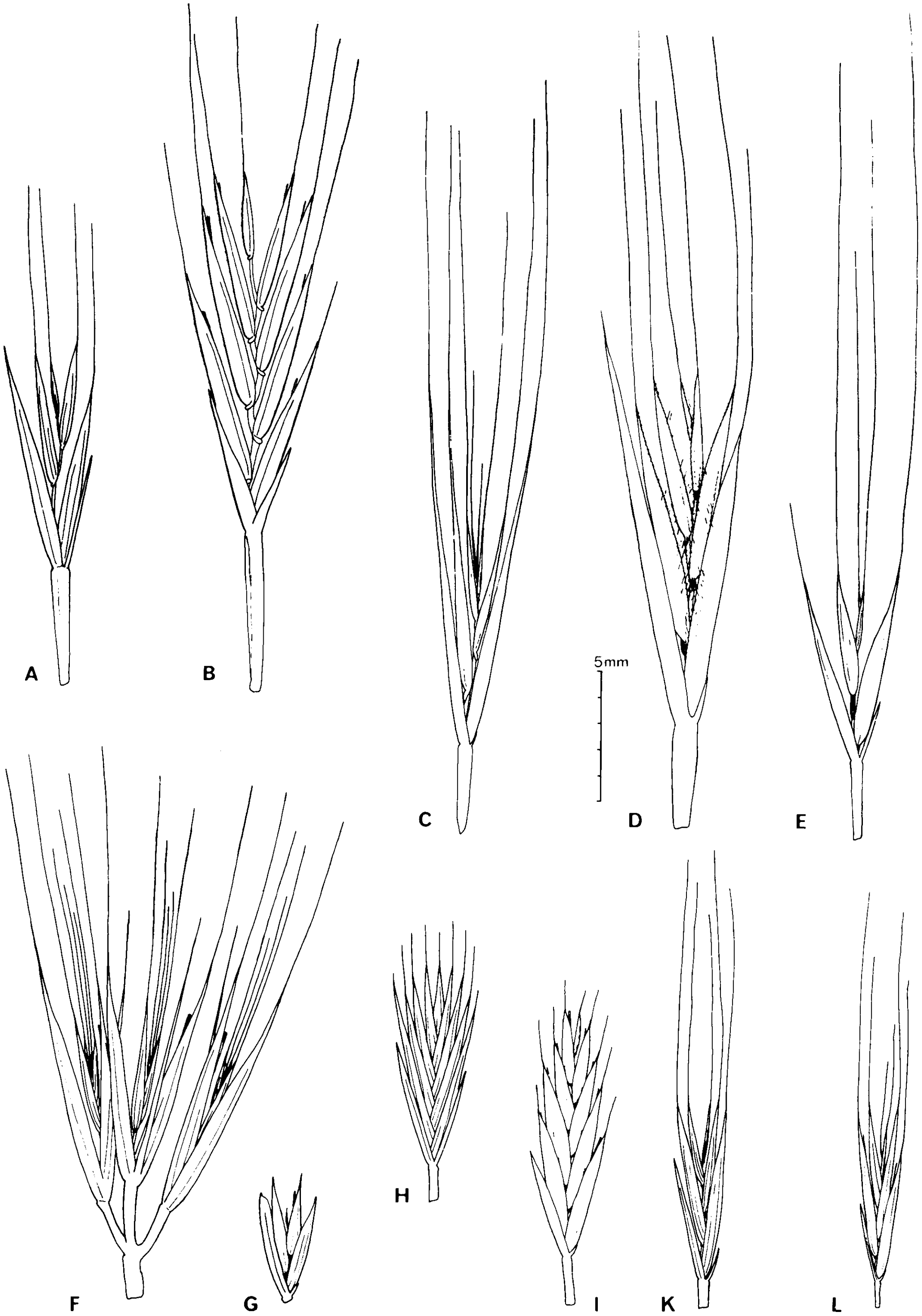
Pedicels. In *Loretia, Spirachne* and three species of *Vulpia* (*V. membranacea, V. fasciculata, V. fontquerana*) the long pedicels are conspicuously dilated and flattened distally (Fig. 1). Dilation is scarcely developed in other species, even where the pedicel is very long.

Pulvini. Well developed pulvini are present in the axils of panicle branches and pedicels in *V. microstachys* agg. (*Vulpia*). These swell after anthesis and cause the branches or spikelets to become strongly divergent or even reflexed. In *Vulpiella* pulvini are present, but the branches do not become reflexed. Pulvini are not found in other species, but are characteristic of certain related genera such as *Scleropoa* and *Cutandia.*

Spikelet groups. In *Spirachne* the spikelets, each with a distinct pedicel, are arranged in constant groups of three on top of a common pedicel-like panicle-branch (Fig. 1F). In all other species the spikelets are borne independently.

Spikelet characters

Aestivation. In most plants of *Spirachne* the normal distichous arrangement of glumes and florets has become twisted so that these parts form a gradual spiral around the rhachilla. This unique character was described in detail by Hackel (1880), when first recognising *Spirachne* as a subgenus of *Vulpia,* although he also recognised a variant which exhibited the normal


A
B
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5mm
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distichous arrangement (var. *subdisticha* Asch. & Hackel, cf. Maire 1955).

Glumes. In all but two species the two glumes are distinctly unequal, the lower being not more than three-quarters the length of the upper. In the genus *Festuca*, on the other hand, the lower glume is almost always more than three-quarters the length of the upper. In *V. inops* (*Spirachne*) the two glumes (including awns) are subequal in length, but the lower glume is much narrower than the upper and has a shorter body and longer awn (Fig. 1 F), while in *V. octoflora* (*Vulpia*) the lower glume is up to 7/8 as long as the upper (Fig. 1 H). It is sometimes more useful to express glume length in relation to the length of the adjacent lemma; *V. sicula* and *V. setacea* may be separated by this character (upper glume longer than adjacent lemma in *V. setacea*, shorter in *V. sicula*).

In extreme cases the lower glume is very short and veinless, or has one minute vein (Fig. 1). This is the case in all species of *Ctenopsis* and in certain species of *Loretia* (*V. alopecuros*, *V. ligustica*) and *Vulpia* (*V. membranacea*, *V. fasciculata*, *V. ciliata*, *V. ambigua*). Nevertheless both *Loretia* and *Vulpia* possess other species with relatively long lower glumes (Fig. 1); up to 3:5 the length of the upper in *V. geniculata* (*Loretia*), up to 3:4 in *V. bromoides* (*Vulpia*), and up to 7:8 in *V. octoflora* (*Vulpia*). In *Vulpiella* the ratio is approximately 3:4 (Fig. 1 B).

Glume-ratio is therefore a very important diagnostic criterion in *Vulpia* and related genera. Care is needed, however, to make measurements only on spikelets which are not terminal on the inflorescence or on its branches, for in such spikelets the lower glume is often much longer than usual.

The number of veins is generally 0–1 in the lower glume and 1–3 in the upper glume, the higher numbers in each case being associated with the longer and broader glumes. In *Spirachne* there are 3 and 5 veins respectively.

In most species the glumes are acuminate or sharply acute at the apex. In *V. ciliata* and *V. ambigua* (*Vulpia*) the upper glume is hyaline at the apex, which frequently breaks off, giving the false impression that the apex is blunt. In *Spirachne* and *V. membranacea* and *V. fasciculata* (*Vulpia*) the upper glume has an awn up to as long as the body, while in *V. fontquerana* (*Vulpia*) and annual species of *Loretia* the upper glume is also characteristically, though more shortly, awned.

The glumes are mostly rounded dorsally but in *Ctenopsis cynosuroides* and *C. pectinella* the upper glume is keeled distally.

Glume pubescence is reviewed under lemma.

Sterile florets. As in most pooid grasses, the 1–2(–3) most apical florets in each spikelet are reduced in size and male or sterile in the majority of the species. However, two other patterns also occur.

In *V. ciliata* and *V. ambigua* (*Vulpia*) there are only 1–3 fertile florets, but 3–7 distal sterile florets. The lemmas of the latter exceed those of the former in length and width (and in *V. ciliata* bear a different pattern of indumentum), but have shorter awns (Fig. 2 B, C). The paleas of the sterile florets are reduced or absent.

In *V. membranacea*, *V. fasciculata* and *V. fontquerana* (*Vulpia*) there is a congested group of 2–6 very small sterile florets (Fig. 1 C, E). This pattern also occurs in *Spirachne*, where there is only one fertile floret, just as there often is in *V. fontquerana*.

Rhachilla. The lowest floret is more or less sessile within the glumes, but the rest are separated by rhachilla segments which provide useful taxonomic characters in terms of length, shape and indumentum. In *V. membranacea*, *V. fasciculata* and *V. fontquerana* (*Vulpia*) and in *Spirachne* the apical group of sterile florets is borne on a long slender rhachilla segment which separates this group from the fertile florets.

Dispersal units. In most species the unit of dispersal is a single floret with the next higher rhachilla segment, the spikelet disarticulating at the base of each floret and leaving the pedicel and two glumes on the parent plant. There is usually no abscission layer at the base of sterile or male florets, so the most distal fertile floret carries

Fig. 1. Spikelets of representative species of *Vulpia* sensu lato. – A: *V. geniculata*. – B: *Vulpiella tenuis*. – C: *V. fasciculata*. – D: *V. alopecuros*. – E: *V. fontquerana*. – F: *V. inops*. – G: *Ctenopsis pectinella*. – H: *V. octoflora*. – I: *Ctenopsis gypsophila*. – K: *V. myuros*. – L: *V. ambigua*.

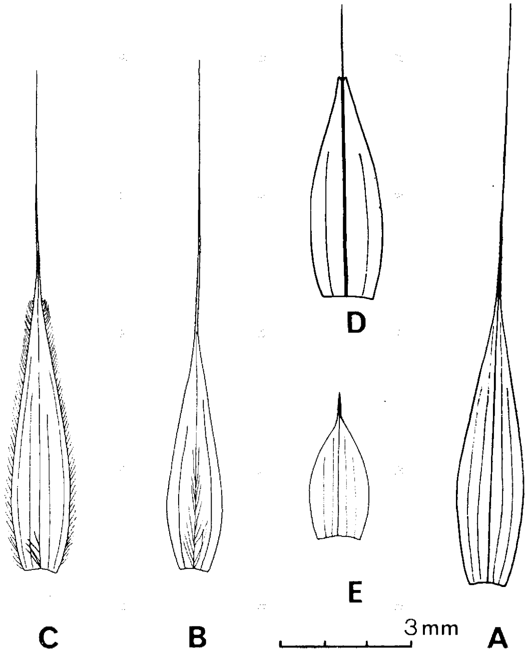


Fig. 2. Lemmas of representative species of *Vulpia* sensu lato. – A: *V. bromoides.* – B: *V. ciliata* (from fertile floret). – C: *V. ciliata* (from sterile floret). – D: *Vulpiella tenuis.* – E: *Ctenopsis gypsophila.*

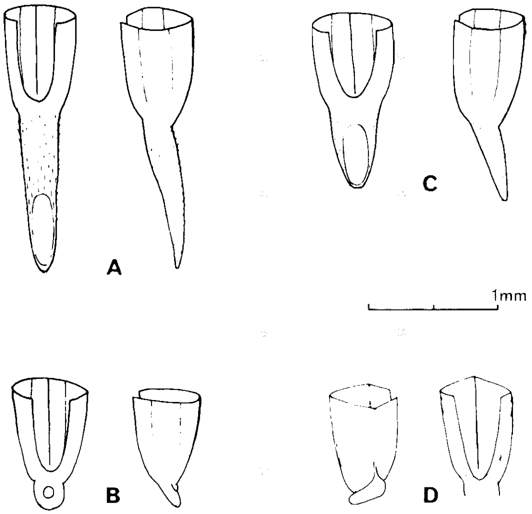


Fig. 3. Adaxial and lateral views of lemma calluses of representative species of *Vulpia* sensu lato. – A: *V. fontquerana.* – B: *V. fasciculata.* – C: *V. bromoides.* – D: *Vulpiella tenuis.*

with it any more distal sterile ones. Such a unit is thus particularly bulky in *V. ciliata, V. ambigua, V. fontquerana, V. fasciculata,* and *V. membranacea* (*Vulpia*). In plants of the first three of these species bearing spikelets with only one fertile floret, all the florets therefore fall as a single unit. In all these species the antrorsely hispid lemmas are efficient in penetrating fur and clothing, etc., and act as a dispersal agency.

In *V. fasciculata* and *V. membranacea* (*Vulpia*) and in *Loretia* abscission occurs less readily below each floret, but in addition there is an abscission layer at the base of the pedicels. Hence the dispersal units are mixtures of single fertile florets, single fertile florets with one or more sterile florets attached, and whole spikelets. The last are particularly characteristic of *V. alopecuros* (*Loretia*). In these species abscission sometimes occurs at the base of each rhachilla segment rather than above it. The antrorsely hispid, distally dilated pedicels are efficient in dispersing whole spikelets.

In *Spirachne* there is little abscission within or below each spikelet, but it regularly occurs at the base of the ultimate panicle branch bearing three spikelets, so that the unit of dispersal is three spikelets (with a total of three fertile florets).

In *Vulpiella* abscission often occurs also at the position of the pulvini, at the base of the pedicels and panicle branches, a feature shared with the related genus *Cutandia* but scarcely developed in the pulvinate *V. microstachys* (*Vulpia*).

Floret characters

Callus. The callus appears to be derived from the most basal part of each rhachilla segment, and the lemma arises from it. In most species the line of disarticulation lies adjacent to and below the callus, so that it forms the most basal part of each separated, ripe floret. In the majority of species considered here it is a thickened, glabrous, horse-shoe-shaped structure, approximately 0.1–0.2 mm in the plane of the longitudinal axis of the lemma (Fig. 3 C, D). However, in *V. alopecuros* (*Loretia*) and *V. fasciculata* and *V. membranacea* (*Vulpia*) it is much longer (0.5–0.8 mm), pointed and antrorsely hispid (Fig. 3 B), while in *V. fontquerana* it is 1–1.5 mm, antrorsely hispid and sharply pointed (Fig. 3 A). In the last case the callus is about as long as the rest of the rhachilla segment, the florets thus being separated by 2–3 mm, and serves as an effective agent of dispersal. In the other three species, on the other hand, the spikelets often fall as a single unit, so the pointed callus plays a much lesser role in dispersal.

Lemma. The usual features of the lemma such as size, shape, number and prominence of veins, length of awns and pubescence are all important diagnostic characters, but many of them vary at or even below the species level.

The longest lemmas (excluding awns) are found in *V. alopecuros* (*Loretia*), *V. fasciculata* and *V. membranacea* (*Vulpia*), where they may be up to c. 18 mm long, and the shortest in *V. sciurea* (*Vulpia*), where they are only 2.5–3.5 mm long. It must be emphasised that these measurements apply to only the two lowest florets, and are extremes of means. More distal florets usually have smaller parts, those of apical, sterile florets often being minute, and exceptional spikelets can often be found where even the basal florets have measurements outside those given above. We consider that mean basal lemma length is the most satisfactory measurement for diagnostic purposes. Lemma width is seldom of diagnostic value, but it can be used to separate *V. bromoides* (1.3–1.9 mm) and *V. muralis* (0.8–1.3 mm) (*Vulpia*).

In *Vulpia, Loretia, Spirachne* and *Ctenopsis* the lemma is narrowed at the apex into an awn of varying length, often longer than the lemma itself (Fig. 2A–C). In *Ctenopsis* (Fig. 2E) and some species of *Vulpia* the awns are shorter, the extreme being found in *C. pectinella,* with awns up to c. 1 mm only. The lemma is mostly very gradually narrowed at the apex, but in *Ctenopsis* and a few *Vulpia* species it is more abruptly so. In *Vulpiella* (Fig. 2D) the lemma is slightly but distinctly notched at the apex, and the awn arises from the termination of the midrib at the base of the notch, as in the genus *Cutandia*.

In *Vulpia, Loretia, Spirachne* and *Ctenopsis* the lemmas are mostly 5-veined and rounded on the back, although in *C. pectinella* they are somewhat keeled and in *V. ciliata* and *V. ambigua* (*Vulpia*) they often possess only 3 veins (Fig. 2B, C). In all cases the veins are usually rather inconspicuous. In *Vulpiella,* on the other hand, the lemmas are conspicuously 3-veined and strongly keeled on all 3 veins (Fig. 3D). In lemma characters, therefore, *Vulpiella* closely resembles the genus *Cutandia*. It must be noted that in both *Cutandia* and *Vulpiella* microscopic examination of cleared lemmas usually shows an extra pair of very weakly developed veins.

Lemma (and glume) pubescence is a very variable character, but its pattern of variation is sometimes of great interest. In some species no variation has been recorded, e.g. *V. membranacea* (*Vulpia*), where the lemmas are glabrous apart from antrorsely directed pricklets on the awn and veins. But in most species variation occurs from totally glabrous to densely pubescent lemmas. The pubescence of the glumes and lemmas, and of the margins, veins and other surfaces of the lemma, often varies independently, so that a great many combinations are possible. These are particularly numerous in *V. alopecuros* (*Loretia*) where they were treated in detail by Maire (1955), and in *V. microstachys* (*Vulpia*), in which many segregates have been described based on these and other characters (Lonard & Gould 1974). *V. megalura* (*Vulpia*) is in fact only a variant of V. *myuros* with ciliate lemmas and we therefore recognise it as only a forma of the latter (Stace & Cotton 1976 b). In most species the variant with densely pubescent lemmas is much less common than the subglabrous variant, but in *V. hirtiglumis* (*Vulpia*) the reverse is the case, only one example of this species without pubescent lemmas having been seen by us. *V. ciliata* and *V. sciurea* (*Vulpia*) and *V. alopecuros* (*Loretia*) are also more often pubescent than not. *V. ciliata* differs from *V. ambigua* mainly in its lemma pubescence, being hairy on the margins and dorsal midline in the former but glabrous or scabrid in the latter. There are also small differences in floral measurements between these two species, which are more or less allopatric. There are, however, occasional glabrous variants of *V. ciliata* (var. *imberbis* (Vis.) Halácsy) which occur among typical variants well outside the geographical range of *V. ambigua*.

Palea. The paleas provide relatively few diagnostic characters. In all the species they are 2-keeled, bifid at the apex and slightly shorter than to as long as the lemmas, but small specific differences in overall shape, degree of apical notching and pubescence do occur. Palea length

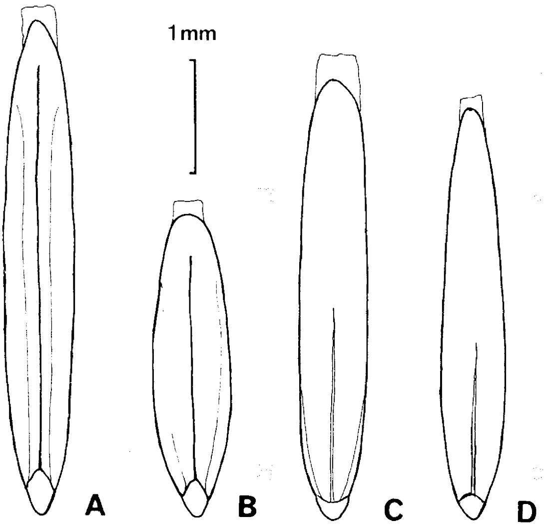


Fig. 4. Adaxial views of caryopses of representative species of *Vulpia* sensu lato. – A: *V. myuros*. – B: *V. octoflora*. – C: *Vulpiella tenuis*. – D: *Ctenopsis cynosuroides*.

may be a slightly better discriminant than lemma length in separating *V. fasciculata* from *V. membranacea* (*Vulpia*).

Stamens. In *Loretia, Spirachne, Ctenopsis* and *Vulpiella* there are usually three stamens, which become exserted at anthesis, although the anther size and the degree of exsertion varies a good deal. Thus in *C. pectinella, C. cynosuroides, C. gypsophila* and *Spirachne* the anthers are only c. 0.4–1.4 mm and appear just beyond the lemma tip at anthesis, whereas in species of *Loretia* they are mostly 2–4 mm and pendent on long filaments. Occasionally, plants of these groups with only 1 or 2 stamens have been recorded (cf. Maire 1955).

In *Vulpia* there is a greater range in such stamen characters. *V. fasciculata* and *V. membranacea* have 1–3 anthers which are 0.7–2 mm and just exserted at anthesis; *V. fontquerana* has 3 anthers 0.5–0.8 mm and also just exserted at anthesis; and the other species have usually a single anther 0.3–0.8 mm and included at anthesis. In the third group occasional specimens are encountered with 2 or 3 anthers, or in which the anther just protrudes at anthesis or slightly exceeds 0.8 mm, but basically it is a group of cleistogamous, self-pollinated grasses. Within it, *V. ciliata* and *V. ambigua* represent extremes; they are ephemeral, cleistogamous grasses with a single anther 0.4–0.6 mm long. However, we have seen specimens of *V. myuros* in England and of *V. muralis* in Sicily with a single, well-exserted anther, and similar examples of the American species have been reported by Lonard & Gould (1974) and Kannenberg & Allard (1967). *V. persica* has 1–3 small anthers, and there is no justification for Bor's (1970) referring it to *Loretia*. The undehisced anthers are either yellowish or deep violet in colour, and we have seen both colour variants on different plants in the same population of several species. Similar variation is found in a great many grasses of varying relationships, and seems to be of very little taxonomic significance.

Ovary and lodicules. These organs provide relatively few taxonomic characters. In *Vulpiella* the lodicules are ovate and rather irregularly toothed at the apex, whereas in *Vulpia, Loretia, Spirachne* and *Ctenopsis* they are usually narrower and are conspicuously bifid, the relative lengths and shapes of the two teeth varying from species to species. In lodicule characters *Vulpiella* resembles the genus *Cutandia* rather than *Vulpia* and its allies.

The ovary is glabrous in most species, and provided with two terminal or subterminal styles. However, in all species of *Loretia* except *V. alopecuros*, in *V. fasciculata* (*Vulpia*), and in *Spirachne* it is conspicuously pubescent at the apex. This character is a constant discriminant between *V. fasciculata* and *V. membranacea*, which are otherwise extremely difficult to separate. It should be noted that in Paunero (1964) the drawings of the spikelets (Figs. 21, 22) of these two species have become transposed, so that the ovary of *V. fasciculata* wrongly appears glabrous.

Caryopsis. The caryopsis varies from linear to narrowly elliptic in outline, with a short embryo visible at the base of the abaxial (dorsal) surface. The species with the relatively broadest caryopsis (ratio c. 1:4) is *V. octoflora* (*Vulpia*) (Fig. 4 B), and those with the narrowest ones (ratio c. 1:7) are *V. membranacea, V. fasciculata, V. myuros* (Fig. 4A), *V. ciliata* and *V. ambigua* (*Vulpia*). Those species with a pubescent ovary-tip retain this characteristic on the ripe caryopsis. According to Paunero (1963) the apex of the caryopsis is papillose in *Ctenopsis delicatula* and *C. cynosuroides,* and smooth in *C. gypsophila* and *C. pectinella,* but we have not observed such a difference.

The abaxial surface is rounded in *Vulpia, Loretia, Spirachne* and *Ctenopsis,* but strongly carinate in *Vulpiella,* producing a more or less trigonous caryopsis. The edges of the caryopsis are rolled round on to the adaxial side to produce a groove which obscures the hilum to varying degrees in different species.

The hilum is very narrow and almost as long as the caryopsis in *Vulpia, Loretia* and *Spirachne* (Fig. 4A, B), but less than half as long in *Ctenopsis* and *Vulpiella* (Fig. 4C, D).

The palea is wrapped round the caryopsis and in *Vulpia, Loretia, Spirachne* and *Vulpiella* is firmly adherent to it, but in *Ctenopsis* the caryopsis remains more or less free from the palea.

Leaf characters

Morphology. Leaf morphology is not very variable. All the species possess flat leaf-blades which, however, become convolute as the season advances. In dry conditions this often takes place well before flowering.

A few species show conspicuously dilated upper leaf-sheaths, this character being particularly well displayed in *V. fasciculata* (*Vulpia*) and to a lesser extent in other species where the inflorescence is partially enclosed in the uppermost leaf-sheath at anthesis.

The membranous ligules show some variation in length, which is particularly useful in separating *C. delicatula* (0.1–0.5 mm), *C. gypsophila* (0.5–1.5 mm) and *C. cynosuroides* (1–2.5 mm).

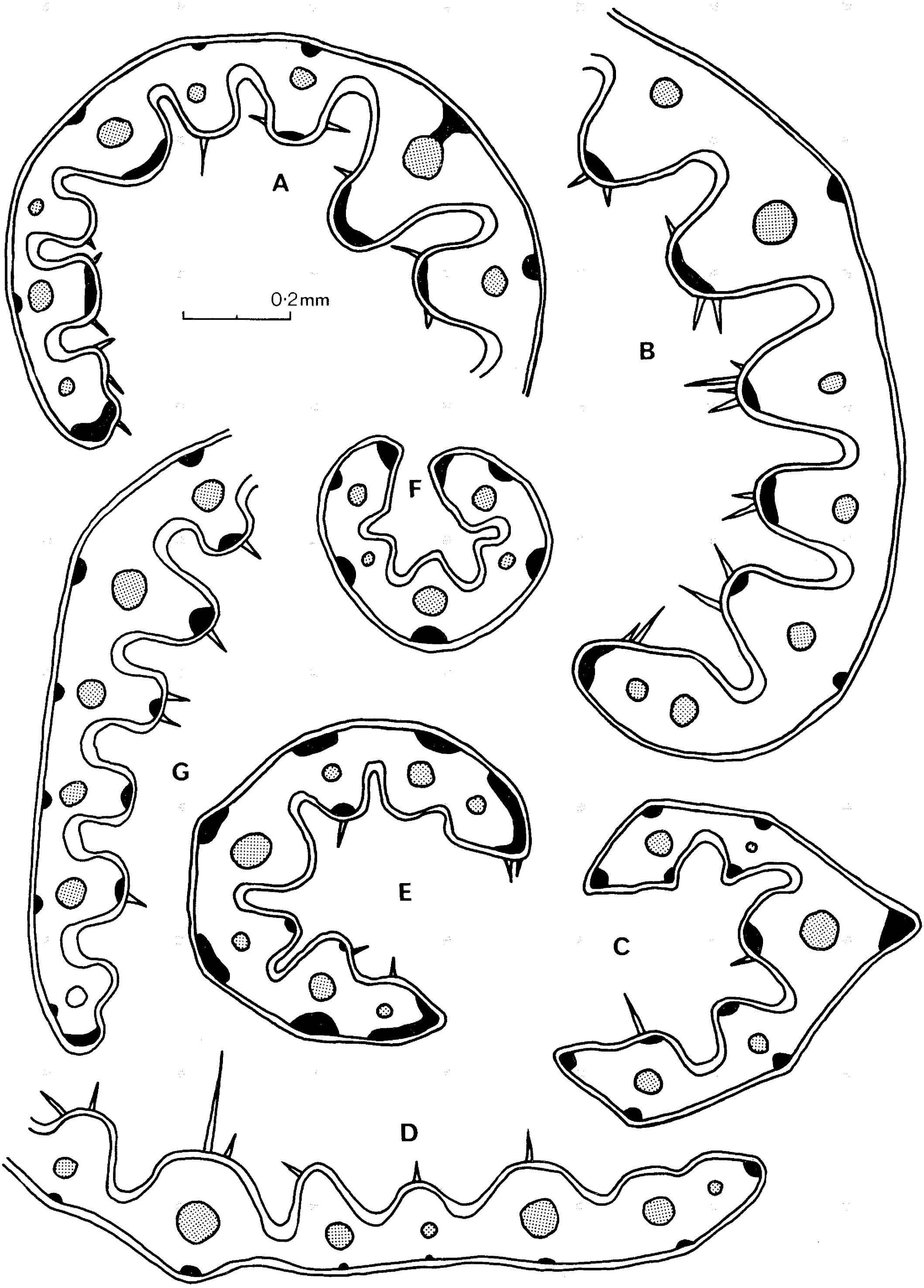
Internal anatomy. The anatomical details of the leaves follow the typical festucoid pattern described by Metcalfe (1960).

The adaxial surface of the leaf-blade is strongly ribbed, each rib corresponding to the position of a vascular bundle, the most prominent of which is the midrib itself (Fig. 5). In most species there are approximately 9–13 veins across the leaf width, the midrib and the third one on either side being larger than the others, but frequently some of the smaller veins are missing or there are extra ones. In *Ctenopsis* and *Spirachne* there are usually only 5–7 veins, which alternate between large and small.

Bundles (caps) of fibres above and below each vein, especially the midrib, and at the leaf margins, are developed to varying extents. They are distinctly better developed in *V. fasciculata, V. membranacea* and *V. fontquerana* (*Vulpia*), *Loretia, Vulpiella* and (especially) *Ctenopsis* than in *Spirachne* and the rest of *Vulpia.* In some cases, especially in *Vulpiella* and *Spirachne,* the epidermal cells contiguous with the sclerenchyma bundles, particularly on the abaxial surface, are lignified and very narrow in cross section, as is equally clearly seen on epidermal preparations. *Spirachne* (Fig. 5C) is also distinctive in that the abaxial leaf surface is keeled on the midrib and major lateral veins, whereas it is more or less rounded or flat in all other species. The differences in the bulliform cells of *V. myuros* f. *myuros* and f. *megalura* given by Lonard & Gould (1974) were not observable in our material.

Epidermis. The epidermal anatomy is again typically festucoid (Metcalfe 1960), but variation within this pattern occurs. The abaxial epidermis exhibits two major zones, costal and intercostal, but on the adaxial epidermis there is a narrow intermediate zone between the two, and the intercostal zone can be subdivided into central bulliform and marginal stomatal regions. On both epidermises long cells, short cells, hairs and stomata may occur.

The epidermises of *Vulpia, Loretia, Spirachne,* and *Ctenopsis* are very similar. On the abaxial epidermis (Fig. 6A) the long cells are very long, parallel sided and have tightly undulate anticlinal cell-walls in the intercostal zones. The short cells vary greatly in abundance, but are generally present in both costal and intercostal zones. They are very short, with smooth walls, and vary in the degree to which they are single or paired; single short cells are either cork-cells or prickle-bases, whereas double short cells consist of two cork-cells, a cork-cell and a silica-cell or a cork-cell and a prickle-base. In the costal zone up to about four adjacent short cells may occur. On the abaxial surface all the hairs are prickles: short, more or less conical, thick-walled hairs arising from a short cell. They are present on the leaf margin and to varying degrees (but never frequent) in the costal and intercostal zones. Stomata are only of sporadic


A
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occurrence on the abaxial epidermis; when present they are confined to the intercostal zones.

On the adaxial epidermis (Fig. 6B), except close to the margins, the long cells are straight-walled, and short cells (apart from hair- or prickle-bases) rather infrequent and more or less confined to the costal and intermediate zones. Hairs are generally much more abundant than on the abaxial epidermis, but may or may not be confined to the costal zone. In almost all cases at least the majority of hairs in the costal zone are macrohairs, often mixed with prickles and sometimes with intermediate types. Microhairs and papillae are absent. The density of macrohairs varies considerably from species to species and to some extent within species and, of course, constitutes the macroscopic character 'leaf pubescence'. Macrohairs are absent from the material seen of *V. sciurea* (*Vulpia*) and *C. pectinella*, and prickles too (except on the leaf margin) from that of the latter; material of all the other species examined possesses both macrohairs and prickles. The stomatal zone consists of modified (shorter) long cells with rows of stomata bearing the typically gramineous paired subsidiary cells. The bulliform cells are large, thin-walled cells with flattened ends.

Within *Vulpia, Loretia, Spirachne* and *Ctenopsis* variation is thus virtually confined to the frequency, distribution and pairing of short cells and the frequency of prickles on the abaxial epidermis, and the frequency and distribution of prickles and macrohairs on the adaxial epidermis, and the quantitative differences observed are not well correlated with any of the four taxonomic groupings. Moreover, it is possible, with the examination of further material, that many of the apparent interspecific differences would disappear. Epidermal characters of this sort, possibly distinguishing *V. fasciculata* and *V. membranacea* (*Vulpia*), have been given by Stace & Cotton (1976 a).

The epidermal characters of the single species of *Vulpiella* (Fig. 6C, D) differ markedly from the above. The main differences are as follows:

(1) Short cells are confined to the costal zones on both epidermises.

(2) Short cells on both epidermises are often in pairs or greater units, or separated by longer short-cells.

(3) Short cells on both epidermises are much longer than in the other taxonomic groups, and mostly with markedly undulate anticlinal walls.

(4) Silica cells all have markedly undulate anticlinal walls and occur in the costal zones of both epidermises.

(5) Long cells on the abaxial epidermis have straight anticlinal walls, and are conspicuously wider at their midpoint than at their ends.

(6) There are more stomata in the intercostal zone on the abaxial epidermis.

(7) Hairs are absent from the abaxial epidermis.

(8) Prickles are present in the costal zone but hairs are otherwise absent from the adaxial epidermis.

The list of differences is impressive, and moreover leads to a much closer resemblance between abaxial and adaxial epidermises of *Vulpiella* than between those of the other four groups.

Table 2. Stomatal length and chromosome number in two species groups of *Vulpia*. Stomatal lengths are ranges of means (in three cases only one collection measured).

Species	2n	Stomatal length (μm)
V. myuros	42	34–57
V. hirtiglumis	42	53
V. bromoides	14	24–39
V. muralis	14	29–43
V. octoflora	14	39
V. fasciculata	28	33–59
V. membranacea	14	26–41
V. fontquerana	14	36

Stomatal length. Although there is not a good overall correlation between chromosome number (Cotton & Stace 1976) and stomatal length, within certain critical species groups of *Vulpia* it is better. Table 2 shows that the hexaploids *V. myuros* and *V. hirtiglumis* have on average longer stomata than the three related diploids, and that the tetraploid *V. fasciculata* has on average longer stomata than its two related diploids.

Fig. 5. Leaf-sections of representative species of *Vulpia* sensu lato. – A: *V. alopecuros*. – B: *V. fasciculata*. – C: *V. inops*. – D: *V. myuros*. – E: *Ctenopsis gypsophila*. – F: *Ctenopsis pectinella*. – G: *Vulpiella tenuis*. – Shaded regions: vascular bundles. Black regions: sclerenchyma.

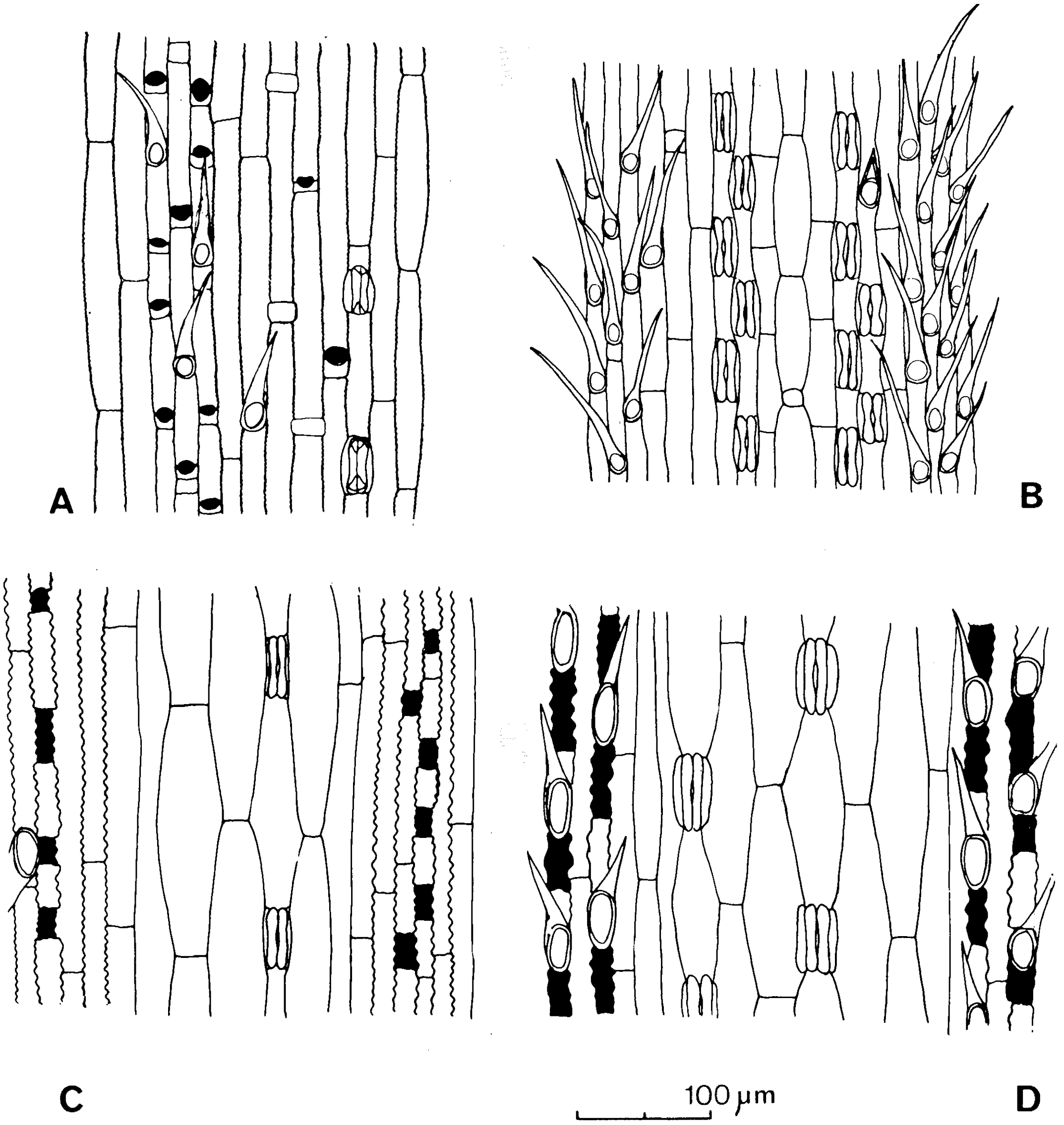

Fig. 6. Epidermises of *Vulpia alopecuros* (A, abaxial; B, adaxial) and *Vulpiella tenuis* (C, abaxial; D, adaxial). – Black regions: silica-cells.

Discussion

The morphological and anatomical characters previously surveyed clearly serve to differentiate taxa at all levels. Hence, it is possible to define each of the five taxonomic groups recognised and various subgroups within some of them, as well as the individual species and infraspecific taxa.

Vulpiella

Of the five groups, *Vulpiella* is clearly the most distinct. It differs from *Vulpia, Loretia, Spirachne* and *Ctenopsis* in the well-developed pulvini at the base of the inflorescence branchlets, at which disarticulation takes place; in the 3-veined, 3-keeled lemmas with a notched apex; in the broad, irregularly toothed lodicules; in the trigonous caryopsis with a short hilum; and in a considerable number of features of the leaf epidermis (notably the straight-walled long cells and the relatively long, undulate-walled silica-cells on both epidermises). Many of these characters are traditionally considered important diagnostic features in the Gramineae, and together they provide convincing evidence that *Vulpiella* and *Vulpia* are not congeneric. In all its important characters the single species of *Vulpiella* most closely resembles the genus *Cutandia*, which will be reviewed in a later paper; it is simply the long awns and non-divaricating inflorescence branches of *Vulpiella* which give it a superficial resemblance to *Vulpia*. We are therefore of the opinion that Duval-Jouve (1880) and Camus (1943) were wrong in placing this species in *Loretia* Duval-Jouve and in *Vulpia* subgenus *Loretia* section *Incrassatae* A. Camus respectively.

Ctenopsis

Ctenopsis differs from the other three groups in its relatively short, broad caryopses which have a short hilum and which lie more or less free from the palea at maturity, although we are not aware that these characters have been stressed by previous workers. Traditionally (cf. Maire 1955) *Ctenopsis* has been treated as a monotypic genus (type species *C. pectinella*), but Paunero (1963) added to it the other three species in Table 1. These have been usually included in *Vulpia*, although the name *Narduretia* has also been coined for them (Huguet del Villar 1925). *C. pectinella* is certainly the most distinctive of the four species, particularly with regard to its sessile spikelets, keeled, shortly-awned lemma apex and glabrous leaf epidermis, but in general the characters surveyed here support Paunero's broader concept of the genus. It is additionally characterized by its simple, secund inflorescence, large abaxial bundles of leaf sclerenchyma, minute lower glume, rather abruptly narrowed lemmas often with rather short awns, keeled upper glume in two species, and 3 short, slightly but distinctly exserted anthers. While arguments could be made for including *Ctenopsis* in *Vulpia*, we feel that at least equally strong arguments exist for recognising it as a distinct genus and we therefore prefer to follow Paunero's treatment.

Vulpia, Loretia and Spirachne

There are good differences between *Loretia* and *Vulpia* if, for the present, we set aside *V. fasciculata, V. membranacea* and *V. fontquerana*. *Loretia* has chasmogamous florets with three long anthers, well developed leaf-sclerenchyma, and distally dilated pedicels with a basal abscission layer, while in *Vulpia* the florets are cleistogamous (or nearly so) with often a single, short anther, the leaf-sclerenchyma is less abundant, and the pedicels are unthickened and lack an abscission layer. These are clear differences which, in the absence of *V. fasciculata* and its two allies, would strongly suggest generic separation for *Vulpia* and *Loretia*.

V. fasciculata and *V. membranacea* are very closely related and have been much confused in the past (Stace & Cotton 1976 a); many authors have not recognised them as distinct species (cf. Maire 1955). *V. fontquerana*, a recently discovered endemic from SW. Spain (Melderis & Stace 1968), is much more distinct, but nevertheless obviously closely related. The three share in common the general facies and short anthers of *Vulpia*, and the well developed leaf-sclerenchyma, distally dilated pedicels and usually 3, exserted anthers of *Loretia*. Moreover, spikelet disarticulation of *V. fontquerana* is as in *Vulpia*, whereas that of the other two species is as in *Loretia*, and the hairy ovary apex of *V. fasciculata* is found elsewhere in *Loretia* but not in *Vulpia*. These facts clearly show that *V. fasciculata, V. membranacea* and *V. fontquerana* form a well-defined taxon somewhat intermediate between *Loretia* and *Vulpia*. This group is further characterized by the well-awned upper glumes, the distinctive apical group of sterile florets and the very well developed, pointed basal callus. It (or those members of it under study at the time) has previously been described as section *Monachne* (Dumortier 1824) and section *Intermediae* (Camus 1943).

Spirachne is clearly most similar to *Monachne* of the above 3 groups, with which it shares the apical group of sterile florets, 3 short, slightly exserted anthers, the awned upper glume and distally dilated pedicels. It is, however, unique in its groups of three spikelets (each usually with a spiral aestivation), subequal glumes and keeled leaves.

Thus, within the genus *Vulpia*, excluding

Vulpiella and *Ctenopsis,* four major groups are recognisable. Within each of these there is variation roughly proportional to the number of species, but in our opinion it does not warrant recognition of further supra-specific categories. Some of this variation is parallel within the four groups. For example the glume ratio shows a wide range of variation in *Vulpia, Monachne* and *Loretia,* the range being greatest in *Vulpia* and least in *Monachne,* and awn-length is similarly variable. The existence of parallel variation within many species, regardless of the group to which they belong, has been pointed out previously, particularly with regard to pubescence.

Within each of the two largest groups, *Vulpia* and *Loretia,* there are species or groups of species with distinctive, exceptional features. Notable among these is the perennial habit in *V. sicula, V. setacea* and *V. litardiereana* (*Loretia*); the characteristic group of apical sterile florets and 3-veined lemmas in *V. ciliata* and *V. ambigua* (*Vulpia*); the subsessile spikelets in *V. persica* (*Vulpia*); and the pulvinate inflorescence branches in *V. microstachys* (*Vulpia*).

Relationship to Festuca

The closest relations of *Vulpia* (including *Loretia, Monachne* and *Spirachne*) are *Ctenopsis,* discussed above, *Nardurus,* to be discussed in a later paper, and *Festuca. Festuca* and *Vulpia* have been traditionally separated by up to six characters, none of which, however, forms an absolute criterion. Hence *V. sicula* and its two allies are perennials, *V. geniculata, V. setacea* and others have well-branched panicles, *Loretia* has chasmogamous florets, *V. octoflora* and *Spirachne* have subequal glumes, *V. octoflora* has rather abruptly narrowed and shortly awned lemmas, and *V. geniculata* and *V. bromoides* have relatively broad caryopses; all these characters are typical of *Festuca.* Nevertheless it is possible to separate the two genera by a combination of characters and, although it is admittedly simply a practical convenience, we prefer this to their amalgamation.

Of the four groups of *Vulpia, Loretia* is obviously the most similar to *Festuca,* forming a link between *Festuca* and the other three groups.

Taxonomic conclusions

We consider *Vulpiella, Ctenopsis* and *Vulpia* to be separate genera, but the status of these and the ranks accorded the four groups within *Vulpia* will remain a matter of subjective judgement unless numerical taxonomic studies can produce an acceptable objective system.

Loretia, Vulpia and *Spirachne* are all distinct groups which might well merit recognition at the generic level but for the fact that *Monachne* clearly links the former two and *Spirachne* seems closer to *Monachne* than to the others. Therefore we recognise these four groups as sections of *Vulpia.* We consider this classification to be the most useful and practical, but it is clearly a phenetic, not a phylogenetic, one.

Within *Ctenopsis, C. pectinella* is distinct from the other three species and the two groups merit sectional status.

The following conspectus sets out the classification we have adopted, together with the most important supra-specific synonyms and an indication of the scope of each taxon. A more detailed taxonomic description of all the taxa, including the species, will be given in a later paper.

Vulpiella (Trabut) Burollet

Basionym: *Cutandia* subg. *Vulpiella* Trabut
Type species: *Cutandia incrassata* (Salzm. ex Loisel.) Bentham = *Vulpiella tenuis* (Tineo) Kerguélen
Other synonyms: *Cutandia* sect. *Vulpecula* Hermann; *Vulpia* subg. *Loretia* sect. *Incrassatae* A. Camus, pro parte excl. typ.
Monotypic

Ctenopsis De Not.

Type species: *C. pectinella* (Del.) De Not.

Sect. **Ctenopsis**

Synonym: *Festuca* subg. *Vulpia* sect. *Pectinula* Hermann
Monotypic

Sect. **Pseudocynosurus** (Willk.) Cotton & Stace, comb. nov.

Basionym: *Vulpia* sect. *Pseudocynosurus* Willk., in Willk. & Lange, Prodr. Fl. Hisp. 1: 91 (1861)
Type species: *V. delicatula* (Lag.) Dumort. = *C. delicatula* (Lag.) Paunero
Other synonyms: *Narduretia* Huguet d. Villar; *Festuca*

subg. *Vulpia* sect. *Ctenopsis* sens. Hermann, non sens. orig.
Other species: *C. gypsophila* (Willk. ex Hackel) Paunero; *C. cynosuroides* (Desf.) Paunero

Vulpia C. C. Gmel.

Type species: *V. myuros* (L.) C. C. Gmel.
Synonyms: *Mygalurus* Link; *Dasiola* Raf.; *Chloamnia* Raf.; *Distomomischus* Dulac

Sect. **Vulpia**

Synonym: *Vulpia* subg. *Euvulpia* sect. *Articulatae* A. Camus
Species included: All species under sect. *Vulpia* in Table 1 with the exception of the three included under sect. *Monachne* below

Sect. **Monachne** Dumort.

Type species: *V. uniglumis* (Ait.) Dumort. = *V. fasciculata* (Forsk.) Samp.
Synonym: *Vulpia* subg. *Euvulpia* sect. *Intermediae* A. Camus
Other species: *V. membranacea* (L.) Dumort.; *V. fontquerana* Melderis & Stace

Sect. **Spirachne** (Hackel) Boiss.

Basionym: *Vulpia* subg. *Spirachne* Hackel
Type species: *V. inops* (Del.) Hackel
Monotypic

Sect. **Loretia** (Duval-Jouve) Boiss.

Basionym: *Loretia* Duval-Jouve
Lectotype species: *L. geniculata* (L.) Duval-Jouve, selected here, = *V. geniculata* (L.) Link
Other synonyms: *Vulpia* subg. *Pseudofestuca* Rouy; *Vulpia* subg. *Loretia* sect. *Festucoides* A. Camus & sect. *Incrassatae* A. Camus, pro parte incl. typ.
Other species: All species under sect. *Loretia* in Table 1.

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Spore-producing and apical meristems in vascular plants – a comparison

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A comparison, mainly based on literature between the organization of spore-producing and apical meristems is made in various groups of vascular plants. The comparison is carried out only with respect to the occurrence of periclinal divisions in the superficial cell layer of the meristems and concerning the pteridophytes also in respect to the number of initials. The two kinds of meristems are reported to be undifferentiated (unstratified) in pteridophytes and differentiated in angiosperms except for the roots of a number of angiosperms. During the evolution a transition from undifferentiated to differentiated apical meristems and spore-producing meristems probably has occurred. In most gymnosperms studied the spore-producing meristems have attained the more advanced stage while the shoot apical meristems of most genera still are quite undifferentiated or show intermediate conditions.

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The distinguished British morphologist, Bower (1896), stated that the study of the sporangia of a vascular plant should be carried out in the light of a knowledge of the segmentation of its apical meristems. He considered that the earliest development of the sporangia in the main corresponds to the growth of the apical meristems of the same plant. According to this view plants with tunica-corpus differentiated (stratified) shoot apices should have sporangia which originate from two separate initial layers (epidermal and subepidermal initials) and that plants with undifferentiated (not tunica-corpus differentiated, unstratified) shoot apices should have sporangia which are derived from the outermost cell layer of the mother organ. Bower's statement also implies that the organization of all apical meristems of a plant is essentially similar. Later Allen (1946), Foster & Gifford (1959) and Fagerlind (1961, 1971) discussed the correlation between the structure of spore-producing meristems and that of shoot apical meristems. However, no detailed comparison between the two types of meristems within different groups of vascular plants has been performed. For that reason this survey of the organization of shoot and root apical meristems as well as spore-producing meristems has been carried out. On the basis of this information an attempt has been made to compare the two kinds of meristems.

Apical meristems are unlimited contrary to spore-producing ones and exhibit various patterns of zonal structure which do not occur in sporangia. On that account no comparison between the meristems is made in regard to cytohistological zonation and to the degree of mitotic activity in different cell complexes except for the rate of periclinal divisions in the outermost cell layer. The comparison is carried out only with respect to the occurrence of periclinal divisions in the superficial cell layer of the meristems and concerning the pteridophytes also with respect to the number of initials. With meristem initial(s) is (are) here meant the cell or the cells from which all meristem tissue ultimately is derived. In this paper the descriptions of vegetative meristems generally refer to fully developed shoots and roots.

Within many systematic groups the information about the organization of apical meristems and/or spore-producing meristems is insufficient or lacking. Since there is very little information on the structure of the meristems in question of one and the same plant the comparison between the meristems has been made between different plants of the species or between different species of the genus. In some cases there are contradictory reports in the literature respecting a certain type of meristem of a species or a genus which may be due to many reasons. The structure of the meristem may be different in different individuals of the species or in various species of the genus. The investigations perhaps do not refer to the same stage of development and the meristem may show different organization during the ontogeny. Furthermore the same meristem may have been interpreted in various ways by different authors. It seems, however, that at least most species of a genus usually show the same organization concerning a certain meristem in regard to the presence or absence of a discrete outer layer and in regard to the number of initials (one or more). Even if the present paper is a preliminary report it will give information on whether Bower's theory is correct.

The reports on the ontogeny of the sporangia are partly based on the author's own investigations (Brunkener 1973, 1975). In the present paper the results from the author's preliminary studies on vegetative shoot apices and on strobili of some gymnosperms are also mentioned. The references concerning a certain taxon in most cases represent only a selection of works.

Pteridophytes

The growth of the pteridophyte shoots is initiated from one or more cells in the superficial layer. In some genera, however, the frequency of periclinal divisions in the surface at the summit of the apex is low or very low. Most investigations about the roots show that there is a single apical initial or a layer of initials immediately inside the root cap. The sporangia in all pteridophytes are initiated from one or more cells in the outermost layer of the mother organ.

Thus the spore-producing meristems and the shoot apical meristems of pteridophytes and the root apical meristems of at least most pteridophytes are undifferentiated which agrees with Bower's theory. Below some reports are mentioned in which the initials of the apical meristems are described to be stratified or to show a tendency to stratification. Moreover, an attempt has been made to compare the number of initial cells (one or more) of the sporangia and of the apical meristems of shoots and roots.

Psilotaceae

The apical meristem of the rhizome and the aerial shoot of *Psilotum* (Ford 1904, Bierhorst 1954) and the rhizome of *Tmesipteris* (Sykes 1908) is reported to possess a single, large apical cell. Wardlaw (1945) found that such a cell usually can be observed but that it is difficult to refer the development of the meristem to the division of a single cell.

Regarding the sporangium Bower (1894, 1908) could not definitely say that there is only one initial cell. Fagerlind (1961) was of the same opinion concerning *Psilotum* while Bierhorst (1968) stated that the sporangium of both genera originates from a group of surface cells. The author's studies on *Psilotum* have shown that the initiation of the sporangium at least sometimes can be traced to the division of a single mother cell.

Lycopodiaceae

Turner (1924) reported that the apical growth of the shoot of *Lycopodium* proceeds from two groups of cells. A few superficial cells give rise to the "dermatogen" and the "periblem" while another group of cells immediately below the surface group produces the "plerome". Härtel (1938) and Freeberg & Wetmore (1967) described a group of superficial initials from which all the stem tissue is ultimately derived. Bhambie & Puri (1963) arrived at the same result but spoke about a more or less discrete superficial layer.

According to Bruchmann (1874), Stokey (1907) and Guttenberg (1964) the root apical meristem grows from four independent superimposed tiers of initials which give rise to calyptrogen, dermatogen, periblem and plerome.

The sporogenous tissue is derived from several initial cells (Bower 1908, Brunkener 1973).

Selaginellaceae

The shoot apical meristem is variable according to the species and sometimes even within the same species (Bruchmann 1909a, Wand 1914, Popham 1951). In certain species a single, usually tetrahedral apical cell has been demonstrated, while in other species two such cells or more often several initials have been described. Bruchmann (1909a) reported that in *Selaginella poulteri* young shoot apices show a single apical cell, whereas older branches may show several initials. In *S. gracilis*, Wand (1914) described a group of initials in the main shoots but a single apical initial in older lateral shoots. Bhambie & Puri (1963), however, never found signs of a single apical initial and believed that throughout *Selaginella* there is a group of large conspicuous initials in the shoot apical meristem.

Also the organization of the root apex seems to vary from species to species. A single apical cell has been demonstrated in some of the few investigated species (Guttenberg 1964, 1966, Webster & Steeves 1967). Webster & Steeves maintained that the number and distinctness of the initials may vary even during the development of the root. In *S. martensii* they found in several roots that the cap is derived from separate initials. Bruchmann (1909 b) described a stratified initial group with two distinct tiers in *S. spinulosa* and three such tiers in *S. lyallii*. According to Guttenberg (1966) species of *Selaginella* with a single apical initial in the shoots also have such a cell in the roots while other species with a group of superficial initials in the shoots exhibit a stratified initial region in the roots. It is, however, too early to propose this, since only a few species have been compared in this respect. Moreover, an investigation of *S. densa* (Webster & Steeves 1963) does not support this view.

The sporogenous tissue arises from a group of initials (Bower 1908, Brunkener 1973).

Isoetaceae

The stem apex of *Isoetes* (West & Takeda 1915, Guttenberg 1966) and *Stylites* (Rauh & Falk 1959) show a few superficial initials, which rarely divide periclinally. Bhambie & Puri (1963) described for *Isoetes* a discrete superficial layer at the summit of the apex but found some periclinal divisions on the sides. They suggested that the zone of cells inside the outermost layer at the summit is a self-perpetuating complex.

In regard to the root apex of *Isoetes* Bruchmann (1874) and Guttenberg (1964) reported a meristem with common initials for calyptrogen and dermatogen and separate initials for periblem respectively plerome. Rauh & Falk (1959) arrived at the same result regarding *Stylites*. In *Isoetes* Paolillo (1963) observed two initial groups, one that produces the procambium and the inner cortex and one that gives rise to the rest of the root. On the contrary, Bhambie (1972) described in *Isoetes* a group of common initials responsible for the formation of all parts of the root.

The sporogenous tissue is derived from a number of initials (Smith 1900, Bower 1908).

Equisetaceae

A tetrahedral apical cell is present in the shoot apex as well as in the root apex. According to the prevalent view this cell is actively dividing. Buvat & Liard (1953) and D'Amato & Avanzi (1968), however, reported that the apical cell in established shoot apices divides very rarely and is devoid of histogenetic potencies.

Regarding the sporangium Bower (1894) and Campbell (1940) always, and Goebel (1880) at least in most cases, found only one initial. Fagerlind (1961) was of the opinion that it is almost impossible to prove this. According to my own studies it appears that at least in some cases there is a single initial.

Ophioglossaceae

Campbell (1911) and Sen (1968) reported that the apex of the rhizome of *Ophioglossum* possesses a central initial that, however, cannot be designated as a typical apical cell. In contrast to this a layer of prismatic superficial initials has been observed by Gewirtz & Fahn (1960), Bhambie & Senger (1971, quoted from Bhambie 1972) and McAlpin & White (1974). Also in the shoot apex of *Botrychium* and *Helminthostachys* a single apical cell (Campbell 1911) or a group of initials (Bhambie & Senger 1971, quoted from Bhambie 1972) has been described. Stevensen (1976 b) stated that the shoot apex of *Botrychium* cytohistologically is composed of three zones of "initials". A zone of surface "initials" usually contains a conspicuous centrally located apical cell, from which all parts of the shoot are derived.

For the root apex of *Ophioglossum* a tetrahedral apical cell has been reported (Campbell 1911, Gewirtz & Fahn 1960, Sen 1968, Bhambie & Rao 1973). Campbell (1911) observed this condition also in *Botrychium* and *Helminthostachys*. He stated, however, that in all three genera the apical cell is replaced by several more or less equivalent initials in older roots. This was confirmed by Bhambie & Rao (1973) with reference to *Ophioglossum*.

The sporangium of *Ophioglossum* generally arises from a few initials but sometimes there is probably only one (Brunkener 1973). *Botrychium* and *Helminthostachys* in most cases show a single initial (Bower 1908).

Marattiaceae

A pyramidal or prismatic apical cell predominates in the apex of the stem of the young sporeling, whereas a group of equivalent initial cells occur in older shoot apices (Charles 1911, West 1917, Campbell 1918).

Corresponding conditions have been described for the root apices (Campbell 1911, West 1917, Guttenberg 1966). In thicker roots, however, there is from the beginning a number of equivalent initials.

The sporangium generally originates from a single initial (Bower 1908).

Leptosporangiatae

According to the classical view on the shoot apex of the leptosporangiate ferns the growth proceeds from a single apical cell with two or three cutting faces (Popham 1951, Wardlaw 1951, Clowes 1961, Guttenberg 1966, Foster & Gifford 1974). The results from several recent investigations support this concept of an active apical cell (Hébant-Mauri 1975, Stevenson 1976a). In *Osmunda,* however, Steeves (1963) found that a distinct apical initial may be identified in dormant shoot apices but cannot be recognized in actively growing ones. McAlpin & White (1974), who examined 19 leptosporangiate genera stated that most of them do not show a single apical cell which divides in a regular, predictable sequence. They described a promeristem consisting of many "initials" but, like many other authors, did not use the term initials for the cell or the cells from which all the tissue of the shoot is ultimately derived. In the shoot apex of *Dennstaedtia* Stevenson (1976a) distinguished a number of "initials" which are derived from a prominent apical cell. He emphasized that the apical cell is a constituent of the fern apical meristem and considered that the efforts of Hagemann (1964), De Albertis & Paolillo (1972), McAlpin & White (1974) and other authors to discount totally the presence of an apical cell is untenable.

In the root apices of the leptosporangiate ferns a single, usually tetrahedral apical initial has been demonstrated. Guttenberg (1966) and Bhambie & Rao (1973), however, found that a single apical initial in young roots of *Osmunda* is replaced by a number of equally prominent initials in older or thicker roots. In *Azolla* the apical cell of the root apex is reported to cut off a single root cap cell (Clowes 1961). Subsequently the root grows partly from the apical cell, partly from a group of cells which originates from the first root cap cell and gives rise to the root cap. According to Avanzi & D'Amato (1967) the single apical cell in the root apex of *Marsilea* behaves as a typical initial only during the early development of the root. Later the cell becomes quiescent in the sense that it does not divide or divides rarely, whereas the surrounding cells still are meristematic. Other authors such as Bhambie & Rao (1973) also found a tendency to the presence of a quiescent centre in the roots of some leptosporangiate ferns. Clowes (1967) stated that the occurrence of a single tetrahedral apical cell and the very obvious derivative pattern in the surrounding tissues does not prove that the apical cell divides to give rise to this pattern. This cell pattern merely shows that there has been a genetic relationship in the past.

The sporangium of the Leptosporangiatae with the exception of the Osmundaceae is derived from a single mother cell. In the Osmundaceae, however, the sporogenous tissue can be traced in origin to a single cell.

Discussion

Shoot apical meristems of vascular cryptogams are undifferentiated. In *Lycopodium* and *Isoetes,* however, there is a weaker or stronger tendency to the elimination of periclinal divisions in the superficial layer at the summit of the apex. In mature roots of *Lycopodium,* a few *Selaginella* species, *Isoetes, Stylites* and *Azolla* a differentiated initial group in the apex has been reported. Bhambie & Puri (1963), however, described a common group of initials in roots of *Isoetes* and Esau (1965) stated that all tissues of the root in vascular cryptogams are derived either from a single apical cell or from a number of initial cells arranged in one tier.

Since a sporangial initial in many pteridophytes in appearance does not diverge from adjacent meristematic cells and since its daughter cells at first are not divergent, it is in many cases very difficult or impossible to determine the number of initials. Often it can be decided that the first sporogenous cells of a sporangium arise through periclinal divisions of a few cells while it is uncertain whether the latter originate from a single sporangium initial. In certain cases it is also

Table 1. Number of initials of shoot and root apices and of sporangium primordia in pteridophytes. – [1] Reports of one initial in some species and more initials in other species. – [2] Reports of one initial in young apices and more initials in older apices of the same plant (species).

Taxon	Shoot apex	Root apex	Sporangium primordium
Psilotum	one	–	one (at least in some cases)
Tmesipteris	one	–	one or more?
Lycopodium	more	more	more
Selaginella	one or more[1] [2]	one or more[1]	more
Isoetes	more	more	more
Equisetum	one	one	one (at least in some cases)
Ophioglossum	one or more[1]	one or more[2]	more (in general)
Botrychium	one or more[1]	one or more[2]	one (in general)
Helminthostachys	one or more[1]	one or more[2]	one (in general)
Marattiaceae	one or more[2]	one or more[2]	one (in general)
Leptosporangiatae (excl. Osmundaceae)	one or more[1]	one	one
Osmundaceae	one or more[2]	one or more[2]	one

difficult to establish whether there is one or more initials in the apical meristems. Accordingly the comparison between the spore-producing meristems and the apical meristems in regard to the number of initials in many cases must be very uncertain. More detailed information about the number of sporangium initials in pteridophytes has been given earlier (Brunkener 1973).

Since there are different opinions about the mitotic activity of the apical cell in the fern shoot and root and since the number of species which have been thoroughly investigated in this respect is low, no satisfactory generalization about the role of the apical cell can be made. White (1971) considered, however, that it seems possible that the single apical cell of the typical fern shoot and root might be active during the early development of the organ but becomes more or less quiescent when the organ matures. This condition has also been reported in the shoot apex of *Equisetum* (Buvat & Liard 1953, D'Amato & Avanzi 1968) and may be observed in all pteridophytes with an apical cell in the shoot and root apex. If the apical cell really loses the ability to divide, the growth of the adult organ consequently proceeds from a group of initials. If the apical cell, however, is not quiescent but divides at times it must be regarded as the single true initial.

The number of initials (one or more) of the apical meristems in shoots and roots and of the spore-producing meristems are summarized in Table 1 which is partly generalized. When a single apical cell is present the cell is here considered to show at least a certain degree of mitotic activity and therefore can be regarded as a true initial. In most groups of pteridophytes the number of initials in the root corresponds to that of the shoot of the same species (genus).

The number of initials (one or more) of the apical meristems and that of the spore-producing meristems agree in *Lycopodium, Isoetes* and many species of *Selaginella* and of the Leptosporangiatae and at least sometimes in *Psilotum* and *Equisetum*. In the Marattiaceae the single initial of the sporangium corresponds to the condition in the apical meristems only in very young plants. In respect to the Ophioglossaceae the number of initials of the spore-producing meristems seems to agree with that of the shoot apices only in some species and with that of either young or old root apices.

In shoot and root apices within the Marattiaceae and the Osmundaceae and in root apices within the Ophioglossaceae a single apical cell is often reported to be gradually replaced by a group of equivalent cells. This ontogenetic development supports the view that a meristem with a single initial represents a more primitive stage than a meristem with a number of initials. The defenders of this opinion also emphasize the occurrence of a single apical cell in many algae and bryophytes. On the basis of this view it can be stated that the more advanced evolutionary stage has been attained in many pteridophytes but in some of them not with regard to all meristems. Thus the transition from the stage with one to the stage with several initials obviously can take place in a meristem independently of the conditions in other meristems. Meristems in which an apical cell is more or less quiescent or is replaced by a number of initials may be regarded as transitional forms between meristems with a single permanent initial and meristems with several permanent initials. In some pteridophytes the spore-producing meristem originates, sometimes from a single initial, sometimes from a few initials. This condition may also be considered a transition from meristems which always show a single initial to meristems which always show two or more initials. On the contrary, however, it can be suggested that a spore-producing meristem with several initials is more primitive than one with a single initial in accordance with the general view that the eusporangiate pteridophytes are phylogenetically more primitive than the leptosporangiate ones.

Gymnosperms

Cycadaceae

All studies on the shoot apices show that the growth proceeds from some initials in the superficial layer (Johnson 1951).

According to the few investigations about the ontogeny of the sporogenous tissue the microsporangia as well as megasporangia arise from two-layered initial groups (Brunkener 1973).

Ginkgoaceae

In both long and short shoots the initials of the apex belong to the outermost layer (Foster 1938).

Starr (1910) reported that the sporogenous tissue of the microsporangium probably originates from a single subepidermal cell. The megasporangium is derived from a two-layered initial group (Brunkener 1973).

Pinaceae

In all investigated genera periclinal divisions are common in the superficial layer of the shoot apex (Korody 1937, Allen 1947, Sacher 1954). My own studies on young male and female strobili in *Pinus mugo, P. sylvestris, Picea abies, P. pungens, Pseudotsuga taxifolia, Tsuga canadensis, Larix decidua* and on young male strobili in *Abies veitchii* as well as my studies on vegetative shoot apices of these species also show that these apical meristems are undifferentiated.

The microsporangium arises from the surface layer. The sporogenous tissue of the megasporangium originates directly (*Pinus, Tsuga*) or either directly or indirectly (*Pseudotsuga, Larix, Picea*) from the superficial layer (Brunkener 1973). In the first case ("direct origin") a cell in the outermost layer cuts off a sporogenous cell. In the latter case ("indirect origin") an inner cell arisen in this way cannot be regarded as sporogenous. On the contrary the cell gives rise to a small group of cells of which the inner cells are somatic and one or a few of the outer cells, that is immediately inside the outermost layer of the ovule, produce the sporogenous tissue (Brunkener 1973 p. 375).

Taxodiaceae

In most of the species studied the initial region of the shoot apical meristem is obviously undifferentiated but the frequency of periclinal divisions in the initials is definitely lower than in the Pinaceae (Cross 1943). In *Taxodium*, however, the periclinal divisions in the outermost layer appear to be absent in the permanent shoots contrary to the deciduous shoots (Cross 1943).

The microsporangium of *Taxodium* (Coker 1903, Vasil & Sahni 1964), *Cryptomeria* (Erspamer 1952, Singh & Chatterjee 1963) and *Cunninghamia* (Brunkener 1973) and the megasporangium of *Cryptomeria* (Singh & Chatterjee 1963) are reported to originate from two initial layers. According to Shaw (1896) the same condition seems to exist in the megasporangium of *Sequoia*.

Cupressaceae

Periclinal divisions in the superficial layer of the shoot apex have been observed in *Chamaecyparis* (Hejnowicz 1957), *Libocedrus* (Jackman 1960), *Callitris, Juniperus, Thuja* (A. Pillai 1963 b) and *Cupressus* (S. K. Pillai 1963). In *Thujopsis*, however, Seeliger (1955) found, with few exceptions, a discrete outer layer. In *Juniperus communis* I have investigated the apical meristem of lateral buds and in *Chamaecyparis pisifera, Thuja occidentalis* and *Callitris* sp. the apical meristem of various lateral branches. In *Juniperus* 147 periclinal divisions (mitoses or cell pairs, which clearly show that mitoses just have occurred) were recorded in the outer layer at the summit of the shoot apex in 109 of the 118 buds studied during the period July–October (147/109-118). The corresponding value was for *Chamaecyparis* 4/4-46 (September, October), for *Thuja* 4/4-38 (July, August) and for *Callitris* 22/16-28 (in greenhouse).

Almost all investigations of the Cupressaceae show that the sporangia arise from two distinct initial layers. The rate of periclinal divisions in the outermost layer of the generative axis of *Juniperus communis* at the time of megasporangium initiation does not seem to be as high as previously (Brunkener 1973) was suggested. Therefore, the megasporangium can be said to arise sometimes directly and sometimes indirectly from the outermost layer (cf. Pinaceae). The microsporangium of *Juniperus communis* is remarkable owing to the occurrence of occasional periclinal divisions in the outer of the two initial layers. The inner cell produced by such a division can give rise to sporogenous cells.

Cephalotaxaceae

Singh (1961 a, b) demonstrated that the shoot apical meristem of *Cephalotaxus* possesses superficial initials, whereas the microsporangium as well as the megasporangium originates from two-layered primordia.

Podocarpaceae

The growth of the shoot apex of *Podocarpus* (Johnson 1951, Jackman 1960, Pillai & Pillai 1974), *Dacrydium* and *Phyllocladus* (Jackman 1960) proceeds from some cells of the outermost layer.

The microsporangium of *Podocarpus* and *Acmopyle* originates from two distinct layers of mother cells (Brunkener 1973) and to judge from the drawings made by Lawson (1923 a, b) the same condition seems to exist for the megasporangium of *Microcachrys* and *Pherosphaera*.

Araucariaceae

In *Araucaria* (Griffith 1952, S. K. Pillai 1964) and *Agathis* (Jackman 1960, Pillai & Pillai 1974) the apical shoot meristems are tunica-corpus organized.

From Burlingame's (1913) illustrations it is evident that the primordium of the microsporangium of *Araucaria* is two-layered.

Taxaceae

In lateral buds of *Taxus baccata* I have found periclinal divisions in the outermost cell layer at the summit of the apex (15/13-22, August, September). In young generative secondary shoots the result was 45/32-40. According to Kemp (1943) the shoot apex of *Torreya* grows from an undifferentiated group of initial cells.

In *Taxus* the mother cells of the microsporangium are arranged in two distinct layers. The same condition is reported for both types of sporangia in *Torreya* (Coulter & Land 1905, Kemp 1959). In *Taxus*, however, the first sporogenous cells of the megasporangium originate directly or sometimes probably indirectly from the outermost layer of the mother organ (Brunkener 1973).

Gnetinae

In *Gnetum* (Johnson 1951, Fagerlind 1954, Pillai & Pillai 1974) and in *Ephedra* (Gifford 1943, Seeliger 1954, Fagerlind 1971, Pillai & Pillai 1974) older shoots have tunica-corpus differentiated meristems. In *Welwitschia* Rodin (1953) and Martens & Waterkeyn (1963) detected occasional periclinal divisions in the superficial layer of the shoot apex. Fagerlind (1954), however, emphasized that the activity of the apical meristem ceases very early and that corresponding young stages of *Gnetum* and *Ephedra* also show periclinal divisions in the outermost layer.

According to the summary of Schnarf (1933) the initials of the microsporangium and megasporangium of the three genera are arranged in two layers. Fagerlind (1961, 1971) who confirmed this with respect to the microsporangium showed that the sporogenous tissue of the megasporangium in the Gnetinae is derived from the superficial cell layer.

The limited amount of information on the apical structure of strobili shows that they are organized as the vegetative apices in respect to the presence or absence of a tunica-corpus (Guttenberg 1966, Gifford & Corson 1971). Fagerlind (1971), however, found occasional periclinal divisions in the "pseudotunica" of both male and female strobili of *Ephedra* which exhibits tunica-corpus differentiated vegetative shoot apices.

Root apical meristems

According to older literature the root apices of gymnosperms have separate initials for the stele (plerome), whereas the other parts of the root are derived from common initials. The reports, however, refer to embryonic roots. Allen (1947) and Wilcox (1954) studied older roots and recognized a group of common initials for all the tissues of the root in *Pseudotsuga* respectively *Abies*. Allen distinguished three and Wilcox two groups of temporary initials which are derived from the central group of permanent initials. Also in the Cycadaceae and *Ginkgo* a common group of initials for all the tissues of the root has been reported (A. Pillai 1963 a). On the basis of available literature Guttenberg (1964) distinguished two separate groups of initials in primary roots of gymnosperms. He considered, however, that the independent initials for plerome later become inactive and that the growth of the root then proceeds from a common group of initials. A. Pillai (1964) studied the root apices of 27 species belonging to 14 genera and 5 families within the Coniferae and found that all species exhibit two separate initiating zones. One central initiating zone is responsible for the growth of the stele and the central region of the root cap (columella). The other zone of initials which is situated around the stelar pole and the proximal end of the columella (as a hollow cylinder) gives rise to the cortex and the peripheral region of the root cap. Thus the two groups of initials distinguished by A. Pillai are not arranged in superimposed tiers as was described in older literature. In the root apex of *Ephedra* A. Pillai (1966) observed three separate groups of initials. There is a discrete layer of stelar initials that is situated immediately above a layer of columella initials. The initiating zone for the cortex and the peripheral region of the cap surrounds the stelar pole and the proximal part of the columella.

A. Pillai (1966) has suggested an evolutionary trend in the organization of the root apex in gymnosperms. The most primitive type with an undifferentiated initial region occurs in the Cycadaceae and *Ginkgo*. The Coniferae exhibits a more advanced type with two separate groups of initials and *Ephedra* which has three such groups probably represents the most advanced type. The occurrence of a quiescent centre in the root apices has been demonstrated in many angiosperms but the available information is yet too insufficient to justify a generalization regarding the presence of such a region in gymnosperm roots.

Discussion

A comparison between the root and shoot apical meristem shows that both types of meristems are undifferentiated in the Cycadaceae and in *Ginkgo*. On the basis of A. Pillai's view (1964) the root apical meristem of the Coniferae with two specially arranged groups of initials agrees neither to the unstratified shoot apex of most conifers nor to the two-layered one in certain other conifers. Nor in *Ephedra* the root apical organization with three groups of initials corresponds to the stratification of the shoot meristem. If, however, Guttenberg's (1964) suggestion that gymnosperms have common initials in the root apex is correct, the organization of the shoot and root apical meristem agrees in most gymnosperms.

In Table 2 the frequency of periclinal divisions in the superficial cell layer of the shoot apex at the summit and of the sporangium primordia is mentioned very approximately. No reports concerning the roots are noted in the table since the roots of most investigated gymnosperms (A. Pillai 1964, 1966) show a special organization that does not occur in shoot apices or sporangium primordia. It must be emphasized that the table is based upon few investigations and therefore is strongly generalized. It is difficult to compare the frequency of periclinal divisions of different studies since the frequency almost always is related with such vague expressions as "periclinal divisions are rather common" or "periclinal divisons occur occasionally". Moreover, in many gymnosperms more or less pronounced seasonal variations can be observed with respect to the rate of periclinal divisions in the superficial layer. During a certain period numerous such periclinal divisions can be detected but during another period the apical meristem gives the expression of being tunica-corpus differentiated. If such variations are reported in the literature the period with the highest frequency is represented in the table. Furthermore the conditions in main and lateral shoots may be different as in *Taxodium*. In certain gymnosperms the megasporangium-producing meristem at first is tunica-corpus organized but later shows a higher or lower frequency of periclinal divisions in the outermost layer. Since these divisions do not give rise to sporogenous tissue they have been neglected in the table. Many genera are incompletely or not at all investigated with reference to the meristems in question. In almost all gymnosperm genera the structure of the sporangia is described but only few studies give information about whether the early primordium is undifferentiated or differentiated. The information in the table, however, presumably corresponds to the condition in most genera within a respective family.

It is evident from the table that the arrangement of the initials of the microsporangium in general corresponds to that of the megasporangium of the same genus (family). Furthermore, it is clear that the structure of the spore-producing meristems on the whole agrees with that of the apical shoot meristems in the Pinaceae. This condition is possibly valid also respecting the Araucariaceae. In the Gnetinae only the meristem of the microsporangium corresponds to that of the shoot apex. In *Juniperus communis* the shoot apex relatively often exhibits periclinal divisions in the superficial layer. Such divisions also occur in the outer layer of the spore-producing meristems but in a much lower frequency. Thus the latter meristems show a strong tendency to tunica-corpus differentiation and one can speak about only a certain degree of accordance between these meristems and the shoot apical meristem. In most gymnosperms it seems to be no such accordance. Some genera, however, such as *Cryptomeria, Taxodium, Chamaecyparis, Cupressus* and *Thuja*, which have sporangium initials arranged in two discrete layers, possess shoot apices which show a stronger or weaker tendency to tunica-corpus organization.

Table 2. The approximate frequency of periclinal divisions in the superficial layer of the shoot apical meristem and of the micro- and megasporangium in gymnosperms. – P = Periclinal divisions are reported to occur very often or often. – (P) = Periclinal divisions are reported to occur occasionally, relatively rarely or rarely. – O = Periclinal divisions are reported to occur very rarely or never (tunica-corpus organization).

Taxon	Shoot apical meristem	Microsporangium primordium	Megasporangium primordium
Cycadaceae	P	O	O
Ginkgoaceae	P	O	O
Pinaceae	P	P	P, (P)
Taxodiaceae			
Taxodium	(P), O	O	–
other genera	P, (P)	O	O
Cupressaceae			
Juniperus	P	(P)	(P)
Thujopsis	O	–	–
other genera	(P)	O	O
Cephalotaxaceae	P	O	O
Podocarpaceae	P, (P)	O	O
Araucariaceae	O	O	–
Taxaceae			
Taxus	(P)	O	(P)
Torreya	P	O	O
Gnetaceae	O	O	(P)
Ephedraceae	O	O	(P)
Welwitschiaceae	O	O	(P)

In all gymnosperm seedlings anticlinal as well as periclinal divisions occur in the superficial cells of the shoot apical meristem (Guttenberg 1961). In some families this condition becomes permanent in the fully developed shoot while in other families the rate of periclinal divisions decreases more or less. Accordingly one can speak about an intermediate type of meristem between, on one side, clearly undifferentiated shoot meristems as in the Cycadaceae and the Pinaceae, and, on the other side, tunica-corpus organized shoot meristems in the Araucariaceae and the Gnetinae. Most investigated genera of the Taxodiaceae and the Cupressaceae and some genera of the Podocarpaceae and *Taxus* appear to have apical shoot meristems of such an intermediate type. The Taxodiaceae and the Cupressaceae seem to be the most heterogeneous families in this connection, since undifferentiated and tunica-corpus differentiated meristems as well as meristems of the intermediate type have been described. The shoot apical meristem of *Taxodium distichum* indicates that even a single plant can be heterogeneous in this respect.

In harmony with the condition in the shoot apices intermediate types also occur between undifferentiated and differentiated sporangium primordia. The microsporangium primordium of *Juniperus communis* and the megasporangium primordium of *Pseudotsuga, Larix, Picea, Juniperus* and *Taxus* can be regarded as belonging to an intermediate type of meristem. The young microsporophyll of *Juniperus communis* has a discrete outer layer and the microsporangium primordium is stratified. However, when the cells of the inner initial layer of the primordium begin to divide periclinally, or at a later point of time, the outer cell layer occasionally can cut off a single cell that can give rise to sporogenous cells. The megasporangium-producing meristem of *Pseudotsuga, Larix, Picea, Juniperus* and *Taxus* is organized in another way. The mother organ does not show a discrete outer layer and the sporogenous tissue is derived directly or indirectly from superficial cells.

Angiosperms

The shoot apical meristems of all investigated angiosperms with a few exceptions are reported to be tunica-corpus organized. The number of layers in which only anticlinal divisions occur may fluctuate during the ontogeny of the plant, in connection with the initiation of leaves and under the influence of environmental factors. Thielke (1951, 1965) detected periclinal divisions in the outermost layer of the apex at the summit in young fast growing shoots in some species of *Saccharum* and *Erianthus*. The organization of the apices, however, changes and later only normal tunica-corpus differentiation can be observed. Also in a few other genera occasional periclinal divisions in the outermost layer of the shoot apex have been reported but may be regarded as pathologic changes. There is relatively little information about the apical meristems of inflorescences and flowers but it seems as if also these meristems are tunica-corpus differentiated (Guttenberg 1960, Esau 1965).

According to Hanstein's histogen theory (1868) the root apical meristem of angiosperms is initiated from a group of mother cells, the histogen initials, which are arranged in three discrete, superimposed tiers. However, in many angiosperms it has been demonstrated that the histogens are not as discrete as was previously thought. Guttenberg (1960) summarized the information on root apical organization in angiosperms and distinguished two principal types, the closed and the open. The closed type exhibits three discrete and superimposed initial groups which are responsible for the development of the plerome, periblem, dermatogen and root cap. The open type has common initials for all tissues of the root or for all tissues except for the plerome. Transitional forms between the two types are also described. Both the principal types are found in dicotyledons as well as in monocotyledons. Guttenberg stated that the two basic types are developed from a closed type in the embryonic root. Later this type of organization is retained or replaced by the open type.

According to Clowes (1959, 1961, 1967) the apical meristem of the root in most angiosperms and perhaps in most vascular plants has a quiescent centre, which consists of many cells which divide rarely or never. The quiescent centre is shaped like a hemisphere and the cells on the surface of this quiescent complex may be regarded as the initials of the meristem. Clowes emphasized that the degree of quiescence in a root may vary and that the boundary between the region and the surrounding initials fluctuates in position. Several other investigators as Byrne & Heimsch (1968, 1970), also described a quiescent centre in the roots of certain angiosperms. Authors as Popham (1958) and Guttenberg (1960, 1964), however, were doubtful about the existence of such a region. Even if there are contradictory views about the structure of the root apex it is evident that a large number of angiosperms shows a differentiated (stratified) root apical meristem that, however, only partly harmonizes with the tunica-corpus organization of the shoot apex. The stratification of the root meristem does not agree with that of the shoot meristem since the divisions in the root "histogens" do not occur in the same manner as in the tunica layers.

Both the microsporangium and the megasporangium are derived from differentiated initial groups which accordingly corresponds to the organization of the shoot meristem.

Conclusions

During the evolution a transition from undifferentiated to differentiated apical meristems and spore-producing meristems probably has occurred. This change can evidently take place at different points of time in apical meristems and spore-producing meristems. In most gymnosperms studied the spore-producing meristems have attained the more advanced stage while the shoot apical meristems of most genera still are quite undifferentiated or show intermediate conditions.

This review shows that Bower's theory about the accordance between the organization of the spore-producing meristems and that of the apical meristems is partly correct. The pteridophytes and angiosperms at large can be regarded as homogeneous groups in this respect whereas the gymnosperms exhibit varying conditions with pteridophyte as well as angiosperm characters. With reference to the organization of the spore-producing meristems and the apical shoot and root meristems the gymnosperms, therefore, as in many other respects, can be considered a transitional group between pteridophytes and angiosperms.

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New finds of Cornucopiae cucullatum (Poaceae) in Europe

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Cornucopiae cucullatum is reported as new to the islands of Crete and Kos (E Aegean region). Its general distribution is reviewed.

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The authors have found the small annual grass *Cornucopiae cucullatum* L. (for description and illustration see Bor 1968 p. 300) as new to the islands of Crete and Kos (E Aegean region). On Crete it was found in April 1976 by WL in the village of Skisma (Schima), c. 7 km W of Aghios Nikolaos, prov. Merabello. On Kos it was found in a number of localities in 1974–76 by AH (Fig. 1).

Cornucopiae cucullatum always grows under rather wet conditions: on the borders of ditches, small ponds and rivulets, and also in areas water-logged during winter but dry in summer. On Kos it is often associated with *Oenanthe prolifera*.

The species has clearly an eastern total distribution (map in Colosante & Ricci 1972) and previous finds in Europe are few and mostly old. It has been found on the islands of Patmos (Sibthorp & Smith 1806) and Rhodes (Fiori 1938) in the E Aegean area, and on the island of Gozo, Maltese Islands (Sommier 1911). There is also a recent record from C Italy, near Latina in Agro Pontini (Colosante & Ricci 1972).

The species might still be present on Patmos and Rhodes since these islands lie within its probable native area. On Gozo only a single plant was found growing in a ditch, and the find probably represents an occasional introduction only. Colosante & Ricci (1972) regard, although with some reservations, the occurrence in Agro Pontini as native. They refer to the fact that a number of other E Mediterranean plants have their westernmost occurrences in C Italy.

Outside Europe *C. cucullatum* is known from Turkey (probably widespread in the S and W parts), Lebanon, W Syria and Israel (Boissier 1884, Post 1896, Post & Dinsmore 1933, Thiébaut 1953, Mouterde 1966), Iraq (Rechinger 1964, Bor 1968) and doubtfully Iran (Parsa 1950, not mentioned by Bor 1970). It is said to be more or less common in Israel and Lebanon (Post 1896, Thiébaut 1953) but from other areas only very few finds have been published and most of them are old. The species is probably much overlooked

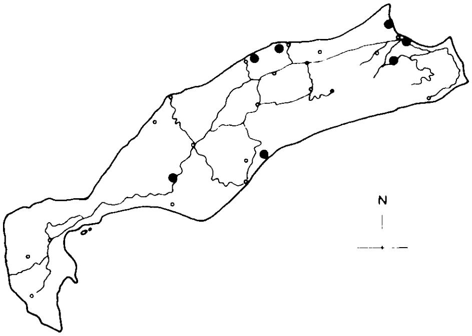

Fig. 1. Localities for *Cornucopiae cucullatum* on the island of Kos. Scale 1:625,000.

and further field work will undoubtedly shed new light on its true distribution and frequency.

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Drawings of Scandinavian plants 115–117

Epilobium L. sect. Epilobium

Alf Oredsson and Sven Snogerup

Oredsson, A. & Snogerup, S. 1977 06 30: Drawings of Scandinavian plants 115–117. Epilobium L. sect. Epilobium. *Bot. Notiser 130:* 205–211. Stockholm. ISSN 0006-8195.

Drawings and descriptions are given for *E. glandulosum* Lehm. and for two Scandinavian form series included under *E. ciliatum* Raf. without taxonomic rank.

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These species are recent introductions in the area, but are well established and spreading. They belong to an American group recognized by its characteristic seed surface, with markedly papillate ridges. Autogamy seems to be dominant in the group, but occasional cross-fertilisation gives rise to hybrids both within the group and with European species. The former at least seem to be relatively fertile, and the taxonomy of the group is difficult. A revision is now being carried out by professor Raven, St Louis. The populations of various minor areas are often quite constant within themselves but differ from one another. This may reflect the introduction of a few presumably rather homozygous biotypes.

The descriptions given below are made on Scandinavian material only and are certainly not valid for the entire American material of these species. Two form series are here presented as *E. ciliatum* form A and *E. ciliatum* form B respectively. They differ in several characters so that in Scandinavia they are just as easily separated as are pairs of related species in other parts of the genus. Professor Raven (pers. comm.), however, states that they will be treated together in his revision. Under these circumstances we find it unwarranted to retain a different taxonomy for the introduced forms in Europe.

115. **Epilobium glandulosum** Lehmann 1830

Perennial herb, (20–)40–90(–110) cm high. Plant sparingly branched, producing one or a few (7–)15–30(–45)-flowered inflorescences, small specimens often unbranched with an apical inflorescence more than half of the plant height. Turions formed late in the autumn, at the surface, sessile or at the end of stolons up to 10 mm long with small spathulate leaves, as dense rosettes of c. 10, broadly obovate, obtuse, glabrous, fleshy, entire to weakly serrate leaves 8–15 mm long, first pale reddish, later dark reddish or in shaded positions pure green.

Stem (1.5–)2.5–4(–6) mm thick, terete, with weak lines below the leaf margins, lines often inconspicuous on older stem parts. Stem subglabrous to sparsely hairy below, often more densely so on the lines, gradually more hairy upwards, in apical part usually rather densely hairy, most hairs glandular, 0–0.3 mm, erect to incurved, some eglandular, incurved to adpressed, 0.2–0.4 mm long.

Lower and middle leaves opposite, most bracts usually alternate, leaves not decurrent, their bases often united. Basal leaves smaller, with a petiole up to 10 mm long, obovate-spathulate to lanceolate, subentire. Middle cauline leaves (35–)50–90 mm long, (15–)20–30(–35) mm broad, sessile or with a petiole up to 2 mm long, ovate to narrowly ovate, acute, basally subentire, in


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middle and upper part sharply but often irregularly serrate with largest teeth usually c. 0.5 mm high. Bracts rather large, like the middle cauline leaves, only the upper ones slightly smaller, more lanceolate in form and often more distinctly petiolated. Basal and middle cauline leaves subglabrous, upper ones sparsely hairy chiefly on petiole, margin and veins, hairs smaller than those of the stem and predominantly glandular.

Pedicels first erect, in fruit erectopatent. Young buds obovoidal, later ± broadly ellipsoidal, with a distinct mucro 0.2–0.3 mm long. Sepals (3.5–)4.5–5 mm, connate to c. 1.5 mm at base, narrowly ovate to lanceolate, green to reddish, usually sparsely glandular, denser on connate part, rarely also with some eglandular hairs. Petals (6–)6.5–7.5(–8.5) mm, notched to 1–2 mm, ± pinkish-purple or often rather light pinkish. Anthers (0.5–)0.7–0.9 mm, long filaments (2.5–)3.5–6 mm, short filaments 1.5–2.7 mm, usually less than half as long as the long ones. Pistil equalling or slightly shorter than the long stamens, stigma capitate.

Capsule stalk (5–)10–15 mm. Capsule 50–60(–70) mm, sparsely to moderately hairy but young ovaries more densely hairy, usually with glandular hairs only but rarely with some eglandular ones as well. Seeds 1.0–1.3(–1.4) mm long, 0.4–0.5(–0.6) mm broad, ± narrowly obovoidal, basally acute, apically obtuse, ventrally flattened with inconspicuous lines, neck inconspicuous or up to 0.05 mm, dorsal surface with c. 25 prominent, papillose edges, chalazal hairs 32–40(–45), 6–7.5 mm long. Flower homogamous, anthers often opening at bud stage.

E. glandulosum has a rather irregular distribution in S and C Scandinavia, with centres around Stockholm and Göteborg, in Västergötland and in S Skåne. It occurs in waste places, loading places, roadsides and similar localities, but in several places has also invaded ditch margins, shores of lakes and rivers etc. It must be regarded as established, and new localities are to be expected anywhere in the area.

E. glandulosum is indigenous in N America.

Known hybrids: with *E. montanum, palustre, parviflorum, roseum* and *tetragonum.*

116. **Epilobium ciliatum** Rafinesque 1808, form A

E. rubescens auct. scand.

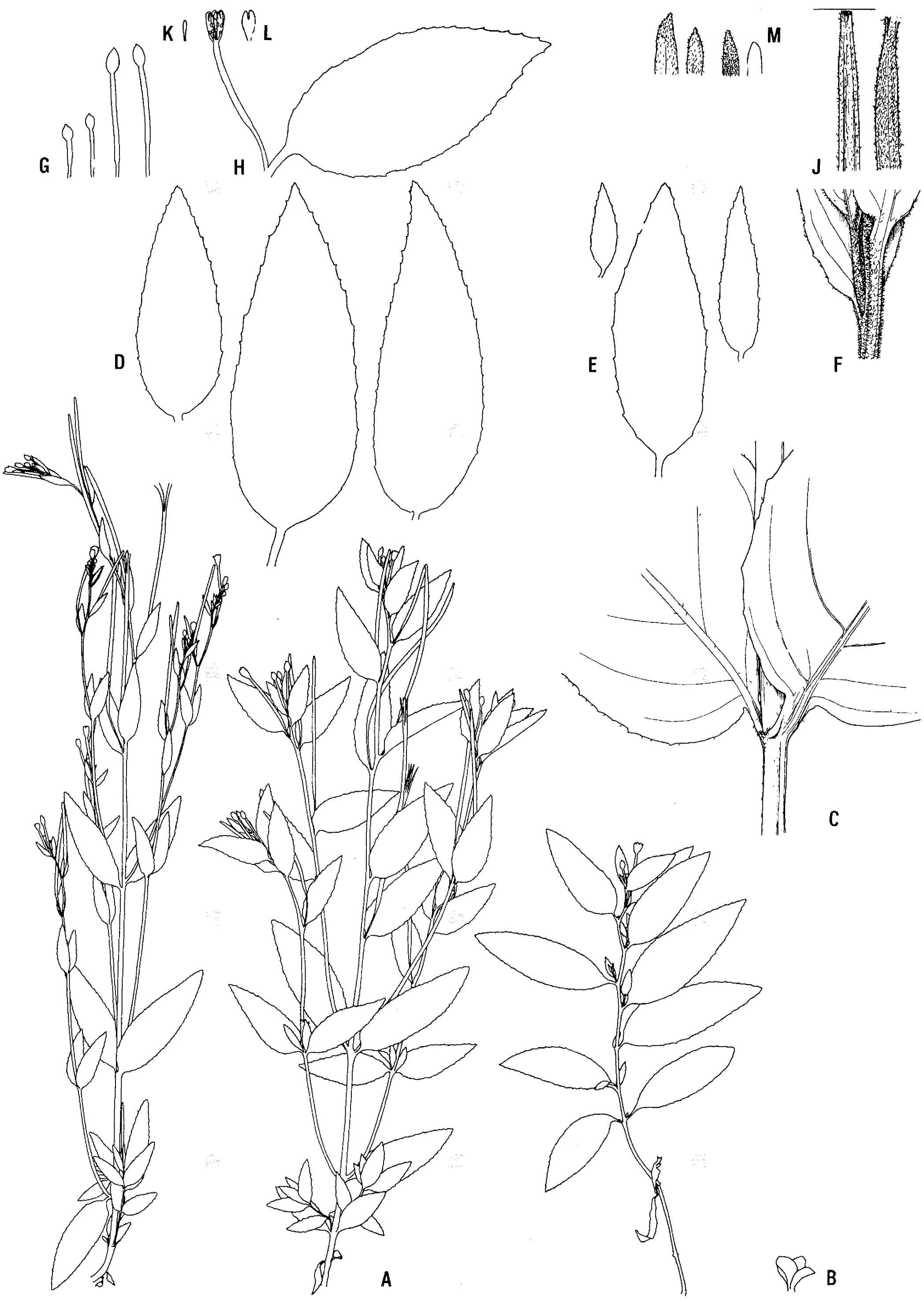
Perennial herb, (15–)30–60(–80) cm high. Plant branching from the base or rarely in denser vegetation only in upper part, with branches emerging at a very sharp angle, producing several or in small specimens only one 5–15(–20)-flowered inflorescences. Often forming adventitious shoots from basal internodes, similar to small individual plants. Turions formed late in the autumn, sessile or on stolons up to 5 mm long, at surface, as rosettes of 5–10 leaves usually broadly obovate, subentire, glabrous, somewhat fleshy, reddish. Sometimes not forming specialized turions but regenerating from the basal parts of the previous year's plants.

Stem 1–5 mm thick, terete, with weak lines below leaf margins, lines inconspicuous in older stem parts. Stem glabrous to subglabrous below, gradually more hairy upwards, apically moderately to densely hairy, with incurved to adpressed eglandular hairs 0.2–0.4 mm long and glandular, patent to incurved ones 0–0.25 mm long.

Basal and middle cauline leaves opposite, most bracts alternate, not decurrent, bases of opposite leaves usually united. Basal leaves smaller, with a petiole 5–10 mm long, obovate-spathulate to lanceolate, subentire. Middle cauline leaves (25–)35–60(–110) mm long, (7–)10–20(–27) mm broad, with a petiole 2–8(–12) mm long, narrowly ovate or rarely lanceolate, acute, sharply but often irregularly serrate in middle and upper part with teeth less than 0.5 mm, in basal part entire to subentire. Upper leaves gradually smaller and often more lanceolate in form. Basal and middle cauline leaves subglabrous to completely glabrous, usually with only few and very small hairs on the margin, upper bracts often slightly more hairy, especially on margins and veins.

Pedicels erect in bud and flower, in fruit erect to erectopatent. Young buds obovoidal, later ± broadly ellipsoidal with a distinct mucro c. 0.2 mm long. Sepals 3–4.5(–5) mm, connate to 1–1.5 mm at base, narrowly ovate to lanceolate, usually reddish especially on the margins, moderately hairy, denser on the basal part, with chiefly

Fig. 115. *Epilobium glandulosum* Lehm. – A: Habit, × 1/3. – B: Winter bud, × 1/2. – C: Stem node, × 2.5. – D: Cauline leaves, × 1. – E: Upper leaves, × 1. – F: Upper stem part, × 2.5. – G: Buds, × 1. – H: Flower, × 1. – J: Apical part of capsule, × 2.5. – K: Style, × 1. – L: Petal, × 1. – M: Sepals, × 2.5.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eglandular hairs. Petals 4.5–6.5 mm, notched to 1–1.5 mm, white or rarely light pink. Anthers 0.5–0.7 mm, long filaments 2.5–4 mm, short filaments 1.2–2.2 mm, usually about half as long as the long ones. Pistil usually shorter than the long stamens, sometimes no longer than the short ones, stigma capitate.

Capsule stalk 10–25(–35) mm in the basal part of the inflorescence, in the apical part shorter. Capsule (50–)60–75(–85) mm, young ovaries densely hairy, ripe fruits moderately so, with both glandular and eglandular hairs like those of the stem. Seeds 1.1–1.3 mm long, 0.4–0.45 mm broad, narrowly obovoidal, basally acute, apically obtuse, with a neck up to 0.05 mm long, ventrally flattened, dorsally with c. 25 prominent, papillose edges, chalazal hairs 30–40, 6.5–8.5 mm long. Flower homogamous, anthers often opening at bud stage.

E. ciliatum form A is commonest around Stockholm and Göteborg and on Gotland, but has also been observed in scattered places all over S and C Scandinavia. It is locally well established and probably spreading. Its relationship to form B requires further investigation. The two forms are normally well separated, but fertile specimens and populations presumed to be intermediate and probably hybridogenous have been observed. Form A occurs in the same sort of habitats as form B and *E. glandulosum* and often together with them.

E. ciliatum form A is indigenous in N America.

Known hybrids: with *E. montanum, palustre, roseum* and *tetragonum*.

117. **Epilobium ciliatum** Rafinesque 1808, form B

E. adenocaulon auct. scand.

Perennial herb, (25–)50–100(–130) cm high. Plant branching apically, or rarely from the base to form several or in dwarfed specimens rarely only one, (5–)10–20(–30)-flowered inflorescences. Turions formed late in the autumn at the surface, sessile or at the end of stolons up to 10 mm long with small, spathulate leaves, as dense rosettes of broadly obovate to elliptical, entire, glabrous, fleshv leaves 10–15 mm long, dark reddish or in shaded position rarely almost pure green.

Stem (1–)2–4(–8) mm thick, terete, with weak lines below the leaf margins, lines often inconspicuous on older stem parts. Stem subglabrous below, gradually becoming more hairy upwards, in apical part moderately hairy with incurved to adpressed eglandular hairs 0.2–0.4 mm long and erect to incurved, glandular ones 0–0.2 mm long.

Most leaves opposite or nearly so, usually only upper bracts alternate, not decurrent, leaf bases usually not united. Basal leaves smaller, with a short or up to 10 mm long petiole, obovate-spathulate, subentire. Middle cauline leaves (30–)50–90(–140) mm long, (8–)15–25(–40) mm broad, sessile or with a petiole up to 3 mm long, narrowly ovate, acute, sharply but often ± irregularly serrate with the largest teeth usually c. 0.5 mm high. Upper leaves gradually smaller and often somewhat narrower in form, usually with a petiole 1–3 mm long. Basal and middle cauline leaves subglabrous or sparsely hairy chiefly on the margin and sometimes also on the veins, upper bracts usually sparsely and sometimes more uniformly hairy, hairs smaller than those of the stem.

Pedicels first erect, in fruit erectopatent. Young buds obovoidal, later ± broadly ellipsoidal, with a distinct mucro c. 0.2 mm long. Sepals (3–)4–4.5 mm, connate to c. 1.5 mm at base, narrowly ovate to lanceolate, green to rather strongly reddish, sparsely to moderately hairy, denser on the connate part, with both glandular and eglandular hairs. Petals 4–6.5(–7.5) mm, notched to 1.5–1 mm, ± pinkish purple or rarely very light pink to white. Anthers 0.6–0.9 mm, long filaments 2.5–3.5 mm, short filaments 1.2–2 mm, usually at least half as long as the long ones. Pistil equalling or slightly exceeding the long stamens, stigma capitate.

Capsule stalk 4–8(–10) mm. Capsule (45–)50–60(–70) mm, sparsely to moderately hairy but young ovaries densely hairy, with glandular as well as eglandular hairs like those of the stem. Seeds (1.0–)1.1–1.3(–1.4) mm long, 0.4–0.45 mm broad, narrowly obovoidal, basally acute, apically obtuse, ventrally flattened with inconspic-

Fig. 116. *Epilobium ciliatum* Raf., form A. – A: Habit, × 1/3. – B: Winter bud, × 1/2. – C: Stem node, × 2.5. – D: Cauline leaves, × 1. – E: Upper leaves, × 1. – F: Upper stem part, × 2.5. – G: Buds, × 1. – H: Flower, × 1. – J: Apical parts of capsules, × 2.5. – K: Style, × 1. – L: Petal, × 1. – M: Sepals, × 2.5.


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uous lines, neck less than 0.05 mm, dorsal surface with c. 25 prominent, papillose edges, chalazal hairs 32–35(–40), 7–9 mm long. Flower homogamous, anthers often opening at bud stage.

E. ciliatum form B is rather common in S and C Scandinavia. It is indigenous in N America and has probably been introduced separately in several different places. It occurs on rubbish heaps, loading places and roadsides, but has also invaded ditch margins, shores of lakes and rivers, tracks and gardens. It is apparently spreading rapidly, and may be found anywhere in the area, generally S of c. 63°N.

Known hybrids: with *E. palustre, parviflorum, roseum* and *tetragonum*.

Fig. 117. *Epilobium ciliatum* Raf., form B. – A: Habit, × 1/3. – B: Winter bud, × 1/2. – C: Stem node, × 2.5. – D: Cauline leaves, × 1. – E: Upper leaves, × 1. – F: Upper stem part, × 2.5. – G: Buds, × 1. – H: Flower, × 1. – J: Apical parts of capsules, × 2.5. – K: Style, × 1. – L: Petal, × 1. – M: Sepals, × 2.5.

Drabopsis verna C. Koch (Brassicaceae) new to Europe

Lars-Åke Gustavsson

Gustavsson, L.-Å. 1977 06 30: Drabopsis verna C. Koch (Brassicaceae) new to Europe. *Bot. Notiser 130:* 213–214. Stockholm. ISSN 0006-8195.

Drabopsis verna C. Koch is reported from Lefka Ori on Crete. This Irano-Turanian species is previously known from C Anatolia and eastwards to W Himalaya. A description of the specimens from Crete is given.

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Drabopsis verna C. Koch

Koch, Linnaea 15: 253 (1841) – *Arabidopsis verna* (Koch) N. Busch, Fl. Cauc. Crit. 3, 4: 457, 460 (1909).

Arabis scapigera Boiss., Ann. Scienc. Nat. Ser. 2, 17: 54 (1842).

Arabis nuda Bel. ex Boiss., Ann. Scienc. Nat. Ser. 2, 17: 54 (1842) – *Sisymbrium nudum* (Bel.) Boiss., Fl. Or. 1: 214 (1867) – *Drabopsis nuda* (Bel.) Stapf, Denkschr. Akad. Wiss. Wien, Math.-Nat. Kl. 51, 2: 298 (1886) – *Arabidopsis nuda* (Bel.) Bornm., Beih. Bot. Centralbl. 28, 2: 535 (1911).

Collection: Crete, Nomos Canea, Lefka Ori, 5.5 km SE–ESE of the village of Omalos. Somewhat moist, stony ground close to snow patches, together with *Crocus sieberi* Gay, on a NW-facing slope, 1800–1850 m, 8.5. 1973, Gustavsson 2196 (LD).

This Irano-Turanian species is new to Europe. It is previously known from C and E Anatolia, Transcaucasia, Iraq, Iran, Afghanistan, C Asia, W Pakistan and W Himalaya. The occurrence on Crete is phytogeographically remarkable in that it extends the distribution of the species more than 1000 km westwards (Fig. 1).

The Irano-Turanian element as a whole is poorly represented on Crete, more richly represented on the S and C mainland of Greece. Among Irano-Turanian species occurring on Crete can be mentioned *Acantholimon androsaceum* (Jaub. & Spach) Boiss., *Atraphaxis billardieri* Jaub. & Spach and *Mattiastrum lithospermifolium* (Lam.) Brand.

D. verna belongs to the group of relict species with a very disjunct distribution on the eastern Mediterranean mountains (cf. Greuter 1972). It probably belonged to the flora of Crete before the island was isolated from the Anatolian continent, i.e. during the upper Miocene to Pliocene (Meulenkamp 1971, Creutzburg 1963).

All the Cretan material was flowering and some specimens bear immature fruits. The plants are extremely small, laying near the lower limit of the range of variation. The siliquae are much shorter than previously described for the species, probably because they are not fully developed. With regard to the most variable characters of the species the morphology of the Cretan plants is as follows: *Stem* single, 0.7–2.0 cm, pubescent, with stalked, branched hairs with 2–4 rays. *Leaves* spathulate to oblong-spathulate, entire, up to 5.5 × 2.1 mm, pubescent, with branched hairs especially on the margins. *Pedicels* in fruit up to 1.0 mm. *Sepals* 1.3–1.5 × 0.6–0.8 mm with simple and branched hairs. *Petals* 1.8–2.2 ×0.5–0.7 mm. *Siliquae* up to 8 mm long and 0.8 mm broad, pubescent, with branched hairs with 2 and 3 rays.

In comparison with the descriptions given in most oriental floras, e.g. Davis (1965) and Rechinger (1968), the plants from Crete also deviate in having pubescent siliquae. Such plants have been described as *Arabidopsis verna* (C.

Fig. 1. Distribution of *Drabopsis verna* in the westernmost part of the total area of distribution, according to literature records and herbarium sheets seen by me.

Koch) N. Busch var. *hebecarpa* N. Busch, in contrast to var. *leiocarpa* N. Busch with glabrous siliquae. According to herbarium material specimens with pubescent siliquae are rare, but do sometimes occur growing together with plants with normally glabrous siliquae. Such mixed collections have been seen from N Iran and Russian Armenia. The specimens of the Cretan collection have constantly pubescent siliquae.

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A study of the Leptopeltidaceae

Lennart Holm and Kerstin Holm

Holm, L. & Holm, K. 1977 06 30: A study of the Leptopeltidaceae. *Bot. Notiser 130:* 215–229. Stockholm. ISSN 0006-8195.

The family Leptopeltidaceae von Höhnel ('Phacidiales') has been amended to comprise unitunicate genera only, viz. *Leptopeltis* von Höhnel s. lat., *Dothiopeltis* E. Müller, and *Ronnigeria* Petrak. *Dothithyrella* v. Höhn., *Leptopeltopsis* Petr., and *Moeszopeltis* Petr. are included in the synonymy of *Leptopeltis*. The following new combinations have been published: *Leptopeltis litigiosa* (Desm.) L. & K. Holm, *L. gregaria* (Petr.) L. & K. Holm, *L. nebulosa* (Petr.) L. & K. Holm, and *L. lunariae* (Fuckel) L. & K. Holm.

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The family Leptopeltidaceae was established by von Höhnel (1917 p. 417, as 'Leptopeltineen') to accommodate 'Phacidiales' with subcuticular ascocarps. With Höhnel's circumscription the taxon was highly heterogeneous, comprising elements as disparate as *Leptopeltis* and *Rhytisma*. No wonder that other investigators, like Theissen & Sydow (1918), and Nannfeldt (1932) did not recognize the group, referring the type genus, *Leptopeltis*, to the 'Hemisphaeriales'; the former authors considered *Leptopeltis* to be related to *Stigmatea*.

The Leptopeltidaceae was revived again as a taxonomic group by Petrak (1947 a) who restricted the family to the genera *Leptopeltis* and *Leptopeltella*, only. He did not express an opinion about its position in the Ascomycete system. Petrak's article is the most thorough study so far devoted to these fungi, and it has definite merits, in addition to the improved circumscription of the family. He noticed the existence of the 'hypostroma' in the host tissues, with differences in different species, which he utilized as taxonomic characters. Moreover, he described two new valid pteridicolous species, viz. *Leptopeltopsis nebulosa*, and *Moeszopeltis gregaria*, referring each of them to a new genus of its own. Petrak had a very narrow generic concept, guided i.a. by presumed differences in spore septation.

In a second article, published simultaneously, Petrak (1947 b) reported on the so-called *Microthyrium arcticum* Oud., a saprophyte on leaves of *Potentilla* spp. He considered this species to be a true member of the Leptopeltidaceae, referring it to the new monotypic genus *Ronnigeria*. We agree with Petrak's classification, though it has been criticized by other workers.

Another noteworthy contribution was made by von Arx (1964) who included some further genera in the family, viz. *Dothithyrella*, and *Dothiopeltis*. The first-mentioned genus had earlier been classified among the Microthyriales, but von Arx rightly recognized its close affinity with the Leptopeltidaceae. *Dothiopeltis* also clearly belongs here. Otherwise von Arx followed Petrak rather closely, though with a somewhat broader generic concept, uniting *Dothithyrella* and *Leptopeltis* (under the name *Pycnothyrium*). Concerning the general relationships von Arx classified the family among the Dothiorales, a view first held by Müller & von Arx (1962).

The Leptopeltidaceae have recently been treated anew by von Arx & Müller, in their survey of the bitunicate Ascomycetes (1975); here the family has been considerably enlarged

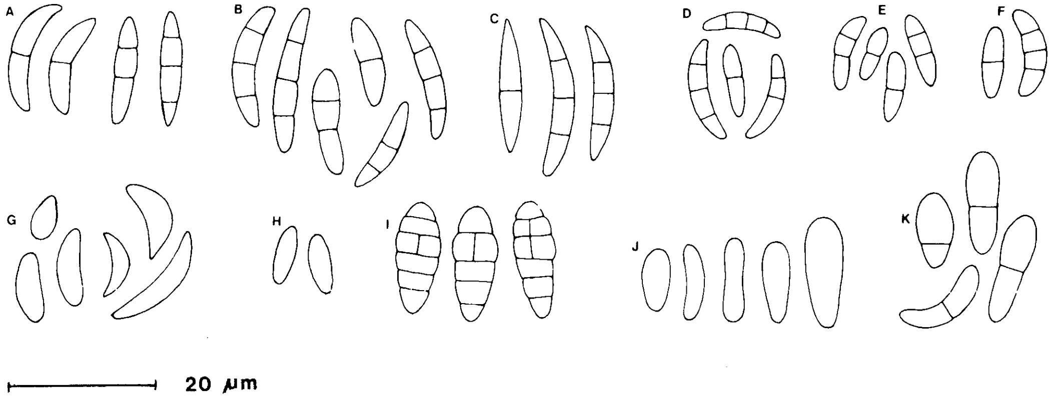


Fig. 1. Spores. – A: *Leptopeltis pteridis*. – B: *L. litigiosa*. – C: *L. filicina*. – D: *L. nebulosa* (on *Athyrium filix-femina*). – E: *L. nebulosa* (on *Lastrea dryopteris*). – F: *L. nebulosa* (on *Dryopteris filix-mas*). – G: *L. gregaria*. – H: *L.* sp., no. 576b. – I: *Dothiopeltis arunci*. – J: *Ronnigeria arctica*. – K: *Leptopeltis lunariae*. – All × 1,000.

again, also including genera such as *Aulographum, Aulographina, Lembosina,* and *Morenoina*.

In our opinion the Leptopeltidaceae should certainly be recognized as a distinct group, appropriately of family rank, but restricted to the genera *Leptopeltis* s. lat., *Dothiopeltis,* and *Ronnigeria,* only. As will be shown the group is quite distinct from other superficial 'Hemisphaeriales' by the ascus structure.

Two morphological problems

Ascus structure

Most hemisphaeriaceous fungi are apparently bitunicate, and the Leptopeltidaceae have also been regarded as such, e.g. by von Arx & Müller (1975), and Luttrell (1973). This view, however, seems to be erroneous. Personally, we have never observed a *Leptopeltis* ascus exhibiting the 'Jack in the box' mode of dehiscence. A negative indication may not be very convincing, but some traits of the ascus microstructure certainly are. We refer to the TEM micrographs in Fig. 6.

For the ultrastructural studies the material (dried herbarium specimens) was prefixed in 2.5 % glutaraldehyde in 0.1 M sodium cacodylate buffer, pH 7.2, at room temperature for 48 h, and postfixed in 2 % $KMnO_4$ for 1 h. It was dehydrated in a graded ethanol series, embedded in Epon, and sectioned with a LKB Ultrotome I equipped with a Du Pont diamond knife. The sections were poststained in 2 % uranyl acetate for 20 min. and in Reynold's lead citrate for 6 min. For examination a JEOL 100 B transmission electron microscope was used, operating at 60 kV.

The ascus wall is thickened at the apex, and the lower part of the thickened region extends downwards as an annular projection into the apical epiplasm. Moreover, traces of a cylindrical ring of electron transparent material can be discerned in the apical thickening. An ascus tip structure of this kind is commonplace among the Unitunicatae, but unknown among the Bitunicatae. The pictures do not permit any definite conclusions as to ascus wall stratification; apparently fresh material is necessary for obtaining unequivocal pictures. However, it is becoming gradually apparent that even the Unitunicatae possess a complex ascus wall, composed of several strata (cf. Bellemère 1975, Codron 1974, Schrantz 1970).

Interthecial threads

Another morphological problem of prime importance is the true nature of the interthecial threads, present in the ascocarps of *Leptopeltis* and *Dothiopeltis*. This question has hardly been discussed, and not much clarification can be obtained from the literature. Petrak (1947 a) called them 'Paraphysoiden', as did von Arx (1964); according to the latter they represent remnants of the interthecial 'tissue': 'Die fädig faserigen Paraphysoiden gehen aus dem durch die Asci verdrängten Binnengewebe hervor' (von

Arx 1964 p. 185). However, the two illustrations in von Arx's paper seem contradictory: fig. 2 (*Leptopeltopsis lunariae*) is in accordance with the cited concept, with interthecial filaments, attached above and below; fig. 1 (*Pycnothyrium litigiosum*) rather illustrates true paraphyses. The term 'paraphyses' is used by von Arx & Müller (1975).

We have found no evidence of the interthecial filaments being true paraphyses but are inclined to interpret them as paraphysoids, in the sense of Chesters (1938), i.e. true filaments, not compressed remnants of a pseudoparenchyma. It is worth noting that they are lacking in *Ronnigeria*, the ascocarp centrum of which seems to be made up of a rapidly dissolving pseudoparenchyma, apparently composed of short-celled, adherent hyphae. It seems conceivable that such hyphae may develop into paraphysoids in the course of evolution. In several bitunicate Hemisphaeriales, on the contrary, the interthecial filaments are reported to be pseudo-paraphyses.

General description and discussion

The Leptopeltidaceae s. str. can be briefly characterized as follows:

Ascocarps supracuticular, or mostly subcuticular, scutate–crustose; scutellum one-layered, of generally radially arranged cells, ± square in surface view; basal layer often poorly developed, hyaline or ± pigmented. No superficial *mycelium*, but often an intramatrical '*hypostroma*'. *Interthecial filaments* numerous–none, septate, often with gelatinous walls. *Asci* oblong, sessile, 'unitunicate', wall apically thickened with an annular 'collar' projecting downwards, I−. *Spores* thin-walled, hyaline, generally allantoid or fusiform, continuous or mostly with 1–3 transverse septa, rarely muriform. *Conidial states* common, generally of the *Leptothyrium*, rarely of the *Pycnothyrium* type.

Saprophytes, particularly common on the petioles of ferns, also in the leaves and stems of various dicotyledons.

Type genus: *Leptopeltis* von Höhnel.

The family seems to be very isolated, and at present we cannot assign it a better place than that given by von Höhnel, among the 'Phacidiales', which is admittedly an expedient for the time being. The Leptopeltidaceae are a very homogeneous group, and it seems reasonable to accommodate most of them in one genus, i.e. *Leptopeltis*. This means a considerable lumping as the generic segregation has been extensive, based mainly on two sets of characters: spore septation and hypostroma structure.

Hypostroma

As regards this vegetative structure the variation in amount as well as in texture is considerable, and each species has its pattern of variation, as rightly pointed out by Petrak, though he overestimated the interspecific differences.

Ronnigeria is altogether devoid of a hypostroma, and *Leptopeltis litigiosa* and *L. lunariae* have at most traces of it, whilst in *Dothiopeltis arunci* it is more in the form of loose hyphae (Fig. 4 B). In the other species it is generally well developed, often completely filling up several host cells, not only in the epidermis, but also in the underlying cortex. Moreover, the hypostroma is not restricted to the matrix cells just beneath the ascocarps but may extend considerably outwards.

The hypostroma is generally pseudoparenchymatous, of ± isodiametric cells, forming a textura angularis or a textura globulosa. In *Leptopeltis nebulosa* and *L. gregaria* it is mainly made up of globose cells (Fig. 5), whilst the angular cells dominate in *L. filicina* and *L. pteridis*. These species were described by Petrak (1947 a) as having a stroma of very small, rather thick-walled cells, a somewhat exaggerated statement. It is true that the cell size is less than in *L. nebulosa* and *L. gregaria*, but it is not as minute as indicated by Petrak, generally being 5–7 μm. In *L. filicina* we have only seen normal thin-walled cells, whilst in *L. pteridis* the hypostroma is, in fact, partly slightly scleroplechtenchymatous, with somewhat thickened cell walls (Fig. 4 A), though thin-walled cells are common. With regard to the hypostroma *L. filicina* and *L. pteridis* are very similar.

Apart from the pseudoparenchymatous tissue there is often a loose hyphal network, or, quoting Petrak (1947 a p. 246), the stroma is 'teils aus reichverzweigten, kurzgliedrigen, durchscheinend grau- oder hell olivenbraun gefärbten Hyphen bestehend, teils pseudoparenchymatisch, durchscheinend olivenbraun'. This statement originally referred to *Leptopeltis nebulosa* only (cf. Fig. 5 A), and the said condition was the basis for the erection of the genus *Leptopeltopsis*, but it also applies to *L. gregaria* (Fig. 5 B), and to some extent even to *L. filicina* and perhaps to other species as well. In fact, *L. gregaria* and *L. nebulosa* are strikingly similar in hypostroma characters, and these by no means justify the assigning of those species to different genera.

To sum up: differences exist in hypostroma structure, but they are not sufficiently clear-cut to justify a generic segregation.

Spore septation

Spore septation is the other parameter employed in generic delimitation within the Leptopeltidaceae. Although extremely important on the specific level, it has, however, been utilized as the basis for a large number of schematic, ill-founded Ascomycete genera. In this case the foundation is particularly shaky, as the alleged differences are largely illusive, based on immature material. Petrak e.g. believed *Leptopeltis filicina* to be amerosporous, and *L. pteridis* (=*L. aquilina*) and *L. nebulosa* to be didymosporous, whilst in fact they are all phragmosporous at maturity. Petrak's misconception largely contributed to his erecting the genera *Leptopeltina* and *Leptopeltopsis*.

The only genus which can be kept apart from *Leptopeltis* on sporological grounds is *Dothiopeltis*, characterized by its muriform spores, and it is chiefly a matter of opinion whether to unite them or not.

The consequences of the above considerations will apparently be a large-scale lumping, resulting in an extensive synonymy. The three genera recognized by us can easily be distinguished.

Key to the genera

1. Dictyosporous .... *Dothiopeltis*
   Amerosporous, didymosporous or phragmosporous 2
2. Interthecial threads present .... *Leptopeltis*
   Interthecial threads absent .... *Ronnigeria*

Leptopeltis von Höhnel

von Höhnel, Ber. Deutsch. Bot. Ges. 35: 418 (in clave) (1917) – *Leptopeltina* Petrak, Sydowia 1: 240 (1947), non Spegazzini 1923 – *Leptopeltinella* Petrak, Sydowia 5: 187 (1951) – Type: *Leptopeltis filicina* (Lib.) von Höhnel, Ber. Deutsch. Bot. Ges. 35: 422.

Dothithyrella von Höhnel, Ann. Mycol. 16: 171 (1918) – Type: *D. litigiosa* (Desm.) von Höhnel.

Leptopeltella von Höhnel, Ber. Deutsch. Bot. Ges. 35: 418 (in clave) (1917) – Type: *L. perexigua* sensu von Höhnel.

Moesziella Petrak, Ann. Mycol. 25: 323 (1927) – Type: *M. pulchella* Petrak.

Moeszopeltis Petrak, Sydowia 1: 241 (1947) – Type: *M. gregaria* Petrak.

Leptopeltopsis Petrak, Sydowia 1: 243 (1947) – Type: *L. nebulosa* Petrak.

Pycnothyrium Diedicke sensu von Arx, Acta Bot. Neerl. 13: 183 (1964), non sensu orig.

Nomenclatural comments

The nomenclature was unfortunately more confused because of Petrak's erroneous typification of *Leptopeltis* by '*L. aquilina*', i.e. *L. pteridis*, with the consequent introduction of the superfluous names *Leptopeltina* and *Leptopeltinella*. Von Höhnel definitely stated that *L. filicina* is the type: unfortunately the wrong typification was accepted and perpetuated by von Arx & Müller.

Another mistake was the adoption of the name *Pycnothyrium*. This genus was established by Diedicke (1913 p. 175) for two imperfect fungi, *Pycnothyrium gracile* Died. (described as new), and *P. litigiosum* (Desm.) Died., the latter name based on *Leptostroma litigiosum* Desm. As pointed out by e.g. von Höhnel, Desmazières's original material in fact represents an immature, perfect state. For this reason von Arx argued that the name *Pycnothyrium* ought to apply to the perfect state, taking precedence over the younger *Dothithyrella*. This argumentation is, however, untenable. As is evident from the description, *Pycnothyrium* is a genus of Fungi Imperfecti; if Desmazières's original material does not fit Diedicke's description, it cannot serve as type for *Pycnothyrium* either (something which von Arx apparently took for granted); then the other species, *P. gracile*, must be selected as the type. Diedicke himself did not designate one.

Infrageneric taxonomy

Generally, the species delimitation does not seem to be very problematic, a condition related to the pronounced host-specificity prevailing in the genus; '*Leptopeltella perexigua*' only, is said to be plurivorous. Useful taxonomic characters can be drawn particularly from the spore type, but also from the hypostroma. Ascocarp shape, on the other hand, is too variable to be of much

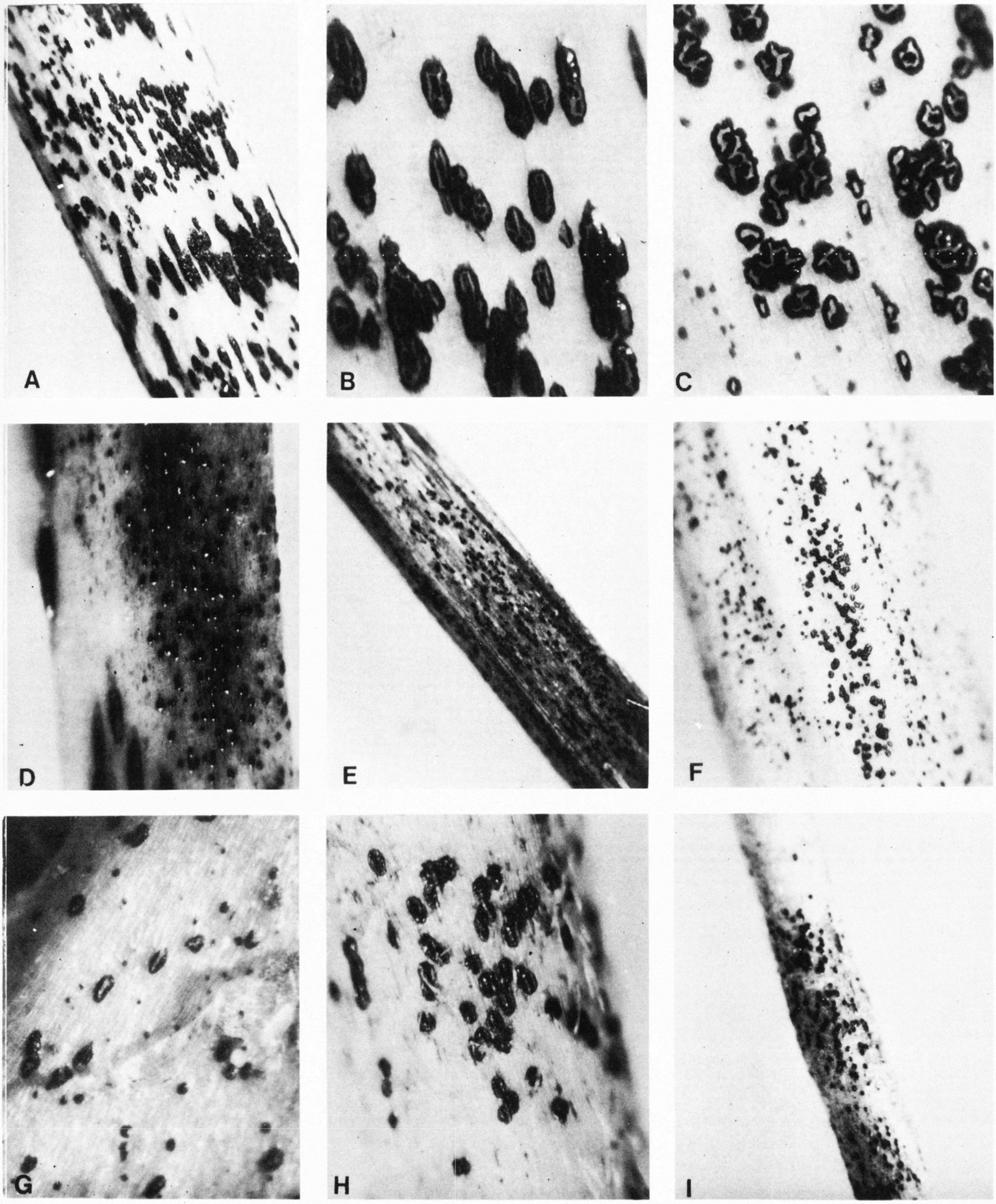


Fig. 2. Ascocarps in surface view. – A: *Leptopeltis pteridis,* ×6. – B: idem, ×25. – C: *L. litigiosa,* ×25. – D: *L. nebulosa,* ×12. – E: idem, ×6. – F: *L. litigiosa,* ×6. – G: *L. filicina,* ×25. – H: *L. gregaria,* ×25. – I: idem, ×6.

value: it can vary from circular to linear and ramified in the same species and within one collection, although a certain type may dominate; for instance most ascocarps of *Leptopeltis litigiosa* are circular. The mode of dehiscence is also very variable. Elongate ascocarps mostly open by an elongate fissure whilst the round ones open by a star-like or circular slit, or completely irregularly (cf. Fig. 2).

A character evidently of some importance is the degree of pigmentation in the basal layer, this being hyaline, if present at all, in *Leptopeltis pteridis, L. litigiosa,* and *L. filicina,* whilst strongly pigmented in *L. lunariae; L. gregaria* and *L. nebulosa* are intermediate in this respect.

Leptopeltis is a small genus, even with our wide circumscription. So far there are only seven known and named species; besides we have a few collections of uncertain status, on *Matteuccia* (see under *L. nebulosa*), and in the *lamina* of *Dryopteris filix-mas* (*Leptopeltis* sp. no. 6). The material at hand is insufficient for formal treatment. No doubt there still remains a great deal to discover – the Leptopeltidaceae have been badly neglected in spite of their frequency. They are easily overlooked though, and above all, they are seldom encountered in a well developed state. Obviously they become rapidly *passés* after ripening – most material collected by us has been either immature or dead, and the same is true for the few herbarium specimens seen.

The recognized species are presented in the following survey, with notes on diagnostic characters, host-range, distribution, and nomenclature; for detailed descriptions we refer mainly to Petrak's and von Arx's papers, though they should be taken with reserve in some respects.

Proposing a formal subgeneric hierarchy seems premature, but some suggestions may be made. A unique position is held by *Leptopeltis pteridis,* on account of its non-radiate scutellum and partly scleroplectenchymatous hypostroma. *L. litigiosa,* too, stands somewhat apart because of its supracuticular ascocarps. The other pteridicolous species, *L. filicina, L. nebulosa,* and *L. gregaria,* are apparently closely allied. *L. lunariae* probably stands close to *'Leptopeltella perexigua'* (a species not seen by us) and may be related to *Dothiopeltis.*

Key to the species of Leptopeltis

1.	On ferns	2
	On dicots	7
2.	Shield distinctly radiate	3
	Mature shield not radiate; on *Pteridium*	1. *L. pteridis*
3.	Ascocarps supracuticular; on *Pteridium*	2. *L. litigiosa*
	Ascocarps subcuticular; on other hosts	4
4.	Spores continuous (always?)	5
	Spores finally septate	6
5.	In petioles of *Lastrea phegopteris*	5. *L. gregaria*
	In the leaf-blade of *Dryopteris filix-mas*	6. *L.* sp.
6.	Spores narrowly fusiform, with ± pointed ends; on *Dryopteris*	3. *L. filicina*
	Spores broadly fusiform, with obtuse ends; on various ferns	4. *L. nebulosa*
7.	Spores 2-celled; on *Lunaria*	7. *L. lunariae*
	Spores 4-celled; on various hosts	8. *'Leptopeltella perexigua'*

1. **Leptopeltis pteridis** (Mouton) von Höhnel

von Höhnel, Ann. Mycol. 15: 304 (1917) – *Gloniella filicina* (Lib.) Mouton f. *Pteridis* Mouton, Bull. Soc. Roy. Bot. Belg. 28(2): 80 (1889) – Type: Belgium, 'sur les stipes morts du Pteris aquilina' (n.v.).

Leptopeltis aquilina Petrak, Sydowia 1: 237 (1947) – *Hypoderma aquilinum* Rehm, Ber. Nathist. Ver. Augsburg 26: 68 (1881) – *Schizothyrium aquilinum* Rehm, Disc.-Fl. 75 (1888) – non *Sphaeria aquilina* Fr., Syst. Mycol. 2: 522.

Exs.: Krieger, F. sax. 1169 (*'Aulographum filicinum'*) (S) – Rehm, Asc. 270 (*'Hypoderma aquilinum'*) (S), Asc. 1227 (*'Aulographum filicinum'*) (S) – Thümen, Myc. univ. 73 (*'Hysterium aquilinum'*) (UPS).

Fig. 1A, 2A, B, 4A.

Ascocarps subcuticular, often densely scattered, ± elliptic, elongated along the petioles or veins, c. 0.3 mm long, mostly several confluent into larger crusts, up to 2–3 mm. *Hypostroma* well developed, partly slightly scleroplectenchymatous, of small cells, mostly 5–7 μm, first hyaline, later dark. *Asci* oblong, up to 30×12 μm, mostly

8-spored, but spore abortion is common. *Spores* mostly allantoid, with obtuse or somewhat acute ends, 12–15 × 3–4 µm, usually 2-celled, but 3- and 4-celled spores occur. *Interascicular threads* numerous.

In dead leaves of *Pteridium aquilinum*, especially the petioles, but also in the foliar veins. Common, as is the imperfect state, *Leptothyrium pteridis* Ehrenb. ex Fr.

This species is generally recognized even macroscopically by the relatively large black ascocarps, looking like tar spots, much more conspicuous than the smaller and lighter *L. litigiosa*, which is always present (see under this species). In the microscope it is easily identified by the non-radiate shield, composed of a textura angularis – not textura epidermoidea, as stated by von Arx & Müller (1975 p. 29). This deviating structure is apparently secondary; originally the scutellum cells are radially arranged.

The ascocarps occur even in the leaf segments, but as far as we have observed, always subcuticularly in the veins – according to Petrak (1947 a p. 235) they may even grow subepidermally in the mesophyll, then considerably deviating in morphology.

With regard to the nomenclature we must admit that the identification with Mouton's fungus may be somewhat problematic. We have followed von Höhnel who apparently had not examined type material, and it cannot be excluded that Mouton's description was at least partly based upon *Leptopeltis litigiosa*. Several authors, such as Rehm and Petrak, and more recently von Arx & Müller, have identified this fungus with *Sphaeria aquilina* Fr., a species taken by others to be a *Mycosphaerella*. Both interpretations are erroneous – as it is apparent from the description and the original material, *Sphaeria aquilina* is a *Leptostroma*.

2. **Leptopeltis litigiosa** (Desm.) L. & K. Holm, comb. nov.

Leptostroma litigiosum Desmazières, Ann. Sci. Nat. Bot. ser. 2, 19: 338 (1843) – *Microthyrium litigiosum* Sacc., Michelia 1: 496 (1879) – *Dothithyrella litigiosa* von Höhnel, Ann. Mycol. 16: 171 (1918) – *Pycnothyrium litigiosum* Died. sensu von Arx 1964 et auct. rec., non sensu Diedicke – Type: Moug. & Nestl., Stirpes Crypt. 673 (UPS!).

Exs.: Desm., Pl. Crypt. Fr. 1327 (n.v.) – Lundell & Nannf., F. exs. suec. 664, 778 (UPS) – Moug. & Nestl. Stirpes Crypt. 673 (UPS).

Fig. 1 B, 2 C, F, 3 A.

Ascocarps densely scattered, supracuticular, generally occurring in abundance and ± covering large parts of the petioles. Solitary ascocarps usually circular, c. 0.1 mm diameter, but often several confluent into crusts up to 1 mm large. *Shield* radiate, splitting irregularly or often with a star-like or circular fissure. *Hypostroma* none or almost none. *Asci* oblong, 25–30 × 10–12 µm. *Spores* generally allantoid, (11–)15–18(–20) × 2.5–3.5 µm, long 2-celled but finally (always?) 4-celled.

On dead petioles of *Pteridium aquilinum*.

An extremely common fungus, at least in Scandinavia, where it seems to be the constant companion of its host. The bracken is cosmopolitan, and *L. litigiosa* also perhaps, but very little is known about its distribution. It is apparently restricted to *Pteridium* – the old unverified record of an occurrence on *Osmunda* (Desmazières 1843) is surely erroneous.

Leptopeltis litigiosa often grows intermixed with *L. pteridis*, but they are easily distinguishable, even by sight, as rightly pointed out by von Höhnel l.c.: 'Während die *Dothithyrella* kleine rundliche, braunschwarze, fast matte Fruchtkörper besitzt, zeigt der zweite Schlauchpilz [=*L. pteridis*] stets längliche oder lanzettenförmige pechschwarze, stark glänzende Stromata'. The difference in brilliancy is due to the difference in habitat – supracuticular, and subcuticular, respectively. Microscopically they are easy to distinguish by the different shield textures, whereas the spores are very similar; *L. litigiosa*, though, seems to have slightly longer and narrower spores, which more often become 4-celled.

An imperfect form was described by Diedicke (1913 p. 175) as *Pycnothyrium litigiosum;* its existence was denied by von Höhnel (1918 p. 171) but confirmed by Grove (1937 p. 198). We have not seen it. Von Arx (1964 p. 185) also reported a conidial state, but according to his description most likely belonging to *Leptothyrium*.

With regard to the nomenclature it can be noted that Desmazières in his protologue cited *Sclerotium pteridis* Pers., but as this name is a *nomen nudum*, the epithet *litigiosum* is not endangered.

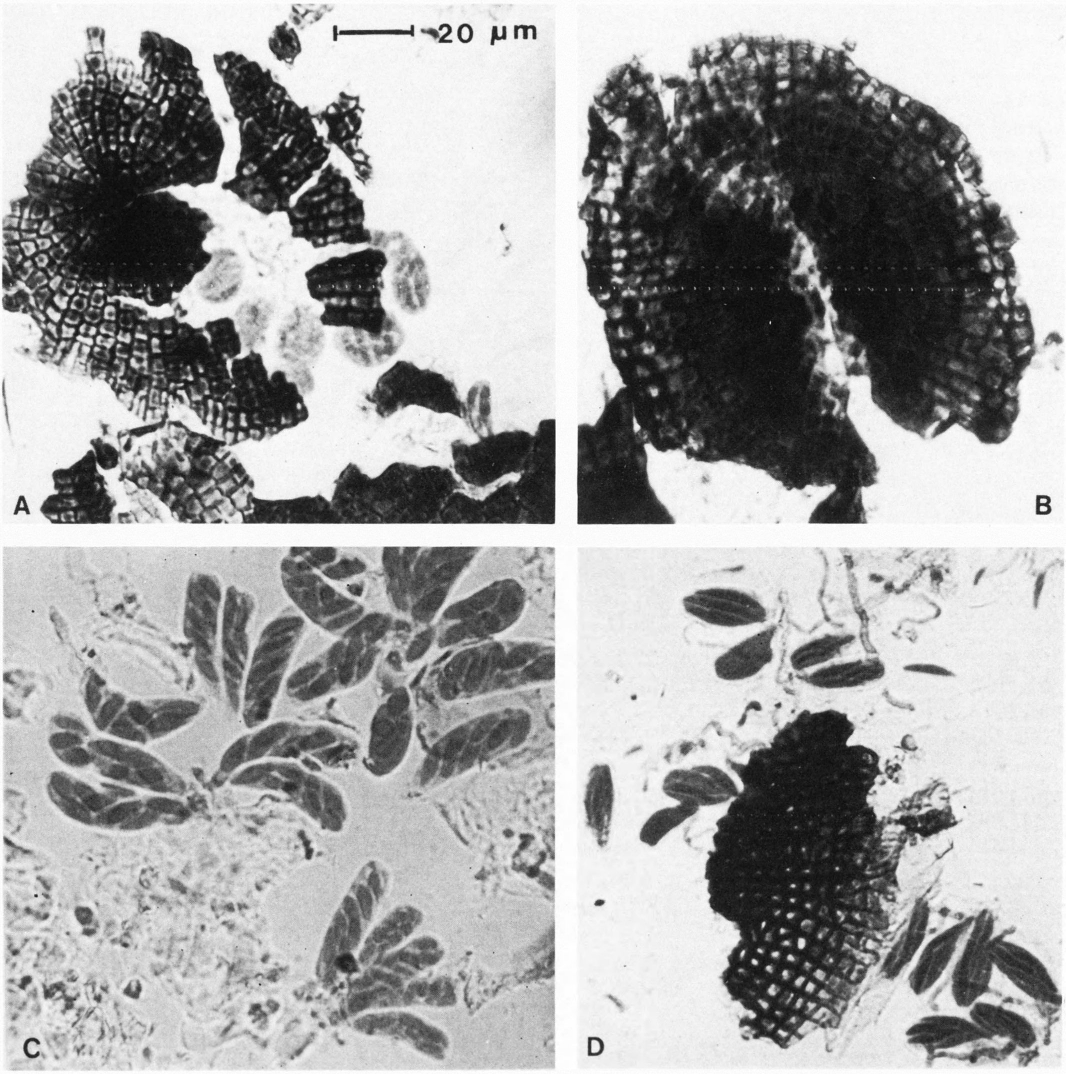


Fig. 3. A: *Leptopeltis litigiosa,* shield and asci. – B: *L. gregaria,* shield. – C: *Ronnigeria arctica,* asci. – D: *L. filicina,* part of shield and asci. – All × 530.

3. **Leptopeltis filicina** (Lib.) von Höhnel

von Höhnel, Ber. Deutsch. Bot. Ges. 35: 358 (1917) – *Aylographum filicinum* Libert, Pl. Crypt. Ard. 275 (1834) – Type: Belgium, 'Ad stipites Aspidii Filicis maris' (BR!!S!).

Aporia Jaapii Rehm, Abh. Bot. Ver. Brandenburg 47: 84 (1905) – *Leptopeltinella Jaapii* Petrak, Sydowia 5: 187 (1951) – Type: Germany, Schleswig–Holstein, Sattenfelde, *Dryopteris spinulosa,* 23.VI.1904, Jaap (S!).

Exs.: Jaap, F. sel. 82 (S) – Libert, Pl. Crypt. Ard. 275 (BR, S) – (Krieger, F. sax. 1169 & Rehm, Asc. 1227 = *L. pteridis*) (S).

Fig. 1C, 2G, 3D.

Matrix: Dryopteris spp., as *D. filix-mas, D. assimilis, D. dilatata, D. spinulosa;* in the petioles and larger veins.

Ascocarps scattered, subcuticular, linear–elliptic. *Hypostroma* mainly of textura angularis, of isodiametric cells, 5–7 µm. *Asci* oblong, c. 30 × 10 µm, 8-spored. *Spores* fusiform, often terminally pointed, 18–20 × 3–4(–4.5) μm, finally (always?) 4-celled.

This species is characterized by its narrow spores, generally pointed at the ends. We can find no support for the recognition of *Aporia jaapii* as a separate taxon – a large amount of material, collected on various members of the *Dryopteris dilatata* complex, seems to agree perfectly with the form on *Dryopteris filix-mas*. When Rehm described *Aporia jaapii* he was evidently ignorant of *Leptopeltis filicina* – otherwise, in all probability, he would have referred his fungus to this species. Certainly Petrak (1947 a) claimed that there were two different taxa, *Aporia jaapii* differing by 'oft etwas kleineren Fruchtkörper und durch die am Rande meist viel heller gefärbten Zellen der Deckschicht, deren Radialwände dicker sind als die Querwände. Auch sind die Sporen der *A. Jaapii* im Durchschnitt etwas grösser' (pp. 239–240). However, these alleged differences are imaginary. Even in the 'true' *L. filicina*, the marginal scutellum cells are almost hyaline, with the radial walls thicker than the transverse ones. Petrak did not see any mature spores, nor did Rehm, who claimed them to be one-celled in *Aporia jaapii*. His type material is immature but 2-celled spores occur.

Leptopeltis filicina is of course easily distinguishable from *L. litigiosa*, and by no means only a 'Substratform', as suggested by von Arx (1964 p. 185). It is probably rather common and widespread in Scandinavia; we have seen material from the Swedish provinces of Skåne, Uppland, Dalarna, and Hälsingland, and from Möre og Romsdal in Norway.

4. **Leptopeltis nebulosa** (Petrak) L. & K. Holm, comb. nov.

Leptopeltopsis nebulosa Petrak, Sydowia 1: 244 (1947) – Type: Czecho-Slovakia, Moravia pr. Podhorn, in dead petioles of *Athyrium filix-femina*, 2.V.1925, leg. Petrak (n.v.).

Fig. 1D–F, 2D, E, 5A, 6.

In aspect similar to the preceding species, *L. nebulosa* is very easily distinguishable, though, by the *spores* which are shorter and relatively broader, with obtuse ends, often allantoid, (8–)10–11 × (2.5–)3–3.5 μm, long 2-celled but finally, at least sometimes (always?), with 3 septa. *Asci* 20–25 × 10–12 μm. *Basal layer* present, ± pigmented below. *Hypostroma* well developed, mostly pseudoparenchymatous, of textura angularis–textura globulosa, cells 5–8 μm diameter, with dark cells.

In the petioles of various ferns.

Leptopeltis nebulosa is apparently a common fungus on *Athyrium filix-femina*, though hitherto known only from the type collection. We have seen a great amount of material on this host from Sweden (Skåne, Uppland, and Gästrikland). Moreover, the species can obviously occur on other hosts too. We have one collection on *Dryopteris filix-mas*, which in every respect is a perfect match of *L. nebulosa*: Norway, Möre og Romsdal, c. 4 km NE of Gjöra, close to the river Driva, 1.VII.1975, 666 a.

The occurrence on *Dryopteris filix-mas* may be exceptional, but this is certainly not the case with another host, viz. *Lastrea dryopteris*. No *Leptopeltis* has so far been recorded on this fern, but we have 5 collections agreeing closely with *L. nebulosa:*

Sweden: Uppland. Uppsala, 25.V.1975, 577 a. – Alunda, pr. Hävermossen, 2.VI.1976, 582. – *Västmanland.* Nora pr. Kerstinbo, 21.V.1975, 571 a. –*Dalarna.* Sundborn, Mjölnarvallen, 884 b.

Norway: Sör-Tröndelag. Oppdal, Gisnafallet, 29.VI.1975, 638.

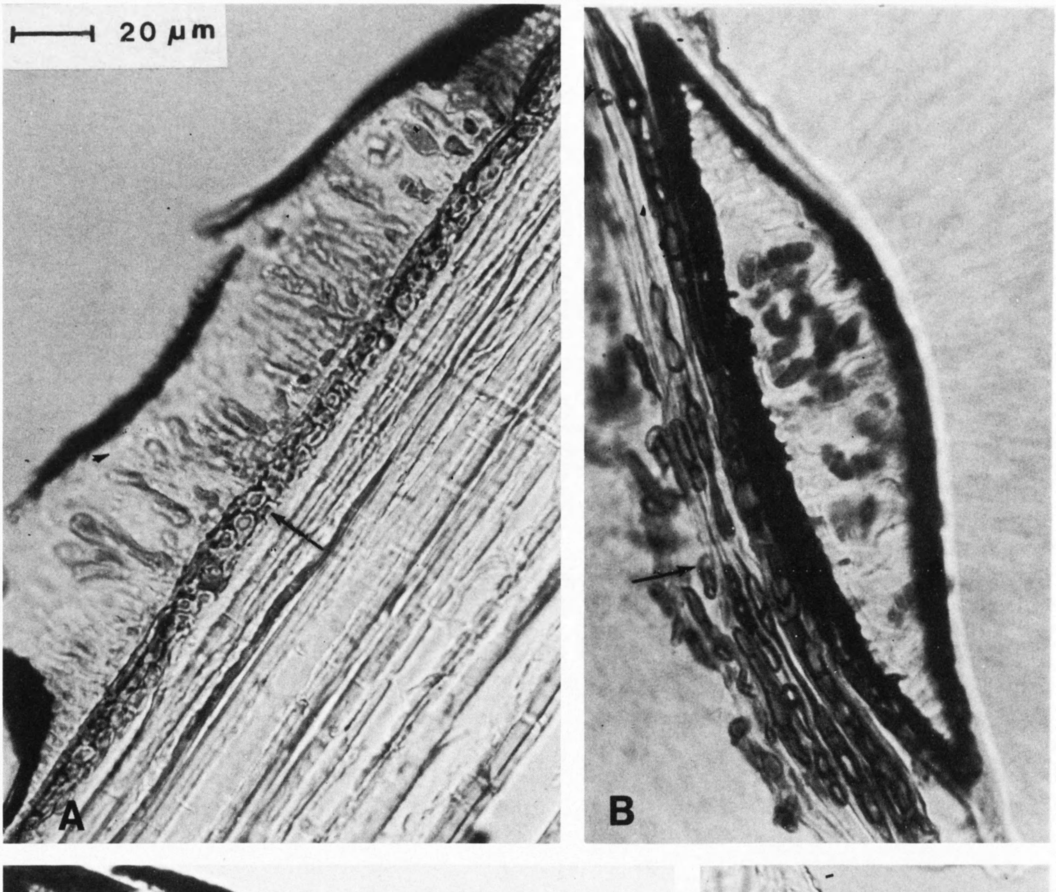
We can also report the occurrence on *Matteuccia struthiopteris* of a *Leptopeltis,* which possibly belongs to *L. nebulosa*. We have 6 Swedish collections, from Uppland, Gästrikland, and Torne Lappmark, but none is in a state to permit a safe determination. The hypostroma is suggestive of *L. nebulosa*.

5. **Leptopeltis gregaria** (Petrak) L. & K. Holm, comb. nov.

Moeszopeltis gregaria Petrak, Sydowia 1: 241 (1947) – Type: Norway, Sogn, Naeröy-dal ['Naerae-Tal, Sagnefjord' l.c.], on dead petioles of *Lastrea phegopteris*, 10.VI.1936, leg. Ade (n.v.).

Fig. 1G, 2H, I, 3B, 5B.

Ascocarps often densely scattered, broadly elliptic–subcircular, usually 100–150 μm long, opening by a longitudinal slit. *Basal layer* present, the cell walls adherent to the substratum being darkly pigmented. *Hypostroma* well devel-


20 µm
A
B
C
D

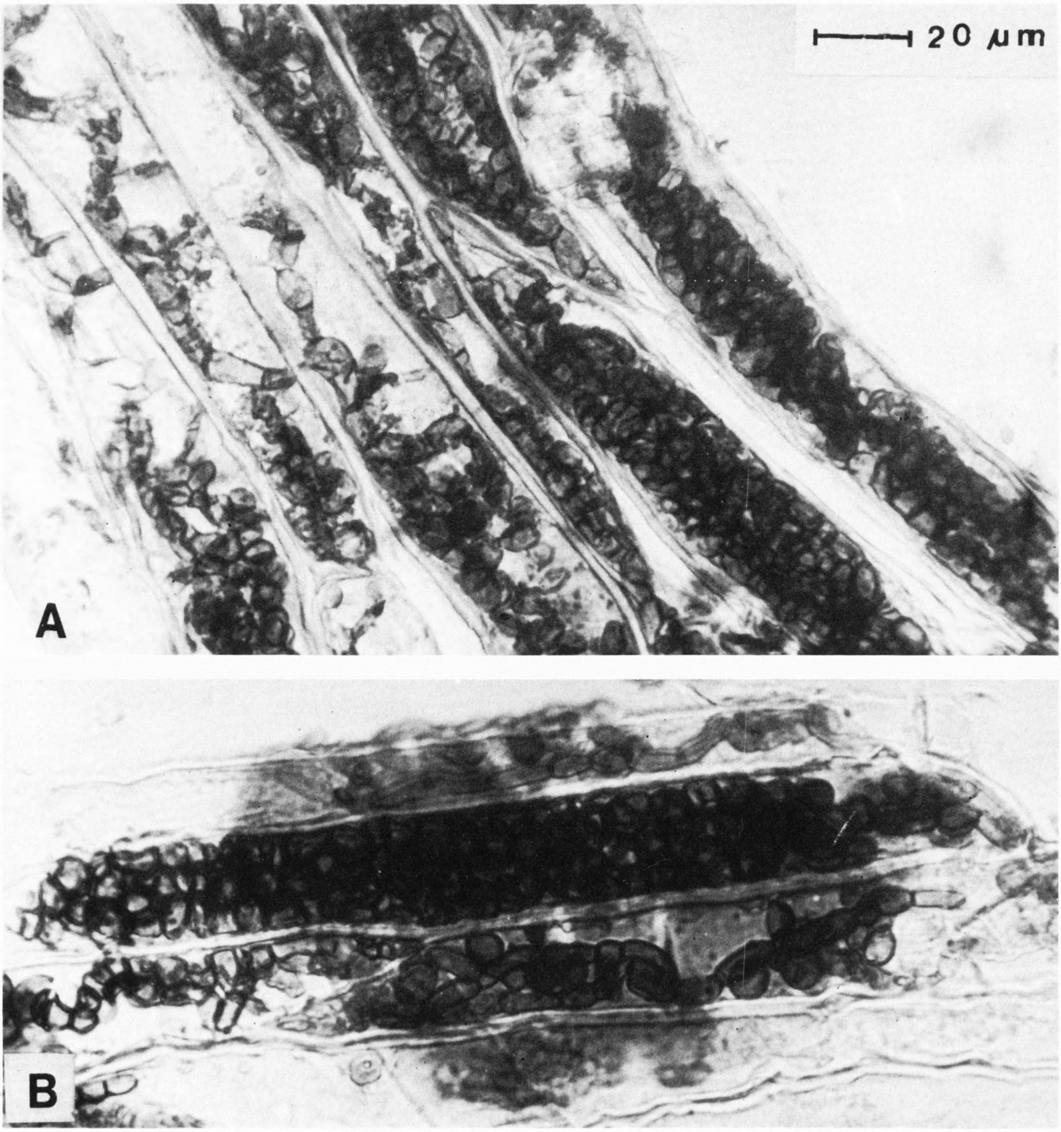


Fig. 5. Hypostromata in host tissue. – A: *Leptopeltis nebulosa*. – B: *L. gregaria*. – All × 610.

oped, mostly of textura globulosa, partly of textura angularis, of comparatively large, dark cells up to 10 µm. *Asci* normally with 8 spores but the number is extremely variable; supernumerary spores are frequent and we have seen asci with up to c. 16 spores. Petrak (1947 p. 243) reported 4- and 6-spored asci. The *spores* are also exceptionally variable in size and shape. Normally they are ± ellipsoidal, 10–12 × 3–4 µm, always(?) continuous.

Fig. 4. Sections of ascocarps. – A: *Leptopeltis pteridis*, hypostroma by the arrow. – B: *Dothiopeltis arunci*, hypostroma by the arrow. – C, D: *Ronnigeria arctica*, with conspicuous basal layer but no interthecial threads. – All × 530.

This species is apparently restricted to *Lastrea phegopteris,* and seems to be rather common, though so far only recorded from the type collection. It is characterized i.a. by the unicellular spores. We do not exclude the possibility of sundry spores becoming septate, but this is apparently exceptional.

Specimens seen: Sweden: Gästrikland. Hille par., Brännsågen, 21.V.1975, 563. –*Dalarna.* Sundborn par., Mjölnarvallen, 22.VI.1974, 198; 21.VI.1975, 596, 597; 23.VII.1975, 708.

Norway: Möre og Romsdal. c. 4 km NE of Gjöra, 1.VII.1975, 662.

6. **Leptopeltis** sp.

Fig. 1H.

Ascocarps subcuticular, densely clustered and often confluent, on both sides of the leaf blade, circular, c. 50 μm diameter, 25 μm high; basal layer pigmented on the underside. No hypostroma. *Asci* oblong, generally 17–20 × 10–12 μm, usually 8-sporous, but supernumerary spores occur. *Spores* oblong, continuous, hyaline, 7–10 × 2.5–3 μm.

Specimen seen: Sweden: Uppland, Uppsala, 'Predikstolen', last year's fronds of *Dryopteris filix-mas,* 25.V.1975, 576 b.

An extremely interesting fungus, unique by its habitat, growing abundantly in the leaf blade, outside the veins. It probably represents a new species, but because of the limited material we confine ourselves to this mention.

7. **Leptopeltis lunariae** (Fuckel) L. & K. Holm, comb. nov.

Microthyrium Lunariae Fuckel, Fungi rhenani 2471 (1872); Jahrb. Nass. Ver. Naturk. 27/28 p. 53 (1873) – *Gloniella lunariae* von Höhnel, Fragm. Mykol. 1004 (1919) – *Leptopeltopsis lunariae* von Arx, Acta Bot. Neerl. 13: 187 (1964) – Type: Austria, Kirchdorf, dead stems of *Lunaria rediviva,* leg. Schiedemayer (S!).

Fig. 1K.

Ascocarps superficial, densely scattered, elliptic, up to 0.3 mm long, but often confluent into larger crusts, intimately mixed with the imperfect form (*Leptothyrium lunariae* Kunze). *Shield* radiate, a thin basal layer present, with dark cell walls. No hypostroma. *Asci* oblong–cylindrical, 40–45 × 12 μm, 8-spored. *Spores* ellipsoid–fusiform, hyaline, 10–14 × 4–5 μm, with one, often submedian septum.

The species is known to us from the type collection only, which, however, is very rich. It is plainly distinct from the pteridicolous species, i.a. by the distinct basal layer, but is probably a close ally of the following species.

8. **'Leptopeltella perexigua'** von Höhnel

von Höhnel, Ber. Deutsch. Bot. Ges. 35: 422 (1917) – *'Pycnothyrium perexiguum'* von Arx, Acta Bot. Neerl. 13: 186 (1964) – non *Hysterium perexiguum* Spegazzini.

?*Moesziella pulchella* Petrak, Ann. Mycol. 25: 323 (1927) – Type: Czecho-Slovakia, Moravia, pr. Weisskirchen (Hranice), dead stems of *Senecio fuchsii,* 1925, leg. Petrak (W?).

Unfortunately no material of this species has been available for study, but judging from the descriptions published, it seems to be a true *Leptopeltis,* characterized i.a. by a distinct, dark basal layer, and by 4-celled spores. According to Petrak and von Arx, it is the perfect state of the very common and plurivorous *Leptothyrium vulgare* (Fr.) Sacc., a fungus, reported by others to be the imperfect form of *Hypoderma commune* (Fr.) Duby (e.g. Grove 1937 p. 163).

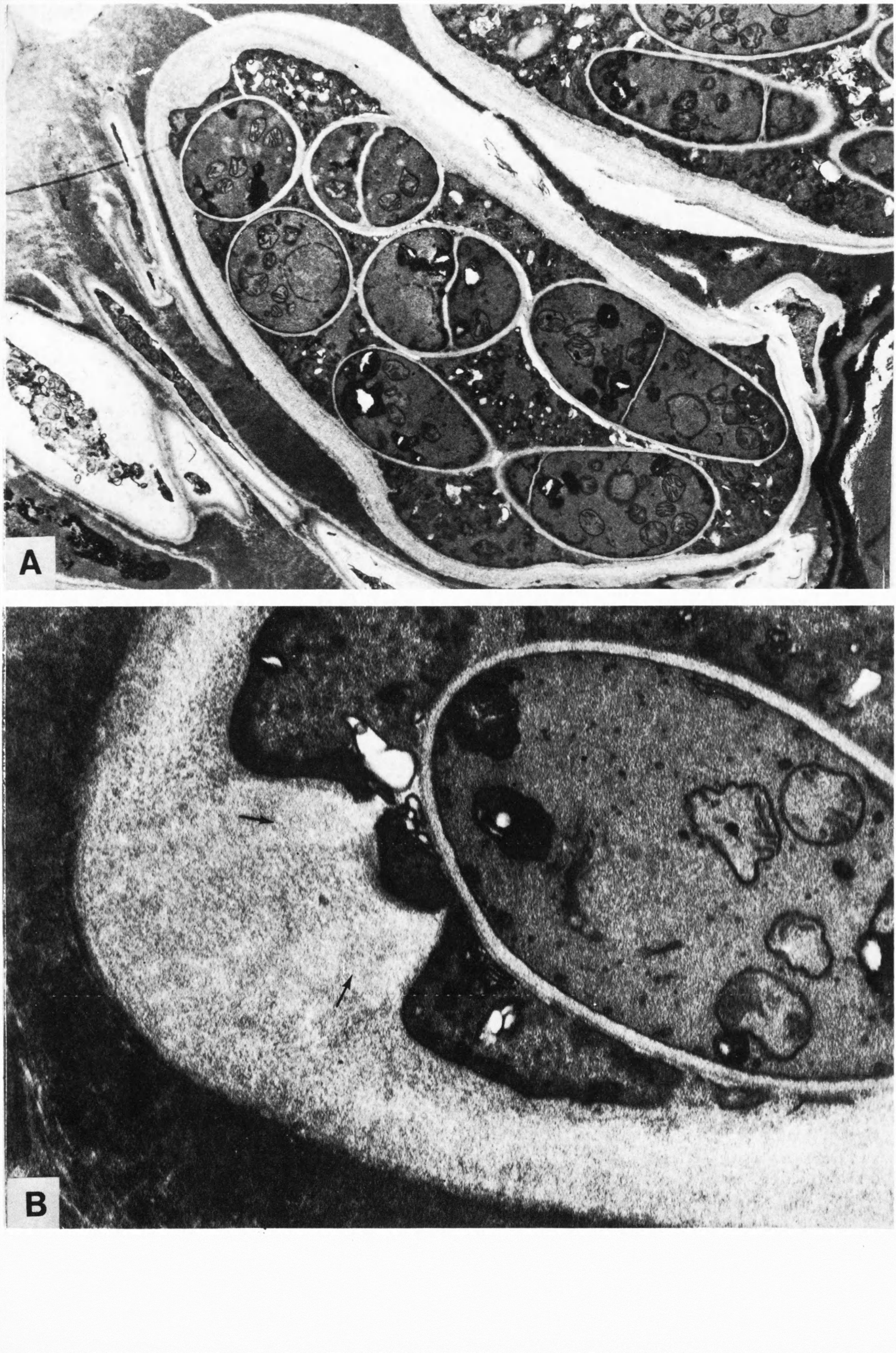
For the time being the fungus is probably devoid of a correct name. The epithet *'perexigua'* must be dropped, as it is based on a misinterpretation: von Höhnel erroneously identified his fungus with *Hysterium perexiguum* Speg. We have examined the type (Italy, Belluno, in dead stems of *Angelica silvestris,* 28. IX. 1879, leg. Spegazzini, LPS!) and can verify that it is hysteriaceous, having nothing to do with the Leptopeltidaceae. Consequently, it is the turn of *Moesziella pulchella* Petr., if it is synonymous, as claimed by Petrak. The correct name would then be *Leptopeltis pulchella* (Petrak), but without an autopsy we refrain from making the formal combination.

Dothiopeltis E. Müller

Müller, Sydowia 10: 197 (1957).

This genus was erected for the sole species *D. arunci* and is still monotypic. It is closely related

Fig. 6. *Leptopeltis nebulosa,* electron micrographs. – A: Ascus, × 8,000. – B: Ascus tip, a cylindrical electron-lucent ring by the arrows. × 30,000.


A
B

to *Leptopeltis* and the taxa might well be united. It seems reasonable, though, to keep *Dothiopeltis* as a separate genus, because of the muriform spores and the well developed basal layer.

Dothiopeltis arunci E. Müller

Müller, Sydowia 10: 197 (1957) – Type: Switzerland, St. Gallen, in dead stems of *Aruncus silvestris*, 25.V.1955, E. Müller & H. Schüepp (UPS isotypus!).

Fig. 1 I, 4 B.

Ascocarps scattered, subcuticular, elliptical in aspect in surface view, up to 0.2 mm long. *Shield* radiate, opening by a longitudinal slit. *Basal layer* well developed, up to 10 μm thick, of 1–2 layers of angular cells with strongly pigmented walls. *Hypostroma* poorly developed. *Interthecial threads* fairly numerous, with 2–3 septa. *Asci* ± oblong, c. 30 × 12 μm, 8-spored. Spores variable in form, ± irregularly ellipsoidal, hyaline, mostly 14–17 × 5–6 μm, generally with 4–5 transverse septa and one longitudinal septum in one or two central segments.

For a detailed description we refer to Müller's paper, though in some respects our findings are at variance with his. We have not seen the basal layer as strongly developed as in his Fig. 1 d, nor are we able to confirm the existence of a 'Mittelsäule', i.e. a central, sterile part of the ascocarp.

Dothiopeltis arunci seems to be a very distinct species, but is so far only known from the type collection.

Ronnigeria Petrak

Petrak, Sydowia 1: 310 (1947). – Type: *Ronnigeria arctica* (Oud.) Petrak l.c.

This genus, so far monotypic, is remarkably deviating by the absence of interthecial threads. The asci, however, are exactly the *Leptopeltis* type, and Petrak was certainly quite right when referring the genus to this family, though the relationship has been denied by von Arx & Müller (1954 p. 399).

Ronnigeria arctica (Oud.) Petrak

Petrak, Sydowia 1: 310 (1947) – *Microthyrium arcticum* Oudemans, Versl. Meddel. Kon. Akad. Wetensch., Afd. Natuurk., ser. 3. 2: 160 (1885) – Type: Novaja Zemlya, *Potentilla fragiformis*, VIII. 1881, M. Weber (n.v.).

Fig. 1 J, 3 C, 4 C, D.

Ascocarps mostly densely crowded, often confluent, amphigenous, subcuticular, solitary ones lenticular, generally 100–125 μm diameter. *Shield* irregularly radiate, basal stratum well developed, of 3–4 cell layers, the undermost one with strongly incrusted walls. No interthecial threads, no hypostroma. *Asci* rather few, ± oblong, c. 35–40 × 10–12 μm, 8-spored. *Spores* continuous, hyaline, 8–12(–15) × 2.5–4(–5) μm, very variable in form and size, oblong–ellipsoidal, often slightly cuneiform.

In dead leaves, especially the lamina, of *Potentilla* spp.

For a full description, see Petrak (1947 b). Evidently the fungus has an arctic-alpine distribution. It is widely spread in the Arctic and is quite common in northern Scandinavia, on *Potentilla crantzii* (even found on *P. hyparctica*). However, it is apparently not coextensive with *P. crantzii;* this plant is common around Uppsala, where the fungus seems to be lacking. Petrak found it on a collection from Austria, Burgenland, which was the first, and still seems to be the sole, record from Central Europe.

Excluded genera

As mentioned in the introduction, several fungi have been wrongly referred to the Leptopeltidaceae by various authors. Most of the 13 genera, originally included by von Höhnel, are evident outsiders and need not be considered; an exception is *Thyriopsis* Theissen & Sydow which was reintroduced by Müller & von Arx (1962) and still kept in the family by von Arx & Müller (1975). In the latter work some further taxa were included, viz. *Aulographum* Lib., *Aulographina* v. Arx & Müller, *Lembosina* Theissen, and *Morenoina* Theissen. These had been placed among the Asterinaceae by the same authors in 1962, a classification which is definitely to be preferred, as they are all bitunicate. This is also the case for *Thyriopsis*, which seems to be fairly closely related to e.g. *Lembosina*.

In 1919 von Höhnel erected the new genus *Lichenopeltella*, based on *Microthyrium maculans* Zopf, a parasite in the thallus of *Umbilicaria hirsuta*. He stated that the fungus 'stellt eine neue Gattung dar, die wegen des fast oberflächlichen Wachstums am besten neben der subcuticulären *Leptopeltella* gestellt werden kann' (1919 p. 553). Von Höhnel was, however, more superficial than the fungus, which in fact is basally immersed in the lichen thallus, as is also illustrated by Müller & von Arx (1962 p. 239, fig. 82), who followed von Höhnel's classification. *Lichenopeltella maculans* has bitunicate asci and seems to be akin to *Mycosphaerella*.

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Flower-visiting lizards on Madeira

Ivar Elvers

Elvers, I. 1977 06 30: Flower-visiting lizards on Madeira. *Bot. Notiser 130:* 231–234. Stockholm. ISSN 0006-8195.

The Madeiran lizard *Lacerta muralis dugesii* has been observed to visit flowers of the introduced species *Aloë arborescens* and of the indigenous *Echium nervosum* in a manner very similar to that of ordinary pollinating visitors. It is suggested that this lizard-flower interrelationship may be looked upon as a possible model of a palaeo-ecological connection between pre-angiosperms and reptilian pre-birds.

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The fauna of the Atlantic island of Madeira includes only one species of reptiles: an indigenous form of the wall lizard, *Lacerta muralis dugesii,* which is very abundant, especially in the vicinity of human settlements. In sunny weather it can be seen on rocky precipices, on house walls, on stone fences etc.

This lizard has been observed visiting the flowers of different plants – obviously to lap up nectar in the flower. A short account of two closely followed cases will be related here.

Observations

Aloë arborescens is a South African shrubby xerophyte, reaching a height of 0.5–2 metres. This species is grown frequently on Madeira as an ornamental plant. From October to February it carries dense, upright racemes of pendant, brightly red flowers. In its native surroundings it is ornithogamous, as is indicated by the vivid colour of the flowers and the very rich nectar production. On Madeira frequent visits are made by honey bees (Fig. 1 A) and sometimes by indigenous birds, this is also true where other introduced plants are concerned (cf. Vogel 1954 p. 328).

On Cape Garajau, a high cliff on the southern shore of Madeira, a religious monument has been erected, surrounded by a horizontal, gravelled plain. On one side of the plain there is a small, stone-walled shed. This shed and the walls supporting the plain is the site of a great number of lizards. Around the place dense populations of *Aloë arborescens* are growing; some of the plants stand very close to the shed (Fig. 1 B).

In December 1976 observations were made of numerous visits of lizards in the flowers of these plants (Fig. 1 C). This *Lacerta* population comprised animals of varying size; the flowers were exploited only by the young, still small individuals, which could poke their heads into the interior of the flowers. The adult lizards, who could no longer enter the legitimate way did not attempt any nectar thefts.

New observations were made on Cape Garajau in February 1977. The *Aloë* specimens along the shed wall were in a postfloral stage and although other plants in the vicinity still carried flowers, no lizards could be seen in them.

However, in the natural vegetation on the slopes of the cape another plant species was now in full bloom, viz. *Echium nervosum.* This shrub, reaching a height of c. 1 metre, is endemic to the Madeiran archipelago. It carries very conspicuous inflorescences: numerous cymes of light blue flowers, densely packed to form a heavy, upright spike-like construction. The nectar production is rich, frequently attracting visitors, viz. pollinating insects.

On one point of Cape Garajau where the stone wall supporting the gravelled plain rises from the surrounding natural ground, two small *Echium* shrubs were flowering. The inflorescences of these were frequently visited by the *Lacerta* population from the adjacent wall (Fig. 1D). In the *Echium* flowers the nectar was available to lizards of any size; they could just sit on the inflorescence and rapidly dip their tongues into the flowers.

The distance between the *Aloë* plants exploited by the shed lizards in December and the *Echium* plants exploited by the wall lizards in February is c. 30 metres. The *Lacerta* population which had become accustomed to nectar drinking in the *Aloë* flowers may have moved over to the *Echium* plants later on. Though it does seem more probable that the populations stick within very limited territories, with the result that the different plants were visited by different lizard populations.

The flower-lizard inter-relationship observed may thus be provoked when a suitable flower grows just in front of a lizard-wall. Two other observations were made under these conditions, indicating such an incentive behind the adaptation of the lizards to the flowers. Firstly a visit of a lizard in flowers of *Echeveria atropurpurea* (in the Madeira Botanical Garden February 1967) was observed, and secondly a group of lizards visiting *Salvia splendens* (in the Sta Catarina Park in central Funchal, February 1977). A fifth plant species where Madeiran *Lacerta* specimens have been observed among the flowers is *Agave attenuata* (observations in February 1967, 1970 and 1977). In this case, however, it cannot with certainty by claimed that the purpose of the visits was that of lapping nectar.

As to the *Aloë*, the *Echium* and the *Salvia*, the lizards were observed to approach the flowers by climbing up along the stems of the plants, as well as by jumping directly through the air from the adjacent stone wall or from other branches of the plants. They showed the same versatile agility in such jumps as may be seen among lizards hunting for insects on the room walls in houses in the tropics.

Discussion

Very little attention has been given to the possibility that reptiles may have any importance as pollinators. The small and agile lizards that can be observed among flowers in the warmer parts of the world are typically carnivorous, and their hard, sleek body surface does not seem at all suitable for pollen carriage. To them the inflorescences of plants probably chiefly mean hunting grounds for insects.

During earlier periods in Earth history the situation may, however, have been different. Coprolites from the Permian and Jurassic indicate that reptiles have been browsing on the flowers of those days (Schweitzer 1968, Harris 1945, 1956, cf. also Faegri & van der Pijl 1966 p. 20). In a recent palaeobotanical treatise on angiosperm origin, reptiles have actually been mentioned as a possible alternative to beetles as original pollinators (Hughes 1976 p. 57).

At the present time birds are important pollinators. If similar ties existed in the Jurassic, they would have involved pre-angiosperms and pre-birds, which underwent a more or less contemporary evolution. In this respect the close relationship between birds and reptiles should be considered; the birds might even be classified as a group among the reptiles (von Huene 1956).

Probably the relationship observed on Madeira is rather unusual: it is so striking that it could hardly have escaped notice had it been of more common occurrence. However, the biological interest of the observations does not primarily lie in the fact that the lizards might bring about some cross-pollination in the few plants they visit. Since their behaviour so closely follows that of ordinary pollinators, it might instead be taken as a sign that an ethological basis for ecological relationships with flowers may be present among reptiles. Thereby is an interesting question raised: is what we today call ornithogamy directly derived from pollination by reptiles among early angiosperms?

The figures are reproductions from part-pictures of pairs of stereoscopic colour photographs. The three-dimensional realism of the originals cannot be communicated. Biologists visiting Stockholm are, however, invited to call upon the author to inspect the originals.

Fig. 1. A: Honey-bee in a flower of *Aloë arborescens*. – B: *Aloë arborescens* at a stone-walled shed. To the left on the sunny side some lizards (*Lacerta muralis dugesii*). – C: An inflorescence of *Aloë arborescens*. A young lizard is sucking nectar. – D: Inflorescences of *Echium nervosum* visited by a lizard drinking nectar. – Madeira, Cape Garajau, December 1976 (A–C) and February 1977 (D). Photo Ivar Elvers.

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Studies in African Cyperaceae XV

Amphicarpy and spikelet structure in Trianoptiles solitaria

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Haines, R. W. & Lye, K. A. 1977 06 30: Studies in African Cyperaceae XV. Amphicarpy and spikelet structure in Trianoptiles solitaria. *Bot. Notiser 130:* 235–240. Stockholm. ISSN 0006-8195.

The morphology of *Trianoptiles solitaria* (C. B. Cl.) Levyns is described and illustrated. This South African plant has basal spikelets, each reduced to a solitary female flower enclosed in a utricle probably representing a modified glume, in addition to the 2-flowered aerial spikelets. New leafy culms and basal spikelets spring together, as multiple buds, in the axils of the leaves. In these features it is highly specialised. The 3- or 4-glumed aerial spikelet shows a monopodial structure particularly clearly and this, rather than a cymose structure, is probably characteristic of other Rhynchosporeae.

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The genus Trianoptiles Fenzl

The genus *Trianoptiles* was described by Fenzl in Endl. Gen. Pl., p. 113 (1836). The type species is *Trianoptiles capensis* (Steud.) Harv. in Gen. S. Afr. Pl. ed. 2, p. 422 (1868), based on *Ecklonea capensis* Steud., in Flora 1829, p. 138. However the generic name *Ecklonea* Steud. had to be rejected because it had previously been used for a genus of seaweeds.

The genus *Trianoptiles* is closely related to *Carpha* R. Br., but differs in having hypogynous bristles feathered at the base, 3-fid at the apex (Clarke 1898 for *Ecklonea*). However, Clarke (1898 p. 271) writes "The structure of the spikelet and flower in this plant is so exactly that of *Carpha* that it might be better to sink the genus in *Carpha*." Pfeiffer (1930) merged the two genera.

However when the basal female flowers were discovered (Levyns 1943), new evidence supporting the separation of the two genera came to light. Verbelen (1970) found the embryo to be of the *Fimbristylis* type in both genera, but in *Trianoptiles* the embryo has a distinct capitellate top-like form. The vegetative anatomy in the two genera also differs in several characters (Metcalfe 1971).

Therefore in this work we have accepted the genus *Trianoptiles* as being separate from *Carpha*, although we realize that they are closely related.

Description

Trianoptiles solitaria (C. B. Cl.) Levyns is a dwarf South African annual growing in seasonally damp areas of the Cape Flats, first described by Clarke (1900 p. 759) as *Ecklonea solitaria*. It is one of the three species of its genus, all rather similar and all confined to the Cape Province (Levyns 1943, Adamson & Salter 1950, Phillips 1951). It produces two kinds of fruit, one aerial, the other at ground level. Thus it is amphicarpous, as are several species of *Bulbostylis* and *Scirpus* recently reviewed by Haines (1971) and Raynal (1976), and now placed in *Abildgaardia* and *Schoenoplectus* (Haines & Lye 1977). It is discussed here because it is a very good example of the habit in the classic sense

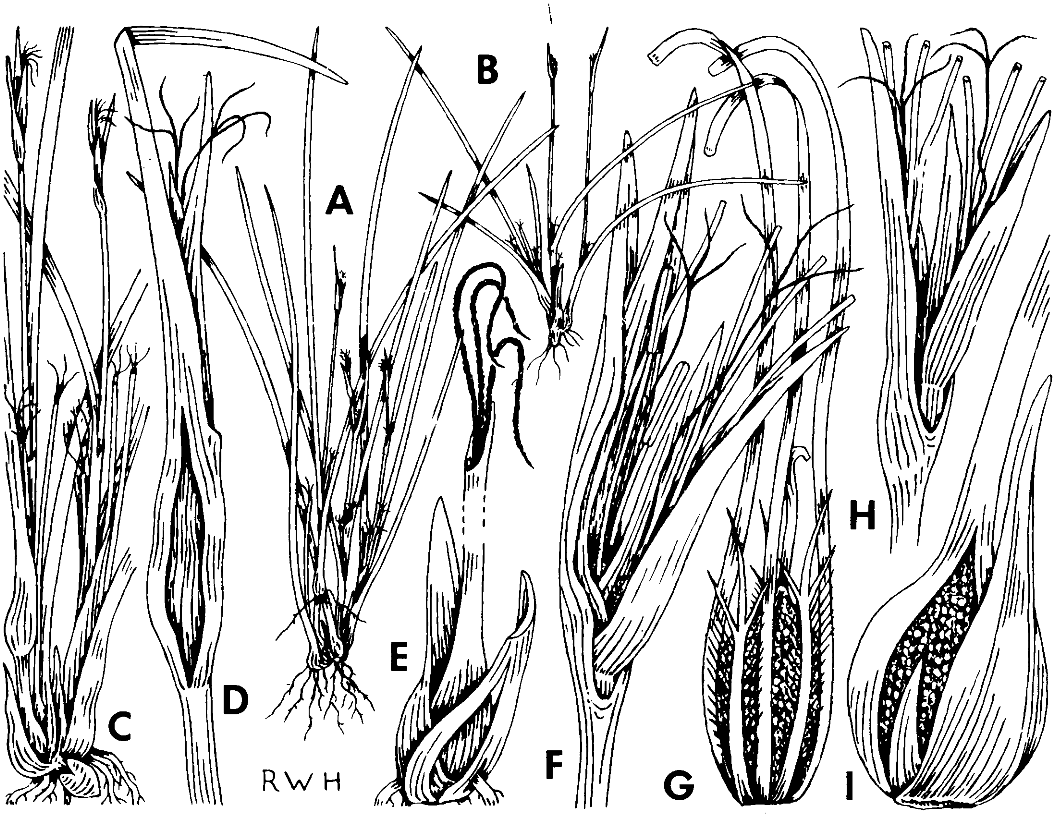

Fig. 1. *Trianoptiles solitaria* drawn from Lye 6697, Rondebosch, Cape Province, S. Africa. – A, B: Habit. – C: Culms and basal flowers, with the achene case from which the seedlings grew. –D: Aerial inflorescence in fruit, the basal glume split. – E: Basal spikelet. – F: Aerial spikelet with 4 glumes. –G: Flower in fruiting stage with perianth and filaments. – H: Aerial spikelet with 3 glumes, the lowermost fertile. – I: Basal fruit with its split utricular base.

of Zohary (1937) and Hylander (1946), as illustrating a possible way by which amphicarpy can be developed and as a basis for reconsideration of the disputed spikelet structure in Rhynchosporeae.

The plant is tufted, new culms developing in the axils of the leaves of the older culms (Fig. 1 A, B). The fruit from which the plant grew may be preserved as a split shell at its base (Fig. 1 C). Each culm bears up to 3 foliage leaves and ends in a 2-flowered spikelet, with or without additional lateral spikelets below. Solitary female flowers are found at the plant base, their stigmas raised high above the ground surface on long styles.

The internodes at the base of the culm are more elongated than in most tufted sedges, so that the roots growing from successive nodes come to form tiers one above the other. Raynal (1967) found similar elongated basal internodes in some specimens of *Lipocarpha chinensis* and noted that they might be mistaken for stolons: "il faut se défier de prendre pour des stolons des tiges allongées verticalement ou presque". They are illustrated in a form of *Abildgaardia* (*Fimbristylis*) *hispidula* by Lye (1971 Fig. 2) and in *Pycreus elegantulus* and *P. lanceolatus* by Haines & Lye (1977). In the *Lipocarpha* Raynal (1967) ascribed their development to "un ensablement dans le lit d'un cours d'eau", the *Abildgaardia* was surrounded by windblown sand and the *Pycreus* plants were growing on silt. In *Trianoptiles* they appear to be normal formations, possibly developed in adaption to life in the rich, though temporary, turf that springs up after rains.

The aerial spikelet may have 3 (Fig. 1D, H) or

4 (Fig. 1 F) glumes, the uppermost always empty, the lowermost also empty when there are 4. The flower bases are hidden in the glumes, only the ends of the long 3-branched styles and the filaments, from which the anthers soon drop, protruding. The flower has a 3-partite perianth of flattened bristles, each bristle trifid at the tip and long-ciliate on the margins (Fig. 1 G). The achenes are elliptic, often splitting the lowest glume as they expand (Fig. 1 D), with a hard coat bearing tubercles in longitudinal rows. At fertilization, which, as usual in Cyperaceae, precedes anthesis, the perianth is poorly developed and its cilia adpressed but later it grows and its cilia spread. The fruit disarticulates with the perianth and persistent filaments remaining attached, possibly as an aid to dispersal.

The solitary female flower at the plant base is reduced to a pistil without trace of any perianth or stamens. It is closely surrounded by a long-necked utricle with an oblique opening from which the style or its 3 branches protrude (Fig. 1 E), the arrangement closely resembling that in *Carex*. Enfolding the swollen base of the utricle there is often a short wide scale, probably a prophyll such as is commonly found at the base of the lateral, as opposed to the terminal, spikelets of Cyperaceae (Haines 1966, Raynal 1971). If this is the case the utricle must be a modified glume, not a modified prophyll as in *Carex*.

When fertilised, presumably by pollen from the aerial spikelets of the same or a neighbouring plant, the basal flowers form globular achenes, heavier than the aerial fruits. Encased in their utricles and old leaf bases they stay in place even after the plant has died. The specimen shown in Fig. 1 C grew from such a fruit. The fruits at the base of each culm ripen before the aerial fruits at its apex.

Clarke found the basal fruits resulting from these flowers in *Trianoptiles capensis* (Steud.) Harv., the type species of the genus. But though he was familiar with the similar fruits in *Bulbostylis humilis* and *B. brevicaulis* and in these species described them correctly, in *Trianoptiles* he described (1898) and figured (1909) the utricle necks and bodies as "slender rhizomes" and "minute bulbils". Schönland (1922) also figured the fruits but without indicating their nature. Later writers have recognised their true nature, but usually make no mention of the utricle, which encloses the pistil so tightly that it appears to have been missed. However, Levyns (1943) describes the female spikelet as "consisting of 2–4 tightly sheathing bracts and a terminal flower, the basal portion of the spikelet subterranean, only the narrow, tubular tip of the uppermost bract and the style branches projecting".

The annual habit and reduced unisexual 1-flowered basal spikelets forming large fruits fixed in place to grow during the next wet season are typical of amphicarpous plants and can be paralleled to *Schoenoplectus lateriflorus* and *articulatus*, for example (Haines 1971, Raynal 1976). The reduction of the aerial inflorescence to one or a few spikelets with only 2 flowers in each is peculiar to the species. The early ripening of the basal fruits is common in amphicarpous species but their enclosure in a utricle is unique.

Development of amphicarpy

In most Cyperaceae the buds in the axils of the lower leaves or sheaths grow into new culms, either directly or by first forming stolons which end in new culms. The buds nearer the culm apex form inflorescence branches of the panicle or anthela as the case may be, subtended by the inflorescence bracts. An intermediate group of leaves either subtend buds which do not develop except in emergencies when the plant apex is destroyed or have no buds at all in their axils. Such an arrangement is described in, for example, *Scirpus sylvaticus* by Irmisch (1855) and Monoyer (1934) and generalised by Mora (1960) and others.

In *Trianoptiles* there are usually no empty axils (Fig. 2 A–C). Haines (1971) suggested that in amphicarpous sedges the "intermediate emergency buds" might "have become specialised to give the basicaulous flowers". But here conditions are more complex, and at the same time more easily examined as the elongation of the internodes makes dissection relatively easy even in the dry specimen.

At the base of each new culm the scales are delicate and soon wither leaving the basal flowers in their axils exposed. No new shoots form in this region but there may be two flowers, each presumably representing a 1-flowered spikelet, in a single axil.

The lowest foliage leaf (Fig. 2A–C, f^1) subtends a complex with a well developed

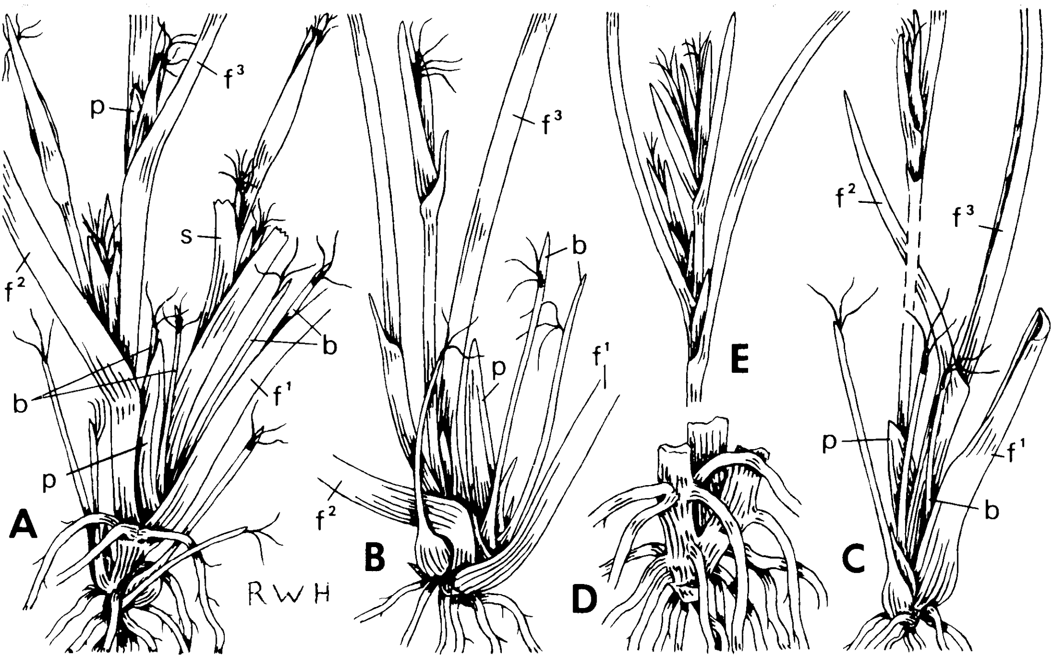

Fig. 2. Branch systems of *Trianoptiles*, the parts spread to expose the axils. – A–C: Culm bases with basal flowers and new culms. – D: Remains of a plant from a previous season. – E: Apex of a strong culm with terminal and lateral spikelets. – b basal flower; f foliage leaf; p prophyll; s leafy shoot.

prophyll (p), one or more basal spikelets (b) and, usually, a new leafy shoot (A and C, s). The second leaf (f^2) may subtend a leafy shoot, a stalked or sessile spikelet or a combination of these, but, in the material investigated, no basal type spikelet. The third and any succeeding leaves subtend only solitary sessile spikelets of an aerial type, or, in the case of the uppermost leaf of weak shoots, they may be empty.

Multiple branching in a single leaf axil is widespread in Cyperaceae. The branches may arise in succession, each from the axil of a prophyll of an earlier axis as in the inflorescence fragments of *Rhynchospora corymbosa* and *Scleria naumanniana* drawn and analysed by Haines (1966). Or the branches may arise independently, each with its own prophyll, as the pair of spikelets placed side by side or one before the other, in tandem, in *Carex utricularia* (Schulz 1887). There may be many branches in complex arrangement as in the inflorescence of *Cyperus papyrus* (Schumann 1892, Raynal 1971), and when they are crowded the prophylls may be lost as in *Schoenus nigricans* (Haines 1966). The arrangement in *Trianoptiles*, with basal flowers and new culms set together in the leaf axils appears unique in Cyperaceae and must be an extreme specialization, probably based on a less developed type of multiple budding in an ancestral species.

Spikelet in Rhynchosporeae

Since the work of Pax (1886) and Čelakovský (1887) the spikelet of Rhynchosporeae and Sclerieae has been considered to be a cymose structure or rhipidium. Each flower above the first was said to terminate an axis springing from the axis below (Fig. 3 E, F) and this produced a major distinction from Scirpeae and Cypereae where the structure was monopodial, with the flowers set laterally on a simple rachilla (Fig. 3G, H).

However, Schumann (1890) and Holttum (1948), on the contrary, found no essential difference in the spikelet structure between Scirpeae and Rhynchosporeae, describing both as being monopodial in structure. Kern (1962)

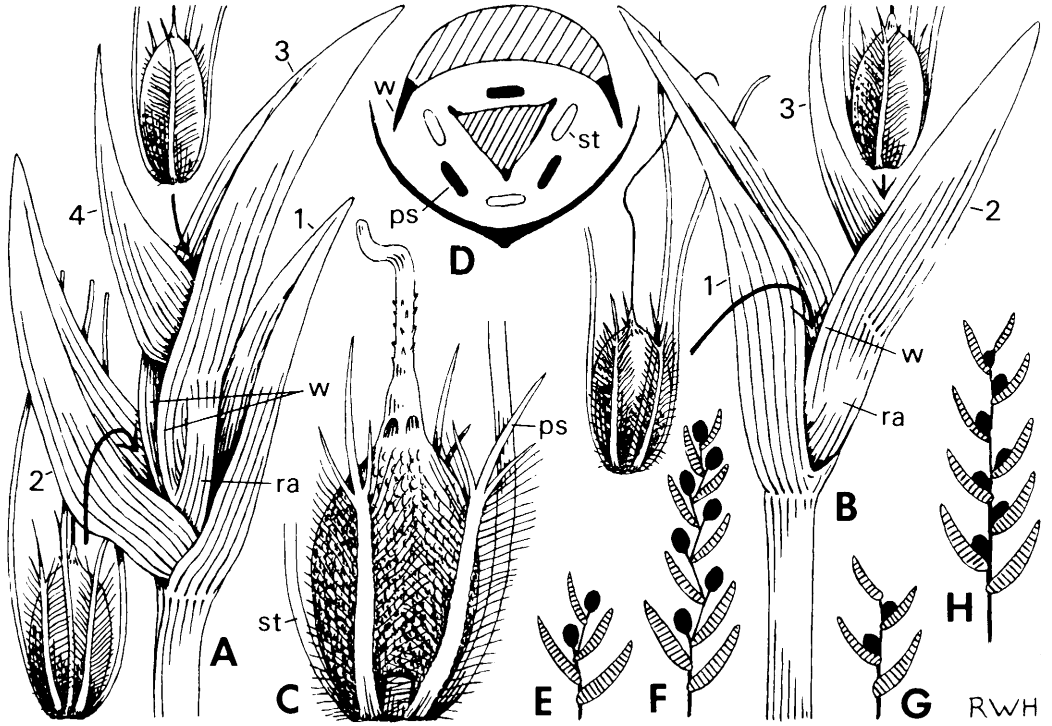

Fig. 3. Spikelet arrangement in *Trianoptiles* and other Rhynchosporeae. – A, B: Dissections of 4- and 3-glumed spikelets. –C: Fruit with perianth bristles. –D: Plan of a flower in position. – E, F: Diagrams of spikelets of cymose structure. –G, H: Diagrams of spikelets of monopodial structure. – ps perianth segment; ra rachilla; st stamen; w wing.

agreed that the spikelets were similar but described both as cymose. Haines (1966) showed in *Schoenus, Rhynchospora* and *Scleria* how each flower was enwrapped by the margins of the glume above that which subtended it, so giving a false impression that it was a terminal structure. Raynal (1971) from new evidence based on the structure of the rachilla, showed that in *Cyperus* at least the structure was monopodial.

Phillips (1951) described the aerial spikelets of *Trianoptiles* as "cymose, with 3–5 more or less distichous bracts and in most cases two perfect flowers associated with the 2 uppermost bracts". However, in reality the simple uncrowded spikelet shows the monopodial structure particularly clearly (Fig. 3 B). The lower flower is enwrapped by wing-like extensions (w) of the glume subtending the upper flower and the uppermost glume is empty.

In a 4-glumed spikelet (Fig. 3 A) the lowermost glume (1) is clearly empty. Glume 2 has a flower in its axil. The rachilla is continued (ra) with a hollow facing the flower and partly enclosing it. A pair of wings (w) are continued downwards from glume 3 along the margins of the rachilla and these help to deepen the hollow. Glume 3 subtends the upper flower which is again enclosed laterally by the wings of the empty glume 4. The flower is set with the median stamen and style-branch abaxial (C, D) as in Scirpeae and Cypereae and the 3 perianth bristles alternate with the stamens as the major segments of a *Fuirena* (Clarke 1898).

Since glume 4 is attached to the rachilla at about the same level as 3 it might be reasonable to consider the upper flower as being set above it, as stated by Phillips. But that would leave glume 3 empty, a most improbable situation. In the 3-glumed spikelet (Fig. 3 B) the arrangement is similar but the lowermost glume 1 of the 4-glumed type is missing. The wing-like extensions of glumes 3 and 4 enwrapping the flowers below are to be found in many species of *Cyperus*, forming Kükenthal's (1936) "alae", considered by him as belonging to the rachilla rather than the glumes. They are less familiar in Rhynchosporeae.

An extension of either the cymose or monopodial system could result in a many-flowered spikelet (Fig. 3 E or G to F or H). But since E is clearly wrong for *Trianoptiles*, F is presumably wrong for Rhynchosporeae with several flowers, up to 5 in *Schoenus* (Haines 1966), over 30 in *Rhynchospora candida* (Haines & Lye 1977). Indeed it is doubtful if the cymose structure would ever have been proposed if such well developed spikelets had been examined by the earlier workers.

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Femsjonia peziziformis (Dacrymycetales) in North Europe

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Femsjonia peziziformis (Lév.) Karst. (Dacrymycetales) is treated with regard to its occurrence in North Europe. *F. peziziformis* is the only known species in this area. A detailed investigation of its morphology has been made. Intraspecific and intergeneric relations are discussed. Notes on the ecology are given, and the distribution in North Europe is mapped. The species is recorded as being new to Denmark and Norway.

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The genus *Femsjonia* was established by E. Fries, who described *F. luteoalba* (Fries 1849) and named the genus after his home parish of Femsjö in Småland. Since then the genus has only appeared once in Scandinavian mycological literature (Karsten 1876). It has therefore been looked upon as being extremely rare in this part of the world. The next report concerning its occurrence in Scandinavia is given by McNabb (1965) who regards three taxa described by Karsten as being synonymous with *Femsjonia luteoalba* and the older *Exidia pezizaeformis* Lév. During the last few years the species has been collected a few times in the Nordic countries. This is also the first report of the fungus from Denmark and Norway. In Estonian SSR several collections have been made during the last three decades (Fig. 5).

Outside Europe two other species have been described, viz. *F. orientalis* Kobay. (Kobayasi 1939 p. 217) and *F. pezizoidea* (P. Henn.) McNabb (McNabb 1965 p. 226). *F. natalensis* Cooke and *F. radiculata* (Fr.) Martin are species excludendae (McNabb 1965 p. 227).

Femsjonia peziziformis (Lév.) Karst.

Karst., Bidr. Finl. Nat. Folk 25 (=Mycologia fennica 3): 352, 1876. – *Exidia pezizaeformis* Lév., Ann. Sci. Nat. Bot. III, 9: 127, 1848.

Femsjonia luteoalba Fr., Summa Veg. Scand. II: 341, 1849. – Neotypus Erikss. & Jacobss. 19602.

Dacrymyces mesentericus Karst., Finl. Basidsv. 459, 1889. – Lectotypus Karst. 1556.

Dacrymyces radicellatus Karst., Hedwigia 29: 178, 1890. – Holotypus Karst. 1559.

Ditiola conformis Karst., Fungi Fenn. Exs. 629; Not. Sällsk. F. Fl. Fenn. Förh. 13 (=Symb. Myc. Fenn. 2): 223, 1873. – Lectotypus Karst. 1554.

Dacrymyces conformis (Karst.) Neuh., Ark. Bot. 28 A(1): 44, 1936.

Fruitbodies single or gregarious, often confluent, sessile or with a short stalk, when fresh mostly 5 to 10 mm in diameter, sometimes larger, at first circular, pustulate to discoid, convex, plane, or slightly concave. Old fruitbodies more irregular (Figs. 1, 2 A, B), bright yellow when young, darkening to dull or brownish yellow when old, fleshy to firmly gelatinous; hymenium at first even and smooth, in old specimens more or less wrinkled (Fig. 2 A); underside white in young fruitbodies, dull yellow in old ones. *Hyphal system* monomitic, hyphae fibulate (Fig. 3 F, G), in the tramal part of the fruitbody thinwalled, 2–3

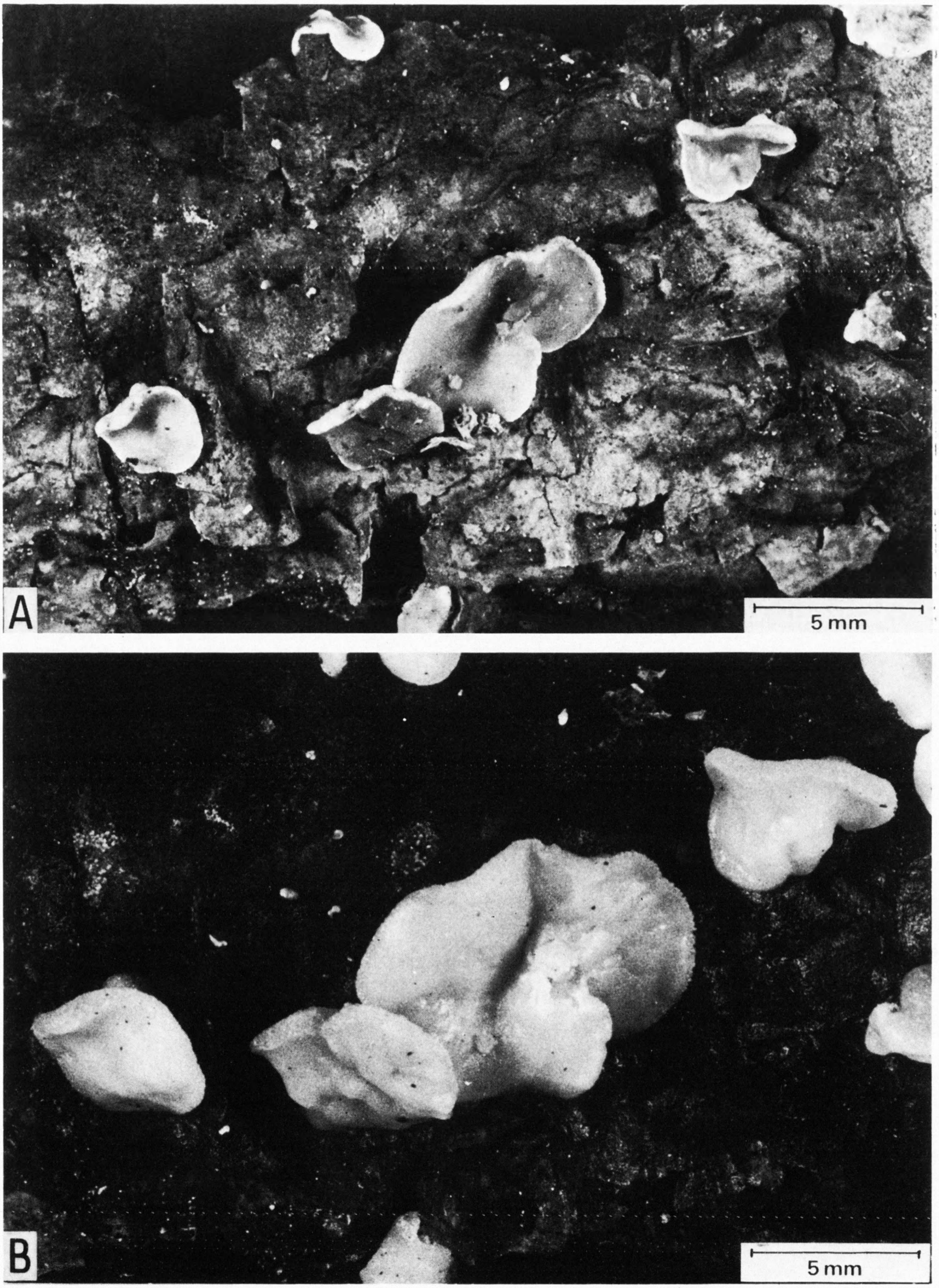


Fig. 1. Fruitbodies of *Femsjonia peziziformis* on *Pinus sylvestris*. – A: Dry specimens. Note the pezizoid shape. – B: The same specimens in wetted state. The fruitbodies have swollen considerably. – Coll. Sunhede 6695. Photo: S. Sunhede.

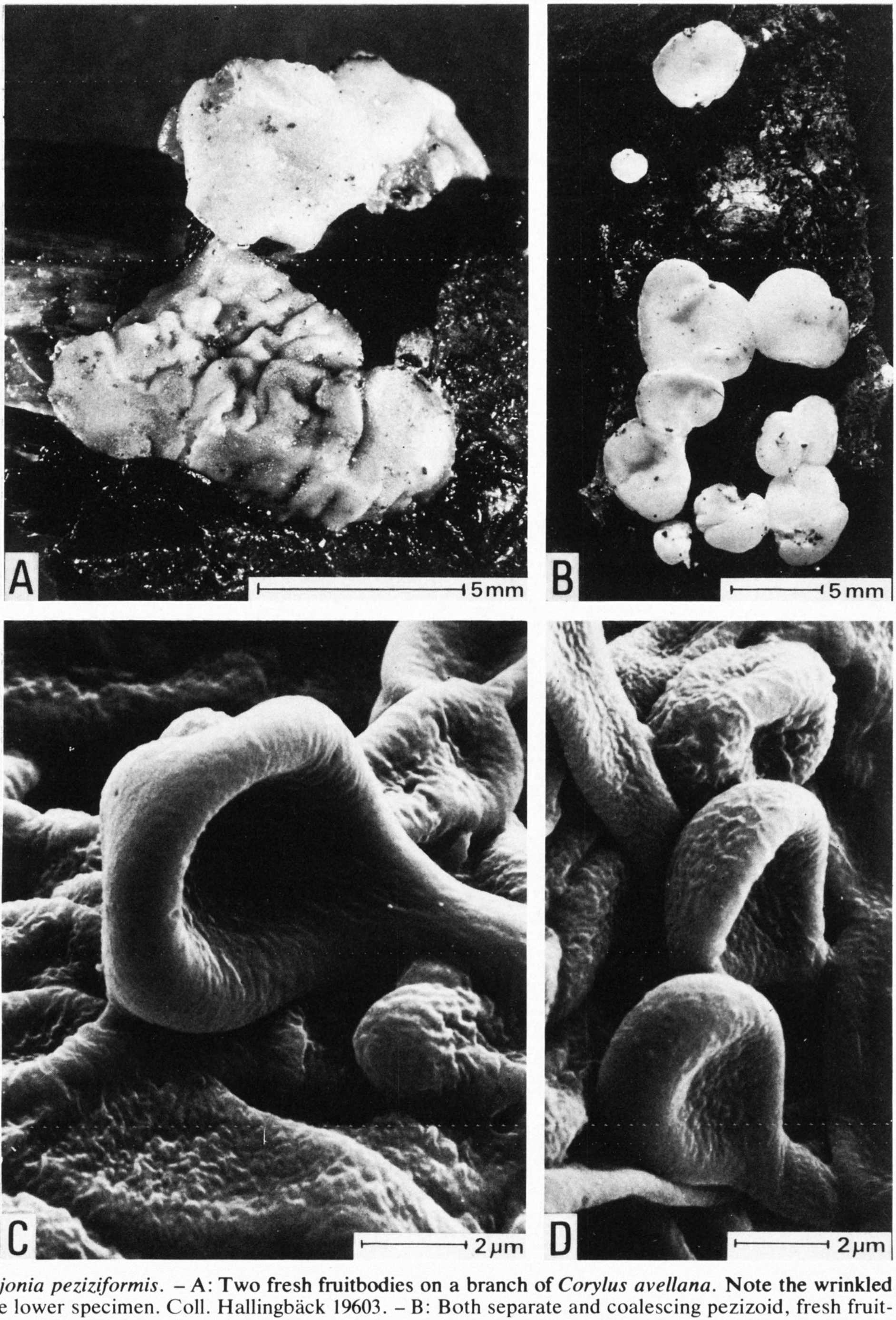
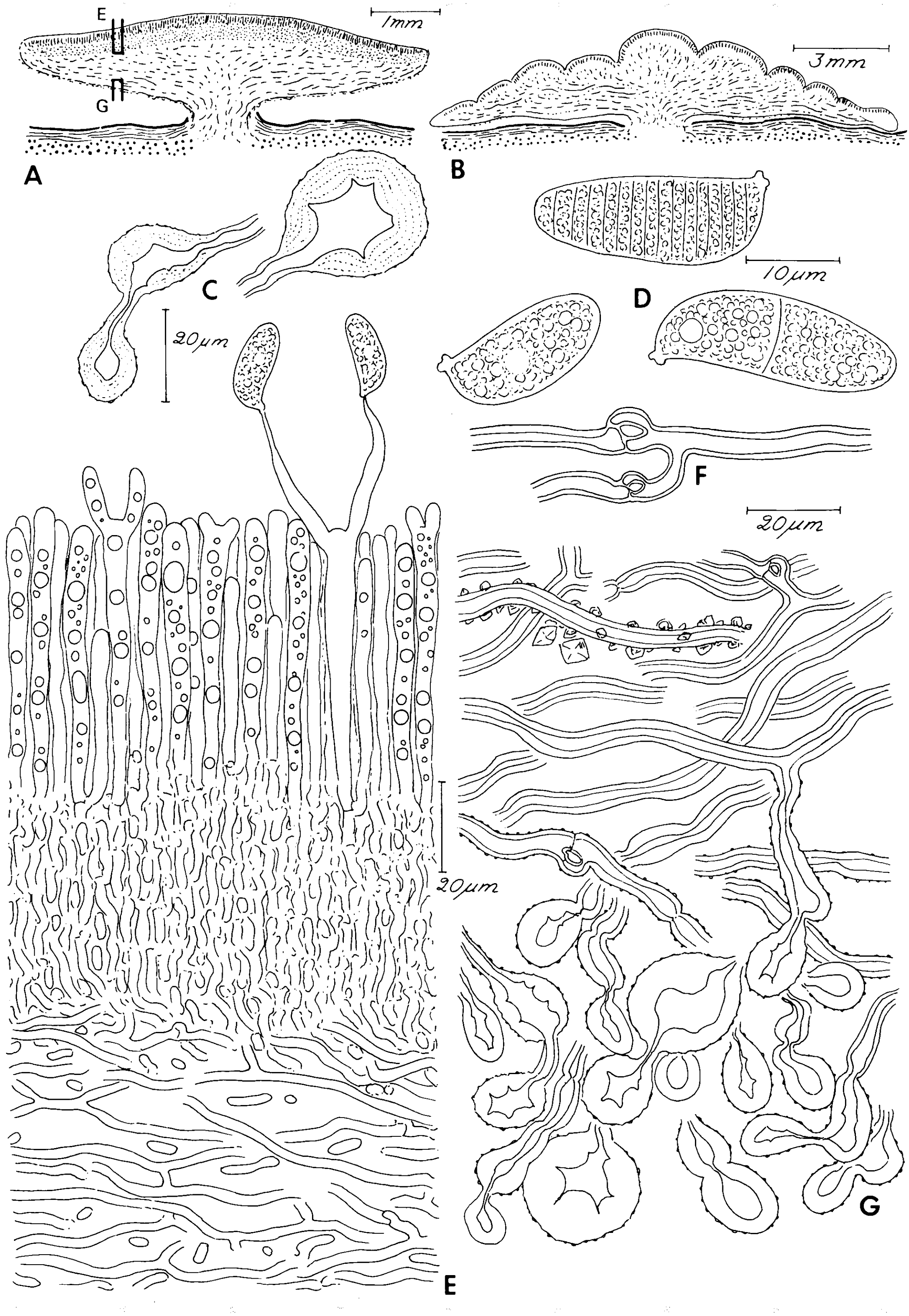


Fig. 2. *Femsjonia peziziformis*. – A: **Two fresh fruitbodies on a branch of *Corylus avellana*. Note the wrinkled** surface of the lower specimen. Coll. Hallingbäck 19603. – B: Both separate and coalescing pezizoid, fresh fruitbodies on a fallen branch of *Quercus*. Coll. Eriksson & Jacobsson 19602. – C, D: SEM-pictures of hyphae from the underside of a fruitbody. C shows one and D three clavate–globose apices of hyphae, all more or less collapsed. Also note the rough, wrinkled or finely tuberculate surface of the hyphae. – Photo: S. Sunhede, T. Hallingbäck & L. Ryvarden.


E
G
1mm
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μm wide, richly branched, arranged more or less parallel, in the subhymenium densely united; hyphae of the white cover of the underside coarser, c. 4–5 μm wide, with thick, gelatinous walls, often encrusted with small grains in mature specimens (Fig. 3G), apically swollen into more or less isodiametric, thickwalled cells with a rough, wrinkled or finely tuberculate surface (Figs. 2C, D, 3G). *Basidia* first cylindrical, then slightly clavate, 65–100 μm long, sometimes more, 5–6 μm wide, with numerous yellow oil-drops in the protoplasm and with a basal clamp; sterigmata two, stout, at first obtuse, then subulate, 25–30 μm long or more, and basally c. 4 μm wide (Fig. 3 E). Basidia in mature specimens forming a dense palisade. No specially differentiated sterile hyphae elements (paraphysoids, dikaryophyses) were observed. The sterile hyphae seen between the basidia are rather young hymenial hyphae, participating in the basidium production (Fig. 3 E). *Spores* narrowly ellipsoid, broadly subcylindrical or slightly subal-lantoid, usually broader towards the base, mostly 25–32 × 8–10 μm but rather variable in size and shape (Fig. 4), thinwalled, smooth, non-amyloid, non-cyanophilous; in microscopical preparations made from hymenial parts several spores septated by thin parallel septa into 2–16 cells (Figs. 3D, 4); spores in the sporeprint studied were non-septate; when these spores were placed in a drop of water most of them became 2–16-septate after 30 hours and initials of germ conidia could be seen, after 48 hours a few developed germ conidia were observed (Fig. 4B, K), the largest ones being ellipsoid, ab. 2 × 1 μm, and filled with yellow oil. One spore attached to a fruitbody was found to have produced numerous oblong conidia (Fig. 4C), reaching a size of 3.5 × 1.5 μm, all conidia developed from the convex, abaxial side of the spore.

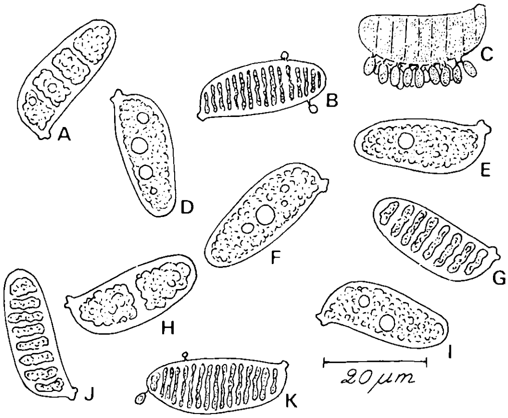

Fig. 4. Spores of *Femsjonia peziziformis*. – A–K: 1-, 2-, 4-, 8-, and 16-celled spores. – B, K: Two 16-celled spores with two young conidia each. – C: Spore with several oblong conidia, all from the convex, abaxial side of the spore. – Del. J. Eriksson.

Femsjonia peziziformis is easily recognized by its conspicuous discoid, bright yellow fruitbodies with white undersides and by its large spores. It looks very much like a Discomycete, e.g. a large species of *Helotium*. It is reminiscent of the closely related genus *Ditiola*, but the fruitbodies are wider and not so obviously stalked. In *Ditiola* fruitbodies are produced in large numbers, often in hundreds, whereas in *Femsjonia* they occur in a much smaller number or even singly.

History and taxonomy

The fungus was described by Fries (1849) and for a long time it was known as *Femsjonia luteoalba*. However, there was a species described earlier by Léveillé (1848) as *Exidia pezizaeformis*. Karsten (1876 p. 352) referred it to the genus *Femsjonia* Fr. Bourdot & Galzin (1928 pp. 71, 72) considered *Femsjonia luteoalba* and *F. pezizaeformis* as distinct species. The former was characterized by aseptate spores and by growing on deciduous wood as *Betula*, *Prunus padus* and *Quercus*. The latter was said to have 12–24-septate spores and to grow on coniferous wood. Later Bourdot (1932 pp. 206, 207) described the spores of *F. luteoalba* as 5–10-septate and those of *F. pezizaeformis* as multiseptate. McNabb (1965 p. 226) expresses a different opinion: "As the spores of *F. peziziformis* are tardily septate, it is doubtful whether these distinctions

Fig. 3. Microanatomy of *Femsjonia peziziformis*. – A: Section through fruitbody, showing position of the Figs. E and G. – B: Section through old fruitbody with wrinkled hymenium. – C: Cellular hyphal apices from the underside of the fruitbody. – D: Spores, 1-, 2-, and 16-celled. – E: Section through part of the hymenium with basidial palisade, subhymenium, and tramal hyphae. – F: Part of hyphae from the underside of the fruitbody. – G: Section through hyphal layer on the underside of the fruitbody. – Coll. Dissing & Sivertsen 7.IX. 1973. Del. J. Eriksson.

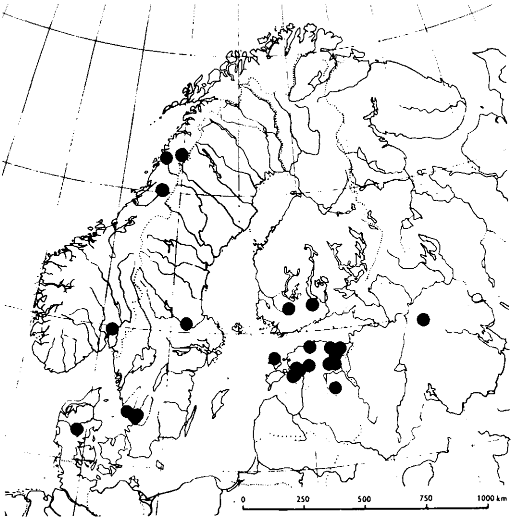

Fig. 5. Known distribution of *Femsjonia peziziformis* in North Europe.

can be maintained, and I prefer to regard Bourdot and Galzin's two species as different-aged collections of a single species."

Léveillé (1848) wrote the epithet *pezizaeformis,* which, however, according to the International Code 1972 art. 73 should be considered to be an orthographic error and should be changed to *peziziformis*. This change was made by McNabb (1965).

As to the generic arrangement with *Femsjonia* as a separate genus, we do not want to make any definite decisions, but we are of the opinion that the genera *Dacrymyces, Ditiola* and *Femsjonia* are very close to each other. The large spores and the general appearance of *Femsjonia peziziformis* make the species easily recognizable but these differences are hardly acceptable for generic separation. Another difference from *Ditiola* is the cellular swellings in the apical part of the sterile hyphae, which as a rule cover the exterior of the fruitbody in *F. peziziformis* (Figs. 2C, D, 3G). The exterior of the fruitbodies of *Ditiola* is also white, composed of coarse hyphae, similar to those in *F. peziziformis* but without the apical swellings. Moreover the hyphae of *Ditiola* are non-fibulate. Whether or not these differences can be looked upon as sufficient for generic separation is a matter for future discussion.

As there seems to be no authentic material left of *Femsjonia luteoalba* Fr. we designate the collection Eriksson & Jacobsson 19602 as the neotype of *Femsjonia luteoalba* Fr. This collection of many well developed fruitbodies is from the same geographic region as the original specimen from Femsjö.

Ecology and distribution

All North European specimens, except for three on *Pinus,* have been found on various deciduous woods, viz. *Alnus incana* (3 specimens), *Betula pubescens* (1), *B. verrucosa* (1), *Betula* sp. (17), *Corylus avellana* (2), *Quercus petraea* (1), and *Quercus* sp. (1). There seems to be no material left from Fries but he notes "Trunc. Betulae ad Femsjö" (Fries 1849 p. 341). All specimens have been found on twigs and trunks of decaying wood.

F. peziziformis is able to grow under very varying climatical conditions, e.g. in the mild, humid climate of Jylland, the oceanic climate of Central and Northern Norway, and the rather continental climate of East Norway, Central Sweden, Estonian SSR and South Finland (Fig. 5). Most of the specimens (26) were collected during August–December but there was also one collection in May. In spite of its rather conspicuous appearance few collections of *F. peziziformis* have been made in North Europe (except for Estonian SSR) indicating that the fungus may be rare at least in some regions. The collections are scattered and there is no definite distributional pattern (Fig. 5). For the distribution outside North Europe see i.a. Martin (1952), McNabb (1965) and Raitviir (1971).

Collections

The herbarium abbreviations are in accordance with Holmgren & Keuken (1974). The Swedish specimens are in the private herbaria of the authors in Göteborg; the Estonian specimens are in TAA, the Finnish ones in H. When possible the specimens are cited from south to north in each country, except for Estonian SSR.

Denmark: Jylland, Aarhus amt, Hörby lunde on *Quercus petraea* 1.X. 1950 B. & J. Eriksson 5004 (UPS).

Finland: Tavastia australis, Tammela, Mustiala, on *Betula* 20.XII. 1865 Karsten 1556; on *Betula* 4.V. 1872 Karsten 1558; on *Betula* 18.IX. 1894 Karsten 1553 – Tammela, Mustiala, Särkjärvi, on *Alnus incana* 20.IX. 1867 Karsten 1552, 1554 – Tammela, Mustiala, Salois, on *Betula* 19.IX. 1890 Karsten 1559 – Hollola, Tiirismaa, on *Betula* 1889? Wainio 1555.

Norway: Oslo, Østmarka, Sølvdobla, on *Betula* 9.IX.

1956 Eftestøl (O) – *Nord-Trøndelag,* Namnsskogan, on *Betula* 24.XII. 1974 Tønsberg (O) – *Nordland,* Rana, – Utskarpen, on *Betula* 12.IX. 1976 Torkelsen 773/76 (O) Rana, Lasken, Rundfjell, on *Betula* 7.IX. 1973 Dissing & Sivertsen (TRH) – Rana, Ørtfjellmoen bro–Rundfjell, on *Betula* 9.IX. 1975 Sivertsen (TRH).

Sweden: Halland, Breared parish, Askarebygget, on *Corylus avellana* 16.XI. 1975 Hallingbäck 19603 – *Småland,* Femsjö parish, "Betulae ad Femsjö" (Fries 1849 p. 341) – *Halland,* Tvååker parish, Sibbarp, on *Quercus* sp. 16.X. 1975 Eriksson & Jacobsson 19602 – *Dalarna,* Garpenberg parish, Garpenbergs gård, on *Pinus sylvestris* 29.VIII. 1974 Sunhede 6695.

Estonian SSR: Distr. Haapsalu, Kulli, on *Betula* 14.VIII. 1960 Raitviir – Virusaar, on *Corylus avellana* 10.X. 1958 Parmasto – *Distr. Harju,* Vikipalu, on *Betula* 14.XI. 1959 Raitviir – *Distr. Hiiumaa,* Tahkuna, on *Betula* 1.IX. 1960 Raitviir – *Distr. Jõgeva,* Enniksaare, on *Betula* 30.IX. 1958 Kalamees – Kurista, on *Betula* 3.X. 1960 Kalamees – Voore, on *Betula verrucosa* 17.IX. 1970 Parmasto – *Distr. Pärnu,* Avaste on *Betula pubescens* 9.IX. 1952 Parmasto – Eidapere, on *Betula 17.X. 1959 Raitviir – Distr. Rakvere,* Jõetaguse, on *Alnus incana* 7.VIII. 1961 Kalamees – Põlula, on *Betula* 11.VIII. 1958 Raitviir – *Distr. Võru,* Sõmerpalu, on *Pinus sylvestris* 19.IX. 1952 Parmasto.

Russian SSR: Distr. *Tikhvin* (Leningrad region), Rugui, on *Pinus* 20.VIII. 1961 Bondartseva (TAA). – One specimen (in H) from the Kola region cited by Karsten as *Ditiola conformis* is *Dacrymyces* sp.

Acknowledgements. We are indebted to the directors and curators of the following herbaria for loan of specimens: H, O, TAA, TRH, and UPS. We are most grateful to Dr J. Lepiksaar, Göteborg and Dr A. Raitviir, Tartu, who have helped us with the mapping of the Estonian localities, to Professor J. A. Nannfeldt, Uppsala for reading the manuscript and to Professor Å. Fridh, Göteborg for discussions on Latin orthography.

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Botanical literature

Jacobsen, H. 1970: *Das Sukkulentenlexikon.* 589 pp, 1063 figs. Gustav Fischer, Jena. Price DM 48:– (cloth).

Although this standard work has been on the market for a number of years, as yet it has not received attention in this journal. It deserves to be mentioned as a useful dictionary of succulent plants, covering about 6,500 species belonging to 355 genera of various families. Only the cacti are excluded, being similarly dealt with in Backeberg's well-known 'Kakteenlexikon'.

The contents have been condensed in order to be accommodated in a single volume. The essential information given includes short descriptions, indications of origin, and hints about cultivation. Larger genera are provided with keys to sections and species.

The extensive list of synonyms at the end may give the impression of a critical treatment throughout, but this is naturally not the case. Where most genera are concerned the author simply lists species in alphabetical order without attempting to evaluate their taxonomic status.

The work claims to cover all succulents (except cacti) described prior to 1970. Irrespective of the hazards of definition however, it must be stated that the coverage is far from complete. Many genera, which have not been subject to recent revision, are quite stepmotherly treated. Take one example from the succulent Liliaceae, only 14 species of *Bulbine* are listed, which is less than half the number of species described. Among the succulent Compositae *Othonna* can be mentioned as a taxonomically intricate and as yet unrevised genus, and many omissions and inconsistencies can also be noted here.

The problem of defining a succulent has been referred to above. Considering the rather incomplete coverage of truly succulent genera, one is surprised to find *Welwitschia* (although with an apology) represented, as well as a number of halophytes lacking horticultural interest. Also, the inclusion of certain bulbous plants seems quite arbitrary (e.g., *Ammocharis, Haemanthus, Litanthus*), as the majority of well-known bulbs are not treated (*Agapanthus, Allium, Lilium, Urginea,* etc.).

Apparently the book should be used with great caution. There are also inconsistencies in the phytogeographical information. In many cases the distribution area is roughly outlined, but all too frequently only the type locality is cited, which may give a false impression where the range is concerned.

The large and phytogeographically important genus *Zygophyllum* is remarkably maltreated. The distribution of the genus is given as the Canary Islands, and the only species mentioned is *Z. fontanesii.*

Unfortunately the nomenclature is not always in accordance with the rules. Some proposed new taxa are apparently not validly published due to the lack of Latin diagnoses, e.g. the new sections and subsections of *Cotyledon.*

The illustrations are mainly black-and-white photographs of cultivated plants. They are plentiful and useful, but not all of them are beautiful.

The above may suffice to warn the reader about uncritical digestion of the contents of this nevertheless impressive work. In spite of numerous errors and shortcomings, the book is a useful source of information and a handy tool for quick reference on a vast subject.

Bertil Nordenstam

Löve, A., Löve, D. & Pichi Sermolli, R. E. G. 1977: Cytotaxonomical atlas of the Pteridophyta. XVIII + 398 pp. J. Cramer, Vaduz. ISBN 3-7682-1103-7. Price DM 150:–.

For many years cytological data on the Pteridophyta have been scattered in several compilations, making it necessary to look up at least 8 sources for information about a particular taxon. This has made the search for information on this group rather inconvenient and time-consuming. Chiarugi's and Fabbri's works have long proved their value as sources of information of this kind, but the rapid accumulation of data since their publications has greatly increased the need for a modern synthesis. The Chiarugi and Fabbri chromosome tables might stand as models for such a work, although one could wish that information on the geography of counted specimens had been added.

Now Löve, Löve & Pichi Sermolli's *Cytotaxonomical atlas of the Pteridophyta* has been published. It deviates in principle and detail from Chiarugi's and Fabbri's works. The points of criticism are too numerous to be dealt with in detail. A few examples of the types of error in which this book abounds will have to suffice.

The authors deliberately exclude hybrids and supposedly incorrect counts although the critieria for exclusion of counts are not clear. Publications before Anno Mantoni (1950) have been omitted unless their information fits in with the classification of the atlas. At the same time many later undocumented counts are included although in my opinion they strongly need reassessment.

Taxa have been arranged according to a forthcoming classification, to be published in *Webbia* by Pichi Sermolli. It represents an extreme splitting into families and genera. This is not the place to discuss classification, but it must be mentioned that the names of original publications have not been followed. Taxa have been distributed according to the new system with the necessary new combinations. The original identification is brought among other synonyms. In some cases the synonymy is incorrect e.g. *Phlegmariurus taxifolius* (Sw.) Löve & Löve is a Tropical American species, not Indian as is the cytologically examined plant quoted. The latter was identified as *Lycopodium hamiltonii* var. *petiolatum* (*Lycopodium taxifolium* Spring nom. non val.)

Sometimes chromosome numbers alone, even very approximate ones, seem to have determined the grouping of species. Thus *Lycopodiella caroliniana* is cited as 2n = 78, in line with the supposed x = 13 of this genus. *Lycopodium meridionale* is cited as 2n = c. 138 which is made to correlate with x = 17 of *Lycopodium*. Far from being members of two different genera these two species are very closely related, perhaps even conspecific, and the actual number is now known to be n = 35 or multiples.

All counts have been cited as somatic numbers, although the majority of counts were made from meiotic material. All meiotic counts except those of known agamosporous species have simply been doubled for the sake of uniform citation. Since meiotic and somatic counts of agamosporous ferns are equal, this practice is a source of error because of the probability of undiscovered agamospory among the cited taxa.

The citation of counts is not always faithful, e.g. Manton 1950 indicated "2n = at least 260" for *Lycopodium selago*. This is cited in the *Atlas* as c. 264.

The practice of giving the supposedly correct number for each species in addition to actual counts is superfluous in most cases, whilst in other cases it is potentially misleading. Misinterpretations of approximate counts have been the cause of taxonomically wrong conclusions as for example the instance of *Lycopodium meridionale* already mentioned. In *Palhinhaea cernua* (*Lycopodium* among friends) it requires a strong faith to find the suggestions of 2n = 208, 260, 338 and 416 convincing as supposedly correct numbers, considering the actual cited counts were 208, 220, 272, c. 330, c. 340, and 416.

The derivation of base numbers presented are often confusing or directly misleading, especially where aneuploid evolution is involved in a group of genera. Thelypteridaceae forms a natural evolutionary group, the lowest meiotic numbers of which form an almost complete aneuploid series 27–36. In the atlas the lowest meiotic number has been given in brackets as a secondary base number in some genera, but not in all. All numbers except prime numbers of the series have been divided to give a lower possible base number. This results in a base number series of 7, 9, 12, 15, 17, 29, 31, which does not make sense without excessive mental acrobatics. The calculations of base numbers seem rather arbitrary.

In Thelypteridaceous genera with n = 36 and multiples, 12 was chosen as the base number although it could equally well be 9 (or 3, 4, 6, or 18!).

The literature references for Lycopodiaceae are seriously confused. I have not been able to check them all, but in the first ten pages I found 10 errors, all referring to counts by Löve & Löve! A count of *Lycopodium selago* was omitted from the book as stated in the introduction p. xi. Later on page 4 the same reference was used for *Lycopodium clavatum*.

I have only examined here Lycopodiaceae s. lat. in detail, but random samples from the rest of the book leave little hope that it is better.

In conclusion it should be said that this book does not meet the need we have for a modern compilation. There are too many omissions, misquotations, misstatements, and misjudgements to be excused, and as a result we still have to check all the same references as before. It is feared that this book will have a harmful influence on future work on the Pteridophyta. It should never have been published.

Benjamin Øllgaard

Sybenga, J. 1975: *Meiotic configurations. A source of information for estimating genetic parameters*. 251 pp. Springer-Verlag, Berlin, Heidelberg, New York. ISBN 3-540-07347-7, 0-387-07347-7. Price DM 68:– (clothbound).

The present volume is the first of a planned series of monographs on theoretical and applied genetics from Springer's publishing house. Several branches of genetics covered by the series are of interest to many plant taxonomists, for example evolutionary genetics, population genetics, ecological genetics, biometrical genetics and cytogenetics.

Sybenga's book is devoted to the quantitative analysis of observations on meiotic configurations with emphasis on their bearing on recombination. The author presents numerous mathematical formulae, diagrams and photomicrographs to help the reader to obtain the maximum amount of information from the slides.

For practical reasons the analysis of crossing-over is dealt with first. Observations at different levels of resolution are taken into account, ranging from direct and exact determination of number and location of chiasmata and of the chromatids involved in specified chromosomes, to indirect estimation of recombination from bivalent number. In the latter case the chiasma frequency can only be inferred from the number of "bound" chromosome arms. The effects at different meiotic stages of structural and numerical deviations are analysed in detail.

Analysis of chromosome pairing is largely dependent on the availability of satisfactory models, since it is rarely possible to observe actual pairing direct. A number of such models are described and applied to various cases, and their merits and shortcomings discussed.

The last part of the book is devoted to the analysis of chromosome orientation and segregation.

The cytogeneticist, or the taxonomist using cytogenetic methods, will certainly gain much from a study of Sybenga's book. Not only will it enable more relevant conclusions to be drawn from the observations but I am also convinced that the researcher will actually see more than before on his slides, after he has been made more aware of the meaning of the microscopically observable features of meiotic configurations.

Anna Weimarck

Cramer, J.(ed.): *Bibliotheca Lichenologica*. A series of original papers and reprints of books on lichens.

1. Hannemann, B. 1973: *Anhangsorgane der Flechten*. Ihre Strukturen und ihre systematische Verteilung. IV + 123 pp., 3 tables, 181 drawings and microphotographs. J. Cramer, Lehre, Germany. Price DM 50:– (paperbound as the following volumes).

2. Awasthi, D. D. 1975: *A monograph of the lichen genus Dirinaria*. IV + 108 pp., 16 distribution maps, 59 figures in 15 plates. Gantner Verlag, Vaduz, Liechtenstein. ISBN 3-7682-5452-6. Price DM 40:–.

3. Wunder, H. 1974: *Schwarzfrüchtige, saxicole Sippen der Gattung Caloplaca (Lichenes, Teloschistaceae) in Mitteleuropa, dem Mittelmeergebiet und Vorderasien.* II + 186 pp., 9

plates. J. Cramer, Lehre. ISBN 3-7682-0924-5. Price DM 40:–.

4. Jürging, P. 1975: *Epiphytische Flechten als Bioindikatoren der Luftverunreinigung, dargestellt an Untersuchungen und Beobachtungen in Bayern.* II + 164 pp., 43 maps, diagrams and tables. Gantner Verlag, Vaduz. ISBN 3-7862-0964-4. Price DM 50:–.

5. De Wit, T. 1976: *Epiphytic lichens and air pollution in the Netherlands.* 115 pp., 114 maps, diagrams and tables. Gantner Verlag, Vaduz. ISBN 3-7682-1059-6. Price DM 60:–.

The various series of botanical works issued by the publisher J. Cramer during the last few decades have included several papers on lichens. *"Dissertationes Botanicae"* is a collection of theses for the Ph.D. degree. Some of them deal with lichenology, viz. No. 4, G. Eigler, *Studien zur Gliederung der Flechtengattung Lecanora* (1969), No. 9, K. Kalb, *Flechtengesellschaften der vorderen Ötztaler Alpen* (1970) and No. 17, V. Wirth, *Silikatflechten-Gemeinschaften im ausseralpinen Zentraleuropa* (1972). The upsurge of interest in lichens during the last few years has resulted in a special series *"Bibliotheca Lichenologica"*.

Anhangsorgane der Flechten is an account of the morphology of the appendix organs of lichens and an effort to use these in taxonomy. The paper has been presented as a Ph.D. thesis at the Free University of Berlin under Professor J. Poelt. The authoress has devoted much attention to the terminology of rhizines, hairs, holdfasts, etc. including a detailed survey of the extensive literature. Many of these organs attach the lichen to its substrate, whereas others have no apparent function.

The terms met with in previous works, for instance by Lindau and Frey, have often been used in different senses. Instead of defining the existing terms the authoress has sometimes preferred to create new ones, such as "Rhizopten", "Rhizohyphen" and "Lichenorhizen". In the reviewer's opinion, the result of this procedure is that the present complex terminology has become still more chaotic.

The concluding chapters contain a comprehensive survey of the lichen system with a discussion of the availability of the appendix organs as auxiliary taxonomic characters.

The majority of the lichen species now referred to the genus *Dirinaria* have mostly been recognized as a subgenus or section of *Physcia.* With the delimitation given in the monograph by Dr D. D. Awasthi (Lucknow, India) it seems to be a well-defined genus in the Physciaceae.

26 species are recorded. 4 species and 4 varieties or forms are described as new. A great many taxa have been recombined. The author has been successful in finding material suitable for lectotypification of all relevant taxa except *D. applanata* and *D. confluens.* In these two cases neotypes have been proposed.

The accepted taxa are fully described together with fairly detailed lists of specimens seen. The taxonomic revision is preceded by brief general chapters on history, morphology, chemistry, ecology, etc.

Dirinaria is a pantropical genus extending to eastern North America, South Africa, eastern Australia and Japan. No species occur in Europe. Distribution maps are provided for all 26 species.

The cosmopolitan genus *Caloplaca* (incl. *Blastenia*) is one of the largest lichen genera including about 500–600 species. Some groups have been studied recently but like many other genera of crustose lichens it is badly in need of a monographic revision.

The present study by Dr H. Wunder was initiated by Professor J. Poelt and has been used as Ph.D. thesis at the Free University Berlin. It has a limited scope treating mainly the *Caloplaca variabilis* group, i.e., saxicolous species (mainly on calcareous rocks) with black apothecia. 8 species are recognized and described in detail, some of them with varieties. The author has seen about 1,600 collections from the major Herbaria in Europe, but only a selected number of stations are quoted.

The numerous taxa described by various authors have been carefully checked. Lectotypes have been selected in almost all cases, and no less than 22 species and 26 varieties are placed in synonymy. Some taxa are recombined. The well known species *C. variabilis* has been neotypified as no type material referable to Persoon has been traced. 3 species described by Hue and probably belonging to this group have been omitted as no types were available in Paris (PC). In the experience of the reviewer most of Hue's material, even from his last years, can be found in PC. However, this requires a personal visit to the Paris Herbarium and a good portion of patience and luck.

The author explicitly states that the group does not constitute a natural unit. In addition, he also treats two species from the *ferruginea* group, which normally have rusty-red apothecia sometimes changing to blackish-brown or black.

The influence of polluted air on the lichen vegetation has been studied for more than a century. The literature on this topic has been exceedingly abundant during the last few decades. A comprehensive survey of the various kinds of research carried out in this field was presented in 1973 under the title of *"Air pollution and lichens"* (ed. Ferry et al.). Cf. review in Bot. Notiser 1974 p. 155.

Many years ago Arnold (*Zur Lichenenflora von München,* 1891–1901) drew attention to the fact that various species of lichens are lacking or are on the decline in the central parts of Munich. The recent work by Dr P. Jürging (Lehrstuhl für Landschaftsökologie, München) gives a broad account of the "air hygienic" situation in the Munich area during the past decade. Following Sernander's classical terminology he has distinguished several zones, viz. "Flechtenwüste", "Innere Kampfzone", "Mittlere Kampfzone", "Äussere Kampfzone" and "Normalzone". His map from 1968 has been followed up by later studies from 1973–1974 showing that certain species of foliose lichens recorded as extinct have reappeared owing to improved air conditions in the central part of the city. The map from 1968 should be compared with maps showing the precipitation of dust and the emission of sulphur dioxide in the same area and at the same time.

Fumigation experiments were performed in nature using some of the most important pollutants, viz. SO_2, HCl, HF, NH_3 and CO. The techniques used and the damage caused to the relevant lichen species are discussed in some detail.

The author has studied the behavior of certain epiphytic lichen species in areas with varying pollution. He has mainly chosen foliose lichens that are sensitive to varying extents, e.g., *Anaptychia ciliaris, Evernia prunastri, Hypogymnia physodes, Lobaria pulmonaria, Xanthoria parietina* and several species of *Parmelia, Physcia* and *Ramalina.* It is remarkable that he draws very little attention to *Lecanora conizaeoides,* otherwise known as the most resistant lichen in polluted areas. The reason is that he seems to consider *L. conizaeoides* to be an ecological modification of *L. varia* caused by the special conditions in urban areas.

Holland is known as one of the most polluted areas in Europe. This fact has been noted in various works, not the least by Dr J. J. Barkman, the eminent specialist in the sociology of epiphytic mosses and lichens. One of his students, Dr T. De Wit, (Rijksinstituut voor Natuurbeheer, Leersum, Holland) has published a thesis which gives a comprehensive survey of the present relation of air pollution to lichen vegetation in this country.

A large number of species of epiphytic lichens on trees throughout the Netherlands have been listed using a 5 km square grid as a basis. Distribution maps of 20 lichen species are given. Comparison with data from around 1950 reveals a decline almost everywhere in the country. The area between Rotterdam and Amsterdam has become especially impoverished.

As in the preceding work results of fumigation experiments are presented. In addition to the gases used by Dr Jürging, Dr De Wit has also used C_2H_4, O_3 and a combination of SO_2 and O_3. Even low concentrations of these air pollutants cause significant morphological damage to the lichen species investigated.

Ove Almborn

Brodo, I. M. & Hawksworth, D. L. 1977: *Alectoria and allied genera in North America.* Opera Botanica 42. Stockholm. 164 pp., 1+67 figures and distribution maps. ISBN 91-546-0211-1. ISSN 0078-5237. Price SKr 87:- (libraries SKr 145:-).

The first attempt to provide a monograph on the North American species of the lichen genus *Alectoria* was made by Howe (1911) who accepted 10 species. Du Rietz (in a preliminary *Synopsis Lichenum,* 1926) recognized 19 species all over the world. In the following decades Gyelnik, Räsänen, Motyka and others (all notorious splitters) ''revised'' the genus, or parts of it, in various ways. Their work resulted in the publication of numerous more or less vague and superfluous taxa. The present volume by I. M. Brodo (Ottawa, Canada) and D. L. Hawksworth (Kew, England) is a necessary clearing-up in this jungle.

There is a tendency today to divide large lichen genera into smaller perhaps more ''natural'' units of generic rank. Poelt et al. have segregated *Physconia* and *Physciopsis* from *Physcia* and *Heterodermia* from *Anaptychia*. Hale has recently proposed a subdivision of *Parmelia* (s. latissimo) into 10 genera. Following this trend Brodo and Hawksworth have split the old *Alectoria* into 4 genera, viz. *Alectoria* Ach. s. str. (8 species in North America), *Bryoria* gen. nov. (the name derived from *Bryopogon* and *Alectoria;* 27 species), *Pseudephebe* Choisy (2 species) and *Sulcaria* Bystr. (1 species). Useful characters for the delimitation of these genera have been found, for example, to be the cortical structure and the presence or absence of certain chemical compounds.

Alectoria s. str. comprises *A. nigricans, ochroleuca* and *sarmentosa* (with ssp. *vexillifera*), etc. Under *Bryoria,* which is divided into 5 sections, we meet with the well-known species *B. chalybeiformis, bicolor, nitidula, simplicior, implexa, fremontii* and others. *Pseudephebe* will hopefully be the permanent generic name for *P. minuscula* and *pubescens,* which for many years have vacillated between *Alectoria* and *Parmelia*. *Sulcaria* is represented by the new species *S. badia,* which is tentatively placed here in addition to *S. sulcata* and *S. virens,* both known from Asia only.

Alectoria nidulifera Norrl. is recorded as *Bryoria furcellata* (Fr.) comb. nov. The Friesian epithet, which is older, can be avoided under *Alectoria* as the combination *A. furcellata* exists for another species. Unfortunately, this procedure has not been possible under *Bryoria*. *A. jubata* is treated as a *nomen confusum* (Art. 69 in the Code of Nomenclature) and *A. prolixa* is considered a synonym of the same taxon.

Among the 38 species recorded from North America 9 are described as new. A great many combinations transferring both North American species and others to the accepted genera are made.

Each species is described in detail often with photographs and always with distribution maps. The numerous taxa described by previous workers have been carefully checked and typified which has resulted in long lists of synonyms. In addition to the maps there are fairly exhaustive lists of localities seen by the authors and represented in the major North American Herbaria.

The taxonomic treatment is preceded by comprehensive and well-illustrated chapters on Anatomy and morphology, Chemistry, Taxonomic concepts, Ecology, Distribution, and Importance to man and nature.

As many of the species treated are widely distributed in the Northern Hemisphere this monograph will also be most useful to the European reader.

The authors have worked jointly on this project since 1970. This method has been somewhat unusual among lichenologists, but has evidently many advantages. Errors and omissions caused by one author can be corrected by the other. The reviewer sincerely recommends this form of cooperation for future monographic works on lichen taxonomy.

Ove Almborn