The distribution of flavonoids in the angiosperms

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Flavonoid distribution in the angiosperms is reviewed. 39 structural classes are defined and the number of genera possessing each class is given for each family. Relationships of families and orders are discussed based upon flavonoid distributions and several observations are made: (1) Many flavonoid types are highly scattered. (2) Many monocot orders show flavonoid patterns different from those in the dicots. (3) Liliiflorae is probably central in monocot evolution. (4) Myricetin often co-occurs with ellagic acid, and both are largely absent from those dicot superorders which possess benzyl isoquinoline alkaloids, polyacetylenes or iridoids. (5) Caryophylliflorae is distinct among polypetalous groups in frequently lacking myricetin and maybe also proanthocyanidins, these are otherwise common in almost all dicotyledons except in the Sympetalae. The superorder is unique in often possessing betalains rather than anthocyanidins. (6) In the Sympetalae the frequent occurrence of 6-hydroxyflavones in the iridoid group and their near absence from the non-iridoid group supports an independent evolutionary history at least for some while. (7) The common occurrence of the rare 5-deoxyflavonoids supports a closer link between Fabales and Rutiflorae. Further suggestions concerning possible relationships of other families are also made.

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Flavonoids comprise a set of biosynthetically related compounds (Fig. 1; for discussion see Hahlbrock & Grisebach (1975)) which occupy an important position among plant constituents as taxonomic characters. Harborne (1967 a) has pointed out that they have certain advantages over many other low molecular weight compounds in that they are widely distributed among the vascular plants, they show much structural variation, they are stable enough to be detected in herbarium specimens and they are usually easily and quickly identifiable. Harborne (1975 a) has recently discussed the use of flavonoids in systematics and has commented on their usefulness at the infra-specific to the ordinal level of classification. He has also stressed the potential value which flavonoids may have when revising existing plant classifications.

This paper is a preliminary survey of the occurrence of various flavonoid types within the angiosperms with a view to contributing, in conjunction with other taxonomic characters, toward a re-evaluation of the relationships of certain groups of plants. The work uses the angiosperm system of Dahlgren (1975 a) to demonstrate the distribution of the different flavonoids, and forms the latest in a series of articles (see Dahlgren (1977 a) for references) which discuss the occurrence and consequent implications of a number of presumably important taxonomic characters. Superorders have the suffix "-iflorae" rather than "-anae" as explained by Dahlgren (1977 b).

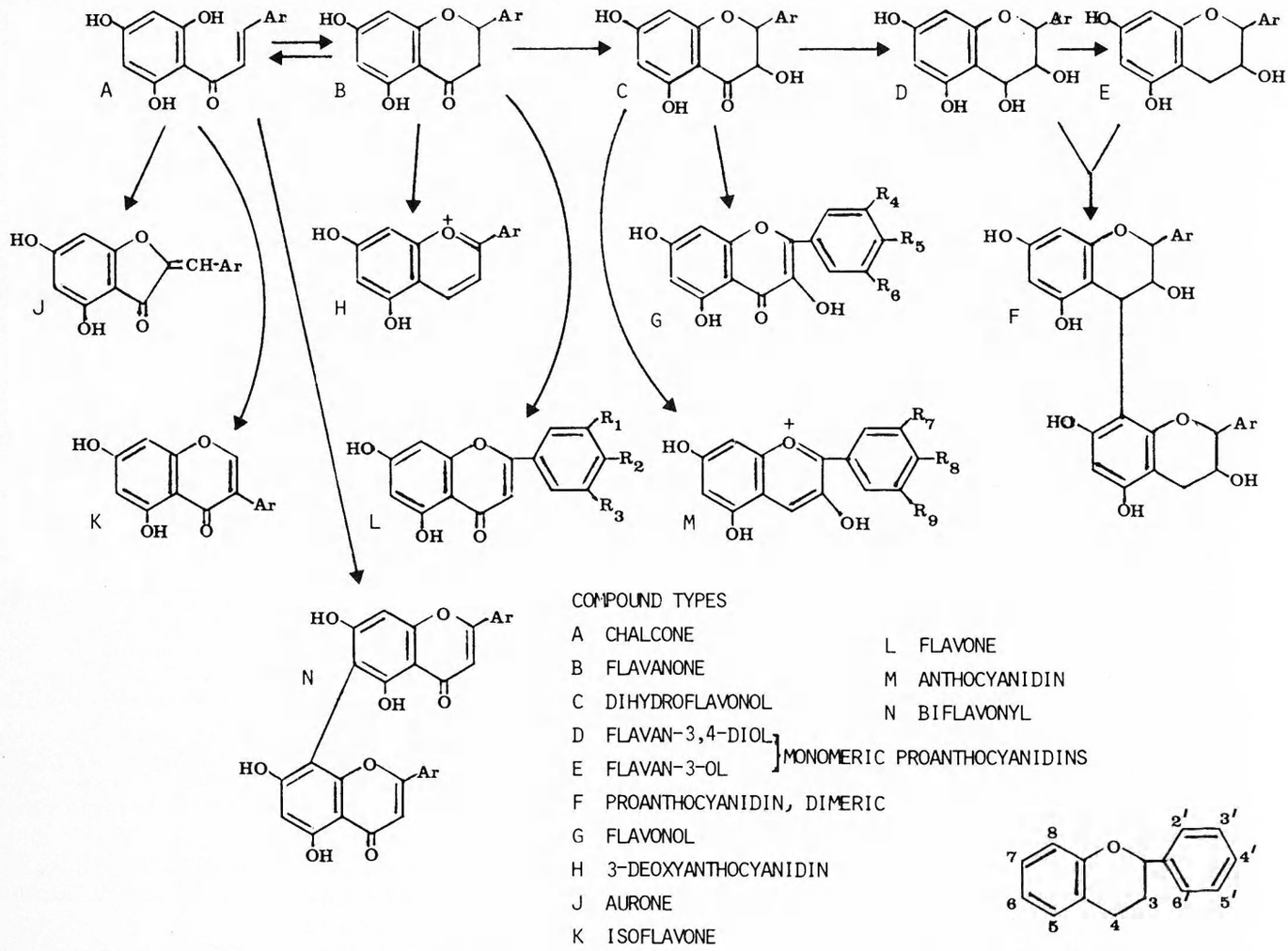

Fig. 1. Biosynthetic relationships between flavonoid types. – Ar = flavonoid B-ring without hydroxylation pattern specified. Examples of specific compounds: luteolin, L, $R_1 = R_2 = OH$, $R_3 = H$; apigenin, L, $R_1 = R_3 = H$, $R_2 = OH$; tricin, L, $R_1 = R_3 = OCH_3$, $R_2 = OH$; myricetin, G, $R_4 = R_5 = R_6 = OH$; quercetin, G, $R_4 = R_5 = OH$, $R_6 = H$; kaempferol, G, $R_4 = R_6 = H$, $R_5 = OH$; delphinidin, M, $R_7 = R_8 = R_9 = OH$; cyanidin, M, $R_7 = R_8 = OH$, $R_9 = H$; pelargonidin, M, $R_7 = R_9 = H$, $R_8 = OH$.

Collection and treatment of data

Reports of flavonoid occurrences were taken from the following books and periodicals:

Bendz, G. & Santesson, J. (eds.) 1973: Chemistry in botanical classification. Nobel Symposium 25. London.

Harborne, J. B. 1967: Comparative biochemistry of the flavonoids. London.

Harborne, J. B., Mabry, T. J. & Mabry, H. (eds.) 1975: The flavonoids. London.

Hegnauer, R. 1962–1973: Chemotaxonomie der Pflanzen. Vols. 1–6. Basel.

American Journal of Botany 47–64 (1960–1977).

Biochemical Systematics and Ecology 1–5 (1973–1977).

Blumea 10–25 (1960–1977).

Botanical Journal of the Linnean Society 56–75 (1958–1977).

Brittonia 12–29 (1960–1977).

Bulletin de la Société Botanique de France 107–124 (1960–1977).

Canadian Journal of Botany 38–55 (1960–1977).

Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, series D, Paris 262–285 (1966–1977).

Indian Journal of Chemistry 3–15 (1965–1977).

Journal of Organic Chemistry 30–42 (1965–1977).

Khimiya Prirodnykh Soedinenii 1–13 (1965–1977).

Lloydia 23–40 (1960–1977).

Mémoires publiés par la Société botanique de France 1960–1977.

Phytochemistry 1–16 (1961–1977).

Plant Systematics and Evolution 123–128 (1974–1977).

Planta Medica 8–31 (1960–1977).

Plantes Medicinales et Phytothérapie 1–11 (1967–1977).

Systematic Botany 1–2 (1976–1977).

Taxon 9–26 (1960–1977).

Tetrahedron 21–32 (1965–1976).

Tetrahedron Letters 1966–1976.

Flavonoids were catalogued by genus which avoided many taxonomic problems over species delimitation and also kept the data base to a reasonably manageable

Table 1. Abbreviations for the different flavonoid structural classes in the data base, including an index to their diagrammatic presentation.

A Delphinidin. Fig. 2	V 6 or 8-O-Methyl flavones. Fig. 11
B Cyanidin and/or pelargonidin. Fig. 3	W 8-Oxygenated flavones. Fig. 12
C O-Methylated anthocyanidins. Fig. 4	X 6-Oxygenated flavones. Fig. 13
D Acylated anthocyanidin glycosides. Fig. 5	Y 2'-Oxygenated flavones. Fig. 14
E Myricetin. Fig. 6	Z 5-O-Methyl flavones. Fig. 14
F Quercetin and/or kaempferol	a Acylated flavone glycosides
G 7, 3', 4' or 5'-O-Methyl flavonols. Fig. 9	b Flavone bisulphates. Fig. 18
H 3, 6 or 8-O-Methyl flavonols. Fig. 11	c Flavanones
J 8-Oxygenated flavonols. Fig. 12	d C-Glycosylation (C-glycoflavones). Fig. 16
K 6-Oxygenated flavonols. Fig. 13	e Isoflavones. Fig. 17
L 2'-Oxygenated flavonols. Fig. 14	f Biflavonyls. Fig. 17
M 5-O-Methyl flavonols. Fig. 14	g 5-Deoxy flavonoids. Fig. 15
N Acylated flavonol glycosides	h 7-Deoxy flavonoids. Fig. 15
P Flavonol bisulphates. Fig. 18	k B-Ring-deoxy flavonoids
Q Dihydro-flavonols	m Proanthocyanidins. Fig. 20
R 3-Deoxyanthocyanidins. Fig. 5	n Betalains. Fig. 5
S Luteolin and/or apigenin. Fig. 7	p Chalcones. Fig. 19
T Tricin. Fig. 8	q Aurones. Fig. 19
U 7, 3', 4' or 5'-O-Methyl flavones (excluding tricin). Fig. 10	r Dihydro-chalcones
	s Isoprenyl flavonoids

size. Information was recorded for over 2200 genera. Except in certain cases, only the aglycone moiety of each flavonoid was recorded. This made the survey more uniform in the detail it encompassed since literature reports vary widely in their thoroughness of identification and use of hydrolytic extraction procedures. The only glycosides recorded were those with acyl groups attached and those where the sugar is bound directly to the flavonoid ring by a carbon-carbon bond (C-glycoflavonoids).

In order to deal with a manageable number of flavonoid types, they were grouped into 39 classes (Table 1). It was considered that these classes would account for most of the structural diversity encountered, but at the same time group together those structures which often co-occur. Thus, for example, quercetin and kaempferol belong to the same class, and flavonols 0-methylated at any or all of the 7-, 3'-, 4'- or 5'-positions are united. 0-Methylation at these positions was distinguished from that at 3-, 6-, or 8-positions because it is far more common. In cases where a structure could be put in several classes, the genus was scored positive for all of them. The only exceptions to this procedure were isoflavones, biflavonyls, chalcones, aurones, C-glycoflavones and dihydroflavonoids whose detailed structures were ignored. The reason for this was that in the first four cases the distributions were highly restricted and further structural detail seemed unnecessary. In the case of C-glycoflavones, the character is meant to demonstrate the distribution of C-glycosylation vs. O-glycosylation, which latter feature is represented by the other 38 classes combined; flavonoid ring structure is immaterial here. In the case of dihydroflavonoids, data were insufficient for a meaningful discussion and hence were excluded from further analysis.

Complete details, on a family basis, of the extent and results of the flavonoid survey are given in the data base. The bubble diagrams (Figs. 2–20) are a pictoral representation of much of the data given there. Two problems were encountered in plotting the data onto the diagrams: (1) incompleteness of survey, where many genera and families have no flavonoid data available; and (2) restricted distribution of certain flavonoid classes to parts of families only. These difficulties were partially resolved by the use of a shading key whose details are as follows: (1) families in which more than 20 % of the genera investigated possess a flavonoid class are shaded according to their size and location in the diagram; (2) families with no reports or recorded to *not* contain the flavonoid class are unshaded; (3) families with 1–20 % occurrence are given an approximately circular shaded area placed within their limits in the diagram. Some differentiation has been made: thus, a large multipunctate circle indicates a large family with more than 10 % occurrence, while a medium septem-punctate circle indicates either a large family with 1–10 % occurrence, or a medium family with 11–20 % occurrence. A small tripunctate circle indicates a small family with 1–10, or occasionally up to 20 % occurrence. Similar principles are followed where hatching is used.

General taxonomic implications

For reasons of space, familial and ordinal relationships are evaluted primarily on the basis of flavonoid distribution patterns, although it is realized that an effective re-appraisal must also encompass data from other sources. The necessary synthesis can partly be made by reference

to the earlier articles in this series which have dealt with the diagnoses of the orders recognized (Dahlgren 1975 a), the occurrence of iridoid compounds (Jensen et al. 1975), embryological characters (Dahlgren 1975 b), sieve-element plastids (Behnke & Dahlgren 1976), uniaperturate pollen grains, successive microsporogenesis, apocarpy, benzylisoquinoline alkaloids, polyacetylenes, centrifugal succession in multistaminate androecia, ellagic acid, epigyny, perigyny and sympetaly (Dahlgren 1977 a).

It is recognized that a review of this scope is outdated quickly, and that one must beware of placing too much emphasis on "absence data", where lack of a compound may be genuine or may merely reflect inadequate investigation. This is especially true of anthocyanidins for which information is particularly poor, and hence discussion here is limited. However, during the course of the review, it has become obvious that certain flavonoid types are rather definitive in their distributions, and in such cases it has been difficult to ignore their absences from various groups; indeed such absences have often been considered important when discussing possible relationships, although we are fully aware that conclusions and speculations based on such data are constantly vulnerable.

Comments on higher categories

The data base and figures show that many of our flavonoid structural classes are polyphyletic and therefore their systematic importance at the suprafamilial level is lessened. However, certain types are more restricted in their distributions and may well help characterize various orders and superorders. Thus, myricetin may be considered typical of Dilleniiflorae, Hamamelidiflorae, Theiflorae, Myrtiflorae, Saxifragiflorae, Plumbaginiflorae, Primuliflorae, Corniflorae (Ericales), Proteiflorae and Rosiflorae (Fabales). It seems to be rare or absent in most monocotyledons, Caryophylliflorae and in the groups Magnoliiflorae, Ranunculiflorae, Araliiflorae, Asteriflorae, Campanuliflorae and Solaniflorae, many orders of which contain benzylisoquinoline alkaloids or polyacetylenes or both (Dahlgren 1977 a). Myricetin is also generally lacking in another group of superorders: Corniflorae (Cornales), Gentianiflorae, Lamiiflorae and Loasiflorae. These produce iridoids (Jensen et al. 1975). The myricetin distribution is remarkably similar to that of ellagic acid (Dahlgren 1977 a) although rather more widespread.

It has been suggested that the Sympetalae comprise two groups: the iridoid-bearing Corniflorae, Gentianiflorae, Loasiflorae and Lamiiflorae; and the non-iridoid-bearing Solaniflorae, Campanuliflorae and Asteriflorae (Jensen et al. 1975; Dahlgren 1977 b). Dahlgren (1977 b) believes that these two groups may have become differentiated from a common ancestor at a relatively early evolutionary stage. Flavonoid data provide some support for these views. Thus, the probability of a common ancestor is reflected in similarities of flavonoid profile shown by the less-derived superorders of both groups: Corniflorae, some Gentianiflorae and Solaniflorae possess a relatively primitive syndrome based on flavonols, including myricetin. The cleavage in the Sympetalae, demonstrated clearly by iridoid distribution, is suggested in a less dramatic manner by the flavonoid types seen in the more advanced members of both groups. Thus, in the iridoid group, at least Gentianiflorae and Lamiiflorae frequently possess 6-hydroxyflavones (6-O-methylflavones may co-occur). In the non-iridoid group, 6-oxygenated flavones are less frequently seen and appear to be restricted to Asteriflorae where they usually exist in the O-methylated state only; i.e. as 6-O-methylflavones. 6-Hydroxyflavones are very rare in this group, occurring in only five of the investigated genera. This approximate correlation in distribution between iridoids and 6-hydroxyflavones supports the contention that the two sympetalous groups have had an independent evolutionary history, at least for some while. The common occurrence in the two groups of luteolin/apigenin and the mutual rarity of myricetin and proanthocyanidins in advanced members would thus likely be the result of convergence.

Some comment may be made at this point about monocot-dicot relationships. The flavonoid syndromes built by the monocot orders are often different from those in their dicot counterparts, being based frequently on a characteristic set of flavone types, including C-glycoflavones, flavone bisulfates, tricin, 5-O-methyl flavones as well as luteolin and apigenin. Nevertheless, monocot-type profiles are found in Nymphaeales and to a lesser extent in Piperales, and certain

similarities between the predominantly flavonol profiles of Magnoliiflorae and Liliiflorae are also evident. These are all groups which have often been considered to have considerable affinity with the monocotyledons.

Magnoliiflorae

Magnoliales, Laurales, Aristolochiales. This is a reasonably homogeneous group whose flavonoid profile is based on the common flavonols, quercetin and kaempferol. Myricetin is noticeably absent, which sets the group apart from Hamamelidiflorae and Dilleniiflorae but links it with Ranunculiflorae, which is also similar in the possession of benzylisoquinoline alkaloids (Dahlgren 1977 a). Flavones occur in Winteraceae, Myristicaceae and Lauraceae. Myristicaceae is distinguished by the presence of isoflavones in *Virola* and *Osteophleum,* compounds normally restricted to Fabaceae and Iridaceae. Lauraceae is unique in the group in that it has the unusual 5-O-methyl flavonols as a major component of its profile. These compounds are otherwise found mainly in Cunoniaceae and Eucryphiaceae (Cunoniales), Juglandaceae, Ericaceae and Plumbaginaceae. Other methylated flavonols appear in only four families (Magnoliaceae, Monimiaceae, Lauraceae and Aristolochiaceae).

Piperales. Flavones and C-glycoflavones characterize Piperaceae which might possibly support a link with some of the similarly endowed monocot families. C-Glycoflavones also occur in Lauraceae. Saururaceae differs in producing flavonols only. However, in both Piperaceae and Saururaceae myricetin is lacking.

Illiciales. This order is characterized by the presence of simple flavonols and in Schizandraceae by myricetin. This sets the order apart from all others in Magnoliiflorae which lack myricetin. Illiciales (notably Schizandraceae) also deviate from most other Magnoliiflorae in having pollen grains with 3 or more colpi.

Ranunculiflorae

Nelumbonales. The flavonoid profile is based on the common flavonols and flavones but is lacking myricetin. In this detail *Nelumbo* agrees with Ranunculales (except Berberidaceae) rather than Nymphaeales.

Ranunculales. The profile of this order is based mostly on the common flavonols and their O-methyl derivatives. The presence of common flavones (luteolin and/or apigenin) and C-glycoflavones in Ranunculaceae may suggest links with Nymphaeiflorae although the latter possesses myricetin and ellagic acid and lacks benzylisoquinoline alkaloids, all of which suggests a position away from Ranunculiflorae. Flavones and C-glycoflavones are reminiscent of those seen in some of the aquatic monocot families (Alismatiflorae), and thus relationships may lie in this direction. Berberidaceae is unique in the superorder in making myricetin and isoprenylated flavonoids. This might possibly indicate a link with Schizandraceae, which has a similar unique position in Magnoliiflorae. Indeed, Cronquist (1968) suggested that Ranunculales finds its closest allies within Magnoliiflorae in Illiciaceae and Schizandraceae.

Papaverales. The profile is based on common flavonols and their O-methyl derivatives (the latter only in Papaveraceae). The presence of 8-oxygenated flavonols in Papaveraceae suggests a connection with Ranunculaceae (*Ranunculus*). The flavonoid syndrome is too simple to venture further comment.

Nymphaeiflorae

Nymphaeales. Flavonols (Nymphaeaceae and Ceratophyllaceae), flavones (Nymphaeaceae) and C-glycoflavones (Nymphaeaceae and Cabombaceae) comprise the flavonoid profile. Flavones and C-glycoflavones suggest links with the aquatic monocots (Alismatiflorae), and with Ranunculaceae although the presence of myricetin and ellagic acid in Nymphaeaceae together with the lack of benzylisoquinoline alkaloids (Dahlgren 1977 a) indicates a position away from Ranunculiflorae.

Rutiflorae

Rutales. Rutaceae and Meliaceae are very similar with a flavonoid profile based on the common flavonols and flavones, together with extra oxygenation and much O-methylation. In some respects this is rather similar to the situation found in Asteraceae, including even the presence of 2′-oxygenated flavones. Rutaceae,

Meliaceae and Simaroubaceae make myricetin, which is also found in other families of this superorder, especially Sapindales. Also isoprenylated flavonoids and flavanones are found in Rutaceae. The other families which have been investigated show less diverse flavonoid syndromes based on the common flavonols, and in Surianaceae, their O-methyl derivatives. This simplification may be artificial and merely reflect the paucity of information. Rutaceae and Simaroubaceae both have C-glycoflavones, a character of sporadic occurrence within Rutiflorae.

Polygalales. Unfortunately, only Malpighiaceae and Polygalaceae have been screened, and then only cursorily. Common flavonols seem to form the major components of the profile. No further discussion is warranted.

Sapindales. The flavonoid profile of Sapindales is based largely on the common flavonols and their O-methyl derivatives. Myricetin is also a major component of all but two of the families investigated (Akaniaceae and Meliosmaceae). Flavones occur only in one genus each of Anacardiaceae and Aceraceae. Aceraceae makes C-glycoflavones, a character found sporadically in Rutales and Geraniales. Anacardiaceae makes biflavonyls which are of rare occurrence in the angiosperms, being known otherwise only in Rhamnaceae, Casuarinaceae, Ochnaceae, Clusiaceae, Euphorbiaceae and Sambucaceae. Anacardiaceae is also distinctive in making 5-deoxyflavonoids. These compounds are found in the Julianiaceae as well and it is this similarity of flavonoid profile, together with morphological and anatomical characters, which has led Young (1976) to recognize Julianiaceae as a subtribe of Anacardiaceae. 5-Deoxyflavonoids are otherwise prominent in Fabales and would support a link as envisaged by Dahlgren (1977 a).

Juglandales. The profile is based on common flavonols and their O-methyl derivatives, including 5-O-methyl ethers, a character found in Rutaceae but also frequently seen in Cunoniales (Hamamelidiflorae). The presence of myricetin is consistent with a position both in Rutiflorae and Hamameliflorae. A careful comparison of the O-methylflavonols reveals a good match between those in Juglandaceae and those in Cunoniaceae and Eucryphiaceae. In Rutaceae 5-O-methylation is usually accompanied by extra oxygenation and methylation in other positions, whilst in Cunoniales and Juglandales it consists solely of O-methylation at the 5-position of the common flavonols. Thus, from a flavonoid standpoint, Juglandaceae appears closer to Hamamelidiflorae, particularly Cunoniales. A Hamamelid alliance has been proposed by Cronquist (1968), Takhtajan (1969), and in an unpublished revision of his system, Dahlgren also places the two groups closer together.

Myricales. Flavonols predominate and myricetin is present. Generally, the profile is ambiguous regarding placement in Hamamelidiflorae or Rutiflorae. However, B-ring deoxyflavonoids are present in Myricales, a character which has been reported from Rutaceae.

Geraniales. The profile is based on the common flavonols and their O-methyl derivatives. Flavones and O-methylflavones appear to be restricted to one genus of Zygophyllaceae (*Larrea*). C-Glycoflavones occur in four families (Zygophyllaceae, Geraniaceae, Linaceae and Oxalidaceae), and 8-oxygenated flavonols occur in both Zygophyllaceae and Geraniaceae. Myricetin is apparently restricted to Ancistrocladaceae and Geraniaceae, but this probably reflects the paucity of observations in related groups. The 5-deoxyflavonoids in Geraniaceae mirror similar compounds in Rutales, Sapindales and Fabales.

Balsaminales. The major compounds are the common flavonols and myricetin. As such, the profile is consistent with a position in Rutiflorae. However, O-methyl anthocyanidins occur and the overall syndrome is reminiscent of that in Myrtales, with which an alliance may exist.

Araliiflorae

Araliales. The major profile consists of common flavonols and in Apiaceae-Apioideae the common flavones as well. A small number of genera in Apiaceae also make O-methyl derivatives of these compounds. Other flavonoid types occur very infrequently and are regarded as being of minor importance although sometimes they are reminiscent of those in Asteriflorae (C-glycoflavones and O-acylated flavonoid glycosides). Isoprenylated flavonoids are in common between Rutaceae, Apiaceae and Asteraceae,

though not common in any of these families. Araliaceae seems to have a much simpler profile based mainly on the common flavonols. Of note in Araliales is the almost total absence of myricetin (only in *Ammi*) and proanthocyanidins (only in *Apiastrum* and *Hacquetia*) which aligns the order with groups such as Asteriflorae and Lamiiflorae.

Pittosporales. The flavonoids consist primarily of common flavonols, sometimes O-methylated. Flavones are present in *Pittosporum*. The occurrence of proanthocyanidins in three of the four genera examined, together with the absence of myricetin, support an intermediate position between the myricetin/proanthocyanidin-bearing Rutiflorae, and Asteriflorae in which myricetin is lacking and proanthocyanidins are extremely rare.

Asteriflorae

Asterales. The flavonoid profile of Asterales consists of common flavones and flavonols together with their extra oxygenated and highly O-methylated derivatives. Overall, the complex is quite similar to that in Rutaceae although the highly methylated flavonoids in this family are mainly found in the fruits (e.g. *Citrus*) whereas the methylated flavonoids in Asteraceae are found in leaf and flower tissue. It is curious that the anthocyanidins in Asteriflorae are mainly the simple cyanidin or pelagonidin with almost no methylation. Myricetin is completely absent and proanthocyanidins have been reported only from *Cosmos*. In these regards Asteriflorae is very similar to Lamiiflorae and Araliiflorae with which latter group it shares *inter alia* the presence of polyacetylenes. Asteriflorae differs from Lamiiflorae by displaying a roughly equal emphasis on flavonols and flavones whereas flavones tend to predominate in Lamiiflorae. Moreover, 6-hydroxyflavones are very rare in Asteriflorae but quite characteristic of Lamiiflorae; this might be indicative of a polyphyletic origin for the Sympetalae (Jensen et al. 1975; Dahlgren 1977 b). Campanulaceae shows certain slight similarities to Asteriflorae in that it can make O-methyl derivatives of flavonols and flavones, but there seems to be no extra oxygenation, nor quite the wide variety of flavonoid types.

Dilleniiflorae

Dilleniales. Dilleniaceae possesses common flavonols and their O-methyl derivatives as major components. Myricetin is present which helps align the family with other myricetin-bearing groups. There are no reports of myricetin in Paeoniaceae, and if this is a genuine absence, it might suggest a link with Ranunculales and Magnoliiflorae. However, tricolporate pollen, scalariform vessel perforations, absence of benzylisoquinoline alkaloids, centrifugal stamen development, etc. all separate *Paeonia* strongly from Ranunculales. Flavonoid data otherwise provide little clue to its affinities, although the presence of flavones may prove significant.

Cistales. The profile consists of common flavonols and flavones with O-methyl derivatives of the former. Myricetin in Cistaceae is consistent with a position in Dilleniiflorae. Bixaceae is distinct in making 8-oxygenated flavones and flavone bisulfates, characters which occur only in Malvaceae within this superorder. In point of fact, in a revised angiosperm system (Dahlgren unpublished) Cistales will be included in Malvales, which is consistent with the flavonoid data.

Malvales. The major compounds present in this order are the common flavonols; flavones and O-methyl derivatives occur to a lesser extent. Myricetin is quite prominent, aligning the order with other myricetin-bearing groups. 8-Oxygenation, especially of flavonols, links Sterculiaceae, Malvaceae and also Bixaceae (Cistales). 3-Deoxyanthocyanidins occur in Sterculiaceae, a character normally associated with New World Gesneriaceae. C-Glycoflavones occur in both Tiliaceae and Malvaceae. In terms of flavonoids Cochlospermaceae would sit just as comfortably in Cistales as in Malvales. Similarly, Elaeocarpaceae could sit well in many of the myricetin-bearing orders.

Urticales. The flavonoids of Urticales consist mainly of common flavonols and flavones. C-Glycoflavones occur in both Ulmaceae and Cannabaceae, although the latter family is often considered isolated within the order. Cannabaceae also shares the presence of myricetin with Ulmaceae and Moraceae. It shares the presence of isoprenylated flavonoids with Moraceae. Moraceae is unique in the order because it

consistently makes 2′-oxygenated flavonols, and to a lesser extent, 2′-oxygenated flavones. This character occurs only sporadically in the angiosperms. In the past Urticales has oscillated between a Dilleniid and a Hamamelid alliance. The flavonoid data would support a link with Dilleniiflorae based upon the regular occurrence of flavones. These compounds are absent from almost all Hamamelidiflorean families.

Euphorbiales. The profile consists of common flavonols and flavones. O-Methyl flavonols are also quite prominent. 8-Oxygenation is present, a character otherwise seen in Malvales. C-Glycoflavones encountered in Euphorbiaceae are also seen in Malvales and Urticales. Euphorbiaceae is unique in the superorder in making biflavonyls.

General points. The flavonoid profile shows a rough 2:1 ratio of flavonols to flavones. O-Methyl derivatives occur at low frequency and chalcones are seen only occasionally (Malvaceae, Moraceae, Cannabaceae, Euphorbiaceae). Myricetin occurs frequently but shows tendencies to be lost in certain families, e.g. Sterculiaceae and Euphorbiaceae. This may be correlated with the evolutionary trend of replacement of flavonols by flavones (Harborne 1977).

Thymelaeiflorae

Thymelaeales. The flavonoid profile of this order is essentially similar to that found in Dilleniiflorae, with an emphasis on flavones as well as flavonols. Myricetin has never been reported which might support a link with the myricetin-poor Euphorbiaceae. The presence of C-glycoflavones is ambiguous and alliances could lie in several directions.

Violiflorae

Violales. The Violalean flavonoid profile is based largely on the common flavonols, flavones and their O-methyl derivatives. Overall, the syndrome is similar to that of Dilleniiflorae except for the almost total absence of myricetin (present in *Viola* only). This character has also been noted by Hegnauer (1973). Datiscaceae, whose position is perhaps debateable, is unique in Violiflorae in making 2′-oxygenated flavonols. It also has B-ring deoxy flavonoids, a character only seen within this superorder in the rather isolated Salicales. 2′-Oxygenated flavonols are otherwise mainly seen in Meliaceae, Anacardiaceae, Fabales and Moraceae. C-Glycoflavones also occur in Violales with some regularity (3 of 8 investigated families) and in neighbouring orders.

Tamaricales. Both Tamaricaceae and Frankeniaceae possess the common flavonols and their O-methyl derivatives. Only the latter has been reported to make flavones and O-methyl flavones. The two families are closely linked from a flavonoid standpoint by the occurrence of flavonol bisulfates. These are rare compounds in the dicots but do occur in for example Cistaceae, Polygonaceae and Malvaceae. Tamaricaceae and Frankeniaceae also lack myricetin, a compound which is rare in Violiflorae.

Salicales. This order is somewhat isolated in Violiflorae. The flavonoid profile consists of common flavonols, flavones and O-methyl derivatives. C-Glycoflavones and myricetin are also prominent. The presence of myricetin distinguishes the order in an otherwise myricetin-poor superorder. Removal of Salicales from Violiflorae on the basis of myricetin and highly methylated flavonoids does present some morphological problems and it is important to note that many of the highly methylated compounds occur in bud secretions rather than in leaf or flower tissue and therefore their taxonomic significance may be lessened.

Capparales. The order is characterized mainly by common flavonols and their O-methyl derivatives. Flavones occur only rarely (at low frequency in Resedaceae and Brassicaceae). Myricetin and proanthocyanidins are notably absent, apart from their occurrence in Limnanthaceae. Perhaps this could be used as evidence for a transfer of Limnanthaceae back to Geraniales, which does have these compounds. Removal of Limnanthaceae would leave Capparales as a myricetin-free order, along with Tamaricales and Violales (excepting *Viola* which has myricetin). However, the presence of glucosinolates in members of Limnanthaceae provides a strong argument for maintaining the family in Capparales where glucosinolate production is widespread if not general. Furthermore, a morphological similarity with Tropaeolaceae helps to

justify a position in Capparales for Limnanthaceae. Insufficient data are available to comment on such problem families as Bretschneideraceae, Salvadoraceae, Bataceae and Gyrostemonaceae. The last named family has been screened for betalains and anthocyanidins but neither type of pigment was found (Goldblatt et al. 1976).

Celastriflorae

Celastrales. Very few families have been investigated so meaningful discussion is difficult. The general profile is dominated by the common flavonols. Myricetin is present at least in Celastraceae which supports a position close to other myricetin-bearing superorders. Celastraceae is unique in the order in making the rare 5-deoxyflavonoids which suggests links with the similarly endowed Fabales, Geraniales and especially with Sapindales. Further similarities which point to a connection between Celastraceae and Sapindales include seed walls, arils, and disc structures. A realignment of Fabales nearer Sapindales, as suggested by Dahlgren (1977 a) would bring groups possessing 5-deoxy flavonoids much closer together.

Santalales. Common flavonols comprise the profile of this order. Myricetin is present in Viscaceae. Flavones or their derivatives are rare, but this may reflect the paucity of investigations. The overall syndrome is consistent with a position in Celastriflorae, where the families may be losing myricetin but not yet being able to make flavones in significant amounts. This would put the order approximately intermediate between Sapindales and Campanulales.

Rhamnales. Dahlgren (1977 a) suggested splitting Vitaceae and Leeaceae away from Rhamnaceae. Flavonoid data would support this proposal. Thus, although all three families have the common flavonols, Rhamnaceae differs in a few, perhaps important respects, namely, the absence of myricetin and the presence of chalcones and biflavonyls, all of which might suggest possible links with Euphorbiaceae (Thorne 1968).

Solaniflorae

Solanales. Major components of the flavonoid syndrome are the common flavonols, together in some families with their O-methyl derivatives (Solanaceae, Polemoniaceae, Boraginaceae). These families also possess flavones to a limited extent. Polemoniaceae is somewhat exceptional in making 6-oxygenated flavonols and C-glycoflavones, although the latter character is also found in Solanaceae. Myricetin occurs very infrequently in Solanaceae and Polemoniaceae. Acylated anthocyanins, although of sporadic occurrence throughout the angiosperms, do show special concentration in Solanales (found in Solanaceae, Convolvulaceae and Polemoniaceae). A more careful search would probably yield additional occurrences.

Campanuliflorae

Campanulales. This order shows a roughly equal emphasis on flavonols and flavones, together with their O-methyl derivatives. Generally, the order is similar to Solanales, although from a flavonoid point of view rather more advanced with the absence of myricetin and a greater emphasis on the synthesis of flavones. Support for a common origin with Solanales is provided by the occurrence of acylated anthocyanins in both Campanulaceae and Lobeliaceae, a character here considered to be typical of Solanales. A common origin of Campanulales and Solanales has also been suggested by Cronquist (1968).

Hamamelidiflorae

Trochodendrales. The profile is characterized by common flavonols; Tetracentraceae also possesses an O-methyl derivative. The presence of myricetin, at least in *Trochodendron,* supports an alliance with the Hamamelidiflorae rather than with the almost myricetin-free Magnoliiflorae.

Hamamelidales. The profile of this order is based on the common flavonols; myricetin is also a dominant compound, which helps align the order with other similarly endowed groups in the superorder.

Casuarinales. This order has a profile based on simple flavonols. The absence of myricetin and the occurrence of biflavonyls in the order perhaps indicate an isolated position for it. Biflavonyls otherwise occur mainly in Theales with

scattered appearances elsewhere, e.g. Euphorbiaceae.

Fagales. The profile is based on the common flavonols, and in Betulaceae on flavones as well. In Betulaceae, both flavones and flavonols show extra oxygenation and a high degree of O-methylation. Perhaps not too much significance should be placed upon this apparent difference from other members of the superorder, because in most cases the highly methylated compounds are found in bud secretions rather than in the leaves (cf. Salicales). The occurrence of myricetin is consistent with this order's place in the myricetin-bearing Hamamelidiflorae. B-Ring deoxyflavonoids are distinctive in Betulaceae (as in Salicales) and C-glycoflavones distinguish Fagaceae.

Cunoniales. The profile is based largely on common flavonols and their O-methyl derivatives. Myricetin is also a major component. Cunoniaceae and Eucryphiaceae possess 5-O-methylated flavonols of the type found in Juglandaceae, Lauraceae, Plumbaginaceae and Ericaceae. Of these families one could argue for a transfer of Juglandaceae from Rutiflorae closer to Hamamelidiflorae, using the 5-O-methylation as contributing evidence. The presence of myricetin in Juglandaceae is also consistent with such a placement.

Rosiflorae

Rosales. Families in this order are characterized by common flavonols and, to a lesser extent by flavones, together with their O-methyl derivatives. Extra oxygenation occurs at very low frequency in Rosaceae, Malaceae and Amygdalaceae. Connaraceae, Melianthaceae and Chrysobalanaceae differ from the other families in lacking flavones, although the absence may well be artificial, reflecting the small number of observations made. Myricetin occurs only in three families (Rosaceae, Chrysobalanaceae: two genera each; and Connaraceae: one genus). If the latter two families were placed elsewhere, e.g. Connaraceae in Sapindales near Anacardiaceae, then Rosaceae would be the only myricetin-bearing member of the order. The rarity of myricetin in Rosales clearly distinguishes it from neighbouring orders, and may well indicate a relationship with Magnoliiflorae. Flavonol bisulfates occur in Rosaceae, as they do in Cunoniaceae (*Davidsonia*). C-Glycoflavones form part of the flavonoid profile of Rosaceae and Malaceae, perhaps reminiscent of their occurrence in Fabales. Isoflavones occur rarely, viz. in Amygdalaceae (*Prunus*) and Malaceae (*Cotoneaster*), otherwise these compounds predominate in Fabaceae. Generally, the flavonoid pattern in Rosales is very diverse; for that reason it is relatively similar to that of Fabales. In many respects flavonoids are consistent with the association of Rosales and Fabales in the same superorder. On the other hand there are some significant differences: 5-deoxy compounds are not known from Rosales whereas they are major constituents of Fabales; and myricetin is much rarer in Rosales than it is in Fabales.

Fabales. The families in this order have similar, diverse flavonoid profiles, akin to those found in Rosales. Thus, there is the same battery of flavonols, flavones and O-methyl derivatives. Extra oxygenation is occasionally seen. Myricetin is rather more common than in Rosales, although the families show definite signs of losing this compound with emphasis shifting toward making flavones. The end point of this trend is exemplified by Fabaceae, which is characterized by the predominance of isoflavones. These compounds do occur, however, to a limited extent in Caesalpiniaceae. C-Glycoflavones are also a major component of the flavonoid picture of Fabales. Isoprenylated flavonoids have been found in several genera of Fabaceae and in one genus of Caesalpiniaceae. Perhaps the major feature of the order as a whole is the occurrence of 5-deoxy flavonoids. This character is fairly prominent in Rutiflorae, and it may well be that a realignment of Fabales nearer this superorder could be justified (Dahlgren 1977 a).

Proteiflorae

Proteales. This order has a very simple syndrome based on common flavonols and myricetin. The presence of myricetin and the absence of flavones could support a Myrtalean affinity as suggested by Cronquist (1968), although the flavonoid profile is rather ambiguous and relationships could lie in other directions, e.g. with Connaraceae and Chrysobalanaceae.

Myrtiflorae

Myrtales. The flavonoid profile is based mainly on common flavonols and their O-methyl derivatives. The latter are especially evident in Combretaceae. Myricetin appears quite frequently; a careful search would probably reveal further occurrences in the order. C-Glycoflavones occur in single genera of Lythraceae, Combretaceae, Myrtaceae and Onagraceae. The general flavonoid syndrome is much like that found in Balsaminales and Theales, although the diversity of anthocyanidin types has not been reported in the latter order.

Elaeagnales. The profile here is based mainly on common flavonols and their O-methyl derivatives. In this respect the order is similar to Myrtales. The chief difference is that myricetin has never been reported from Elaeagnales. This absence, if real, adds weight to the suggestion that the order is related to Thymelaeales (Cronquist 1968) which also appears to lack myricetin.

Trapales. Flavonoids of this order are based upon the common flavonols and C-glycoflavones. The small amount of data precludes useful discussion, although the absence of flavones is consistent with a Myrtalean affinity.

Haloragales. The flavonoid profile is based on common flavonols but again too little data are available to suggest relationships, although the apparent lack of flavones is consistent with a Myrtalean affinity.

General. Myrtiflorae is characterized by flavonols; flavones are very rare.

Saxifragiflorae

Saxifragales. The flavonoid profile of this group consists mainly of flavonols and their O-methyl derivatives. Extra oxygenation is seen in Crassulaceae and Saxifragaceae, including 2′-oxygenation in the latter (*Chrysosplenium*). Further similarities between Crassulaceae and Saxifragaceae include the presence of flavones and acylated flavonol glycosides. Myricetin occurs widely in the order, although it has not been reported from certain families including Fouquieriaceae, Brexiaceae and Greyiaceae. Dahlgren (1977 a) has suggested placing Fouquieriaceae near the Ericales, some of whose families also appear to lack myricetin. An array of anthocyanidins is seen in Saxifragales, reminiscent of those found in Myrtales. B-Ring deoxyflavonoids in Greyiaceae could indicate a link with other, similarly endowed families (Rosales?).

Gunnerales. This profile consists of common flavonols only. Further investigations are needed.

Balanophoriflorae

Balanophorales. Common flavonols, dihydroflavonols and flavanones make up the flavonoid profile. Again, however, too little data exist for effective discussion.

Plumbaginiflorae

Plumbaginales. The two families in this order are characterized mainly by flavonols and their O-methyl derivatives. A wide range of anthocyanidin types is also present. Myricetin is a major constituent in both families, indicating an alignment away from Caryophylliflorae which is poor in this compound. Differences between the families seem to lie in the restriction of 5-O-methylation to Plumbaginaceae and flavones, C-glycoflavones, chalcones and aurones to Limoniaceae. These latter characters could serve to link the order to Polygonaceae, Rhamnaceae or Primulaceae. The 5-O-methylated flavonols are very similar to those found in Ericaceae, Juglandales and Cunoniales.

Polygonales. Flavonols and their O-methyl derivatives comprise the flavonoid profile of this order. 8-Oxygenation occurs which might provide a link with Primulaceae. 5-O-Methylation may indicate links with Plumbaginaceae and the occasional presence of flavones, C-glycoflavones and chalcones may suggest a relationship with Limoniaceae. The presence of myricetin confirms the alignment of Plumbaginiflorae with other similar orders, and as being quite distinct from Caryophylliflorae. Flavonol bisulfates occur in *Polygonum*. The anthocyanidin complement of Polygonales is much simpler than that in Plumbaginales.

Primuliflorae

Primulales. The profile is based mainly on flavonols. O-Methyl derivatives occur in Aegiceratáceae and occasionally in Primulaceae. Thorne (1977) misquoted Harborne (1967 b) by saying that the flavonoids of Plumbaginaceae and Primulaceae are similar. In fact the reverse is true, a point clearly stated by Harborne (1967 b). Superficially the anthocyanidins in the two families are similar, both making delphinidin, cyanidin/pelargonidin and O-methylated derivatives. However, whereas Primulaceae anthocyanidins are methylated at the 7-, 3′- or 5′-positions, those in Plumbaginaceae are frequently methylated at the 5-position only. A further major difference lies in the fact that Plumbaginaceae possesses 3- and 5-O-methylated flavonols whereas Primulaceae does not, but instead makes 8-oxygenated flavonols. However, Ericaceae may provide a connecting link between the two families because it makes both 8-hydroxy and 5-O-methyl flavonols. Indeed, Thorne (1968) included all three families in his Theiflorae; the notable occurrence of 8-hydroxy flavonols in Theaceae would support an alliance, at least for Primulaceae, in this direction. Myricetin occurs in Myrsinaceae and Primulaceae which provides a link with other myricetin-bearing groups but not with Caryophylliflorae. Primulaceae seems to be unique in the order in making a variety of deoxygenated flavonoids which are found in the farina on the undersides of the leaves. It is also the only family in the order from which flavones and their derivatives (*Primula*) and C-glycoflavones (*Steironema*) have been reported.

Ebenales. The flavonoid picture is based on the common flavonols and myricetin. The syndrome is similar to that found in many families of Primulales, e.g. Myrsinaceae.

Theiflorae

Theales. Only a few families of this order have been studied but it seems that the common flavonols predominate along with occasional occurrence of their O-methyl derivatives. Myricetin is quite prominent and is probably more widespread within the order than is known at present. Its presence and the major emphasis on flavonols is consistent with a placement of this order near Myrtales. This position has recently been supported by studies on leaf venation and tooth structure (Hickey & Wolfe 1975). Flavones have been reported only from Ochnaceae and Clusiaceae. These two families show a further similarity in their capacity to make biflavonyls. These are otherwise rare in the angiosperms. Theaceae is unique in the order in making 8-oxygenated flavonols (which may indicate a link with Primulaceae), and 3-deoxyanthocyanidins. C-Glycoflavones occur in Ochnaceae (*Brackenridgea*) and Theaceae (*Thea*).

Nepenthales. Only *Nepenthes* has been investigated; the common flavonols and proanthocyanidins were reported. Further examination is needed to establish the presence or absence of myricetin.

Droserales. The sparse data (common flavonols and proanthocyanidins) offer no help in aligning this order or its constituent families.

Corniflorae

Ericales. This order exhibits mainly flavonols, and in Ericaceae, their 5-O-methyl derivatives. Ericaceae, Cyrillaceae and Epacridaceae all make myricetin, but this compound has so far not been reported from the other families. Its apparent absence from Monotropaceae and Pyrolaceae, which are considered advanced over Ericaceae, may suggest that it is being lost from the order. Its scarcity in Cornales (Hydrangeaceae only) and Gentianales perhaps supports this view. Ericaceae is unique in the order in making 5-O-methylated derivatives. This character is otherwise concentrated in Lauraceae, Juglandaceae, Cunoniales and Plumbaginaceae. Three families (Ericaceae, Diapensiaceae and Empetraceae) make 8-oxygenated flavonols which could be considered to link them with Primulales, Theaceae, or possibly Polygonales. A similar array of anthocyanidins to that in Ericales is found in Primulales to add further weight to the above suggestion.

Sarraceniales, Eucommiales. Scarcity of investigations on these groups hinders effective discussion. However, both orders possess common O-methyl flavonols, compounds which have not been reported from either Ericales or Cornales, although 5-O-methyl flavonols occur in Ericaceae.

Cornales. The profile is based on common flavonols. No flavones have been reported which aligns the order with other flavone-free orders such as Ericales, Myrtales, Ebenales, etc. Sambucaceae is unique in making biflavonyls and C-glycoflavones (in both cases *Viburnum* only). Myricetin occurs only in Hydrangeaceae, as far as is known, and this attribute makes it unusual in the order. It may provide a link to Hamamelidiflorae, however.

Gentianiflorae

Dipsacales. The flavonoid profile comprises mainly flavonols, flavones, and their O-methyl derivatives. The emphasis on flavone types is quite pronounced linking the order to others in the superorder and indeed to Lamiiflorae. 6-Hydroxyflavones in Valerianaceae are suggestive of those widespread in Lamiiflorae. C-Glycoflavones occur in Dipsacaceae only. Myricetin has never been reported from the order which is consistent with loss of this compound and a concomitant increase in flavone synthesis.

Oleales. Oleaceae is unusual in possessing both myricetin and flavones. As such it perhaps could be seen as intermediate in the myricetin-loss/flavone-gain trend. Thus, the family fits well between the myricetin-bearing Corniflorae and the myricetin-free Lamiiflorae. The presence of chalcones may be significant in this respect.

Goodeniales. Very little flavonoid information is available, except that the anthocyanidins include delphinidin and O-methyl derivatives. 3-O-Methylflavonols are present and there have been no reports of flavones. In many ways, therefore, the order is similar to Solanales with which it shares O-methyl anthocyanidins and 3-O-methyl flavonols (in Solanaceae, Polemoniaceae and Boraginaceae), and delphinidin. Further investigations should consider the possibility of O-acylated anthocyanins in Goodeniaceae.

Gentianales. This order is characterized by flavonols, flavones and their O-methyl derivatives. Extra oxygenation occurs in Loganiaceae, Buddleiaceae, Rubiaceae and Apocynaceae. Interestingly, the first three named families make 6-hydroxyflavones, a character dominant in Lamiiflorae. B-Ring deoxyflavonoids occur in both Rubiaceae and Apocynaceae. Myricetin is relatively rare and appears to have been lost by many families, which instead show a considerable synthesis of flavones. This situation is also typical of Lamiiflorae. The proper position of Menyanthaceae has often been debated. Unfortunately, flavonoids offer little help; its profile is similar to that found in Apocynaceae and Asclepiadaceae, but differs from Gentianaceae in not making flavones or C-glycoflavones.

Loasiflorae

Loasales. Only common flavonols have been reported; neither myricetin nor flavones have been seen. This type of profile is typical of Violiflorae, with some of whose families Cronquist (1968) has associated Loasaceae in the past, although the simple flavonoid profile does occur in Menyanthaceae, Apocynaceae and Asclepiadaceae (Gentianiflorae). The embryology and the presence of secoiridoids in Loasaceae firmly links the family to the Corniflorae-Gentianiflorae group of superorders.

Lamiiflorae

Scrophulariales, Lamiales. The general flavonoid profile for these two orders is very similar. There is a major emphasis on flavones and their O-methyl derivatives whilst flavonols and their O-methyl derivatives occur slightly less often; this is especially so in Lamiales. There is often extra hydroxylation, especially at the 6-position, indicating a link with Gentianiflorae. The possible significance of this character in indicating a polyphyletic origin for the Sympetalae has already been discussed. Myricetin is notably absent. A range of anthocyanidin types occur, notably O-acylated glycosides in Scrophulariaceae, Orobanchaceae and Lamiaceae. This may indicate a link with Solanales. As in most taxa of Solanales, Asterales, Araliales, Oleales and Dipsacales, proanthocyanins are lacking. New World Gesneriaceae and Bignoniaceae are distinctive in making 3-deoxyanthocyanidins, a character which is thought to be linked to hummingbird pollination in the tropics. B-Ring deoxy compounds occur at a low frequency in many families which reflects a link with Gentianales (e.g. Rubiaceae) where a similar situation exists. As might be expected of such a large group, a wide array of flavonoids is made

although many types are restricted to one or two genera only.

Hippuridales. Only flavonols and the common anthocyanidins have been reported. If the absence of flavones, especially 6-oxygenated flavones, is genuine, then the order is unusual in Lamiiflorae.

Caryophylliflorae

Caryophyllales. The most striking feature of this group is the replacement of anthocyanidins by betalains in all but two families (Caryophyllaceae and Molluginaceae). This feature sets the superorder apart from the rest of the angiosperms. The families have only been cursorily investigated for the other flavonoid types. However, the profile seems to consist mainly of common flavonols and their O-methyl derivatives. 6-Oxygenation occurs in Aizoaceae and Chenopodiaceae. Myricetin is almost totally absent (seen only in *Mesembryanthemum* s. lat., Aizoaceae). Flavones are relatively rare, occurring in one genus each of Chenopodiaceae, Amaranthaceae and Caryophyllaceae. C-Glycoflavones occur in Molluginaceae, Caryophyllaceae and Chenopodiaceae. Isoflavones occur in one genus each of Amaranthaceae and Chenopodiaceae. In general, the flavonoid profile of this order is fairly similar to that of Ranunculiflorae or Violiflorae, although the presence of betalains and the rarity of proanthocyanidins clearly set it apart.

Alismatiflorae

Alismatales, Hydrocharitales, Zosterales, Najadales. This is a reasonably coherent group from the standpoint of flavonoid pigments. It possesses a characteristic syndrome based chiefly on flavone types: luteolin/apigenin, their common O-methyl derivatives, flavone bisulfates and C-glycosyl derivatives. This profile resembles that of Arecales, except that in this order tricin is also present as a major component. Flavone bisulfates and the lack of myricetin distinguishes the superorder from Nymphaeales. Flavonols appear to be restricted to Alismatales and Hydrocharitales, being absent from the more highly specialized Zosterales and Najadales. The flavonols might indicate a link with Liliiflorae or indeed with Magnoliiflorae. Proanthocyanidins are notably absent from Alismatales which, together with the presence of lactifers, multiaperturate pollen grains and distinctive embryo curvature, serves to distinguish it from Hydrocharitales and Zosterales.

Liliiflorae

Dioscoreales, Stemonales, Haemodorales. These three orders show simple profiles based on the common flavonols with myricetin being absent. As such, their relationships seem to lie with Liliales–Asparagales, and possibly also Magnoliiflorae.

Liliales, Asparagales. Although these two orders have a syndrome based mainly on common flavonols, their O-methyl derivatives and to a lesser extent flavones (which is reminiscent of the situation in Magnoliiflorae), they also possess at low frequencies compounds usually characteristic of Alismatiflorae, Commeliniflorae and Areciflorae (e.g. flavone bisulfates, C-glycoflavones, and tricin). The flavones luteolin/apigenin are quite prominent in Asphodelaceae, Anthericaceae, Hyacinthaceae (Asparagales) and in Colchicaceae and Melanthiaceae (Liliales). Within these families the genera have either flavones or flavonols, rarely both. Iridaceae is distinguished by its isoflavones, a flavonoid type which is common in Fabaceae but also occurs in Myristicaceae (Magnoliales). The flavonoid data bear directly on a major question of monocot evolution, namely, whether Alismatiflorae represents the most primitive monocot stock, as viewed by Takhtajan (1969), or whether the Liliiflorae could be the direct modern-day descendants of the group that was central to monocot evolution, as suggested by Thorne (1977). According to Harborne (1977) the presence of flavones represents an evolutionary advancement over the presence of flavonols. Liliales-Asparagales are characterized mainly by flavonols, whereas the superorders Alismatiflorae and Commeliniflorae are predominantly flavone-bearing. Thus, Liliales-Asparagales could be central in monocot evolution with Alismatiflorae lying on one side and a series of orders, including Zingiberales, Orchidales, Commelinales, the Cyperales-Juncales-Poales complex and Arecales, which show an in-

creasing emphasis on flavones, lying on the other.

Bromeliales. The flavonoid profile is quite varied, based mainly on the common flavonols and, to a lesser extent, on flavones and O-methyl derivatives of both. This part of the profile is consistent with a position close to Liliales-Asparagales. Unusual flavonoid types involving extra oxygenation at the 8-, and especially at the 6-position, occur infrequently. These structural characteristics appear, albeit rarely, in Cyperaceae, Commelinaceae, Restionaceae, Orchidaceae and Eriocaulaceae. Relationships between Bromeliaceae and Commelinaceae have been suggested before (Cronquist 1968, Takhtajan 1969). C-Glycoflavones are present at a low frequency, similar to their occurrence in Liliales-Asparagales. Generally, therefore, Bromeliaceae shows most affinity to this group, although rare occurrences of flavonoids with extra oxygenation clearly distinguish it. The presence of myricetin in two genera is notable and may indicate relationships with other myricetin-bearing monocot groups (Iridaceae, Typhaceae and two Zingiberalean families).

Orchidales. The major flavonoid components of this order are the common flavonols and C-glycoflavones. The prominence of the common flavonols together with the rare occurrences of luteolin and tricin provide a clear link with Liliales-Asparagales. The C-glycoflavones and the sporadic occurrence of 6-oxygenated flavones suggest that alliances could also lie with Cyperaceae, Commelinaceae and Bromeliaceae. Overall, therefore, the order sits well in Liliiflorae but shows possible relationships with certain groups in Commeliniflorae. The presence of flavonoid bisulfates (in *Restrepia*) as C-glycoflavone derivatives rather than as the common flavone variants (found widely in Juncaceae and Arecaceae) is interesting and makes the order unique. As far as the data go, they do not support the recognition of separate families within Orchidales.

Typhiflorae

Typhales. This again is a simple flavonol-bearing order. Of note is the capacity of Sparganiaceae to produce myricetin, a character occasionally shared by Iridaceae (Liliales), Zingiberaceae and Marantaceae (Zingiberales) and Bromeliaceae. The primary emphasis on flavonols and the occurrence of myricetin supports a position between Liliales–Asparagales and Zingiberales, but offers no indication of a close relationship with Juncales-Cyperales.

Zingiberiflorae

Zingiberales. This order has a predominantly flavonol syndrome with no conspicuous difference between the 5–6-staminate and the 1–2-staminate families. Some families, however, do produce distinctive flavonoids. Musaceae makes 3-deoxyanthocyanidins, a character rarely found in the monocots, occurring only sparingly in Poaceae and Cyperaceae. The genus *Alpinia* in Zingiberaceae shows similarities with Juncaceae and Cyperaceae in making 5-O-methyl flavones. The co-occurrence of myricetin in Zingiberales, Typhales and Bromeliales has already been mentioned. C-Glycoflavones in Costaceae and Marantaceae are reminiscent of those found in Commeliniflorae, Areciflorae and Ariflorae. Furthermore, Marantaceae also occasionally makes flavone bisulfates, which are major compounds in Alismatiflorae, Arecales and Juncales, and occur moderately often in Poales and infrequently in Liliales-Asparagales. Generally, therefore, the data support a position for Zingiberales between the Liliiflorae-Typhiflorae on the one hand, and Commeliniflorae-Areciflorae on the other.

Commeliniflorae

Commelinales. Simple flavonols and C-glycoflavones are the main compounds seen in this order. This syndrome is therefore compatible with a position between Liliiflorae (Liliales-Asparagales) and the other orders in Commeliniflorae.

Eriocaulales. The occurrence of flavonols only might suggest a relationship with certain Zingiberalean families such as Heliconiaceae or Strelitziaceae. However, the presence of 6-oxygenation distinguishes the order and a general affinity with the bulk of Liliiflorae is indicated. Only one genus has been investigated and so speculations are even more unreliable than usual.

Juncales. Flavonols and flavones are produced, but the order shows extra elaboration with the production of 5-O-methyl flavones as a major component of the flavonoid syndrome. Flavone bisulfates are also occasionally produced. 5-O-Methyl flavones are found quite frequently in Cyperaceae, which indicates a close relationship between these two groups. Flavone bisulfates occur regularly in Alismatiflorae and Arecaceae and to a lesser extent in Poaceae, the latter two groups being situated in the general vicinity of Juncales.

Cyperales. This order is very similar to Juncales in flavonoid profile, with flavonols, flavones, 5-O-methyl flavones, and occasionally flavone bisulfates. C-Glycoflavones are more prominent than in Juncales. These compounds form major components of the syndromes in Poales, Orchidales and Arecales, and minor ones in Commelinales. Tricin in Cyperaceae is a major compound and indicates a similarity with Poaceae and Arecaceae.

Poales. Flavonols are a minor component while flavones predominate, especially in the form of tricin, C-glycoflavones and to a lesser extent flavone bisulfates. Aurones in Restionaceae might suggest a link with Cyperaceae.

General comments. The orders of Commeliniflorae show diverse relationships with each other, and characteristic flavone types support their recognition as a reasonably coherent unit, which nevertheless shows links with Liliiflorae and Zingiberales through Commelinales-Eriocaulales. The latter two orders show a greater emphasis on flavonols than do the others, and in fact Cronquist (1968) would unite Zingiberales and Commeliniflorae.

Areciflorae

Arecales. This order has a flavonoid profile very similar to Alismatiflorae, except that in Arecales tricin is a major component, being absent from Alismatiflorae. The co-occurrence of flavone bisulfates in such diverse groups strongly suggests convergence. Harborne (1975 b) suggested that these compounds may play a role in the maintenance of ionic balance in cells of plants growing in habitats with high salt concentrations, e.g. aquatic habitats, sea-shores, and very arid regions. The major occurrence of tricin links the syndrome with that of Cyperales, and especially with that of Poaceae. An association with Poaceae was suggested by Clifford (1977) on the basis of a cluster analysis of the monocots, using 51 morphological characters.

Ariflorae

Arales. Araceae has flavonols as major components of its flavonoid profile with C-glycoflavones as minor ones. Lemnaceae show further advancement and has flavonols as minor components and flavones and C-glycoflavones as major ones. This syndrome is compatible with a position close to Marantaceae-Zingiberales and the C-glycoflavone-rich Arecales. The predominance of flavonols in Araceae may point to a relationship not only with Zingiberales, but also with Liliiflorae, as discussed by Clifford (1977).

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Data base

Occurrence of flavonoids within the angiosperms. Directly after the family name a quotient is given, e.g. 2/7 which means that 2 out of a total of 7 genera in that family have been examined for flavonoids. The letter and number codes (e.g. C1 F3) indicate which flavonoids are known from the family in question: the letter designates the flavonoids according to Table 1, and the number indicates the number of genera in which that flavonoid has been found. E.g. C1 F3 means that O-methylated anthocyanidins have been found in one genus, and quercetin and/or kaempferol have been found in three genera. A '+' indicates presence in an unspecified number of genera.

Magnoliiflorae

Magnoliales – Winteraceae 2/7 F2 Q1 S2 ml – Degeneriaceae 0/1 – Himantandraceae 0/1 – Magnoliaceae 4/12 B1 C1 F3 G3 ml – Annonaceae 4/120 F3 N1 cl m2 – Canellaceae 0/5 – Myristicaceae 6/18 F1 S3 cl e2 ml – Eupomatiaceae 1/1 ml
Laurales – Monimiaceae 4/20 F4 G1 ml – Trimeniaceae 0/4 – Lauraceae 16/32 C1 F12 G1 H1 M11 Q4 V1 W1 X1 Z1 cl d2 k2 m8 p3 rl· – Idiospermaceae 0/1 – Austrobaileyaceae 0/1 – Gomortegaceae 0/1 – Amborellaceae 0/1 – Calycanthaceae 2/2 B1 F2 – Hernandiaceae 1/2 F1 – Lactoridaceae 0/1 – Chloranthaceae 1/5 B1 – Gyrocarpaceae 0/2
Aristolochiales – Aristolochiaceae 2/7 B1 C1 D1 F2 G1 H1
Piperales – Saururaceae 2/5 F2 ml – Piperaceae 1/8 U1 c1 d1 k1 p1
Illiciales – Illiciaceae 1/1 F1 m1 – Schizandraceae 2/2 B1 E1 F2 m1

Rafflesiiflorae

Rafflesiales – Rafflesiaceae 0/8 – Hydnoraceae 0/2

Ranunculiflorae

Nelumbonales – Nelumbonaceae 1/1 F1 S1 m1
Ranunculales – Lardizabalaceae 3/7 B2 D2 F2 m1 – Menispermaceae 2/65 F1 U1 – Sargentodoxaceae 0/1 – Kingdoniaceae 0/1 – Ranunculaceae 17/50 A4 B2 C1 D1 F16 G3 J1 N2 S2 d4 m1 – Circaeasteraceae 0/1 – Hydrastidaceae 0/2 – Glaucidiaceae 0/1 – Podophyllaceae 1/6 F1 G1 – Nandinaceae 1/1 m1 – Berberidaceae 3/4 A1 B1 E2 F3 G1 m2 sl
Papaverales – Papaveraceae 9/26 B1 F8 G3 J2 – Hypecoaceae 1/1 F1 – Fumariaceae 3/16 B1 F2

Nymphaeiflorae

Nymphaeales – Cabombaceae 1/2 dl – Nymphaeaceae 3/4 A1 B2 E1 F2 S1 d1 m2 – Barclayaceae 0/1 – Ceratophyllaceae 1/1 A1 B1 C1 F1 m1

Rutiflorae

Rutales – Rutaceae 30/150 A2 B3 E6 F15 G9 H9 J6 K5 M5 Q2 S1 U13 V5 W2 X5 Y1 Z5 c7 d4 g1 h3 k2 m7 p2 s4 – Cneoraceae 1/2 F1 – Surianaceae 1/1 F1 G1 – Simaroubaceae 7/20 E5 F4 d1 m3 – Kirkiaceae 0/1 – Burseraceae 1/16 F1 m1 – Meliaceae 7/50 E2 F4 G1 L1 Q1 U1 V1 X1 Y1 m1
Polygalales – Malpighiaceae 3/60 F2 m2 – Trigoniaceae 0/4 – Vochysiaceae 0/6 – Xanthophyllaceae 0/1 – Polygalaceae 2/12 A1 B1 F1 – Krameriaceae 0/1 – Emblingiaceae 0/1
Sapindales – Coriariaceae 1/1 E1 F1 – Anacardiaceae 23/60 A3 B3 C3 E5 F9 G2 L1 N2 Q5 S1 c3 f2 g16 m7 p2 q15 – Podoaceae 0/2 – Julianiaceae 1/2 E1 F1 g1 p1 q1 – Akaniaceae 1/1 F1 m1 – Uapacaceae 0/1 – Sapindaceae 5/150 E1 F5 G1 H1 K1 m5 – Aitoniaceae 0/1 – Aceraceae 2/3 B1 E1 F2 S1 d1 m2 – Hippocastanaceae 1/2 E1 F1 G1 H1 N1 m1 – Sabiaceae 0/1 – Meliosmaceae 1/2 F1 m1 – Koeberliniaceae 0/1
Juglandales – Rhoipteleaceae 0/1 – Juglandaceae 3/7 E1 F2 H1 M1 Q1 c1 m1
Myricales – Myricaceae 2/3 E2 F2 k1 m1 p1 r1
Leitneriales – Leitneriaceae 0/1
Geraniales – Zygophyllaceae 5/22 F4 G2 H2 J2 N1 S1 U1 d1 – Nitrariaceae 1/1 F1 G1 – Peganaceae 0/1 – Balanitaceae 1/1 F1 G1 – Erythroxylaceae 1/2 F1 G1 m1 – Dirachmaceae 0/1 – Geraniaceae 3/5 B1 C2 E2 F2 G1 H1 J1 d1 g1 m2 – Ledocarpaceae 0/3 – Vivianiaceae 0/1 – Biebersteiniaceae 0/1 – Ixonanthaceae 0/8 – Humiriaceae 0/8 – Hugoniaceae 0/1 – Linaceae 1/12 A1 B1 C1 F1 d1 – Lepidobotryaceae 0/1

– Averrhoaceae 1/3 m1 – Oxalidaceae 1/3 F1 d1 m1 q1 – Hypseocharitaceae 0/1
Balsaminales – Balsaminaceae 1/4 A1 B1 C1 D1 E1 F1 m1

Araliiflorae

Araliales – Araliaceae 7/55 A1 B3 F6 c1 – Torricelliaceae 0/1 – Apiaceae 148/275 B14 C1 D11 E1 F120 G13 N1 P2 S44 U12 a1 b3 c3 d5 e2 m2 s2
Pittosporales – Pittosporaceae 4/9 F4 G2 S1 m3

Asteriflorae

Asterales – Asteraceae 156/900 A5 B20 D3 F88 G46 H49 J15 K47 M3 N5 P3 Q5 S79 T1 U30 V27 W9 X29 Y9 a2 c13 d14 e+ g3 h1 k7 m1 p15 q8 s1

Dilleniiflorae

Dilleniales – Paeoniaceae 1/1 B1 C1 F1 S1 p1 – Dilleniaceae 7/10 E1 F6 G3 M1 Q2 m4
Cistales – Cistaceae 4/8 E3 F4 G2 H1 P1 S1 m4 – Bixaceae 1/1 S1 W1 b1 m1
Malvales – Sphaerosepalaceae 0/2 – Cochlospermaceae 1/2 E1 F1 S1 c1 m1 – Elaeocarpaceae 4/12 A1 B1 C1 E1 F2 G1 m2 – Sterculiaceae 11/60 B3 F11 G1 J2 R1 S2 X1 m6 – Huaceae 0/1 – Tiliaceae 6/50 E1 F5 G1 N3 Q1 S2 U1 d1 m5 – Dipterocarpaceae 6/15 E4 F4 m4 – Bombacaceae 4/20 B2 C1 F2 m1 – Malvaceae 14/75 A2 B5 C1 E1 F8 G2 H1 J6 M1 P1 Q1 U1 W1 b1 d1 m6 p1 – Neuradaceae 0/3
Urticales – Ulmaceae 8/15 E2 F6 Q1 d2 m7 – Hymenocardiaceae 0/1 – Moraceae 13/53 A2 B3 C1 E3 F5 L8 Q7 S2 U1 Y1 c2 e1 m2 p1 s4 – Cannabaceae 2/2 E2 F2 S2 a1 c1 d2 m1 p1 s1 – Urticaceae 6/45 F5 S2 U1 m6
Euphorbiales – Euphorbiaceae 22/300 A1 B4 E1 F13 G6 H2 J2 N1 S2 c2 d3 f3 m5 p2 – Pandaceae 0/4 – Aextoxicaceae 0/1 – Picrodendraceae 0/1

Thymelaeiflorae

Thymelaeales – Dichapetalaceae 0/5 – Thymelaeaceae 5/50 F3 S1 U2 c2 d1 m1

Violiflorae

Violales – Flacourtiaceae 11/93 F5 S4 U1 m7 – Passifloraceae 1/12 A1 B1 C1 F1 S1 d1 m1 – Dipentodontaceae 0/1 – Scyphostegiaceae 0/1 – Violaceae 6/22 A1 B1 C1 D1 E1 F6 G2 S1 U1 d1 m2 – Turneraceae 3/7 F1 S1 m1 – Malesherbiaceae 0/1 – Achariaceae 0/3 – Cucurbitaceae 7/110 F4 S3 U1 d3 – Begoniaceae 1/5 B1 F1 H1 m1 – Datiscaceae 1/1 F1 G1 L1 k1 – Caricaceae 1/4 F1 m1
Tamaricales – Tamaricaceae 3/4 B1 F3 G2 N1 P3 m2 – Frankeniaceae 1/4 A1 C1 F1 G1 P1 S1 U1 m1
Salicales – Salicaceae 2/3 A1 B2 C1 E2 F2 G2 H1 Q1 S2 U2 a1 c2 d1 k1 m2 p2 r1
Capparales – Limnanthaceae 2/2 E2 F2 G2 m1 – Tropaeolaceae 1/2 B1 F1 – Bretschneideraceae 0/1 – Salvadoraceae 1/3 F1 – Moringaceae 1/1 F1 G1 – Resedaceae 1/6 F1 G1 S1 – Tovariaceae 0/1 – Capparaceae 3/30 F3 – Pentadiplandraceae 0/1 – Brassicaceae 22/375 B3 C1 D3 F18 G8 Q1 S1 U1 c1 d1 – Gyrostemonaceae 0/5 – Bataceae 1/1 G1

Celastriflorae

Celastrales – Buxaceae 3/4 F3 – Simmondsiaceae 0/1 – Stylocerataceae 0/1 – Didymelaceae 0/1 – Barbeyaceae 0/1 – Geissolomataceae 0/1 – Avicenniaceae 0/1 – Staphyleaceae 2/5 B1 F2 m1 – Sphenostemonaceae 0/1 – Aquifoliaceae 1/3 B1 F1 – Celastraceae 6/55 B1 E1 F6 N1 g1 m5 – Stackhousiaceae 0/3 – Siphonodontaceae 0/1 – Goupiaceae 0/1 – Lophopyxidaceae 0/1 – Montiniaceae 0/2
Santalales – Olacaceae 0/25 – Opiliaceae 0/8 – Loranthaceae 4/25 F4 m1 – Misodendraceae 0/1 – Santalaceae 5/30 F5 G1 Q1 – Eremolepidaceae 0/3 – Viscaceae 2/18 E1 F1 U1 m1
Rhamnales – Rhamnaceae 10/58 C1 F7 G1 Q1 U1 f1 m3 p1 q1 – Vitaceae 4/12 A2 B2 C2 D2 E2 F1 Q1 d1 m1 – Leeaceae 1/1 E1 F1 m1

Solaniflorae

Solanales – Solanaceae 26/90 A4 B5 C6 D6 E1 F23 G3 H2 N1 Q1 S4 U1 d1 – Goetzeaceae 0/5 – Nolanaceae 1/2 F1 – Convolvulaceae 4/55 B3 C1 D2 F3 – Cuscutaceae 1/1 F1 m1 – Cardiopterygiaceae 0/1 – Cobaeaceae 1/1 F1 m1 – Polemoniaceae 17/18 B2 D1 E3 F13 G8 H11 K10 S1 U4 d8 – Hydrophyllaceae 3/18 F2 U1 c1 – Ehretiaceae 0/13 – Boraginaceae 21/100 C1 F21 G1 H1 Q1 S1 c1 – Wellstediaceae 0/1 – Lennoaceae 0/3 – Hoplestigmataceae 0/1

Campanuliflorae

Campanulales – Campanulaceae 5/35 A2 D1 F3 G2 S4 U1 – Pentaphragmataceae 0/1 – Lobeliaceae 3/30 A1 B1 D1 S1 m1 – Sphenocleaceae 0/1

Hamamelidiflorae

Trochodendrales – Trochodendraceae 1/1 E1 F1 m1 – Tetracentraceae 1/1 F1 G1 Q1 m1 – Eupteleaceae 1/1 F1 m1 – Cercidiphyllaceae 1/1 F1 Q1 m1
Hamamelidales – Myrothamnaceae 1/1 F1 m1 – Hamamelidaceae 9/22 A1 E8 F9 Q1 m6 – Platanaceae 1/1 A1 B1 E1 F1 N1 Q1 m1 – Altingiaceae 1/2 A1 B1 E1 F1 Q1 m1 – Daphniphyllaceae 1/1 A1 F1 – Rhodoleiaceae 0/1
Casuarinales – Casuarinaceae 1/2 F1 f1 m1
Fagales – Fagaceae 4/8 B1 E1 F4 G1 Q1 c1 d1 m2 p1 r1 – Corylaceae 1/1 E1 F1 m1 – Betulaceae 4/5 E2 F4 G3 H3 J1 K3 Q1 S2 U3 V2 W1 X2 c2 k1 m2 p1
Balanopales – Balanopaceae 0/1
Cunoniales – Cunoniaceae 22/27 A2 B13 E6 F22 G1 M4 P1 S1 m17 – Iteaceae 1/2 A1 B1 F1 m1 – Brunelliaceae 0/1 – Eucryphiaceae 1/1 F1 G1 H1 M1 Q1 c1 m1 – Baueraceae 1/1 E1 F1 m1 – Bruniaceae 0/12

Rosiflorae

Rosales – Crossosomataceae 0/1 – Rosaceae 29/80 A3 B15 C1 D1 E2 F27 G4 J1 K1 N1 P4 S2 U3 V1 X2 d3 m18 r2 – Malaceae 24/25 B5 D1 F19 G1 H2 J2 M1 S5 U1 c6 d8 e1 k2 m11 r2 – Amygdalaceae 4/5 B2 C1 F4 G1 H1 J1 K1 Q2 S1 U1 c3 e1 k1 m3 p1 – Connaraceae 1/25 E1 F1 m1 – Melianthaceae 1/2 F1 – Chrysobalanaceae 3/10 E2 F3 m3
Fabales – Mimosaceae 10/45 E2 F5 G2 H3 J2 K3 L1

Q4 S1 V1 W1 d1 g4 h1 m4 p6 q1 – Caesalpiniaceae 31/150 B5 C3 E7 F10 G3 H3 K4 L2 M1 Q7 S4 T1 U1 c6 d4 e4 g7 m9 p2 s1 – Fabaceae 111/450 A12 B7 C10 D1 E12 F60 G18 H3 J3 K5 M1 N1 Q8 S29 T1 U10 V1 X1 c17 d28 e65 g25 k1 m17 p20 q4 r2 s12

Proteiflorae

Proteales – Proteaceae 14/62 E3 F11 Q1 m14

Myrtiflorae

Myrtales – Lythraceae 4/25 A1 B3 C3 F1 U1 d1 – Punicaceae 1/1 A1 B1 – Rhizophoraceae 5/16 B1 E1 F2 m3 – Dialypetalanthaceae 0/1 – Crypteroniaceae 0/2 – Combretaceae 6/19 B3 C1 E1 F4 G2 H2 J2 K1 d1 g1 m2 – Oliniaceae 0/1 – Melastomataceae 20/240 A3 B6 C13 D14 E1 F5 N1 m3 – Penaeaceae 0/5 – Myrtaceae 27/100 A7 B17 C11 E6 F12 G1 Q2 c1 d1 m10 – Onagraceae 14/21 A2 B3 C4 E4 F10 H2 d1 m1 p5
Elaeagnales – Elaeagnaceae 2/3 C1 F2 G1 m1
Trapales – Trapaceae 1/1 B1 F1 d1
Haloragales – Haloragaceae 2/6 B1 F2 m1

Saxifragiflorae

Saxifragales – Crassulaceae 8/35 B1 E2 F6 G3 H2 J2 N1 U1 X1 c1 m2 – Penthoraceae 1/1 F1 m1 – Saxifragaceae 12/30 A3 B4 C2 E8 F12 G3 H2 K2 L1 N3 Q1 S3 m9 – Fouquieriaceae 1/2 A1 B1 D1 F1 m1 – Francoaceae 0/2 – Brexiaceae 1/3 m1 – Cephalotaceae 1/1 E1 F1 – Tremandraceae 2/3 C1 E2 F2 – Vahliaceae 0/1 – Ribesiaceae 1/1 A1 B1 D1 E1 F1 G1 m1 – Greyiaceae 1/1 F1 H1 k1 m1
Podostemales – Tristichaceae 0/5 – Podostemaceae 0/45
Gunnerales – Gunneraceae 1/1 F1

Balanophoriflorae

Balanophorales – Balanophoraceae 1/18 F1 Q1 c1 – Cynomoriaceae 0/1

Plumbaginiflorae

Plumbaginales – Plumbaginaceae 4/4 A2 B3 C2 E3 F4 G1 H1 M3 m2 – Limoniaceae 6/6 A1 B2 C2 E5 F5 G1 H2 S1 d1 m5 p1 q1
Polygonales – Polygonaceae 11/40 B4 E3 F10 G3 J2 K1 M1 P1 S1 U1 X1 d3 m4 p1

Primuliflorae

Primulales – Myrsinaceae 5/35 A2 B1 C2 E3 F4 m3 – Aegiceritaceae 1/1 G1 – Theophrastaceae 2/5 F2 – Primulaceae 17/20 A3 B4 C6 E4 F17 G1 J3 Q1 S1 V1 W1 X1 Y1 d1 g4 h4 k3 m16 – Coridaceae 1/1 F1 m1
Ebenales – Ebenaceae 1/2 E1 F1 m1 – Sapotaceae 9/60 E4 F9 Q3 m7 – Lissocarpaceae 0/1 – Styracaceae 2/12 F2 m1

Theiflorae

Theales – Stachyuraceae 1/1 F1 m1 – Ochnaceae 3/40 B1 S1 d1 f2 m1 – Quiinaceae 0/4 – Medusagynaceae 0/1 – Scytopetalaceae 0/5 – Sarcolaenaceae 2/8 E2 F2 – Strasburgeriaceae 0/1 – Oncothecaceae 0/1 – Theaceae 6/16 A1 B2 E2 F5 G2 J2 R1 d1 m4 – Pentaphylacaceae 0/1 – Marcgraviaceae 2/5 E1 F2 m1 – Caryocaraceae 0/2 – Pelliceriaceae 0/1 – Napoleonaceae 0/2 – Bonnetiaceae 0/3 – Foetidiaceae 0/1 – Lecythidaceae 4/15 A2 B2 F2 m1 – Symplocaceae 1/2 F1 G1 m1 – Clusiaceae 7/40 E2 F1 G1 S2 b1 f4 m4 – Ancistrocladaceae 1/1 E1 F1 m1 – Elatinaceae 1/2 F1 m1
Nepenthales – Nepenthaceae 1/2 F1 m1 – Dioncophyllaceae 0/3
Droserales – Droseraceae 2/4 B2 F1 m1 – Lepuropetalaceae 0/1 – Parnassiaceae 1/1 F1 m1

Corniflorae

Ericales – Actinidiaceae 1/3 F1 m1 – Clethraceae 1/1 F1 m1 – Cyrillaceae 1/3 E1 F1 m1 – Roridulaceae 0/1 – Ericaceae 47/50 A2 B8 C3 D1 E24 F47 H4 J16 M11 N2 Q18 S1 c2 d1 m12 p1 r3 – Monotropaceae 2/12 F2 – Pyrolaceae 3/3 F3 Q2 m1 – Epacridaceae 21/30 A11 B17 C1 E9 F19 m3 – Diapensiaceae 5/7 F5 J1 m1 – Byblidaceae 0/1 – Empetraceae 3/3 A1 B1 C1 F3 J3 m1 – Grubbiaceae 0/2
Sarraceniales – Sarraceniaceae 1/3 F1 G1 m1
Eucommiales – Eucommiaceae 1/1 G1 m1
Cornales – Garryaceae 0/1 – Alangiaceae 0/2 – Cornaceae 6/12 A1 B2 F4 m3 – Davidiaceae 1/1 F1 m1 – Nyssaceae 0/2 – Icacinaceae 3/58 F1 m2 – Escalloniaceae 4/7 F3 Q1 m3 – Columelliaceae 0/1 – Stylidiaceae 1/5 F1 – Hydrangeaceae 6/17 A3 B3 E2 F6 m4 – Alseuosmiaceae 0/3 – Sambucaceae 2/2 B2 F2 S1 d1 f1 m1 r1 – Adoxaceae 0/1

Gentianiflorae

Dipsacales – Caprifoliaceae 10/12 B2 F9 S6 U1 d1 m3 – Valerianaceae 2/13 F2 G1 S1 U2 X1 a1 – Triplostegiaceae 0/1 – Dipsacaceae 4/8 A1 F3 S2 U1 d4 – Morinaceae 0/1 – Calyceraceae 0/4
Oleales – Oleaceae 10/29 B1 C2 D1 E1 F9 S3 c1 p1
Goodeniales – Goodeniaceae 3/14 A3 C3 H1
Gentianales – Loganiaceae 2/7 F1 X1 – Buddlejaceae 3/10 E1 F2 S1 U2 W1 X2 – Retziaceae 0/1 – Rubiaceae 35/500 A1 B6 E1 F25 G7 H1 J1 K1 Q1 S1 U4 V1 W1 X2 a1 c1 d1 h1 k1 m10 s1 – Menyanthaceae 3/5 F3 G1 m1 – Gentianaceae 4/80 A1 B1 F3 S1 d2 – Apocynaceae 33/180 B1 C2 E1 F32 G4 S1 V1 W1 Z1 k1 m10 – Asclepiadaceae 14/130 B2 C1 F13 G1 m1 s1

Loasiflorae

Loasales – Loasaceae 3/15 F3

Lamiiflorae

Scrophulariales – Scrophulariaceae 29/220 A5 B12 C4 D2 F9 G3 H2 J2 K1 S9 U10 V4 X5 Z1 a1 c2 d2 k1 p1 q3 – Selaginaceae 0/1 – Globulariaceae 2/2 F1 S1 U1 V1 X2 – Lentibulariaceae 2/4 S2 U1 W1 X2 – Plantaginaceae 1/3 F1 S1 V1 X1 k1 – Pedaliaceae 3/12 S1 U2 V2 X2 – Trapellaceae 0/1 – Martyniaceae 1/3 F1 – Orobanchaceae 2/14 A2 B2 C1 D1 S1 T1 – Gesneriaceae 35/120 A5 B19 C11 F1 R14 S18 U1 c1 k2 p5 q4 – Bignoniaceae 20/120 A1 B7 C1 F9 Q1 R2 S7 U3 V2 W1 X8 Z1 a1 c1 k3 – Henriqueziaceae 0/2 – Myoporaceae 2/4 F2 G1 H1 K1 Q1 S1 c1 k1 – Acanthaceae

11/250 A1 C2 F2 S9 U2 V1 W1 X1 Y1 c1 d1 h1 k1 p2
Hippuridales – Hippuridaceae 1/1 B1 F1
Hydrostachyales – Hydrostachyaceae 0/1
Lamiales – Verbenaceae 13/75 A1 B3 C1 F1 G3 H3 J1 K4 S6 U5 V4 X6 d1 k1 – Callitrichaceae 1/1 S1 – Lamiaceae 57/180 A3 B6 D5 F12 G2 H2 K1 S33 U14 V8 W6 X26 Y1 Z2 a4 c5 d2 k3

Caryophylliflorae

Caryophyllales – Phytolaccaceae 4/12 F2 G1 n4 – Agdestidaceae 1/1 n1 – Stegnospermataceae 1/1 n1 – Achatocarpaceae 1/2 n1 – Nyctaginaceae 11/30 F3 m1 n10 – Aizoaceae 23/110 E1 F2 G1 H1 K1 m>3 n22 – Molluginaceae 2/14 B1 d1 – Didieraceae 4/4 n4 – Cactaceae 33/150 F2 G4 H1 n32 – Portulacaceae 10/19 F3 m1 n10 – Hectorellaceae 1/2 n1 – Basellaceae 2/4 F1 n2 – Chenopodiaceae 14/102 F7 G1 H1 K1 U1 d1 e+ n12 – Dysphaniaceae 1/1 n1 – Halophytaceae 1/1 n1 – Amaranthaceae 11/65 F2 V1 X1 e1 n10 – Caryophyllaceae 17/70 B8 C9 D1 F9 G2 S1 d8 m1 p1

Alismatiflorae

Alismatales – Alismataceae 6/9 B1 F1 b2 d6 – Limnocharitaceae 1/4 d1
Hydrocharitales – Butomaceae 1/1 d1 m1 – Hydrocharitaceae 6/16 B3 F3 S3 U3 b2 d2 m3 – Aponogetonaceae 1/1 B1 F1 m1
Zosterales – Scheuchzeriaceae 1/1 S1 d1 – Juncaginaceae 0/5 – Potamogetonaceae 2/3 S1 U2 d2 m1 – Zosteraceae 1/2 S1 U1 b1 – Posidoniaceae 1/1 m1 – Zannichelliaceae 1/3 S1 U1 b1 – Cymodoceaceae 1/5 m1
Najadales – Najadaceae 1/1 B1 d1

Liliiflorae

Dioscoreales – Dioscoreaceae 1/7 B1 D1 F1 m1
Stemonales – Stemonaceae 0/3 – Trilliaceae 2/4 F2
Asparagales – Smilacaceae 1/4 F1 m1 r1 – Philesiaceae 1/7 F1 – Ruscaceae 2/3 F2 G1 d1 – Convallariaceae 4/22 B1 C1 F4 G1 d1 m1 – Asparagaceae 1/3 B1 C1 F1 – Dracaenaceae 4/13 F4 m2 – Hypoxidaceae 0/10 – Tecophilaeaceae 0/8 – Phormiadeae 1/3 F1 m1 – Xanthorrhoeaceae 1/8 F1 m1 p1 – Aphyllanthaceae 1/1 F1 – Asphodelaceae 5/19 F2 S3 d1 – Anthericaceae 4/31 F2 S2 d1 m2 – Ixioliriaceae 0/2 – Agavaceae 4/15 F4 – Hemerocallidaceae 1/1 A1 B1 F1 – Hyacinthaceae 15/37 A2 B3 D3 F4 Q1 S10 T2 U2 b2 d1 – Alliaceae 5/26 B1 C1 F5 – Amaryllidaceae 15/55 B5 F12 G1 N1
Taccales – Taccaceae 0/1
Haemodorales – Haemodoraceae 1/16 F1 m1 – Pontederiaceae 2/7 A1 m2 – Philydraceae 2/4 F1 G1 m1
Liliales – Colchicaceae 5/17 B2 F1 S5 T1 U1 – Iridaceae 16/60 A3 B6 C6 D1 E3 F4 G1 S1 T1 U1 d3 e4 m5 – Alstroemeriaceae 2/4 F2 – Liliaceae 7/15 A1 B3 F7 G1 p1 – Melanthiaceae 5/25 F3 S1 d1 m1
Triuridales – Triuridaceae 0/7
Burmanniales – Burmanniaceae 0/9 – Corsiaceae 0/2 – Thismiaceae 0/8
Orchidales – Apostasiaceae 0/2 – Cypripediaceae 1/4 d1 – Orchidaceae 82/729 A2 B11 C3 D5 F23 G1 N1 Q1 S2 T1 U2 V2 X2 b1 d52 m1
Bromeliales – Bromeliaceae 18/60 B+ C+ E2 F17 G3 H2 J1 K2 S4 U1 V1 X3 d2 – Velloziaceae 1/5 F1

Typhiflorae

Typhales – Sparganiaceae 1/1 B1 E1 F1 m1 – Typhaceae 1/1 B1 F1 G1

Zingiberiflorae

Zingiberales – Lowiaceae 0/1 – Heliconiaceae 1/1 F1 – Musaceae 1/2 A1 B1 C1 F1 R1 m1 – Strelitziaceae 2/3 A1 F2 m1 – Zingiberaceae 15/45 B3 C2 E3 F10 G4 H2 M1 Q1 Z1 c2 k1 m10 p1 – Costaceae 1/4 B1 F1 d1 m1 – Cannaceae 1/1 B1 F1 m1 – Marantaceae 9/30 A3 B2 C1 E1 F5 S2 b2 d5 m4

Commeliniflorae

Commelinales – Commelinaceae 10/38 A1 B+ D1 F5 U1 X1 d2 m4 – Cartonemataceae 0/1 – Mayacaceae 1/1 F1 – Xyridaceae 1/2 B1 F1 N1 d1 – Abolbodaceae 0/2 – Rapateaceae 0/16
Eriocaulales – Eriocaulaceae 1/13 F1 G1 H1 K1
Juncales – Juncaceae 7/9 F4 S5 U2 Z4 b4 d1 g2 m2 – Thurniaceae 0/1
Cyperales – Cyperaceae 41/90 A1 B6 F8 R3 S11 T21 X1 Z8 b1 c2 d26 m20 p1 q10
Centrolepidales – Centrolepidaceae 0/5
Poales – Restionaceae 7/28 B1 C1 F1 J2 W1 b1 m1 q4 – Ecdeiocoleaceae 0/1 – Flagellariaceae 2/2 A1 B1 F1 – Joinvilleaceae 0/1 – Poaceae 131/620 A3 B17 C6 D5 F21 G3 N1 P1 R2 S21 T113 U5 b26 d117 g1 m23

Areciflorae

Arecales – Arecaceae 68/217 F21 G1 P1 S47 T31 b35 d60 m49
Pandanales – Pandanaceae 0/3
Cyclanthales – Cyclanthaceae 0/11

Ariflorae

Arales – Araceae 18/115 B13 C1 F9 c2 d2 m1 – Lemnaceae 4/4 B2 C1 F1 S4 d3

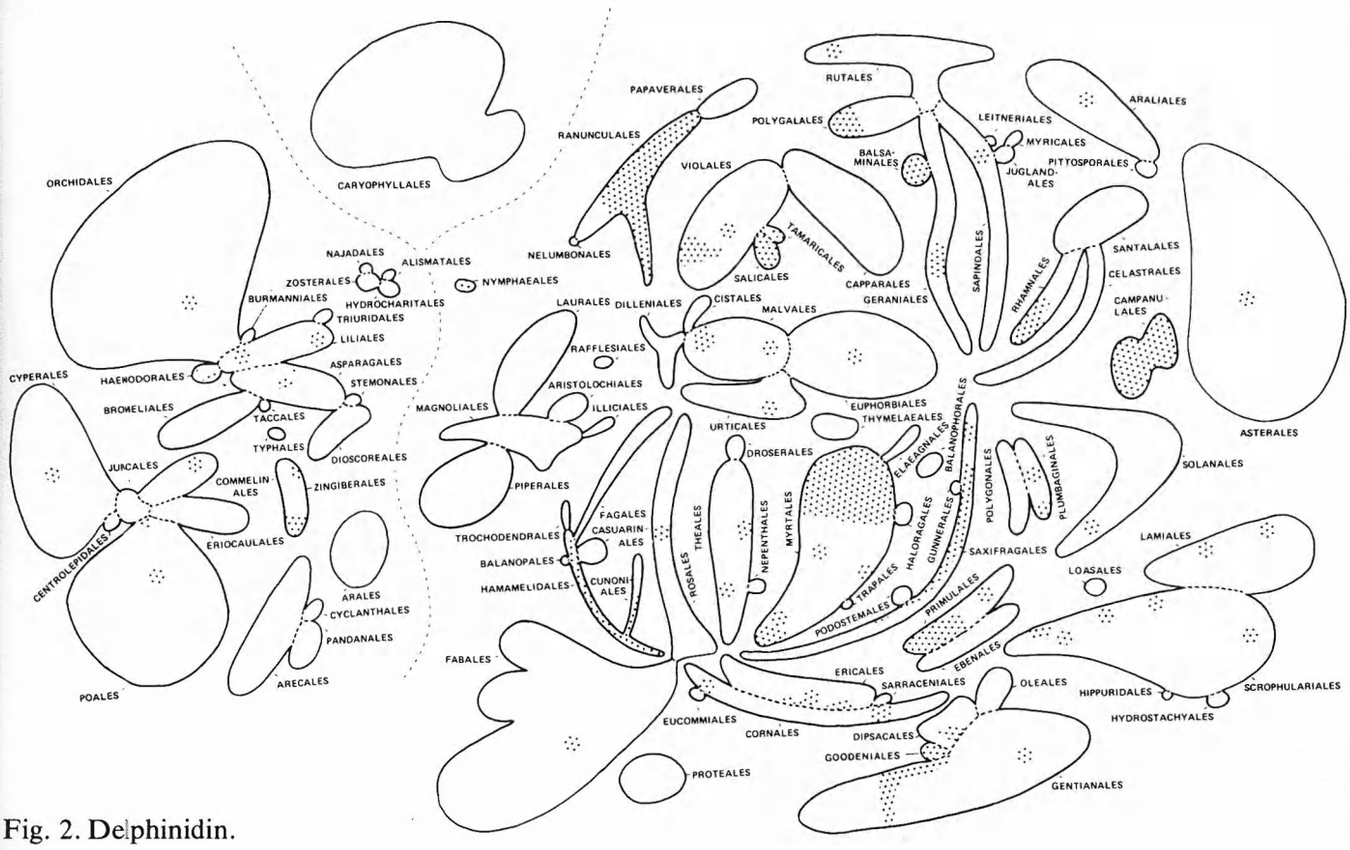

Fig. 2. Delphinidin.

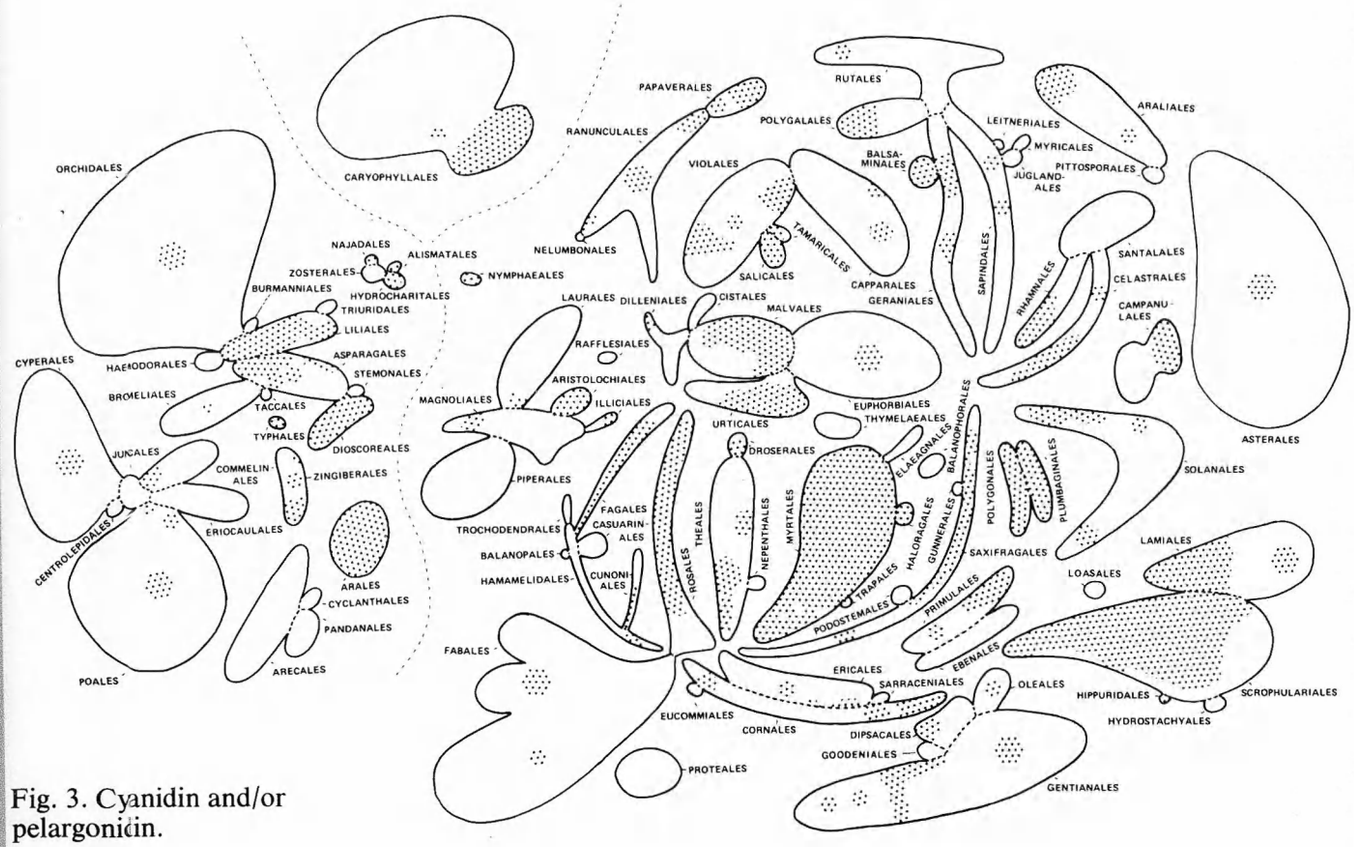

Fig. 3. Cyanidin and/or pelargonidin.

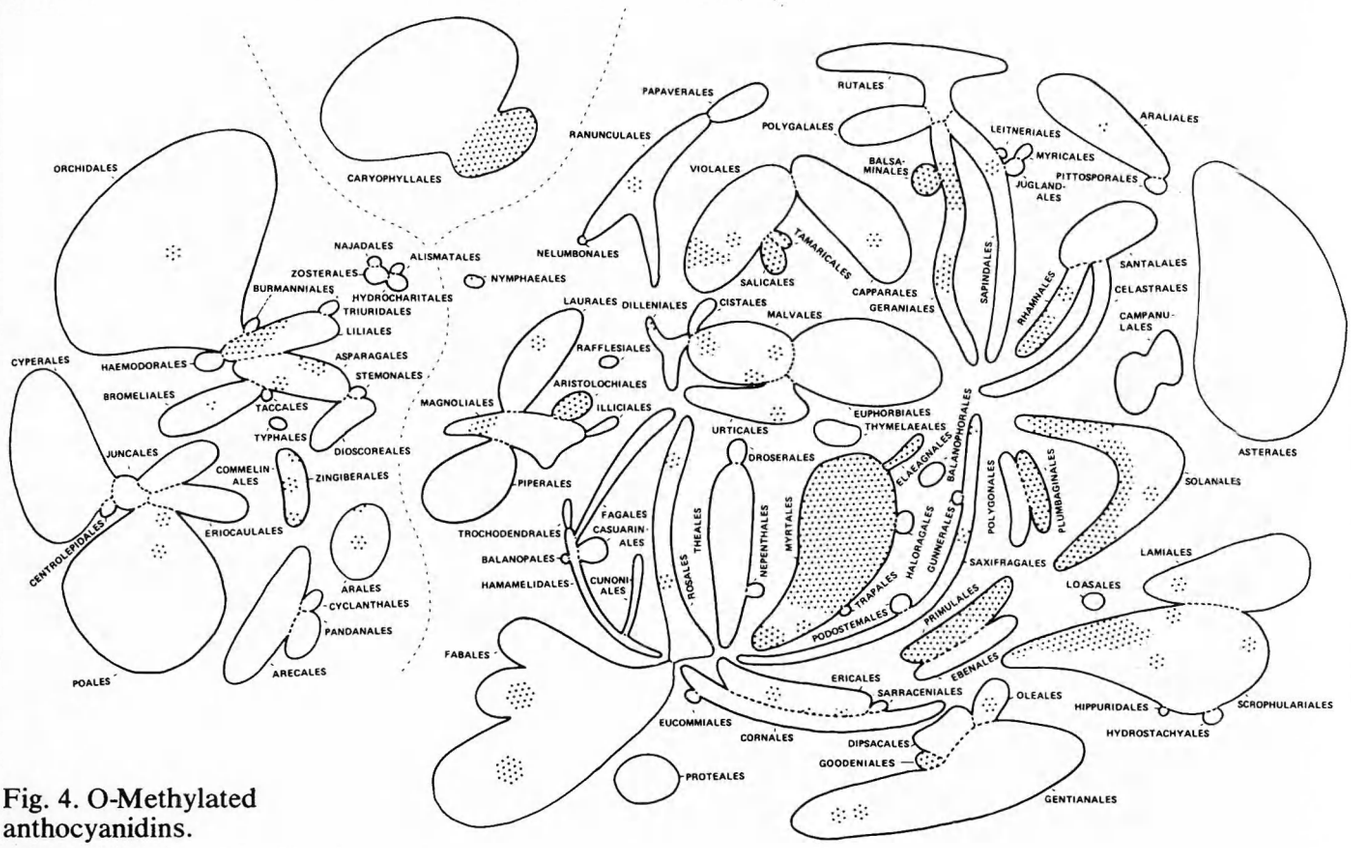

Fig. 4. O-Methylated anthocyanidins.

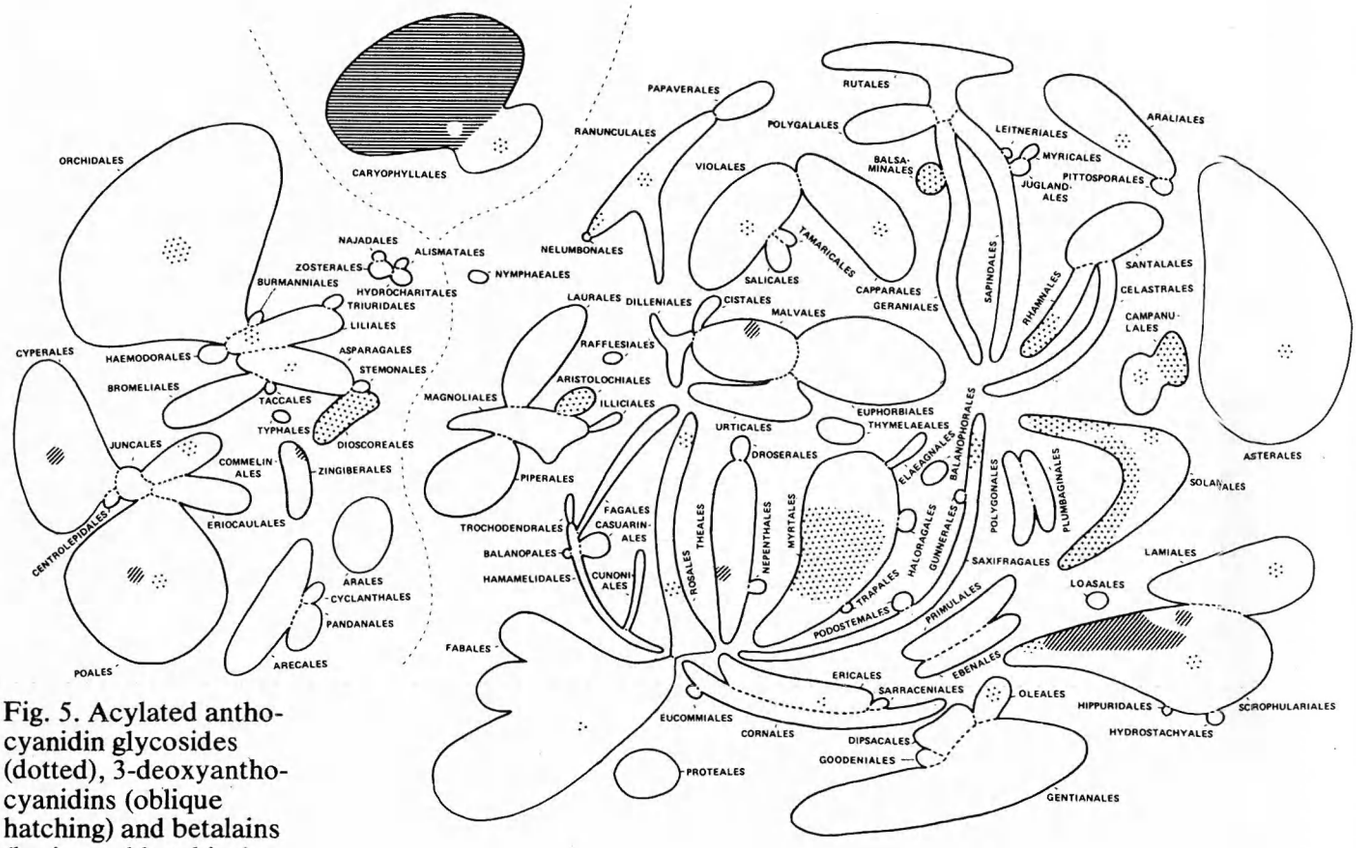

Fig. 5. Acylated anthocyanidin glycosides (dotted), 3-deoxyanthocyanidins (oblique hatching) and betalains (horizontal hatching).

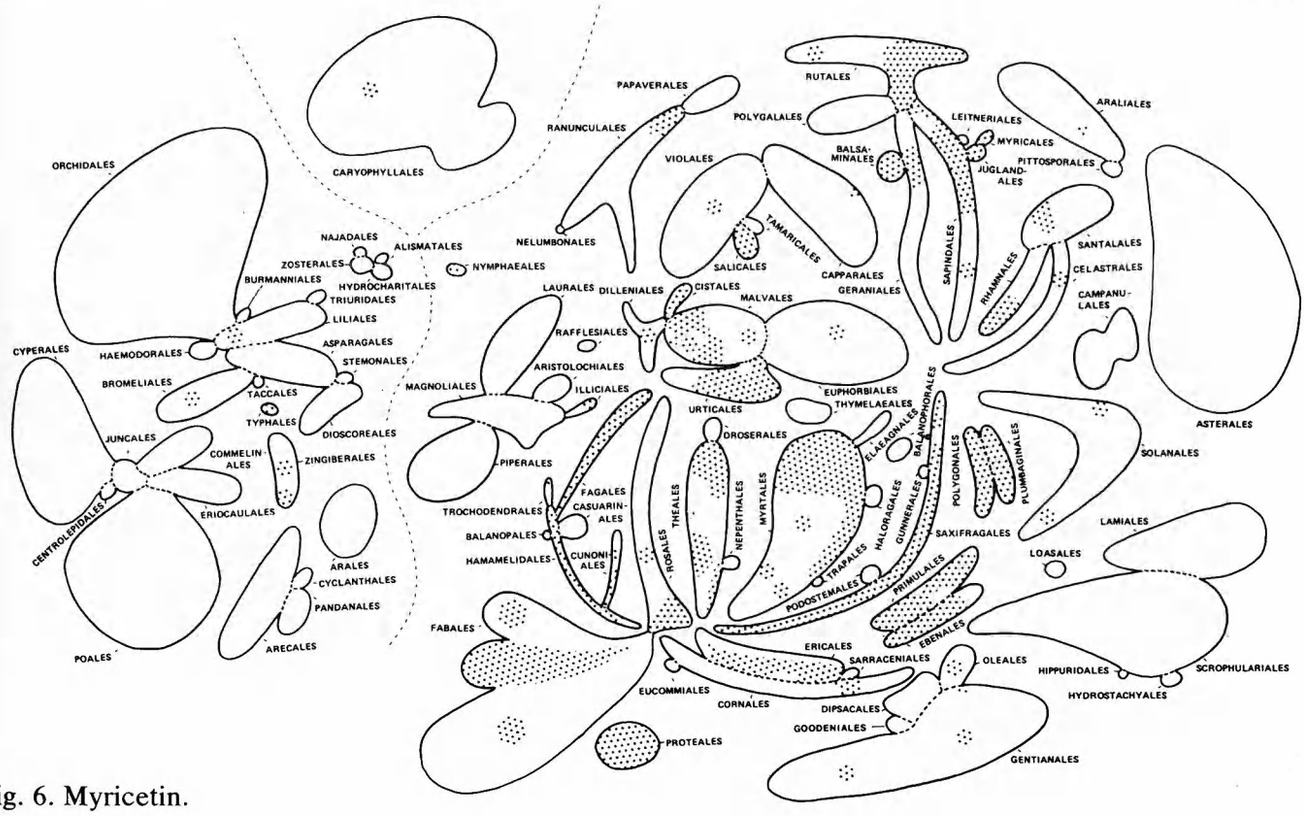

Fig. 6. Myricetin.

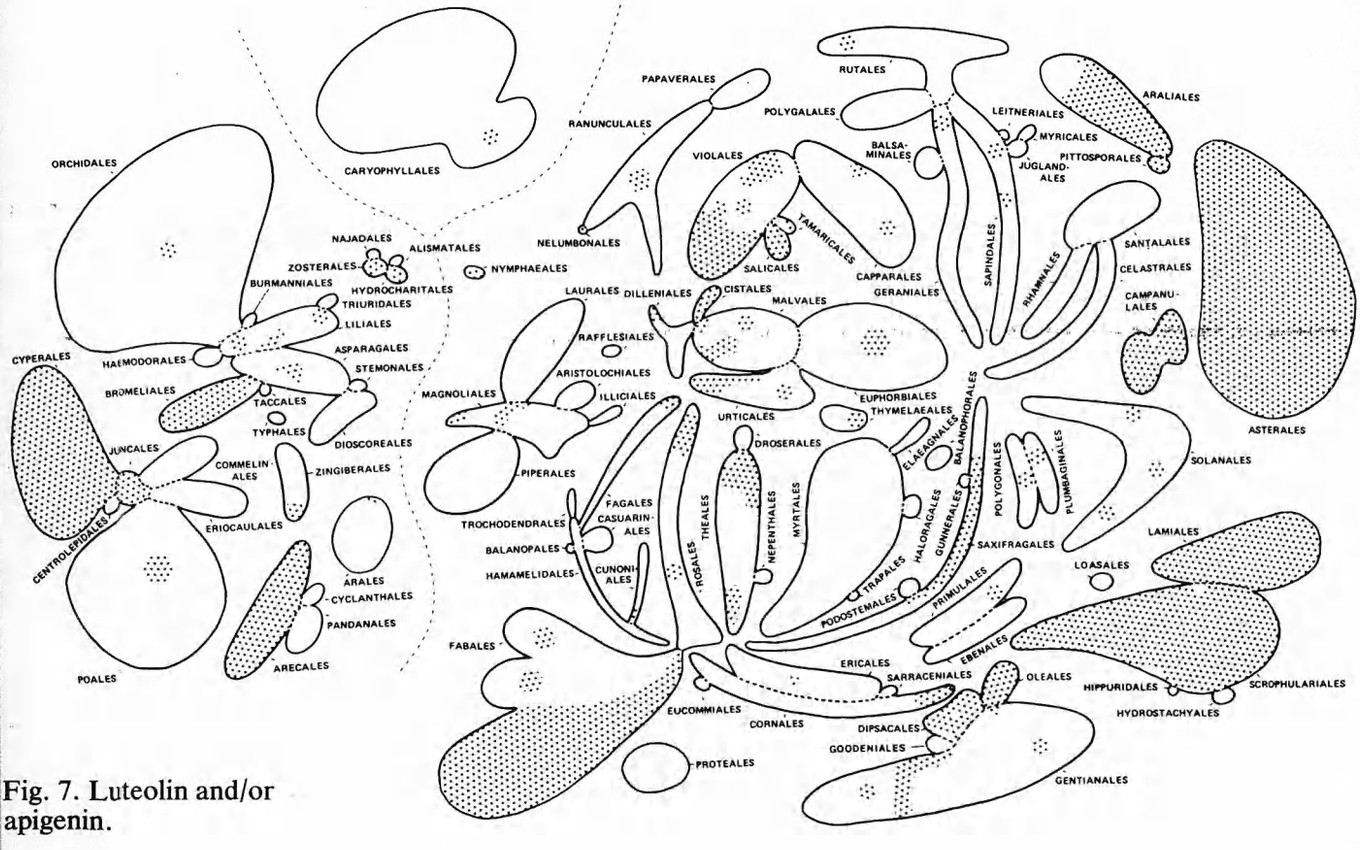

Fig. 7. Luteolin and/or apigenin.

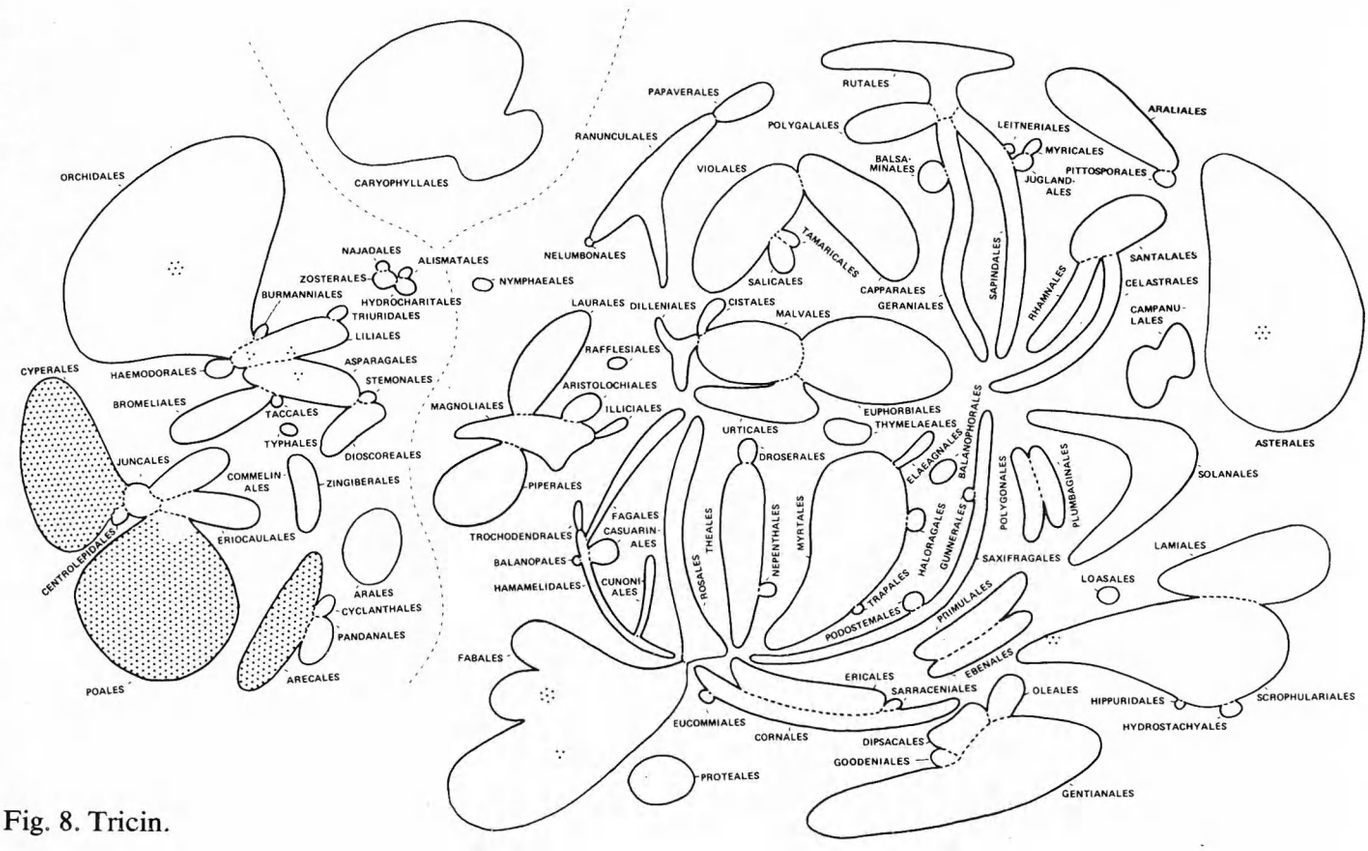

Fig. 8. Tricin.

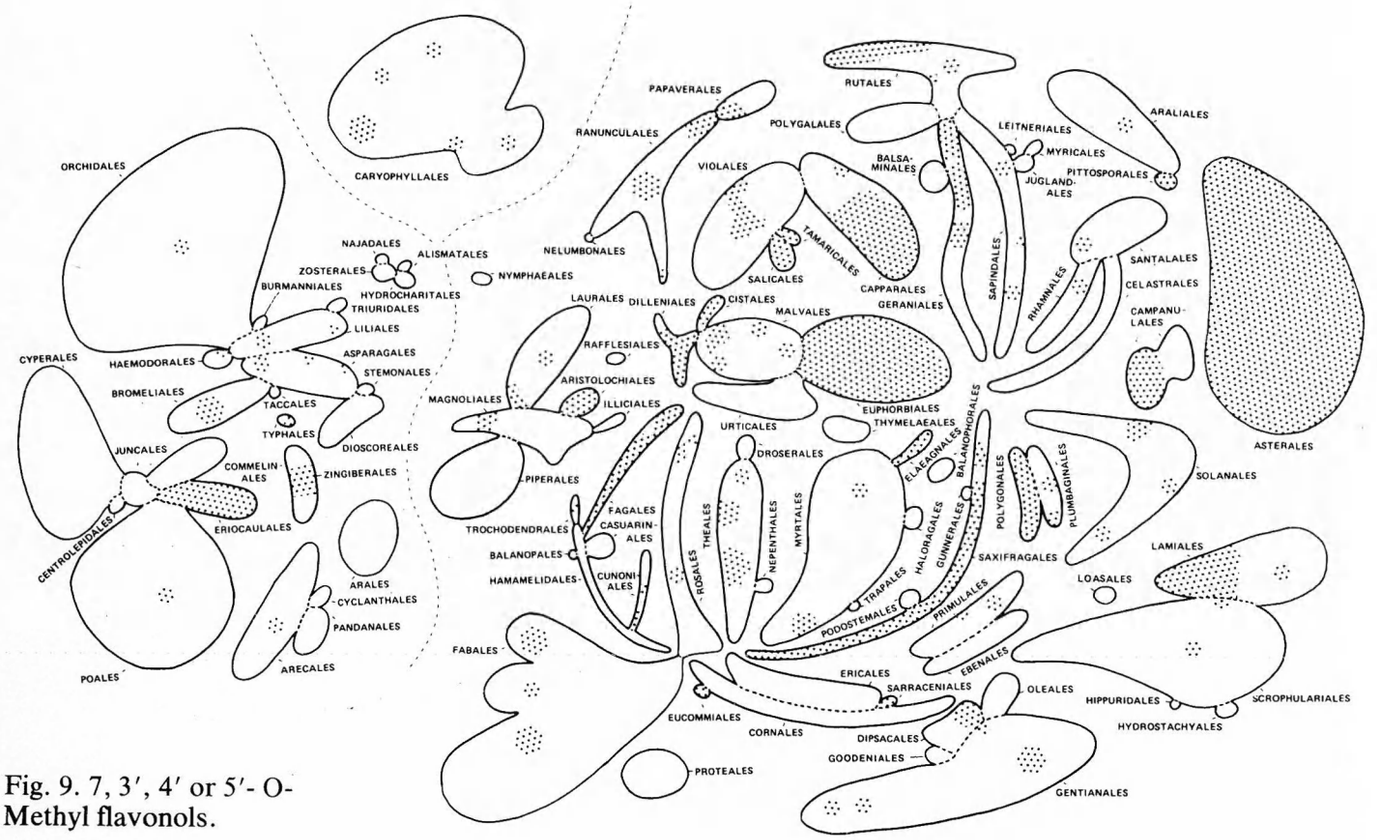

Fig. 9. 7, 3′, 4′ or 5′- O-Methyl flavonols.

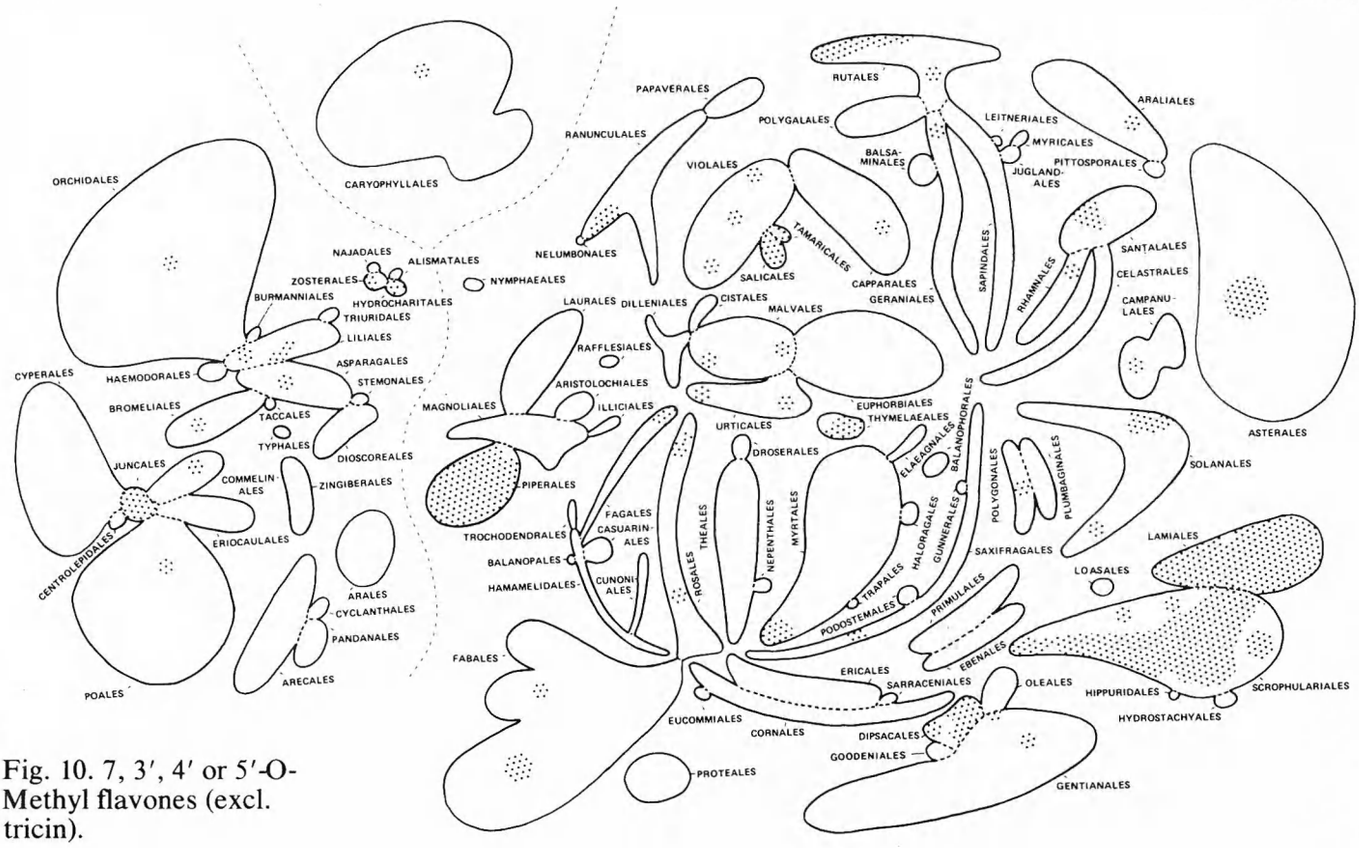

Fig. 10. 7, 3′, 4′ or 5′-O-Methyl flavones (excl. tricin).

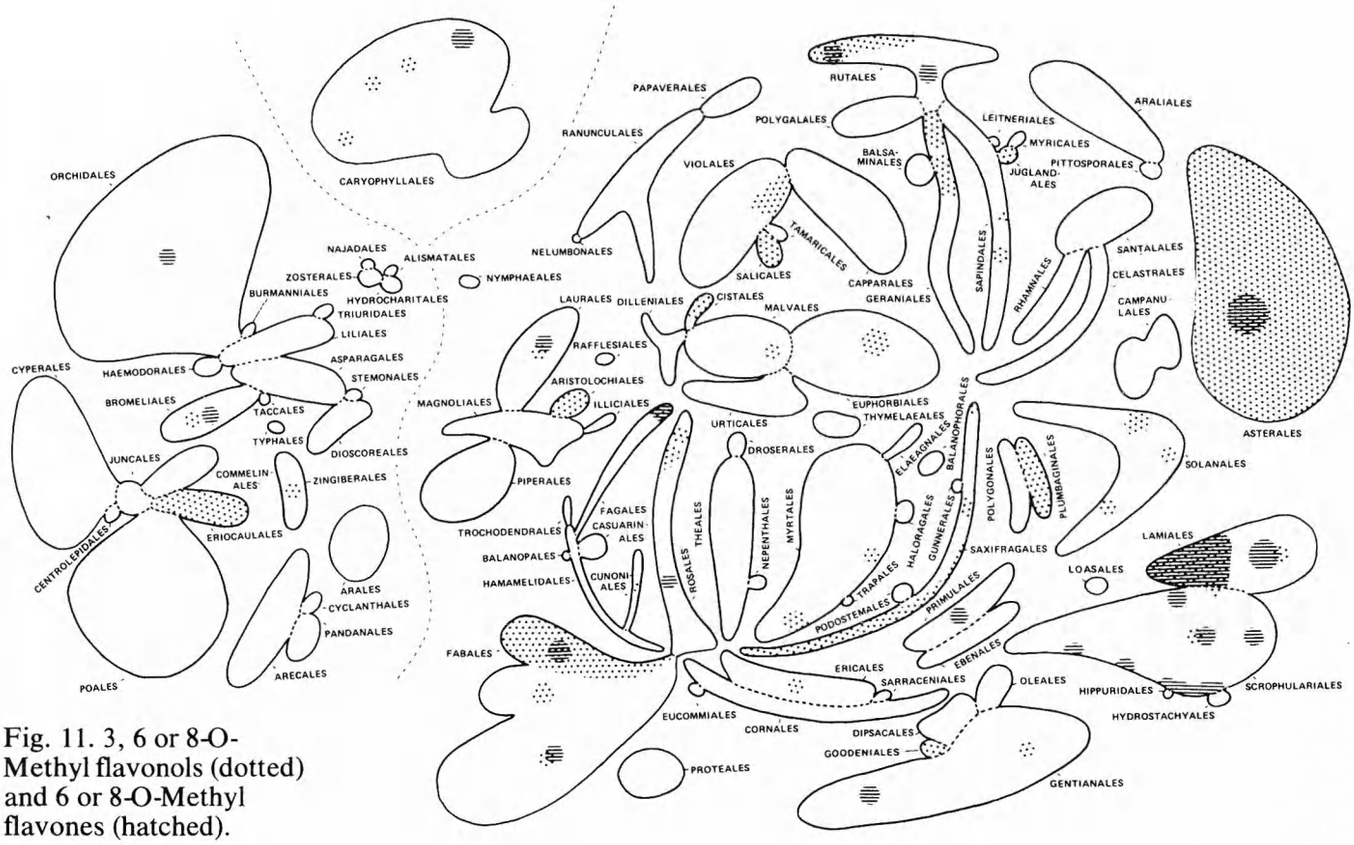

Fig. 11. 3, 6 or 8-O-Methyl flavonols (dotted) and 6 or 8-O-Methyl flavones (hatched).

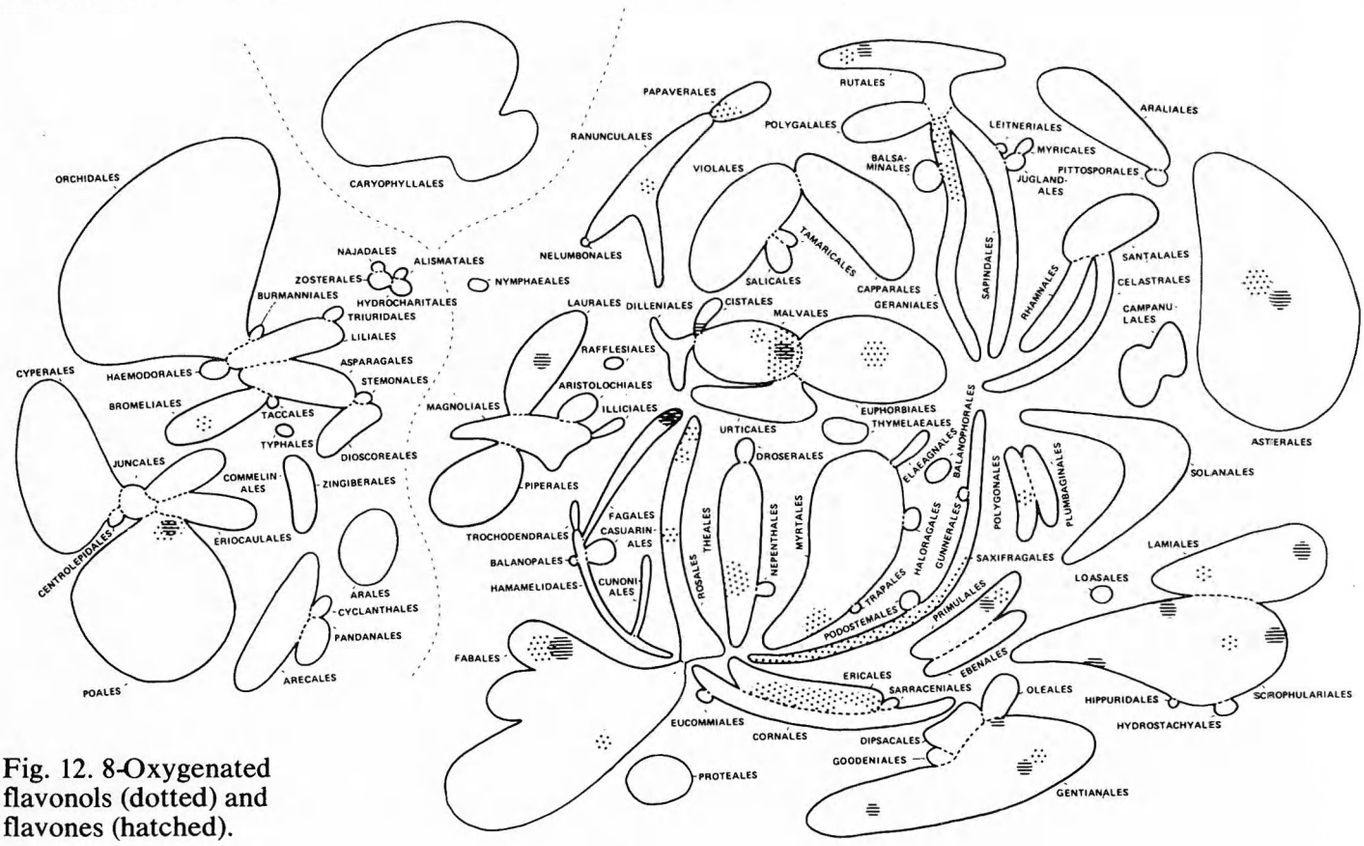

Fig. 12. 8-Oxygenated flavonols (dotted) and flavones (hatched).

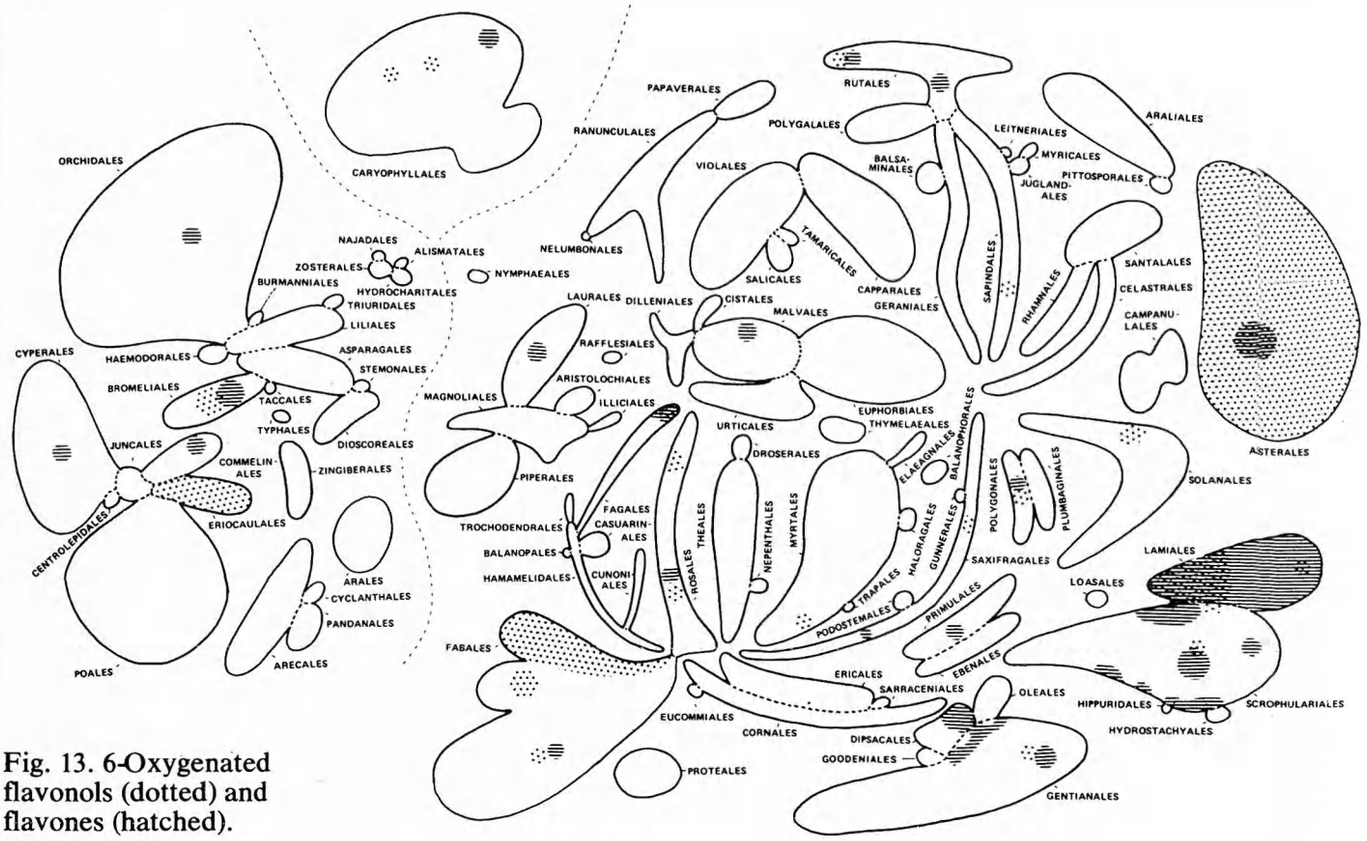

Fig. 13. 6-Oxygenated flavonols (dotted) and flavones (hatched).

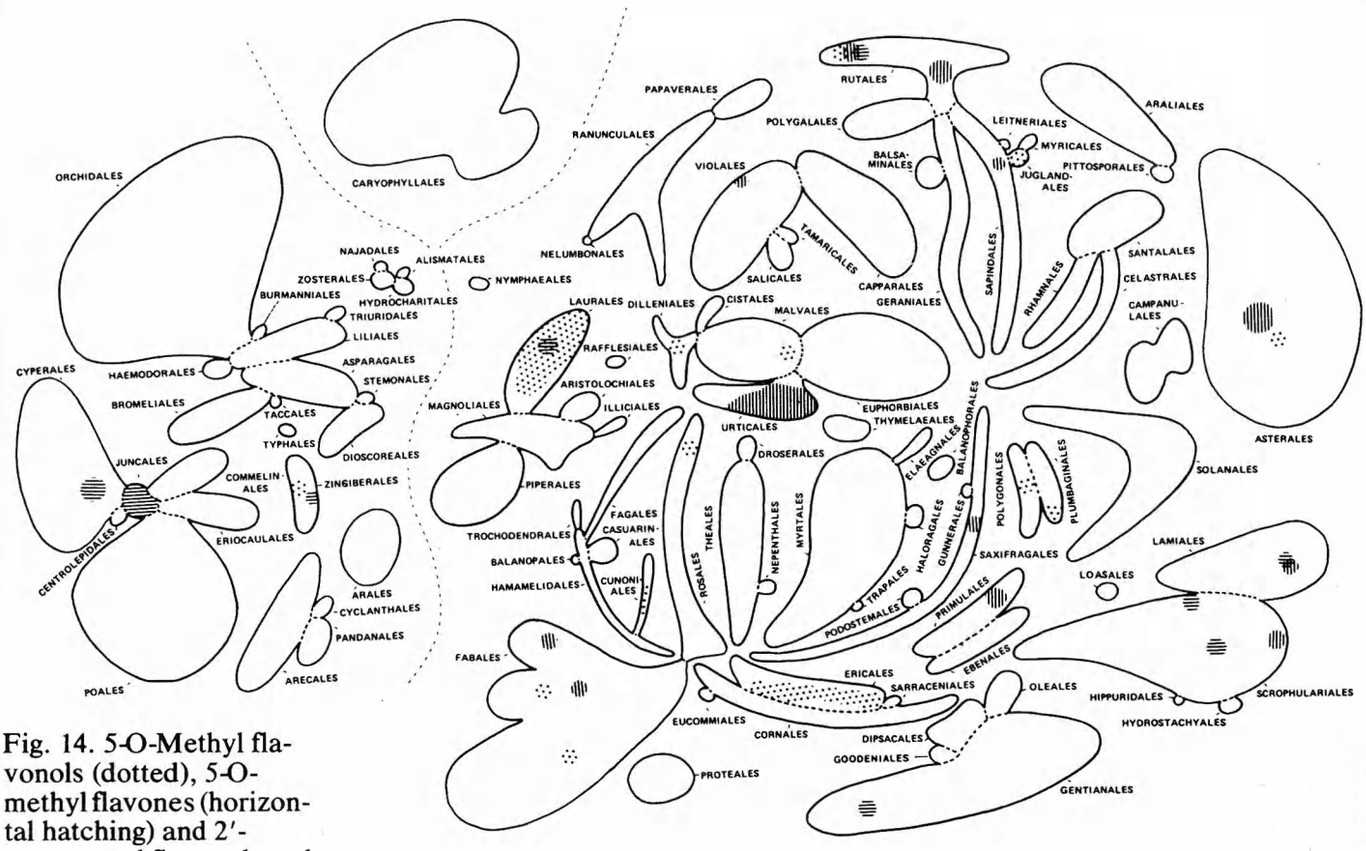

Fig. 14. 5-O-Methyl flavonols (dotted), 5-O-methyl flavones (horizontal hatching) and 2′-oxygenated flavonols and flavones (vertical hatching).

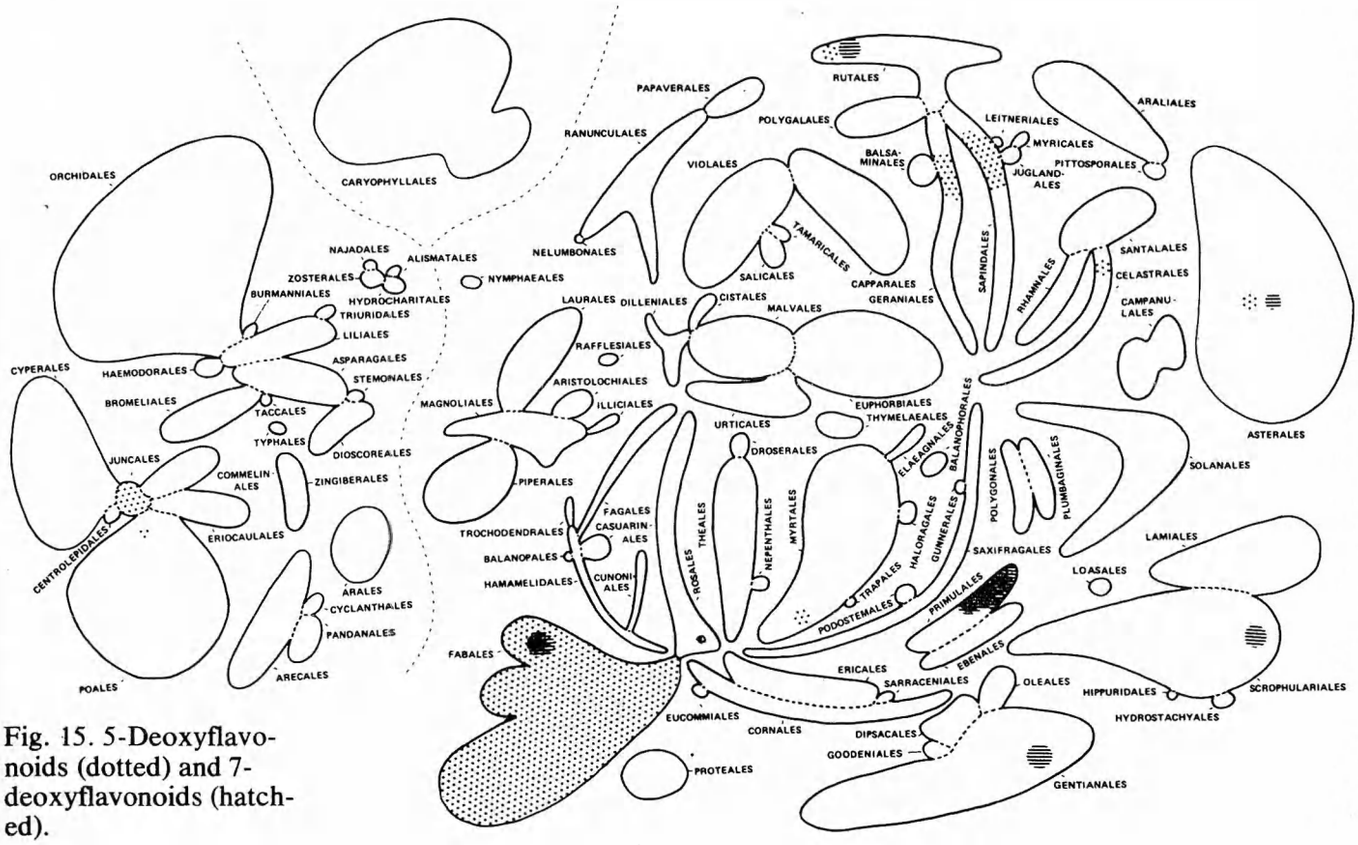

Fig. 15. 5-Deoxyflavonoids (dotted) and 7-deoxyflavonoids (hatched).

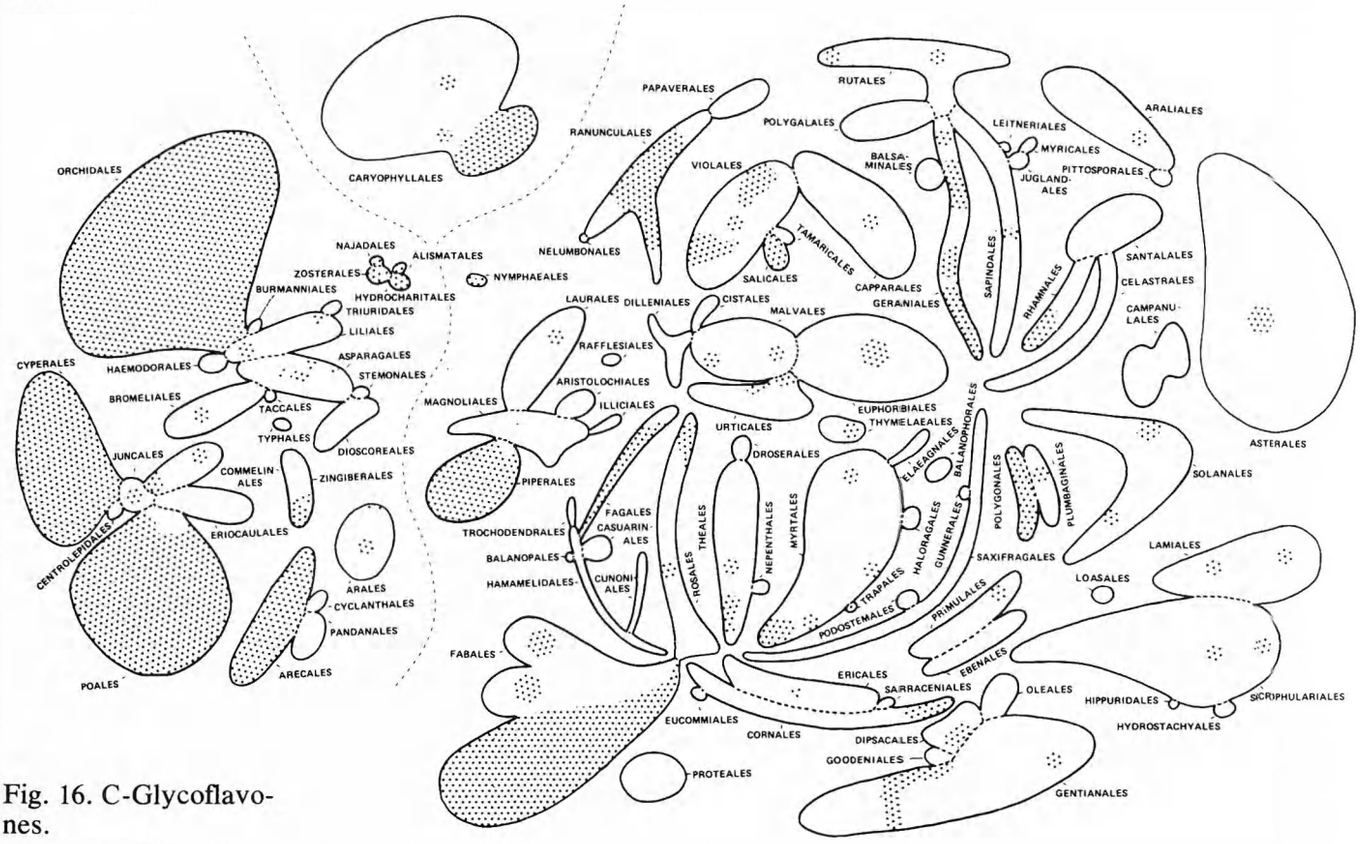

Fig. 16. C-Glycoflavones.

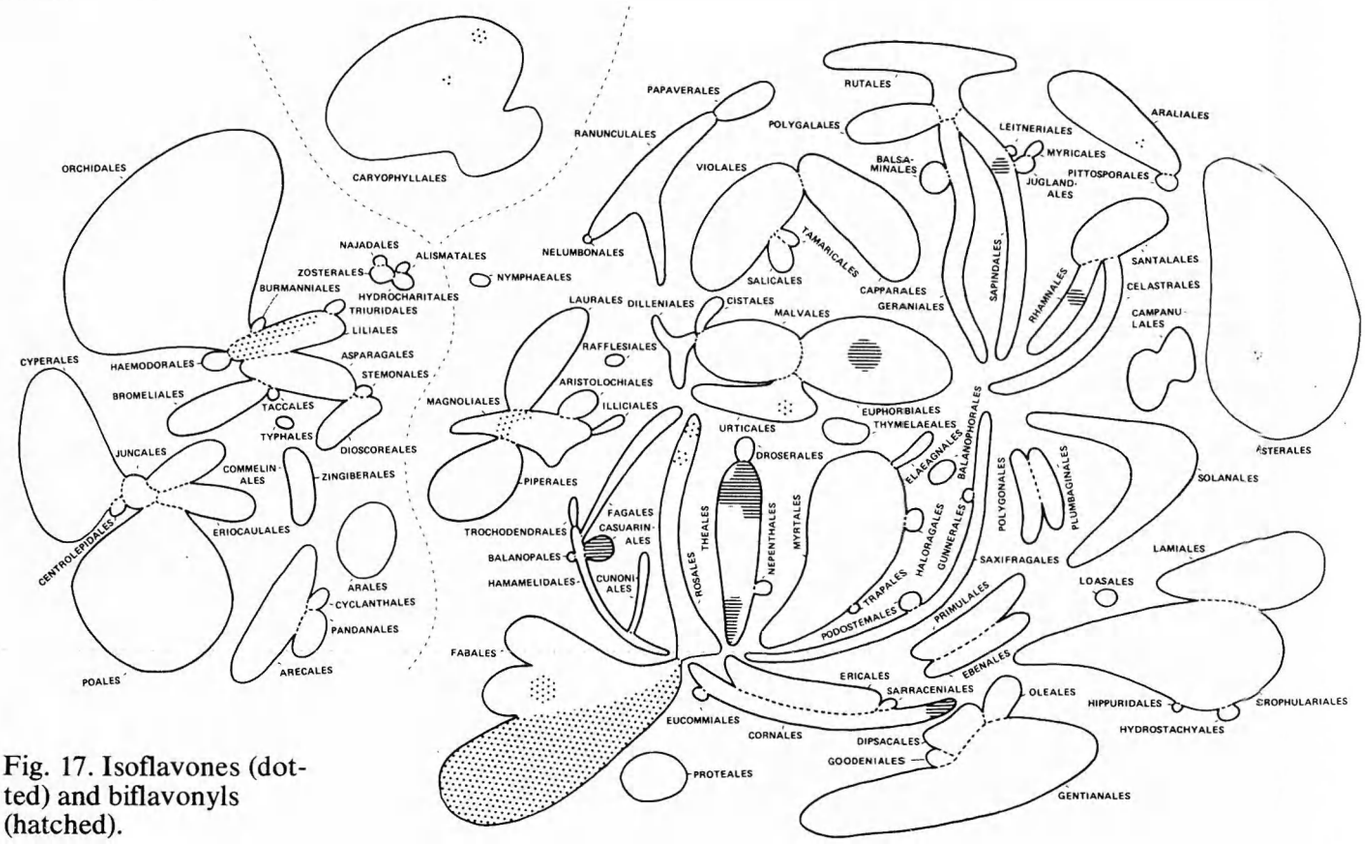

Fig. 17. Isoflavones (dotted) and biflavonyls (hatched).

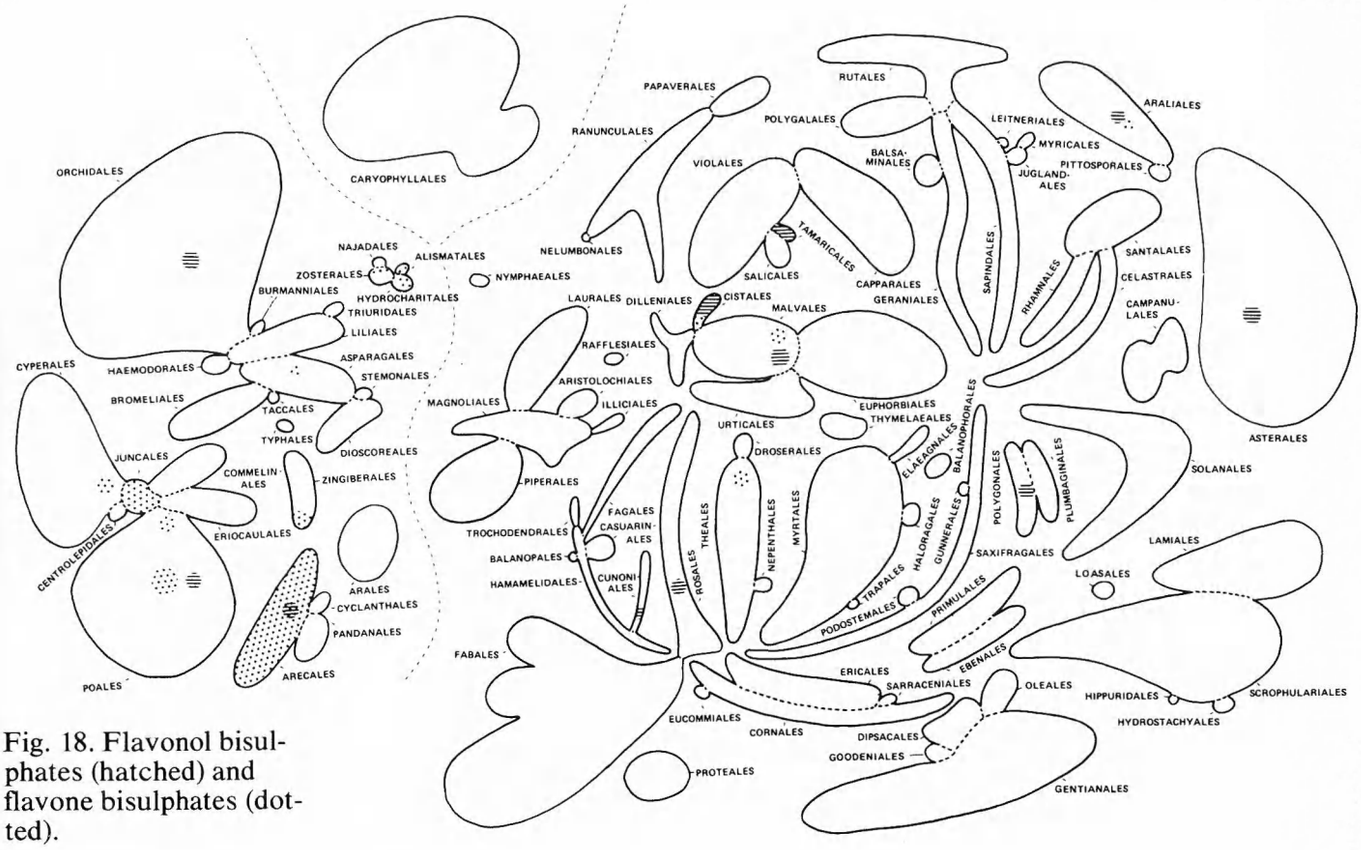

Fig. 18. Flavonol bisulphates (hatched) and flavone bisulphates (dotted).

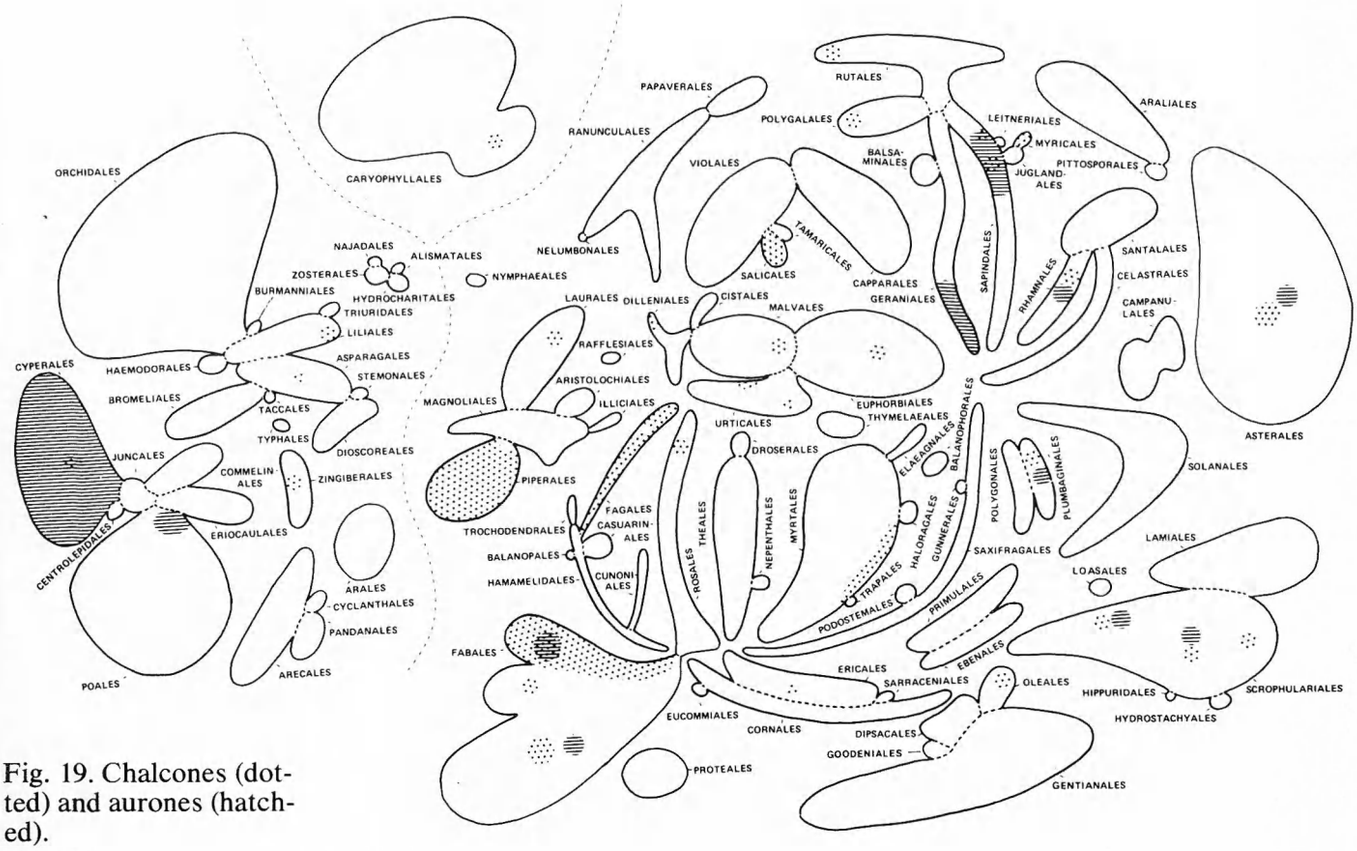

Fig. 19. Chalcones (dotted) and aurones (hatched).

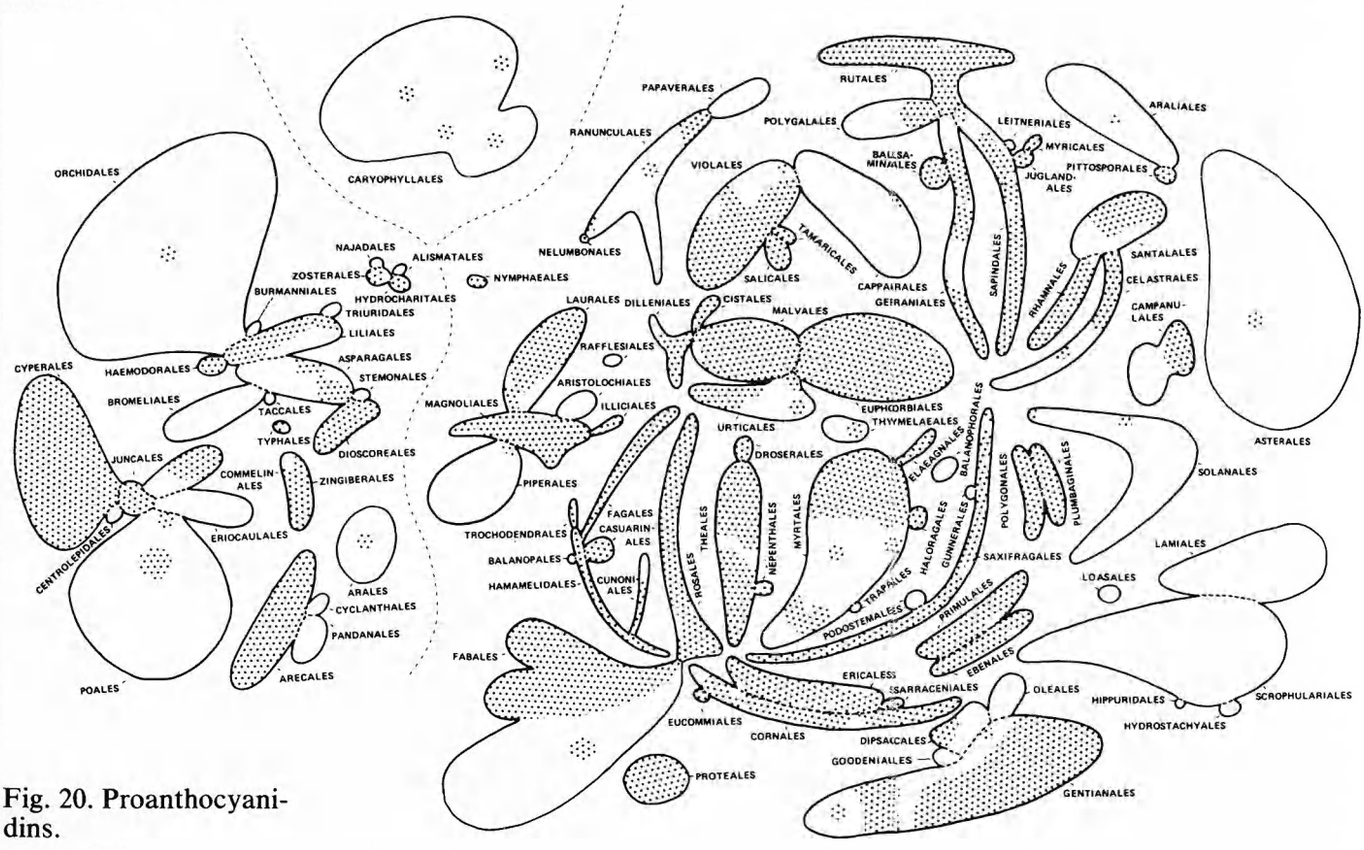

Fig. 20. Proanthocyanidins.

The genus Calceolaria in NW South America

III. The sections Symplocophylla and Dermatophylla

Ulf Molau

Molau, U. 1979 02 15: The genus Calceolaria in NW South America. III. The sections Symplocophylla and Dermatophylla. *Bot. Notiser 132:* 31–48. Stockholm. ISSN 0006-8195.

Two sections of *Calceolaria* (Scrophulariaceae) in NW South America are revised, viz. sect. *Symplocophylla* and *Dermatophylla,* both with coriaceous leaves. Sect. *Symplocophylla* is characterized by sessile, connate leaves and comprises two species, one of which occurs in the investigated area. Sect. *Dermatophylla,* with distinctly petiolate leaves, comprises seven species in NW South America. Three species are described as new, viz. *C. phaeotricha, C. oxyphylla* and *C. pedunculata,* and three new combinations are made, viz. *C. nivalis* subsp. *cerasifolia* (Bentham) Molau, *C. microbefaria* subsp. *fruticosa* (Pennell) Molau and *C. microbefaria* subsp. *tatamana* (Pennell) Molau. The chromosome number 2n = 36 is reported for *C. nivalis* subsp. *nivalis*.

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Sect. 6. **Symplocophylla** Pennell

Pennell 1951 a p. 2 – Type species: *Calceolaria connatifolia* Pennell.

Scandent shrubs. Leaves coriaceous, sessile and at least partially connate. Cymes 4-flowered; cyme bracts lacking. Sepals internally with a short-tomentose border along the margin. Corolla yellow, without spots. Anthers opening throughout; thecae equal.

The section *Symplocophylla* is restricted to southernmost Ecuador and northern Peru, and comprises two allopatric species separated by the Piura Divide. *Calceolaria connatifolia,* the southern counterpart to *C. semiconnata,* does not occur in the investigated area. It is recognized by completely connate leaves with the blades widest at the nodes. At present, this species is known from five collections from the departments of Cajamarca and Amazonas in northern Peru.

In leaf and sepal morphology sect. *Symplocophylla* shows certain affinities to sect. *Dermatophylla,* to which it is probably closely allied. Furthermore, the peculiar corolla of *C. semiconnata* resembles that of *C. nivalis,* a species of sect. *Dermatophylla.*

1. **Calceolaria semiconnata** Pennell

Pennell 1951 b p. 154 – Orig. coll.: Camp E-218 (PH holotype, NY).

Calceolaria lucida Pennell 1951 b p. 154 – Orig. coll.: Espinosa 338 (PH holotype).

Illustrations. Fig. 1; Pennell 1951 b pp. 152, 155 Figs. 22–23.

Scandent *shrub;* stems glabrous, up to 3 m; lateral branches ± patent. *Leaves* lanceate, 9.0–13 × 2.5–3.4 cm, slightly acuminate, rounded at base and connate by a 2–4 mm wide junction on either side of the node; above bright green and glabrous (except for some brownish tomentum on the proximal part of the midrib); beneath pale green, glabrous, reticulate-venose; margins entire or sparsely denticulate. *Inflorescence* terminal, comprising 2 pairs of 4-flowered cymes on strongly diverging peduncles 1.0–4.0 cm long. Pedicels 1.0–2.1 cm, glabrous or sparsely puberulous. *Sepals* ovate, 4.8–6.0 × 3.2–4.2 mm, acute to slightly acuminate, greenish, externally glabrous. *Corolla* bright yellow

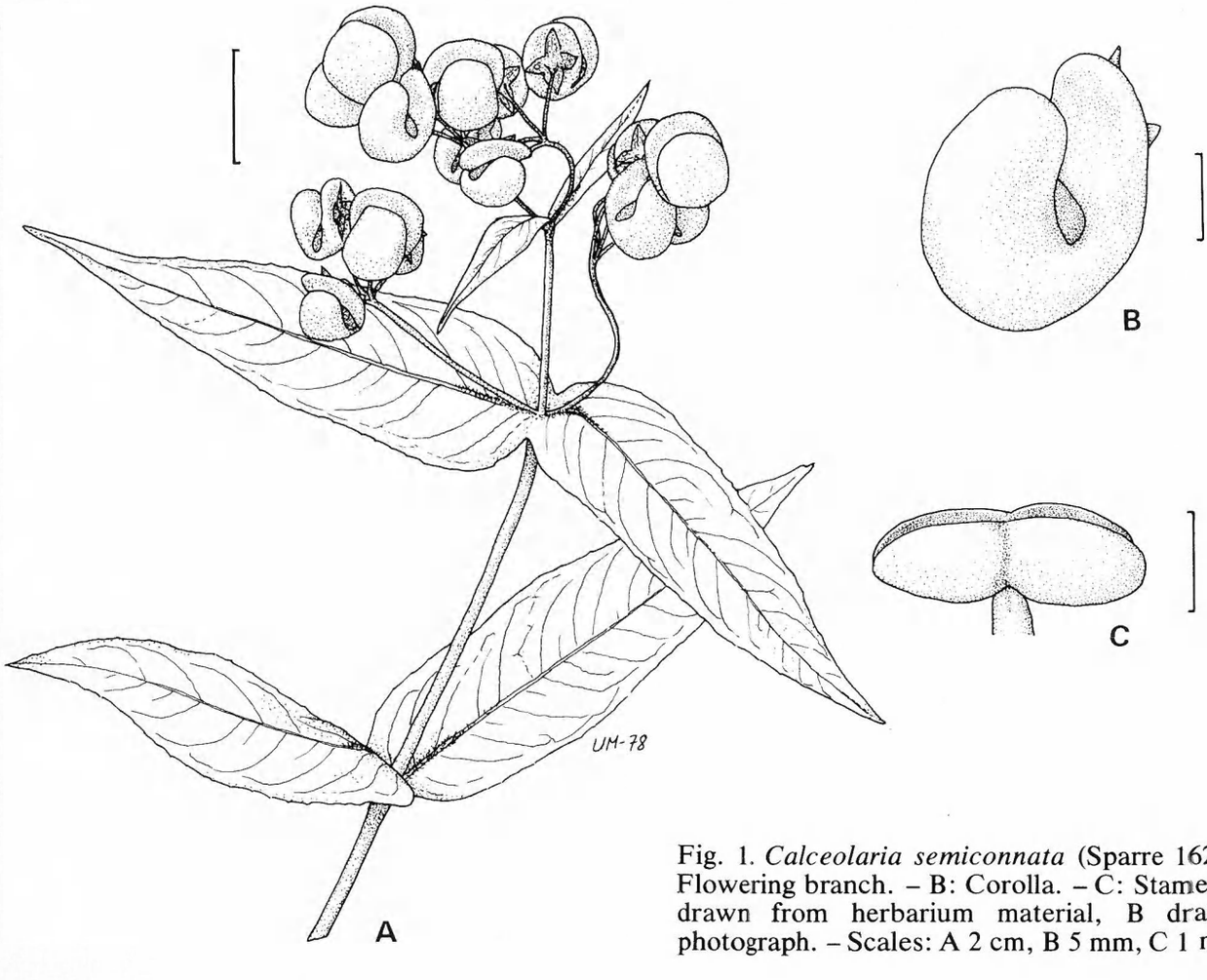

Fig. 1. *Calceolaria semiconnata* (Sparre 16238). – A: Flowering branch. – B: Corolla. – C: Stamen. – A, C drawn from herbarium material, B drawn from photograph. – Scales: A 2 cm, B 5 mm, C 1 mm.

(upper lip paler than lower), externally glandular; upper lip 6–10 × 9–12 mm, hooded, frontally flattened; lower lip 12–20 × 11–15 mm, saccate in about 1/2 of its length, inflated, upcurved, ± closing the orifice. *Anthers* 2.4–3.0 mm, buffish to yellow-brown; thecae divaricate. *Filaments* 0.7–0.9 mm. *Style* 1.5–2.6 mm. *Capsule* glutinous, not seen mature.

Habitat. Dry mountain scrub at altitudes between 2250 and 2900 m.

Distribution. Fig. 2. Restricted to a small area in the province of Loja, southern Ecuador. Not common.

Remarks. Relying upon three collections only, Pennell (1951 b) recognized two sympatric species of sect. *Symplocophylla* in southernmost Ecuador. According to his key *Calceolaria lucida* and *C. semiconnata* can be separated by means of patent versus ascending branches and flattened versus raised venation on the lower leaf surface. In the present material these differences are very slight and the characters do not seem to be correlated. I therefore regard the two forms as conspecific and have chosen to retain the epithet *semiconnata,* especially since the type material of this is in better condition.

Specimens studied. Ecuador. Loja: Cerro Villonaco W of Loja, 2450– 2900 m, 28.VI.1944, Camp E-218 (NY, PH) – Cajanuma, S of Loja, 2400 m, 7.V.1946, Espinosa 338 (PH) – Zamora-Huaico, 3 km S of Loja, 2250–2300 m, 17.VII.1946, Espinosa 631 (PH) – "Obuble", Loja, Poortman s.n. (P) – Cerro Villonaco, 20 km W of Loja on road to Catamayo, 2500 m, 16.V.1967, Sparre 16238 (S).

Sect. 7. **Dermatophylla** Pennell

Pennell 1951 b p. 113 – Type species: *Calceolaria salicifolia* R. & P.

Scandent or erect shrubs. Leaves coriaceous, distinctly petiolate. Sepals internally with a short-tomentose border along the margin (absent in *Calceolaria deflexa* and *C. stricta*). Corolla yellow, without spots. Anthers whitish to dark brown; thecae divaricate to deflexed, equal or subequal.

The section *Dermatophylla* is a well-defined group, ranging from Costa Rica to Bolivia. It comprises about fifteen species, seven of which occur in the investigated area. In Central America it is represented by a single species, *Calceolaria irazuensis* Donn. Sm., restricted to the highlands of Costa Rica and Panama.

Within this section smaller groups of closely allied species can be recognized. In NW South America such a group is formed by *C. nivalis* and *C. sotarensis*. These two species have a peculiar type of corolla: the upper lip is flattened and circular, while the lower lip is inflated and upcurved. This feature (with some modifications) is also found in species of other sections, viz. *C. hyssopifolia* (*Thamnobia*), *C. semiconnata* (*Symplocophylla*) and *C. fusca* (*Phaeanthera*).

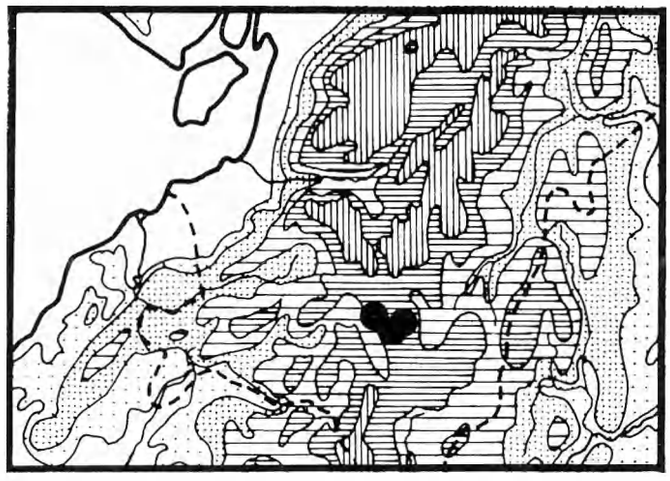

Fig. 2. Known distribution of *Calceolaria semiconnata*.

Another well-defined group of species occurs in the Andes of northern Peru, S of the Piura Divide. It comprises *C. salicifolia, C. tetragona, C. dentifolia* and *C. solanifolia,* large-flowered species with long, pale anthers opening to connective. None of these is found in the investigated area, which still more confirms the importance of the Piura Divide as a phytogeographical border-line.

The Peruvian species of sect. *Dermatophylla* are unsatisfactorily treated by Edwin (1971) in Macbride's *Flora of Peru*. Most of the shortcomings were obviously due to difficulties in obtaining type material of species described long ago. Thus, the number of species was overestimated. Since all the types of the species in question have now become available, most of the problems can be solved. The following Peruvian species do not occur in the investigated area and will not be treated in this paper (synonyms within brackets):

C. boliviana (Rusby) Pennell
C. deflexa R. & P.
C. dentifolia Edwin
C. salicifolia R. & P. (*C. involuta* R. & P.)
C. solanifolia Edwin
C. tetragona Bentham (*C. endopogon* Kränzlin, *C. myrtilloides* Kränzlin, *C. riccioi* López Guillén)
C. viscosa R. & P. (*C. arborescens* Edwin)

Key to the species of sect. Dermatophylla

1. Leaves 7.5–15 × 2.7–5.8 cm; sepals completely glabrous ..... 6. *C. stricta*
– Leaves usually smaller; sepals internally with a short-tomentose border along the margin ... 2
2. Upper lip of corolla flattened, circular; lower lip inflated, upcurved, closing the orifice 3
– Upper lip of corolla arched, ± globose; lower lip projecting or pendent 4
3. Thecae buffish or yellow-white, divaricate ..... 1. *C. nivalis*
– Thecae dark brown, deflexed ..... 2. *C. sotarensis*
4. Primary peduncles 8–15 cm, usually largely exceeding the subtending leaves . 5. *C. pedunculata*
– Peduncles less than 6 cm 5
5. Thecae globose, divaricate ..... 7. *C. microbefaria*
– Thecae elliptic, divaricate or deflexed 6
6. Leaves acute; peduncles and pedicels tomentose with ± brownish hairs ..... 3. *C. phaeotricha*
– Leaves acuminate; peduncles and pedicels glabrous ..... 4. *C. oxyphylla*

1. **Calceolaria nivalis** H. B. K.

Scandent *shrub* 0.5–3 m high; the whole plant glutinous. Stems glabrous, much branched. *Leaves* ovate to lanceate, glabrous, acute, at base truncate (rarely cuneate) and often somewhat dimidiate; margins serrate, ± deflexed, sometimes revolute. Petioles dorsally pubescent.

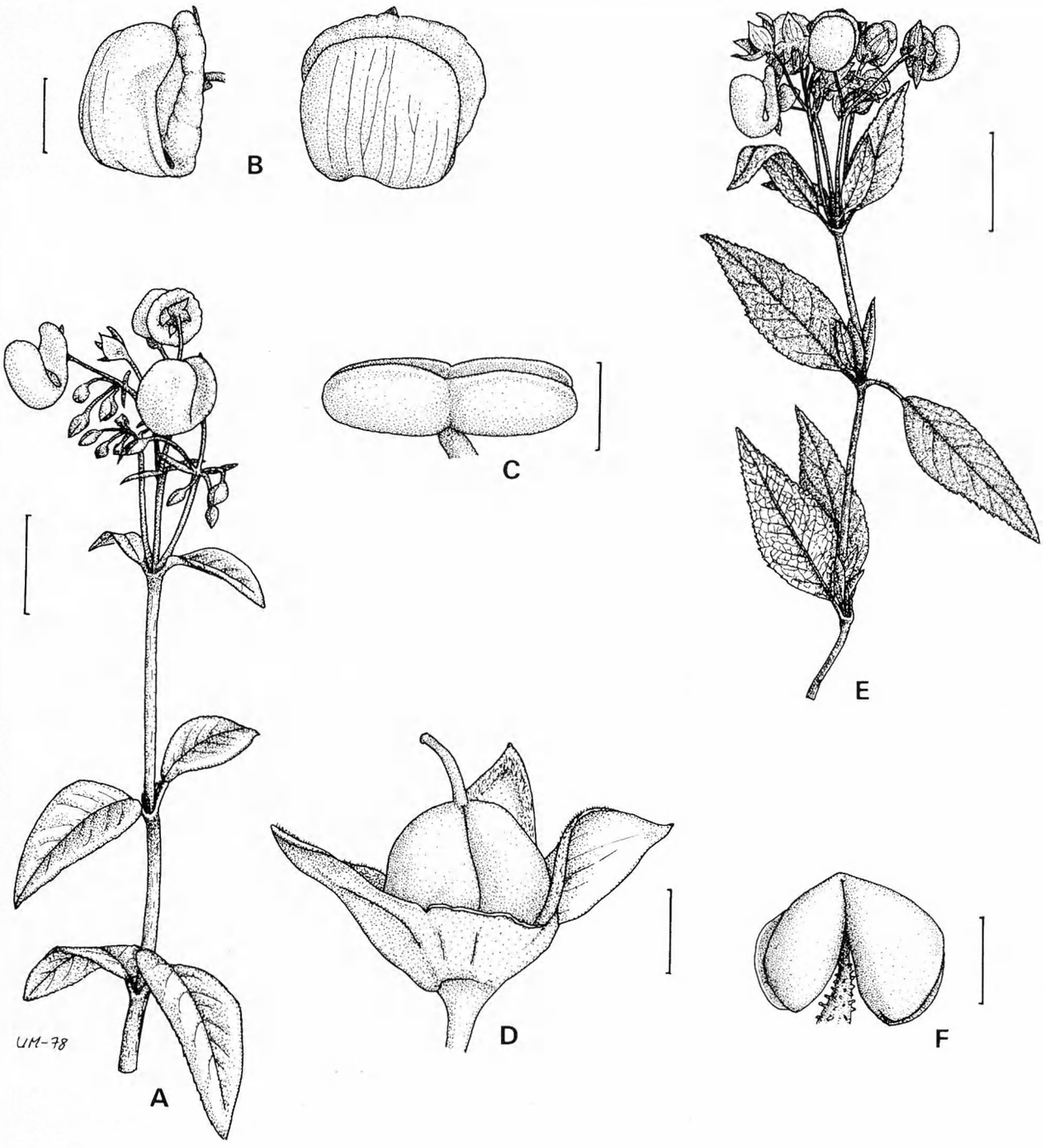

Fig. 3. A–D: *Calceolaria nivalis* subsp. *nivalis*. – A: Flowering branch. – B: Corolla. – C: Stamen. – D: Capsule. – A–C: Harling et al. (leg. Molau) 14970; D: Harling & Andersson 14536. – E–F: *C. sotarensis* (Lehmann 3690). – E: Flowering branch. – F: Stamen. – A drawn from photograph, B, C drawn from fixed material, D–F drawn from herbarium material. – Scales: A, E 2 cm, B 5 mm, C, F 1 mm, D 2 mm.

Inflorescence terminal. Peduncles and pedicels glabrous. Cyme bracts present. *Sepals* ovate, acute, mucronate, greenish, externally glabrous, internally with a short-tomentose border along the margin. *Corolla* bright yellow, externally glabrous; upper lip hooded, flattened and almost circular (saucer-like); lower lip inflated, upcurved, ± closing the orifice, saccate in 1/3–2/5 of its length. *Anthers* opening throughout; thecae equal, divaricate.

Remarks. *Calceolaria nivalis* ranges from central Ecuador to central Peru. In many places it is common in the mountain scrubs. It comprises two distinct subspecies, separated by the Piura Divide.

Key to the subspecies

1. Leaves pinnate-venose beneath; petioles dorsally tomentose with short greyish or buffish hairs ..... 1 A. subsp. *nivalis*
– Leaves pinnate- or reticulate-venose beneath; petioles and young axillary shoots densely villous or lanate with usually ferrugineous hairs ..... 1 B. subsp. *cerasifolia*

1 A. **Calceolaria nivalis** subsp. **nivalis**

Calceolaria nivalis Humboldt, Bonpland & Kunth 1818 p. 381 – *Fagelia nivalis* (H. B. K.) Kuntze 1891 p. 460 – Orig. coll.: Bonpland 3269 (B-WILLD lectotype, P).

Calceolaria padifolia Humboldt, Bonpland & Kunth 1818 p. 380 – *Fagelia padifolia* (H. B. K.) Kuntze 1891 p. 460 – Orig. coll.: Bonpland s.n. (P holotype).

Calceolaria fuchsiaefolia Hemsley 1879 p. 258 – Orig. coll.: Rodger et al. s.n. (K holotype).

Illustrations. Fig. 3 A–D; Hemsley 1879 Pl. 173; Hooker 1879 Tab. 6431; Hemsley 1881 p. 269 Fig. 49.

Leaves 4.0–7.5(–11) × 1.4–3.2(–5.8) cm; above dark green, nitidous; beneath greenish white, pinnate-venose. Petioles 6–18(–38) mm, dorsally tomentose with buffish or greyish white hairs. *Inflorescence* comprising 1–3 (usually 2) pairs of 4–12-flowered cymes on primary peduncles 1.5–5.7 cm long. Pedicels 0.6–3.0 cm. *Sepals* 4.4–6.2(–7.2) × (2.5–)3.0–4.7 mm at anthesis, later enlarged, reaching 9.0 × 6.0 mm; one of the sepals usually narrower than the other three. *Corolla* bright yellow; upper lip 6–11 × 10–15 mm, often paler than the lower when dried; lower lip 13–17 × 10–16 mm. *Anthers* buffish or yellow-white, 2.6–3.4 mm. *Filaments* c. 1 mm. *Style* curved, 2.0–3.0(–4.1) mm. *Capsule* glabrous, conical, 5–6 mm long.

Chromosome number. 2n = 36. – Voucher: Harling et al. (leg. Molau) 15075 (GB). – The same chromosome number has previously been reported by Srinath (1939 p. 106).

Habitat. Mountain scrub in relatively humid areas, at altitudes between 1700 and 3650 m.

Distribution. Fig. 4. A disjunct taxon, in Ecuador ranging from the provinces of Bolívar and Chimborazo to Azuay. A small distribution area is also present immediately N of the Piura Divide in the department of Piura, northern Peru. In all, 86 specimens from 49 collections have been studied.

Remarks. In its main distribution area *Calceolaria nivalis* subsp. *nivalis* grows at altitudes between 2500 and 3650 m, and has leaves 4.0–7.5(–9.2) cm long and petioles 6–18 mm. In the isolated southern distribution area in Piura it is known from altitudes between 1700 and 2850 m. Specimens from that area usually possess larger leaves (4.5–11 cm long) and longer petioles (5–38 mm), the largest measurements obtained in collections from the lowermost altitudes. Probably it was these slight differences in size that caused Humboldt, Bonpland and Kunth to recognize *C. padifolia* as a separate

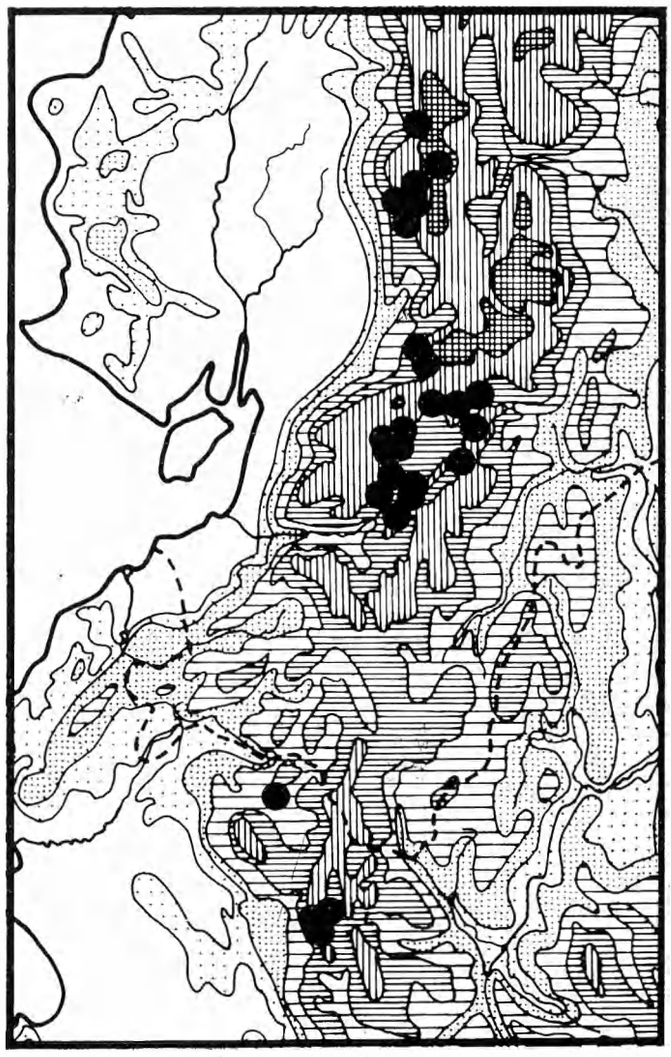

Fig. 4. Known distribution of *Calceolaria nivalis* subsp. *nivalis*.

species. However, the above variation is readily obtained in greenhouse by changing the environmental conditions. Leaf-blade size and petiole length seem to be influenced by temperature and moisture as well as exposure to wind and sunlight. The unusual distribution pattern present in this taxon is probably due to climatic conditions; the two distribution areas correspond in moisture. In the intervening, much drier parts of the Andes, subsp. *nivalis* is absent. In the province of Loja (southernmost Ecuador) it is replaced by some endemic species, viz. *C. oxyphylla, C. stricta* and *C. semiconnata*.

During the nineteenth century subsp. *nivalis* was introduced to Europe, where it was cultivated and described under the name of *C. fuchsiaefolia*.

Representative specimens. Ecuador. Bolívar: Balsapampa–San Miguel road, 2800 m, 16–17.V.1968, Harling et al. 9552 (GB) – Road between San Juan and Guaranda, 3600 m, 26.IV.1942, Haught 3277 (NY, PH). – *Chimborazo:* W Cordillera above Balsapampa, 2600 m, VIII,1934, Rimbach 217 (B, NY). – *Cañar:* Near El Tambo, 2900–3050 m, 5.VII.1945, Camp E-3978 (G, K, MO, NY, P, PH, S, UC) – Between Taday and Azogues, 3000–3300 m, 4.II.1977, Harling et al. (leg. Molau) 15021 (GB) – Tipococha, 3200 m, 10.VII.1939, Penland 998 (GH, PH). – *Azuag:* Valley of Río Surucuchu, 18–20 km W Cuenca, 3000–3150 m, 16.VII.1945, Camp E-4204 (BM, NY, PH, U, VEN) – Portete de Tarqui, 2700–2950 m, 5.IV.1974, Harling & Andersson 13207 (GB); 2600–2700 m, 3.II.1977, Harling et al. (leg. Molau) 14970 (GB) – Páramo de Tinajillas, km 67 S of Cuenca on Pan American Highway, 3250 m, 4.V.1973, Holm-Nielsen et al. 4938 (AAU, GB, MO). – *Morona-Santiago:* Road Gualaceo–Limón (General Plaza), W slope, 2600 m, 2.IV.1974, Harling & Andersson 13081 (GB). – *Peru. Piura:* Ayabaca, Bonpland s.n. (P) – Between Tambo and Canchaque, 2000–2600 m, 18.IX.1964, Hutchison & Wright 6657 (F, MO, NY, UC) – Above Canchaque, 1700–1900 m, 21–23.III.1948, Pennell & Ferreyra 14914 (GH, PH) – Huancabamba, 2600 m, VIII.1943, Sandeman 4263 (K, OXF).

1 B. **Calceolaria nivalis** subsp. **cerasifolia** (Bentham) Molau comb. nov.

Basionym: *Calceolaria cerasifolia* Bentham 1846 p. 218 – *Fagelia cerasifolia* (Bentham) Kuntze 1891 p. 459 – Orig. coll.: Mathews 1684 (K holotype, CGE, OXF).

Leaves 4.0–12 × 1.3–5.0 cm; above bright or dark green, nitidous; beneath pale green or greenish white, pinnate- or reticulate-venose. Petioles 5–20 mm, villous or lanate with usually ferrugineous hairs. *Inflorescence* comprising 2–3 pairs of 8–16-flowered cymes on primary peduncles 1–9 cm long. *Sepals* and *corolla* as in subsp. *nivalis*. *Anthers* 2.3–3.0 mm long, brownish yellow to yellow-white. *Filaments* c. 1 mm long.

Habitat. Thickets, rocks and pastures, at altitudes between 2450 and 4200 m.

Distribution. Andes of northern and central Peru; ranges from the central parts of the departments of Cajamarca and Amazonas to the department of Lima, very common in the north. In all, 161 specimens from 74 collections have been studied.

Remarks. *Calceolaria nivalis* subsp. *cerasifolia* is the southern counterpart to subsp. *nivalis* and has not been found N of the Piura Divide. Along its continuous distribution area in the Andes of northern Peru it shows a clinal variation. Specimens from Cajamarca and Amazonas have ± ovate leaves, often with pinnate venation beneath; towards the south (departments of La Libertad, Ancash and Lima) the leaves are always lanceate and reticulate-venose, and the petiole pubescence is paler.

Representative specimens. Peru. Cajamarca: On the road to Balsas, 13 km above Celendín, 3000 m, 20.V.1964, Hutchison & Wright 5207 (F, K, MO, NY, UC, US) – Between Paso Credo and Huambos, prov. Chota, 2450 m, 22.V.1965, López & Sagástegui 5286 (MO) – Paso de Gavilán, S of Cajamarca, 10.IV.1948, 3200 m, Pennell & Anderson 15089 (PH); 2850 m, Pennell & Anderson 15099 (PH) – Llama, Cutervo, 2290 m, VII.1943, Sandeman 4100 (K, OXF). – *Amazonas:* E slope of Cerro Calla-Calla, 2.VI.1966, Edwin & Schunke 3634 (F, G, NY); 3636 (F, NY); 3638 (F, NY); 3642 (G); 3643 (F, NY); 2535 m, 27.V.1964, Hutchison & Bennett 4632 (F, MO, NY, UC) – Cerro Puma-Urco, SE of Chachapoyas, 2400–2900 m, 18–19.VI.1948, Pennell 15503 (BM, G, K, LE, M, NY, PH, S); 20.V.1962, Wurdack 429 (F, K, NY, S, UC). – *La Libertad:* Río Chusgón valley, 21 km above and E of Pullac on the road to Buldibuyo, 3000 m, 7.VIII.1964, Hutchison et al. 6156 (K, M, P, S) – Rio Marañón canyon, 4 km SE of summit above Aricapampa on road to Huamachuco, 3900 m, 10.VIII.1964, Hutchison et al. 6277 (K, M, MO, P, UC). – *Ancash:* Slopes below Laguna de Llanganuco in Quebrada de Llanganuco, c. 25 km above Yungay, 2800–3900 m, 27.VI.1966, Edwin & Schunke 3816 (F, G, NY, W); 3837 (F); 3839 (F, GH, NY). – *Lima:* Central Highway between San Mateo and Matucana, 9 km E of Matucana, 22.VI.1966, Edwin & Schunke 3802 (BM, F, W).

2. **Calceolaria sotarensis** Pennell

Pennell 1951 b p. 116 – Orig. coll.: Lehmann 6135 (K holotype).

Illustration. Fig. 3E–F.

Slender *shrub* at least 0.5 m high; stems glabrous. *Leaves* lanceate to ovate, 3.0–5.3 × 1.2–2.0 cm, acute or slightly acuminate, at base cuneate or rounded; above dark green, minutely rugose, glutinous, tomentose on the proximal part of the midrib; beneath pale green, reticulate-venose, glabrous; margins serrate. Petioles 4–7 mm long, dorsally brownish tomentose. *Inflorescence* terminal, comprising 2 pairs of 6–10-flowered cymes on glabrous primary peduncles 2.0–3.8 cm long. Cyme bracts small or lacking. Pedicels glabrous, 0.7–1.8 cm. *Sepals* ovate, 6.0–8.0 × 3.8–6.0 mm, acuminate, green, externally glabrous, internally with a short-tomentose border along the margin. *Corolla* yellow, externally glabrous except for some short pubescence on the lower lip around the orifice; upper lip 7–10 × 10–12 mm, hooded, flattened and almost circular in outline; lower lip 12–15 × 10–15 mm, saccate in about 1/2 of its length, inflated, upcurved. *Anthers* dark brown, 2.0–2.3 mm long, opening throughout; thecae deflexed, equal or subequal, c. 2 mm long. *Filaments* 1.3–1.5 mm. *Style* 3.8–4.0 mm, curved. Mature capsule not seen.

Habitat. Mountain scrub, at altitudes between 2700 and 3200 m.

Distribution. Fig. 5. Restricted to a small area in the Colombian Andes in the department of Cauca, comprising Volcán Sotará and adjacent mountains in Cordillera Central.

Remarks. *Calceolaria sotarensis* is probably most closely related to *C. nivalis*, but the aberrant anther morphology along with vegetative characters support its treatment as a separate species. Furthermore, the first inflorescence internode is often very much shortened and the four primary peduncles consequently originate from approximately the same place, a condition never found in *C. nivalis*.

Specimens studied. *Colombia*. *Cauca:* Quebrada Flantos, between Chapa and Río Blanco (S of Sotará), 2720 m, 13.VII.1944, Core 898 (NY) – "Alto de los Motilones", Sotará, 3000 m, 21.II.1884, Lehmann 3690 (BM, G, K, LE, PH) – Volcán Sotará, 3000–3200 m, Lehmann 6135 (K).

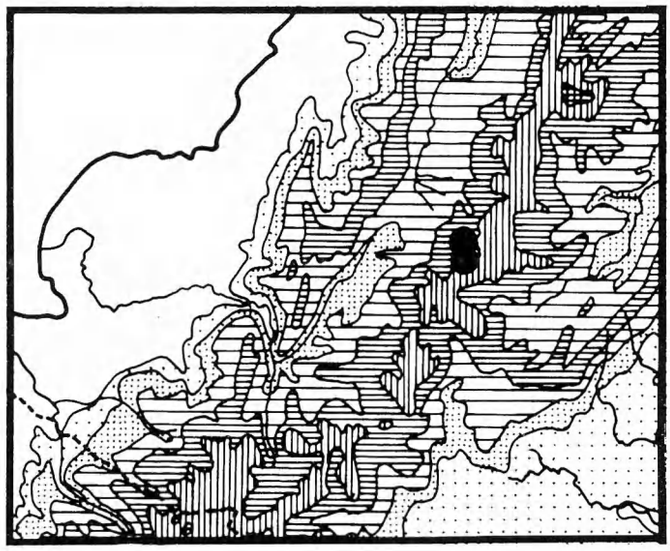

Fig. 5. Known distribution of *Calceolaria sotarensis*.

3. **Calceolaria phaeotricha** Molau sp. nov.

Orig. coll.: Harling & Andersson 13124 (GB holotype).

Illustration. Fig. 6 A–C.

Frutex erectus vel scandens, 0.5–3 m altus. Pedicelli et pedunculi partesque distales caulis pubescentes, pilis fuscis septatis. Folia ovata–lanceata, 3.5–5.7 × 1.2–1.8 cm, acuta, ad basin cuneata; supra viridia, glutinosa, glabra, distincte rugosa; infra albovirentia, glabra, pinnato- vel leviter reticulato-venosa; margine serrato dentibus mucronulatis. Petioli 3–8 mm, dorsali parte tomentosa. Inflorescentia terminalis, 1–2 paria cymarum 4–6 florum complectens; pedunculis primariis 1.3–4.0 cm longis. Bracteae cymarum adsunt. Pedicelli 1.2–3.0 cm. Sepala ovata, 4.0–6.2 × 2.5–3.5 mm, acuta–admodum obtusa, subviridia, extra glabra, intus vitta marginali breviter tomentosa obsita. Corolla flava, extra glabra; labio superiore 5–10 × 6–11 mm, arcuato; labio inferiore 11–18 × 6–14 mm, ad 2/5 fere longitudinis saccato, ± pendenti. Antherae fuscae, 2.0–3.8 mm longae, totae dehiscentes; thecae deflexae, aequales vel subaequales, 1.5–2.0 mm longae. Filamenta c. 1.5 mm. Stylus 3.8–5.0 mm, rectus vel leviter curvatus. Capsula ovoides, 4–5 mm longa, glabra, glutinosa.

Erect or scandent *shrub*, 0.5–3 m high. Pedicels, peduncles and distal parts of stems tomentose or shortly villous with brown or buffish, septate hairs (colour intensity depending on the staining of the septa). *Leaves* ovate to lanceate, 3.5–5.7 × 1.2–1.8 cm, acute, at base cuneate; above dark green, glutinous, glabrous, distinctly rugose; beneath whitish green, glabrous, pinnate- or faintly reticulate-venose; margins serrate with mucronulate teeth. Petioles 3–8 mm, dorsally tomentose. *Inflorescence* terminal, comprising 1–2 pairs of 4–6-flowered cymes on

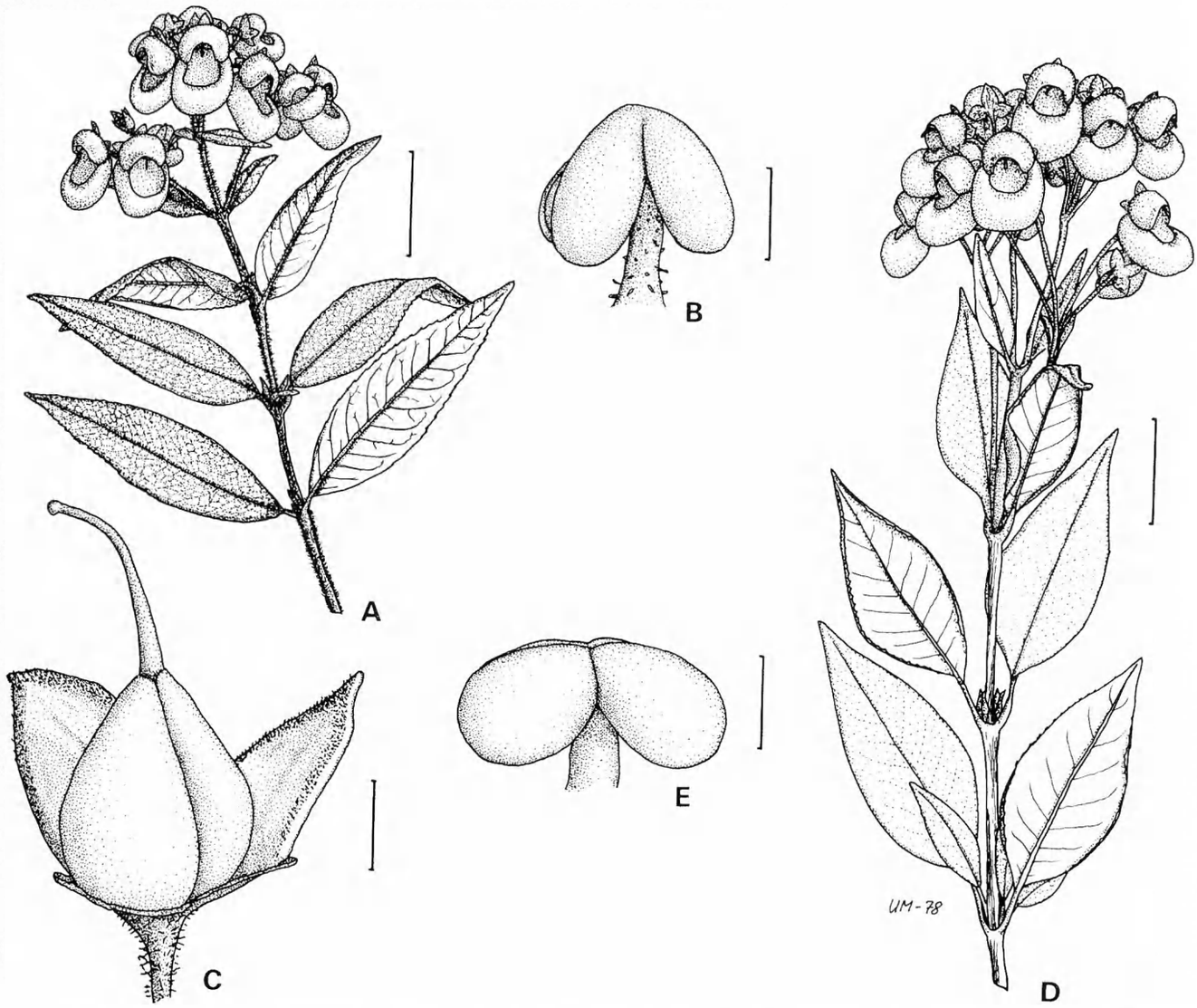

Fig. 6. A–C: *Calceolaria phaeotricha*. – A: Flowering branch. – B: Stamen. – C: Capsule. – A, B: Harling & Andersson 13124; C: Camp E-4858. – D–E: *C. oxyphylla* (Harling & Andersson 13513). – D: Flowering branch. – E: Stamen. – All drawings made from herbarium material. – Scales: A, D 2 cm, B, E 1 mm, C 2 mm.

primary peduncles 1.3–4.0 cm long. Cyme bracts present. Pedicels 1.2–3.0 cm. *Sepals* ovate, 4.0–6.2 × 2.5–3.5 mm, acute to somewhat obtuse, pale green (turning red in full exposure), externally glabrous, internally with a short-tomentose border along the margin. *Corolla* bright yellow, externally glabrous; upper lip 5–10 × 6–11 mm, arched; lower lip 11–18 × 6–14 mm, saccate in about 2/5 of its length, ± pendent. *Anthers* dark brown, 2.0–3.8 mm long, opening throughout; thecae deflexed, equal or subequal, 1.5–2.0 mm long. *Filaments* c. 1.5 mm. *Style* 3.8–5.0 mm, straight or slightly curved. *Capsule* ovoid, 4–5 mm long, glabrous, glutinous.

Habitat. Páramo and mountain scrub, at altitudes between 2800 and 3700 m.

Distribution. Fig. 7. Restricted to a small part of Cordillera Oriental in the provinces of Azuay and Morona-Santiago, southern Ecuador.

Remarks. *Calceolaria phaeotricha* is distinguished from all other species of sect. *Dermatophylla* by the rugose leaves and brown-tomentose inflorescence.

Specimens studied. Ecuador. Azuay: Between Galápagos and El Pan, Cordillera Oriental, 21.VII.1943, Acosta-Solís 5118 (F) – Páramo del Castillo, Sevilla de Oro, 3350 m, 21.VIII.1945, Camp E-4858 (M, NY, PH, S); 3700 m, 29.VI.1947, Harling 1263 (S) – Páramo and sub-páramo area N and NW of the Páramo del Castillo (c. 6–8 km N–NE of Sevilla de Oro), 3050–3400 m, 31.VIII.1945, Camp E-5136 (NY, PH). – *Morona-Santiago:* Road Gualaceo–Limón (General Plaza), 2800–3000 m, 2.IV.1974, Harling & Andersson 13124; km 29, 3000–3100 m, 20.IX.1967, Sparre 18766 (S).

4. **Calceolaria oxyphylla** Molau sp. nov.

Orig. coll.: Harling & Andersson 13513 (GB holotype).

Illustration. Fig. 6 D–E.

Frutex scandens, 0.7–1 m altus; caules glabri, ramosi. Folia ovata–lanceata, 3.2–8.0 × 1.5–2.7 cm, glabra, acuminata, ad basin cuneata et ± dimidiata; supra viridia, glutinosa; infra albovirentia, pinnato-venosa; margine serrulato. Petioli 7–18 mm, glabri. Inflorescentia terminalis, 2–3 paria cymarum 4–10 florum complectens; pedunculis primariis glabris 2.0–3.2 cm longis. Bracteae cymarum plerumque adsunt. Pedicelli 0.9–2.8 cm, glabri, valde glutinosi. Sepala ovata, 4.2–5.7 × 3.0–4.8 mm, subviridia, acuta–obtusa, extra glabra, intus vitta marginali breviter tomentosa obsita. Corolla flava, extra glabra excepta brevi pubescentia circa orificium praesertim in labio inferiore; labio superiore 6–10 × 8–11 mm, arcuato; labio inferiore 10–18 × 7–13 mm, ad tertiam fere partem longitudinis saccato, proiecto vel pendenti. Antherae fuscae, 2.5–3.2 mm longae, totae dehiscentes; thecae divaricatae vel leviter deflexae, aequales, c. 2 mm longae. Filamenta c. 2 mm. Stylus 3.0–4.3 mm, paene rectus. Capsula ovoides, 4–5 mm longa, glabra.

Scandent *shrub*, 0.7–1 m high; stems glabrous, much branched. *Leaves* ovate to lanceate, 3.2–8.0 × 1.5–2.7 cm, glabrous, acuminate, at base cuneate and ± dimidiate; above dark green, glutinous; beneath whitish green, pinnate-venose; margins serrulate. Petioles 7–18 mm, glabrous. *Inflorescence* terminal, comprising 2–3 pairs of 4–10-flowered cymes on glabrous primary peduncles 2.0–3.2 cm long. Cyme bracts usually present. Pedicels 0.9–2.8 cm, glabrous, strongly glutinous. *Sepals* ovate, 4.2–5.7 × 3.0–4.8 mm, light green, acute to obtuse; externally glabrous, internally with a short-tomentose border along the margin. *Corolla* bright yellow (upper lip somewhat paler than the lower when dried), externally glabrous except for some short pubescence on the lower lip around the orifice; upper lip 6–10 × 8–11 mm, arched; lower lip 10–18 × 7–13 mm, saccate in about 1/3 of its length, projecting or pendent. *Anthers* dark brown, 2.5–3.2 mm long, opening throughout; thecae divaricate or slightly deflexed, equal, c. 2 mm long. *Filaments* c. 2 mm. *Style* 3.0–4.3 mm, almost straight. *Capsule* ovoid, 4–5 mm long, glabrous.

Habitat. Shrubby mountain forest and protected places in grass páramo, at altitudes between 2400 and 3450 m.

Distribution. Fig. 7. Restricted to the lower Andes of southern Ecuador in the provinces of Loja and El Oro.

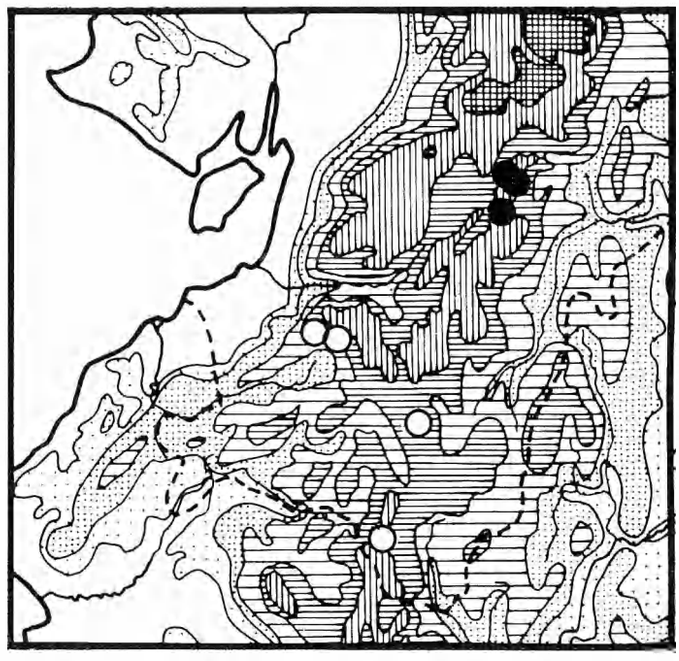

Fig. 7. Known distribution of *Calceolaria phaeotricha* (●) and *C. oxyphylla* (○).

Remarks. In floral characters *Calceolaria oxyphylla* resembles *C. phaeotricha*. However, *C. oxyphylla* is distinct in several important vegetative characters, viz. acuminate, non-rugose leaves and glabrous inflorescence.

Specimens studied. *Ecuador. El Oro:* Between Corredores and Cashatambo (N of Zaruma), c. 2500 m, 10.IX.1947, Espinosa 2231 (NY, PH). – *Loja:* Chepel (NE of Zaruma, between Payama and Tioloma), 2950 m, 30.VIII.1947, Espinosa 2022 (F) – Cordillera Oriental, E of Loja, c. 2400 m, 27.XII. 1947, Espinosa 2278 (PH) – Loja–Zamora road, on the border to prov. Zamora-Chinchipe, 2600–2800 m, 13.IV.1974, Harling & Andersson 13513 (GB) – Muletrack Amaluza–Palanda, W slope, near the pass, 3350–3450 m, 22.IX.1976, Øllgaard & Balslev 9694 (AAU).

5. **Calceolaria pedunculata** Molau sp. nov.

Orig. coll.: Harling et al. 14890 (GB holotype).

Illustration. Fig. 8.

Frutex laxus, scandens, ramis floriferis extra protrudentibus. Caules 0.5–2 m longi, sparse ramosi. Folia lanceata, 4.0–11 × 1.6–3.4 cm, glabra, acuminata, ad basin cuneata; supra viridia, glutinosa; infra subviridia (siccata in colorem vivide flavovirentem conversa), pinnato-venosa; margine acute dentato dentibus mucronulatis. Petioli 5–13 mm longi, dorsali parte breviter hirsuti. Inflorescentia terminalis, 1(–2) paria cymarum 8–10 florum complectens; pedunculis primariis 8–15 cm longis, glutinosis, plerumque admodum flexuosis et longitudinem foliorum subtentorum aliquantum excedentibus. Bracteae cymarum adsunt. Pedicelli 0.5–2.6 cm, glutinosi, glabri vel puberuli pilis glanduliferis.

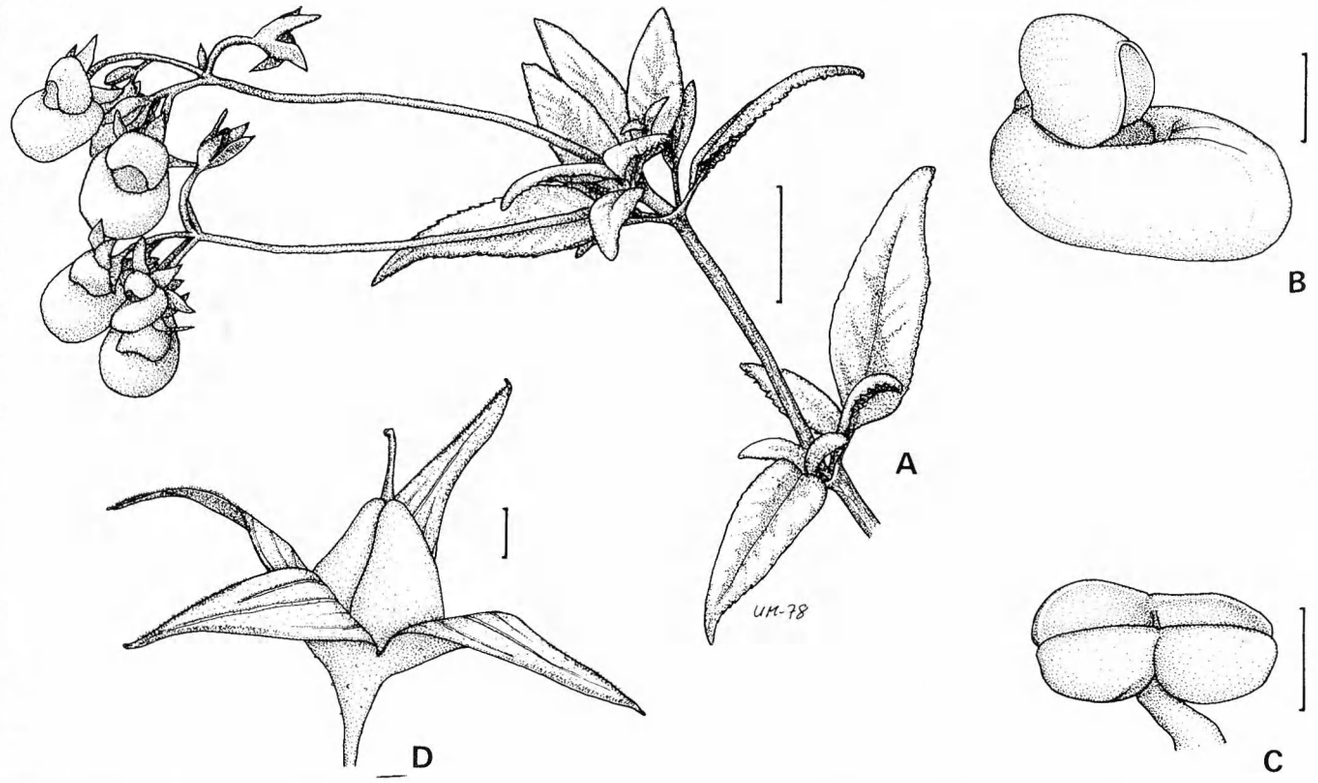

Fig. 8. *Calceolaria pedunculata*. – A: Flowering branch. – B: Corolla. – C: Stamen. – D: Capsule. – A–C: Harling et al. (leg. Molau) 14890; D: Holm-Nielsen et al. 5597. – A drawn from photograph, B, C drawn from fixed material, D drawn from herbarium material. – Scales: A 2 cm, B 5 mm, C 1 mm, D 2 mm.

Sepala lanceata, attenuata, (4.5–)6.0–9.0 × 2.5–3.5 mm in anthesi, subviridia; extra glabra, glandulosa; intus distali parte vitta marginali breviter tomentosa obsita. Corolla flava, extra glabra; labio superiore 5–8 × 9–10 mm, arcuato; labio inferiore 15–25 × 10–15 mm, ad 1/2–2/3 longitudinis saccato, proiecto. Antherae subfuscae, 2.2–3.0 mm longae, totae dehiscentes; thecae divaricatae, aequales. Filamenta c. 1 mm. Stylus 2.4–3.2 mm, paene rectus. Capsula late ovoides, 4–5 mm longa, glabra, glutinosa.

Lax, scandent *shrub,* flowering branches often hanging out of supporting growth. Stems 0.5–2 m long, sparsely branched. *Leaves* lanceate, 4.0–11 × 1.6–3.4 cm, glabrous, acuminate, at base cuneate; above dark green, glutinous; beneath light green (turning bright yellow-green when dried), pinnate-venose; margins sharply serrate with mucronulate teeth. Petioles 5–13 mm, dorsally short-hirsute. *Inflorescence* terminal, comprising 1(–2) pairs of 8–10-flowered cymes. Primary peduncles 8–15 cm long, glutinous, usually somewhat flexuose and largely exceeding the length of the subtending leaves. Cyme bracts present. Pedicels 0.5–2.6 cm, glutinous, glabrous or puberulous with gland-tipped hairs. *Sepals* lanceate, attenuate, (4.5–)6.0–9.0 × 2.5–3.5 mm at anthesis, light green (turning red in exposure); externally glabrous, glandular; internally with a tomentose border along the margins at the distal end. *Corolla* bright yellow, externally glabrous; upper lip 5–8 × 9–10 mm, arched; lower lip 15–25 × 10–15 mm, saccate in 1/2–2/3 of its length, projecting. *Anthers* brownish, 2.2–3.0 mm long, opening throughout; thecae divaricate, equal. *Filaments* c. 1 mm. *Style* 2.4–3.2 mm, straight to slightly curved. *Capsule* widely ovoid, 4–5 mm long, glabrous, glutinous.

Habitat. Mountain rain forest and shrub vegetation, often in steep slopes, at altitudes between 1800 and 3500 m.

Distribution. Fig. 10. Andes of northern Ecuador; restricted to Cordillera Occidental in the provinces of Carchi, Imbabura and Pichincha. In all, 41 specimens from 25 collections have been studied.

Remarks. In Pennell's (1951 b) revision, this species is treated under the name of *C. fallax* Kränzlin. As pointed out in a previous paper (Molau 1978 p. 298), *C. fallax* is synonymous with *C. crenata* subsp. *crenata* (sect. *Thamnobia*).

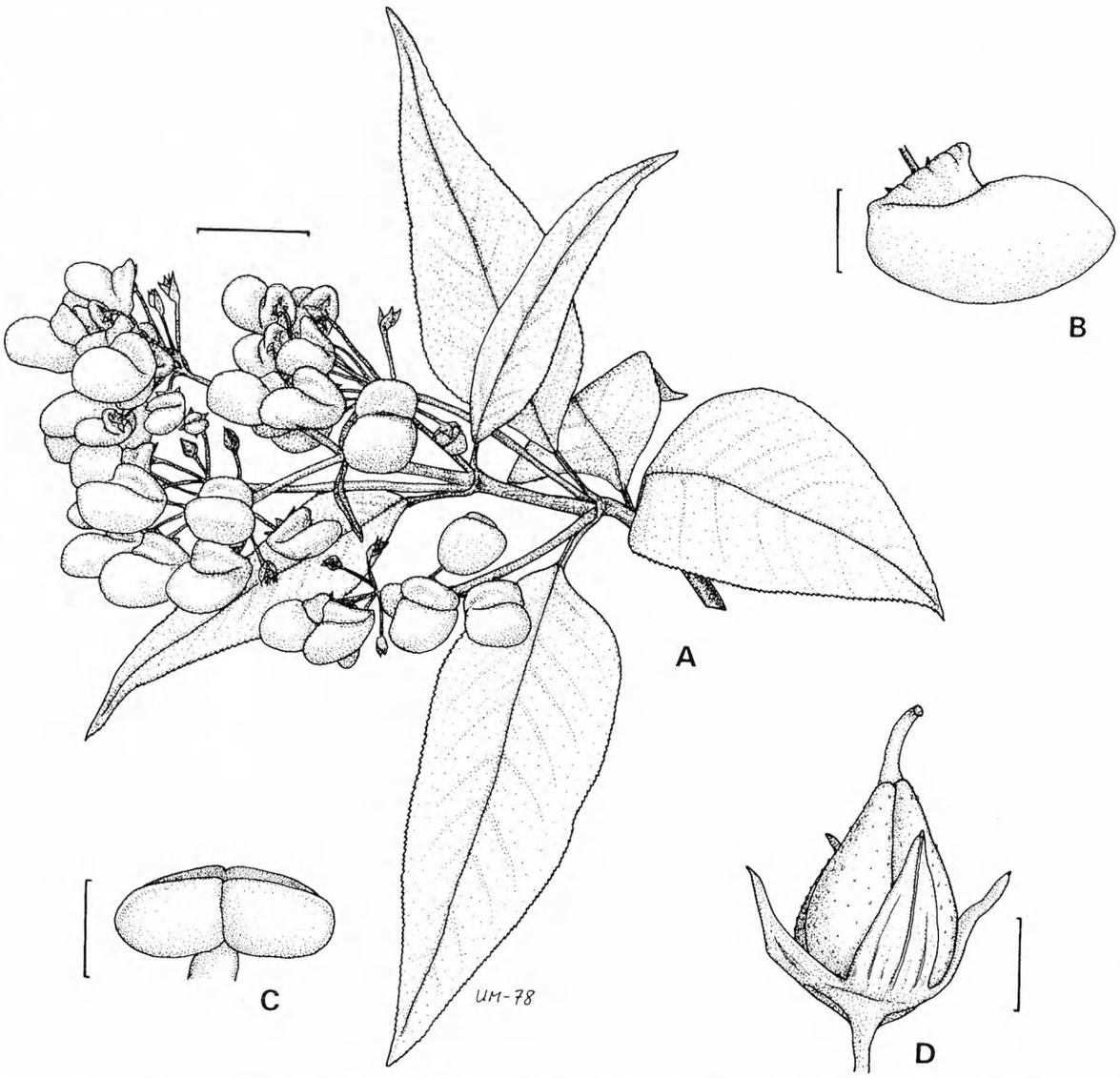

Fig. 9. *Calceolaria stricta*. – A: Flowering branch. – B: Corolla. – C: Stamen. – D: Capsule. – A–C: Harling et al. (leg. Molau) 15430; D: Sparre 16289. – A drawn from photograph, B, C drawn from fixed material, D drawn from herbarium material. – Scales: A 2 cm, B 5 mm, C 1 mm, D 2 mm.

C. pedunculata is distinct from all other species of this section in a number of important characters, viz. leaf colour, sepal shape and the unusually long peduncles. When two pairs of cymes are present, the first inflorescence internode is very short, the four primary peduncles apparently originating from the same place (as in *C. sotarensis*).

Representative specimens. Ecuador. Carchi: Tulcán–Maldonado road, 2900–3100 m, 2.III.1974, Harling & Andersson 12424 (GB); 3150–3250 m, 17–18.V.1973, Holm-Nielsen et al. 5581 (AAU, GB); 5597 (AAU, GB, MO); 3100–3200 m, 31.VII.1976, Øllgaard & Balslev 8309 (AAU). – *Imbabura:* Cotacachi–Apuela road, 33–36 km from Cotacachi (Intac valley), 2900–2950 m, 11.VIII.1976, Øllgaard & Balslev 8723 (AAU) – Otavalo–Apuela road, slopes of Cotacachi, c. 2700 m, 5.XII.1976, Davis 287 (GH, S). – *Pichincha:* Road Quito–Santo Domingo via Chiriboga, below San Juan, 3250 m, 27.IV.1955, Asplund 16089 (S); 15 km NE of Chiriboga, 2480 m, Croat 38716 (MO); 3000 m, 30.III.1942, Haught 3199 (F, NY, PH, US); between Chiriboga and San Juan, 3000–3100 m, 28.I.1977, Harling et al. (leg. Molau) 14890 (GB) – Corazón, 3000 m, 14.I.1881, Lehmann 476 (G) – Sine loco, 2750 m, 1856, Jameson 337 (BM, E, FI, G, K, P).

6. **Calceolaria stricta** H. B. K.

Humboldt, Bonpland & Kunth 1818 p. 380 – *Fagelia stricta* (H. B. K.) Kuntze 1891 p. 460 – Orig. coll.: Bonpland s.n. (P lectotype, B-WILLD).

Illustration. Fig. 9.

Shrub, 0.5–2 m high; the whole plant glabrous. *Leaves* elliptic to lanceate, 7.5–15 × 2.7–5.8 cm, acuminate, at base attenuate; above smooth,

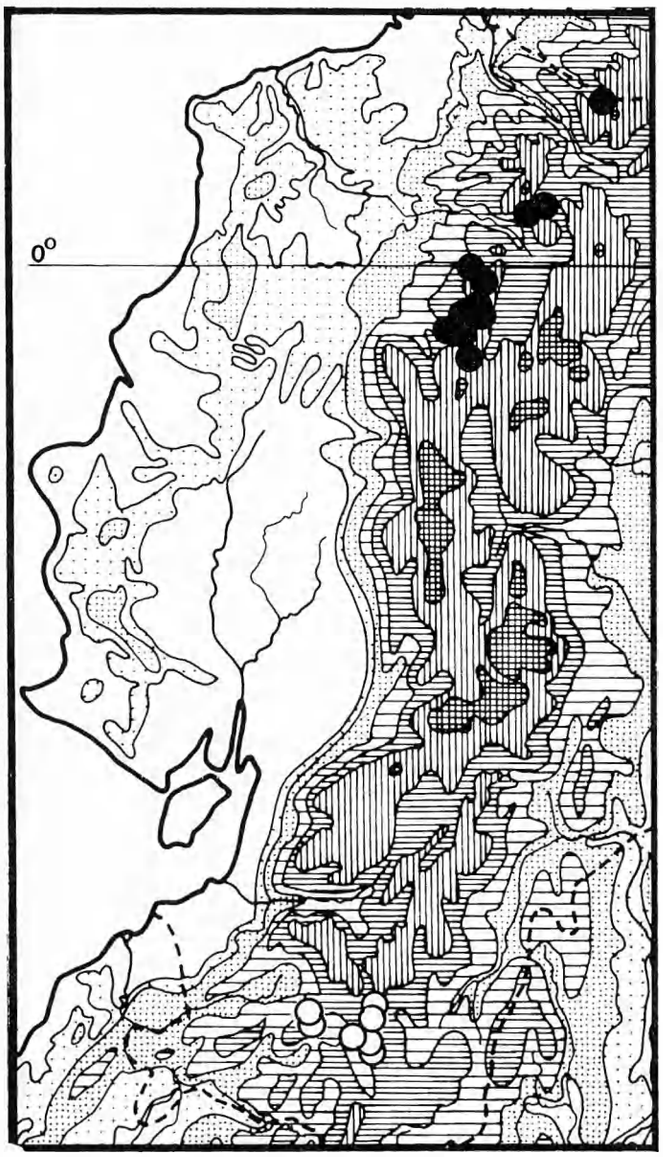

Fig. 10. Known distribution of *Calceolaria pedunculata* (●) and *C. stricta* (○).

glutinous, bright green; beneath pale green, closely reticulate-venose; margins regularly serrulate. Petioles 9–27 mm. *Inflorescense* terminal, comprising 1–2 pairs of 16–36-flowered cymes on primary peduncles 3.0–10 cm long. Cyme bracts absent. Pedicels 0.7–2.8 cm. *Sepals* triangular, 2.5–3.4 × 1.5–2.0 mm at anthesis, acuminate, green, entirely glabrous. *Corolla* bright yellow, externally glabrous; upper lip 5–8 × 6–9 mm, hooded; lower lip 15–20 × 10–15 mm, saccate in 1/2 of its length, inflated, projecting, ± closing the orifice. *Anthers* buffish to yellow-brown, 2.3–2.8 mm long, opening throughout; thecae divaricate, equal. *Filaments* 0.8–0.9 mm. *Style* 1.3–2.2 mm, slightly curved. *Capsule* ± conical, glutinous, 4–6 mm long.

Habitat. Dry shrub forest, at altitudes between 2000 and 2700 m.

Distribution. Fig. 10. Restricted to the mountains of the province of Loja, southernmost Ecuador; locally common. In all, 45 specimens from 25 collections have been studied.

Remarks. *Calceolaria stricta* is the largest-leaved taxon within the section *Dermatophylla*, even when compared with Peruvian species. Furthermore, it possesses unusually large numbers of flowers in each cyme and it has small, glabrous sepals. In corolla shape it resembles *C. rosmarinifolia* (sect. *Thamnobia*).

Representative specimens. *Ecuador. Loja:* Between Río Vinayacu and Loja, c. 2000 m, 1802, Bonpland s.n. (B-WILLD, P) – Nudo de Cajanuma, 7 km S of Loja, 2450–2550 m, 9.VII.1944, Camp E-116 (NY); 2400 m, 7.V.1946, Espinosa 313 (PH); 2400 m, 21.V.1967, Sparre 16583 (S) – Cerro Villonaco, 2600–2700 m, 12.IV.1974, Harling & Andersson 13453 (GB); 3.XI.1887, Poortmann 63 (P, S); 2200 m, 16.V.1967, Sparre 16289 (S) – Loja–Zaruma road near Las Chinches, 2400–2500 m, 30.IV.1974, Harling & Andersson 14086 (GB); 13.II.1977, Harling et al. (leg. Molau) 15430 (GB) – Sine loco ("in montis Loxa"), 1842, Hartweg 821 (BM, CGE, E, FI, G, K, LD, OXF, P, W).

7. **Calceolaria microbefaria** Kränzlin

Much branched, scandent *shrub*, 0.3–3 m high, strongly glutinous throughout. *Leaves* glabrous, acute; above dark green, nitidous, finely rugose; beneath pale greyish green; margins serrate with mucronulate teeth, often somewhat revolute. Petioles dorsally brownish tomentose. *Sepals* ovate, acute or slightly acuminate, green to greenish yellow, externally glabrous, internally with a short-tomentose border along the margin. *Corolla* bright yellow, very variable in size; upper lip arched, subglobose; lower lip pendent or projecting, exposing the orifice. *Anthers* brown of buffish with paler margins, opening throughout; thecae equal, globose, about as high as long, divaricate.

Remarks. In the northern Andes *Calceolaria microbefaria* is one of the most widespread species of subgenus *Cheiloncos*, and ranges from Venezuela to central Ecuador. It is split up into three subspecies, each one occupying one of the three distinct cordilleras of the Colombian Andes. *C. microbefaria* subsp. *microbefaria*

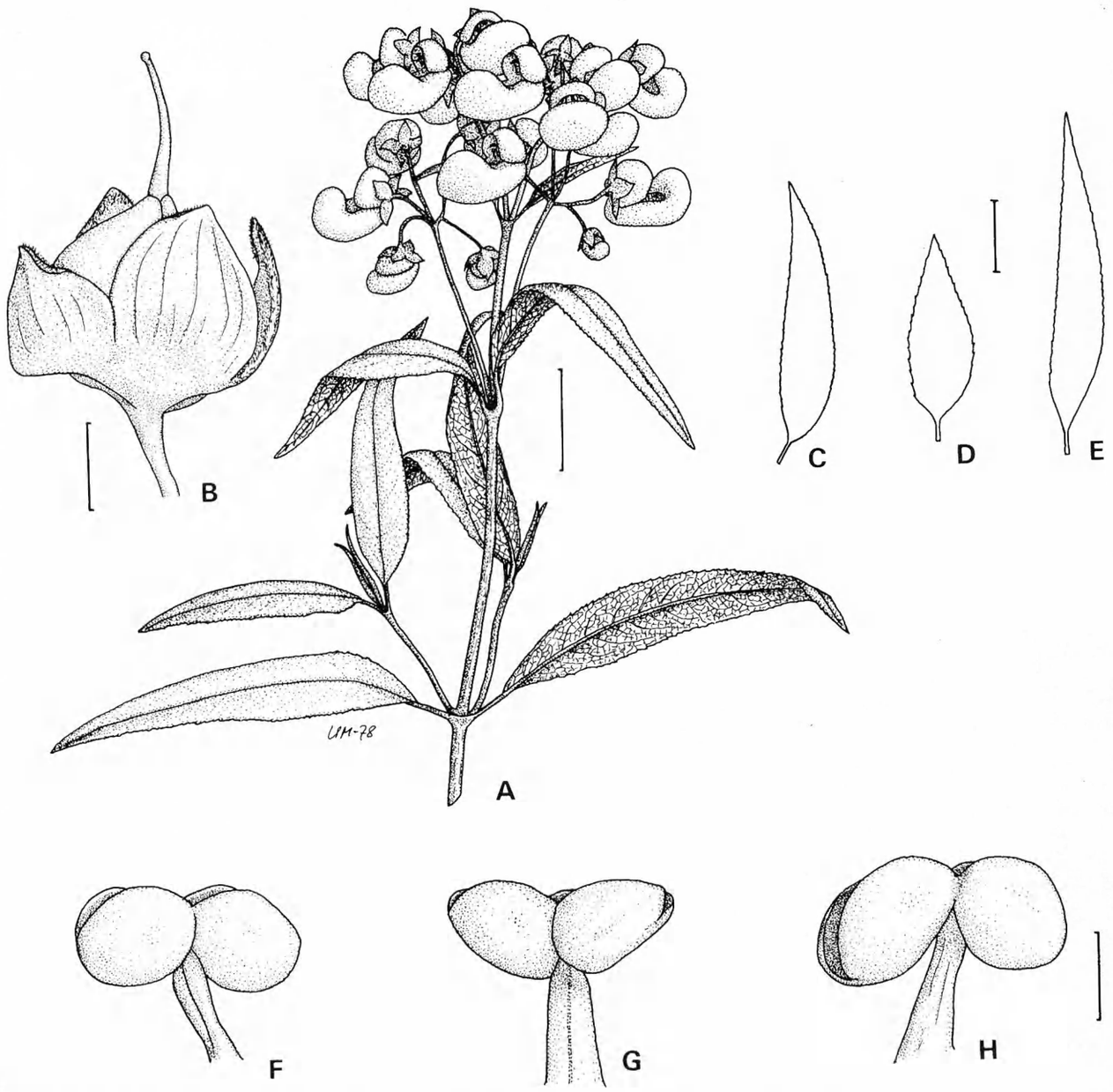

Fig. 11. *Calceolaria microbefaria*. – A–C, F: subsp. *microbefaria;* D, G: subsp. *fruticosa;* E, H: subsp. *tatamana*. – A: Flowering branch. – B: Capsule. – C–E: Outlines of leaves. – F–H: Stamens. A, C, F: Killip & Smith 15582; B: Killip & Smith 17556; D: Core 208; E, H: Pennell 10527; G: Holm-Nielsen & Jeppesen 1380. – All drawings made from herbarium material. – Scales: A, C–E 2 cm, B 2 mm, F–H 1 mm.

ranges throughout the Cordillera Oriental into its north-eastern extension in Venezuela. *C. microbefaria* subsp. *fruticosa* is confined to the Cordillera Central, and extends south to the Andes of Ecuador. However, subsp. *microbefaria* also occurs in a restricted area in Cordillera Central, near the junction of the two mountain chains. This is possibly a relict from an ancient páramo, occupying a wider area than today (van der Hammen 1974). Intermediates are known from where both subspecies occur. The third subspecies, subsp. *tatamana,* is restricted to Cordillera Occidental in central Colombia.

All subspecies have the same, very unusual anther-shape (Fig. 11 F–H), and are also similar in other floral characters. Since morphology of stamens and corolla has turned out to be of great importance at the species level in *Calceolaria,* the three taxa are most conveniently regarded to constitute a single species. The subspecies are separated mainly by corolla size, pubescence of peduncle and pedicel, and leaf shape.

In this complex Pennell (1951 b) recognized no less than four species: *C. microbefaria, C. fruticosa* (with four subspecies), *C. pachycyta* and *C. tatamana*. The subspecies of *C. fruticosa* are not distinguishable according to his key, nor is it possible to separate *C. microbefaria* from the subspecies of *C. fruticosa* occuring in the Cordillera Oriental and in Venezuela. In my opinion, *C. microbefaria* subsp. *microbefaria* should include also *C. fruticosa* subsp. *reticulata,* subsp. *attenuata* and subsp. *pamplonensis*. Furthermore, the collection of *C. fruticosa* subsp. *fruticosa* from Cordillera Oriental cited by Pennell (Sandeman 6030) also has to be referred to this taxon.

The remaining collections from Cordillera Central (referred to by Pennell as *C. fruticosa* subsp. *fruticosa*), however, are readily separated from subsp. *microbefaria* and should be recognized as *C. microbefaria* subsp. *fruticosa*.

Within its area of continuous distribution, subsp. *fruticosa* shows a clinal variation in some characters. Specimens from central Colombia possess reticulate-venose leaves and externally puberulous corolla, while specimens from prov. Cotopaxi and Chimborazo in Ecuador have pinnate-venose leaves and glabrous corolla. Specimens from Ecuador also have slightly larger flowers than have specimens from Colombia. At the time of Pennell's revision, no collections were known from the area between dept. Cauca, Colombia, and prov. Pichincha, Ecuador. As his material showed a discontinuous variation and distribution, Pennell recognized the Ecuadorean specimens as a distinct species, *C. pachycyta*. Since the time of his revision many collections from the intervening area have accumulated, which completely bridge the gap between the two extreme forms.

The fourth species recognized by Pennell, *C. tatamana,* was considered distinct from the others mainly because of the large flowers. However, corolla size varies considerably in the specimens of the type collection. More material is required to elucidate whether or not corolla size is useful in defining this taxon.

Key to the subspecies

1. Peduncles and pedicels glabrous or puberulous; cymes usually 4-flowered 2
– Peduncles and pedicels tomentose or villous with brownish hairs; cymes 4–16-flowered ..... 7 B. subsp. *fruticosa*
2. Leaves reticulate-venose beneath ..... 7 A. subsp. *microbefaria*
– Leaves pinnate-venose beneath ..... 7 C. subsp. *tatamana*

7 A. **Calceolaria microbefaria** subsp. **microbefaria**

Calceolaria microbefaria Kränzlin 1907 p. 193 – *Fagelia microbefaria* (Kränzlin) Pennell 1920 p. 171 – Orig. coll.: Linden 730 (W holotype, BM, FI, G, GH, K, OXF, P, PH, S).

Calceolaria fruticosa subsp. *attenuata* Pennell 1951b p. 122 – Orig. coll.: Pittier 13174 (US holotype, G, K, M, MO, NY, PH, S, VEN).

Calceolaria fruticosa subsp. *pamplonensis* Pennell 1951 b p. 123 – Orig. coll.: Olsson 9 (PH holotype, BM, GH, MO, P, US).

Calceolaria fruticosa subsp. *reticulata* Pennell 1951 b p. 121 – Orig. coll.: Pennell 2570 (PH holotype, GH, K, NY, P, PH).

Illustrations. Fig. 11 A–C, F; Vareschi 1970 p. 341 Fig. 106 (as *C. stricta*).

Leaves lanceate or lanceolate, 4.0–8.5(–12.5) × 1.0–2.3 cm, at base attenuate or cuneate; beneath reticulate-venose. Petioles 4–7(–11) mm. *Inflorescence* terminal, comprising 2–3 pairs of 4(–8)-flowered cymes on glabrous primary peduncles 1.1–5.5 cm long. Cyme bracts absent. Pedicels 0.5–3.4 cm, glabrous or finely puberulous. *Sepals* 3.3–5.2(–6.0) × 2.8–4.0 mm at anthesis; proximal part of calyx glabrous. *Corolla* externally glabrous; upper lip 5–10 × 7–12 mm; lower lip projecting, 11–20 × 8–16 mm, saccate in 2/5–1/2 of its length. *Anthers* 2.0–3.3 mm. *Filaments* 1.5–2.5 mm. *Style* 2.8–5.0 mm. *Capsule* widely ovoid, 5–8 mm long.

Habitat. Protected sites in páramo, mountain scrubs and forests, sometimes in open rocky slopes. The altitudinal records range from 2500 to 4200 m.

Distribution. Fig. 12. Cordillera Oriental, Andes of Colombia and Venezuela; the collections available range from the state of Trujillo, Venezuela, to the departments of Cundinamarca and Meta, Colombia. It is known also from two

collections from Volcán Puracé, Cordillera Central, in the department of Cauca, Colombia. In all, 202 specimens from 80 collections have been studied.

Representative specimens. Venezuela. Trujillo: NW slopes of La Reinosa, above La Mesa de Esnujaque, 2750 m, 28.III.1947, Box & Alayon 3811 (BM, VEN). – *Mérida:* Chachopo, 2750 m, 1846, Funck & Schlim 859 (BM, G, LD, MPU, P, W); 16.I.1929, Pittier 13174 (G, K, M, MO, NY, PH, S, US, VEN); 3200 m, 31.X.1977, Vareschi 8693 (VEN) – Páramo de Mucubaji, vicinity of Laguna Negra, 3400–3500 m, 21.XI.1968, Oberwinkler 13549 (M, VEN). – *Táchira:* Río Quinamarí, SE of Santa Ana, 2500–2700 m, 15.I.1968, Steyermark & Dunsterville 100944 (VEN). – *Colombia. Norte de Santander:* Río Chitagá, Quebrada de Presidente, 3100–3300 m, 28.XI.1941, Cuatrecasas 13481 (F, G, P, PH, S) – Ocaña, 2500–3000 m, 1846, Schlim 391 (BM, G, K, P). – *Santander:* Las Vetas, 3000 m, X.1846, Funck & Schlim 1336 (BM, G, LD, MPU, P, PH, S, W); 3100–3250 m, 16–20.I.1927, Killip & Smith 17253 (F, GH, NY, PH); 17338 (NY, PH); 17342 (NY, PH); c. 3300 m, 1842, Linden 730 (BM, FI, G, GH, K, OXF, P, PH, S, W). – *Boyacá:* Valle del Cocuy, SW slopes, 3100–3750 m, 8.IX.1938, Cuatrecasas 1257 (F) – Páramo Rusia near Rumania, c. 3600 m, 20.VIII.1953, Langenheim 3156 (UC, US). – *Cundinamarca:* La Calera, Páramo de Placio (La Siberia), 17.XI.1965, Forero 207 (AAU, NY) – 3–6 km SW of Sibaté, 2800–2900 m, 13–15.X.1917, Pennell 2389 (F, GH, K, MO, NY, P, PH, US). – *Meta:* Páramo de Sumapaz, 3450 m, 25.I.1972, Cleef 1037 (U). – *Cauca:* "Canaan", Volcán Puracé, 2900–3100 m, 11–16.VI.1922, Killip 6748 (GH, NY, US) – Puracé, 3300 m, II.1938, von Sneidern 1909 (s).

7 B. **Calceolaria microbefaria** subsp. **fruticosa** (Pennell) Molau comb. nov.

Basionym: *Fagelia fruticosa* Pennell 1920 p. 172 – *Calceolaria fruticosa* (Pennell) Standley 1936 p. 174 – Orig. coll.: Pennell 2998 (PH holotype, GH, K, P).

Calceolaria pachycyta Pennell 1951 b p. 117 – Orig. coll.: André 3722 (K holotype, NY).

Illustration. Fig. 11 D, G.

Leaves ovate to lanceate, 3.0–7.7 × 1.0–3.0 cm, at base truncate or cuneate; beneath pinnate- or reticulate-venose. Petioles 4–10 mm. *Inflorescence* terminal, comprising 2–3 pairs of 4–16-flowered cymes on primary peduncles 1.8–5.3 cm long. Cyme bracts sometimes present in the lowermost cyme-pair. Pedicels 0.9–2.5 cm. Peduncles, pedicels and proximal part of calyx tomentose or villous with coarse, brownish hairs. *Sepals* 3.2–5.8 × 2.6–4.5 mm at anthesis. *Corolla* externally glabrous or minutely puberulous; upper lip 5–8 × 6–12 mm; lower lip 11–20 × 9–18 mm, saccate in 1/3–2/5 of its length, projecting, often pendent towards the end of the anthesis. *Anthers* 2.0–3.3 mm. *Filaments* 1.5–2.5 mm. *Style* 3.4–5.0 mm. *Capsule* globose, 4–5 mm long.

Habitat. Páramo, mountain scrub and shrubby cloud forest, at altitudes between 2600 and 3900 m.

Distribution. Fig. 13. Cordillera Central in Colombia and the Andes of northern Ecuador, ranging from the department of Antioquia (Colombia) to the province of Chimborazo (central Ecuador). In all, 67 specimens from 27 collections have been studied.

Representative specimens. Colombia. Caldas: Páramo del Quindio, 3700–3900 m, 13.VIII.1922, Pennell 9708 (B, BM, GH, LE, NY, PH, S) – Manizales, 2750 m, I.1948, Sandeman 5669 (K). – *Tolima:* Páramo de Ruiz, 3200–3500 m, 16–17.XII.1917, Pennell 2998 (GH, K, P, PH) – Nevado del Tolima, 3120 m, VIII.1917, Tracey 187 (K). – *Cauca:* Puracé, 3000 m, 17.IV.1939, Alston 8094 (BM, S); 3700 m, II. 1938, von Sneidern 1910 (S) – Valley of Río Cocuy, W slopes of Páramo de Puracé, 3100 m, 26.V.1944, Killip & Lehmann 38513 (K, PH). – *Nariño:* Volcán La Galera, 3200–3600 m, 22.VII.1964, Soejarto 1011 (ECON, GH); 1036 (ECON, GH). –*Ecuador. Carchi:* Valle de Maldonado, km 53 on the Tulcán–Maldonado road, 3150–3250 m, 17–18.V.1973, Holm-Nielsen et al. 5574 (AAU, GB, MO). – *Imbabura:* Lago San Marcos, Cayambe, 3400 m, 28.XI.1961, Cazalet & Pennington 5385 (K, NY, UC) – Ibarra–Mariano Acosta road, E of the pass, 3500–3600 m, 9.VIII.1976, Øllgaard & Balslev 8571 (AAU). – *Pichincha:* Corazón, André K.612 (F, K, NY); K.613 (F, K); 3722 (K, NY) – "Quito", Jameson 177 (BM, CGE, FI, G, K, OXF, PH, W). – *Cotopaxi:* Quevedo–Latacunga road, Zumbagua, 3300 m, 2.V.1968, Harling et al. 8887 (GB) – Pilaló–Latacunga road, at timberline on the W slopes of the Andes, 3400 m, 6.VII.1968, Holm-Nielsen & Jeppesen 1380 (AAU, C, GB, S). – *Chimborazo:* Track Riobamba–Huamboya, Pungalá, 17.I.1949, Scolnik 1538 (G, PH).

Intermediate specimen

Colombia. Cauca: Puracé, Cordillera Central, 3300 m, 4.IV.1939, von Sneidern 2617 (S). – This specimen is obviously intermediate between *Calceolaria microbefaria* subsp. *microbefaria* and subsp. *fruticosa*. Volcán Puracé is the only area known at present where the two subspecies meet.

7 C. **Calceolaria microbefaria** subsp. **tatamana** (Pennell) Molau comb. nov.

Basionym: *Calceolaria tatamana* Pennell 1951 b p. 118 – Orig. coll.: Pennell 10527 (PH holotype, BM, GH, K, NY).

Illustrations. Fig. 11 E, H; Pennell 1951 b p. 119 Fig. 5.

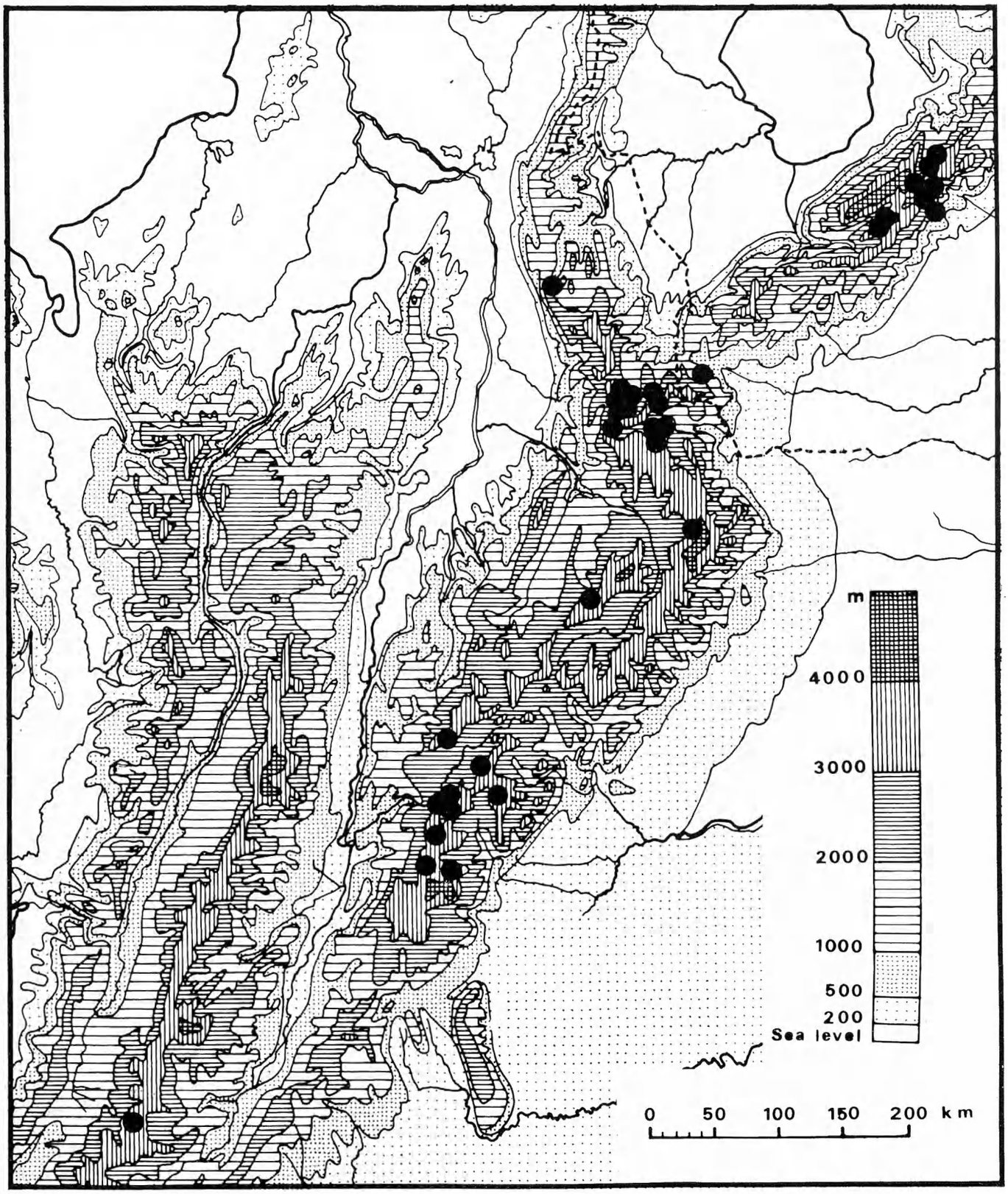

Fig. 12. Known distribution of *Calceolaria microbefaria* subsp. *microbefaria*.

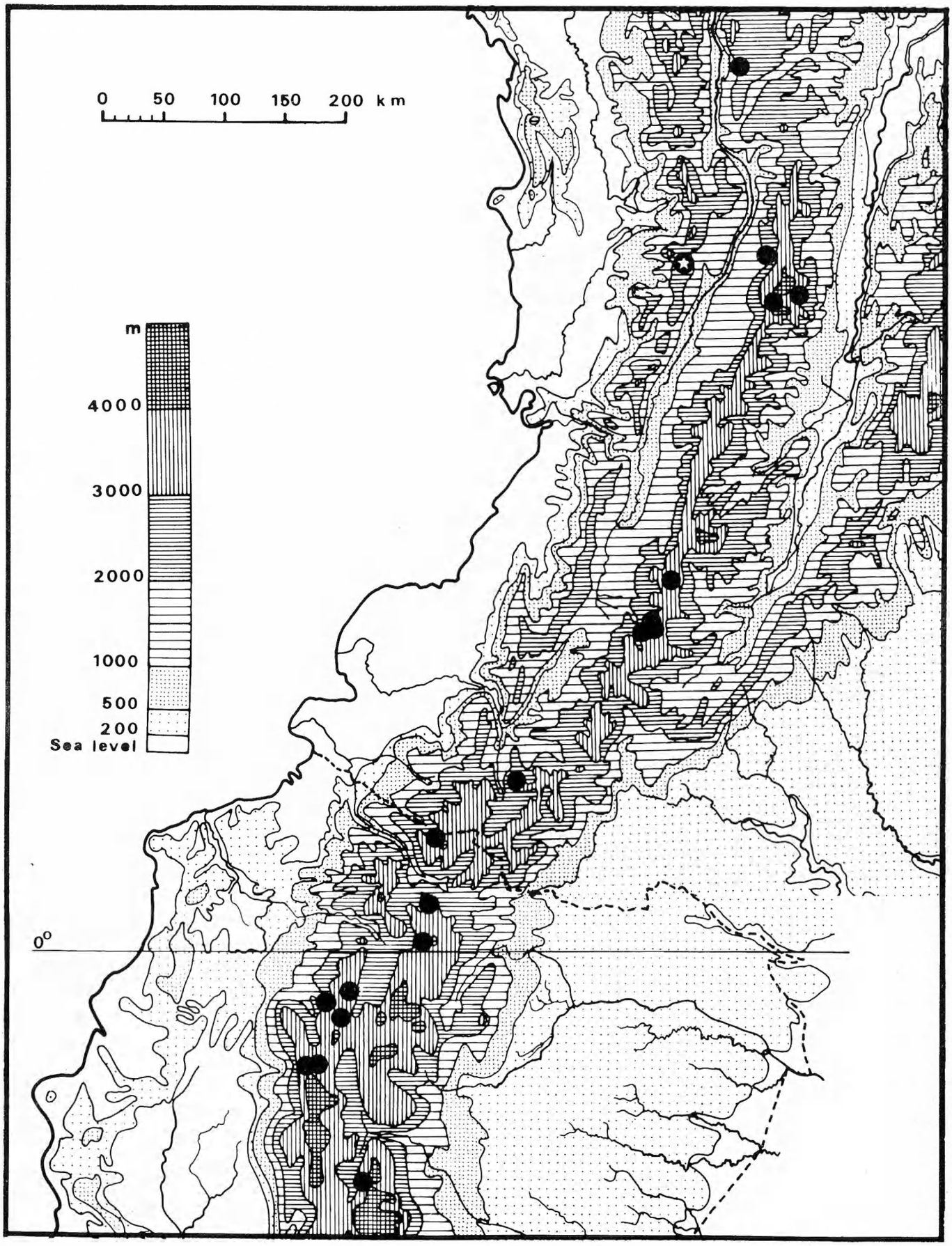

Fig. 13. Known distribution of *Calceolaria microbefaria* subsp. *fruticosa* (●) and *C. microbefaria* subsp. *tatamana* (✪).

Leaves lanceolate, 6.5–10.5 × 1.1–1.5 cm, attenuate at both ends; beneath pinnate-venose. Petioles 5–7 mm. *Inflorescence* terminal, comprising 2 pairs of 4–8-flowered cymes on glabrous primary peduncles 2.5–4.2 cm long. Cyme bracts absent. Pedicels glabrous, 1.0–2.5 cm. *Sepals* 5.0–6.0 × 3.5–4.0 mm at anthesis; proximal part of calyx glabrous. *Corolla* externally glabrous; upper lip 8–12 × 11–20 mm; lower lip ± pendent and slightly upcurved in the distal end, 15–25 × 15–21 mm, saccate in 2/5–1/2 of its length. *Anthers* 2.8–3.4 mm. *Filaments* 2.0–2.2 mm. *Style* 3.5–4.5 mm. Mature capsule not seen.

Habitat. Mountain scrub, 3300–3500 m.

Distribution. Fig. 13. Andes of Colombia, restricted to Cordillera Occidental. These mountains are floristically poorly known, and the distribution is probably wider than might be expected from the single collection so far known.

Specimens studied. Colombia. Caldas: Cerro Tatamá, shrub-zone below páramo, 3300–3500 m, 8–10.IX.1922, Pennell 10527 (BM, GH, K, NY, PH).

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A new species of Polypleurum (Podostemaceae) from India

C. R. Nagendran and G. D. Arekal

Nagendran, C. R. & Arekal, G. D. 1979 02 15: A new species of Polypleurum (Podostemaceae) from India. *Bot. Notiser 132:* 49–50. Stockholm. ISSN 0006-8195.

Polypleurum munnarense Nagendran & Arekal, sp. nov. is described from Kerala, S India.

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Polypleurum munnarense Nagendran & Arekal, sp. nov. – Fig. 1.

Orig. coll.: India, Kerala State, Idukki Distr., rocks in a waterfall 4 km N of Munnar on Munnar–Chinnar road, 10°06'N, 77°03'E, 1820 m, 26.12. 1972, Nagendran 49 a (holotype) in the Central National Herbarium, Howrah -3 (CAL), 49 b–f (isotypes), in the Herbarium of the Postgraduate Department of Botany, University of Mysore, Manasa Gangotri, Mysore-6, India.

Thallus complanatus, repens, basi affixus; partes natantes liberae ca 10 × 1 cm. Surculi secundarii distichi, ca 5 cm longi, filamenta gracilia ferentes. Folia aggregata, carnosa, spathulata, 4 cm longa, ter gemellata; gemellus infimus parvus; gemelli superiores successive ampliores; omnes gemelli filamentis unicis praediti. Flores solitarii, terminales, pedicellati, 1 cm longi. Stamina 2; antherae 2-lobatae; staminodia 2, opposita. Ovarium ellipsoideum, bicarpellatum, syncarpum, biloculare; ovula multa; stylus absens; stigmata 2, linearia; placentatio axilis. Capsulae isolobae ca 1×2.5 mm, 8-costatae, pedicellis ca 1 cm longis. Semina numerosa, minuta, obovoidea, plana, laevia.

Thallus flat, creeping, attached at base; floating parts free, c. 10 × 1 cm. Secondary shoots distichous, c. 5 cm. *Leaves* closely set, simple, fleshy, spathulate, up to 4 cm, in three pairs; lowest pair small, upper two pairs successively larger, each pair of leaves with a single filament. *Flowers* solitary, terminal, pedicellate, 1 cm. *Stamens* 2; anthers bilobed; staminodes 2, one on each side of a common axis. *Ovary* ellipsoidal; style absent; stigmas 2, linear; ovules many; placentation axile. Capsule isolobate, 8-ribbed, c. 1 × 2.5 mm; pedicel c. 1 cm. *Seeds* numerous, minute, obovoid, flat, smooth.

The new taxon differs from *Polypleurum agharkarii* (Nandi) Nagendran et al., *P. dichotomum* (Gardn.) Hall, *P. filifolium* (Ram. & Joseph) Nagendran et al., *P. minus* (Wedd.) Nagendran et al., *P. stylosum* (Wight) Hall and *P. wallichii* (R. Br. ex Griff.) Warming as follows: leaf tips persist on the secondary shoots during the flowering stage. The African *P. submersum* Hall has only a single stamen, which is much longer than the ovary.

The specific epithet refers to the locality at which the new species was first discovered. It was growing together with *Zeylanidium lichenoides* (Gardn.) Engl. and *Z. olivaceum* (Gardn.) Engl.

Acknowledgements. We thank Dr K. Subramanyam for his confirmation of the new species and Dr C. J. Saldanha, Bangalore, for the Latin description.

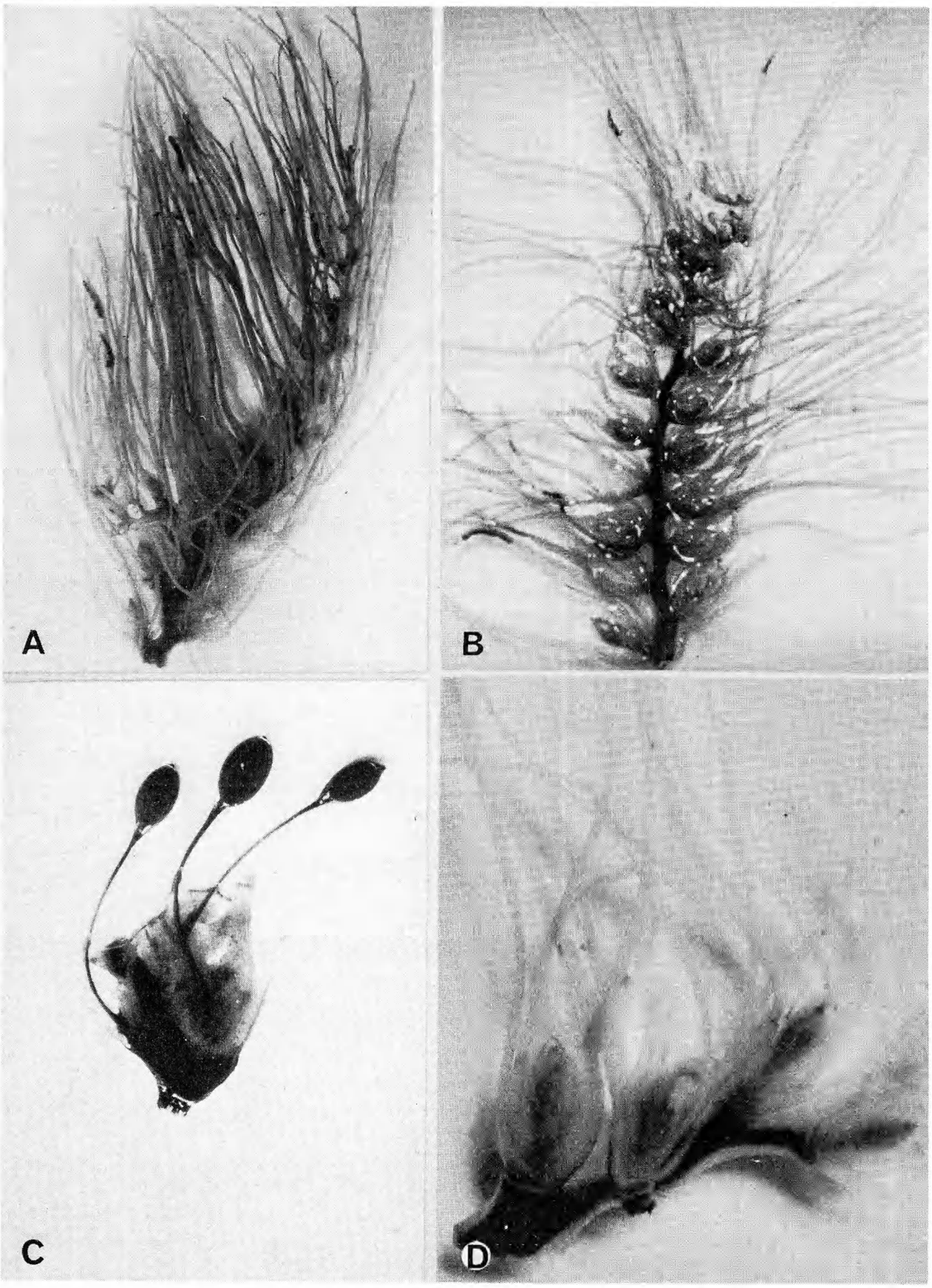

Fig. 1. *Polypleurum munnarense*. – A: Part of thallus at vegetative stage, ×2. – B: Part of thallus with flower buds, ×2. – C: Capsules, ×4. – D: Flower buds, ×3.5.

Embryology of Adenostemma, Elephantopus and Vernonia (Compositae)

T. Pullaiah

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Embryology of *Adenostemma rugosum* Wt., *A. lavenia* (L.) Kuntze, *Elephantopus scaber* L., *Vernonia elaeagnifolia* DC. and *V. divergens* Benth. was studied. The archesporium is hypodermal and consists of a single row of 4–6 cells. The anther wall development corresponds to the Dicotyledonous type. Tapetum is of the Periplasmodial type. Both isobilateral and tetrahedral pollen tetrads occur. Mature pollen grains are 3-celled and tricolpate, with a spinous exine. In *E. scaber* two ovules per overy were observed in a few cases. The female archesporium is single-celled and the embryo sac development is of the Polygonum type. The synergids are hooked. There are either two or three antipodal cells; they are persistent. *E. scaber* shows synergid and antipodal haustoria. Fertilization is porogamous. The endosperm is Nuclear in *E. scaber* and Cellular in the others. The embryo development conforms to the Senecio variant of the Asterad type. The structure and development of seed coat and pericarp are described.

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The tribe Vernonieae, which comprises 41 genera (Hoffmann 1894), is characterised by the presence of homogamous heads. Embryological information about members of this tribe is rather scanty and is mainly restricted to the genus *Vernonia;* and even in this genus, with a total of some 1,000 species, only four have been investigated, viz. *V. chinensis, V. cineraria* (Dahlgren 1924, Palm 1925), *V. cinerascens* and *V. cinerea* (Tiagi & Taimni 1960, 1963). In addition Misra (1972) studied the development of the seed and fruit in *V. anthelmintica.*

Similarly, although the tribe Eupatorieae comprises 42 genera (Hoffman 1894), embryological investigations are hitherto limited to only three, viz. *Eupatorium* (Holmgren 1919, Ghosh 1974, Maheswari Devi & Pullaiah in press, *Mikania* (Dutta 1939, Mitra 1974) and *Ageratum* (Dahlgren 1920, Mitra 1947).

In the present account the complete embryological development of *Vernonia elaeagnifolia* DC., *Elephantopus scaber* L., *Adenostemma rugosum* Wt. and *A. lavenia* (L.) Kuntze, and the development of the male and female gametophytes in *Vernonia divergens* Benth. have been described. A common description is given, unless stated otherwise. *Vernonia* and *Elephantopus* belong to the Vernonieae, *Adenostemma* to the Eupatorieae.

Material

The capitula of *Vernonia elaeagnifolia* were collected from plants cultivated in the gardens of Andhra University. Material of *Adenostemma lavenia* was collected from the Punyagiri Hills; material of *A. rugosum, Vernonia divergens* and *Elephantopus scaber* were collected from the Anantagiri Hills in the Visakhapatnam district, Andhra Pradesh, India.

Species were identified from the *Flora of Madras Presidency* (Gamble 1918) and later verified by reference to the Director, Central National Herbarium, Howrah. Voucher specimens have been deposited in the Herbarium of the Botany Department, Andhra University, Waltair.

Microsporangium, microsporogenesis and male gametophyte

The anther is tetrasporangiate. In cross section the young anther shows an oval-shaped mass of

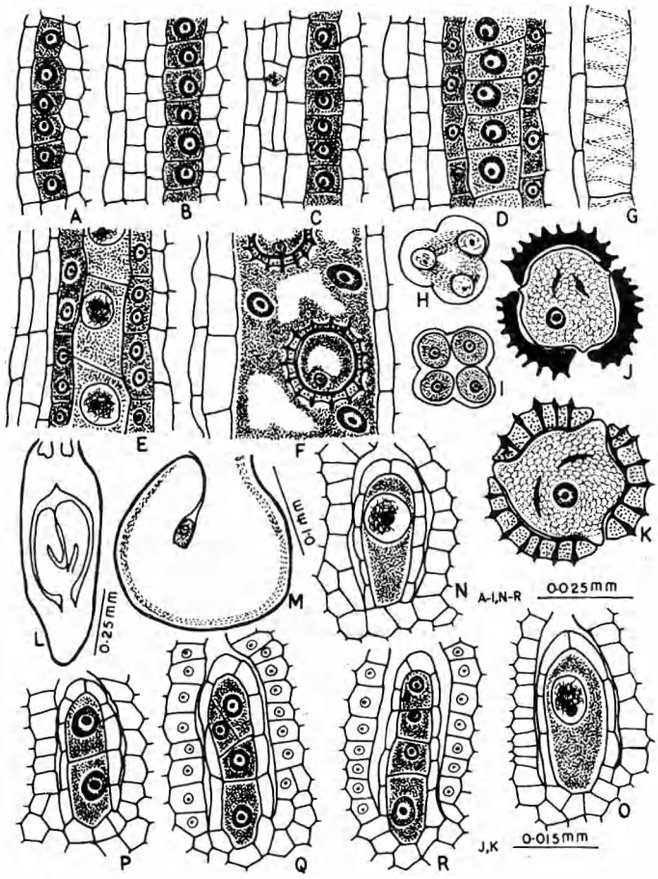

Fig. 1. A, F, G, I, K, L, R: *Elephantopus scaber*. – B–D, H, M, N, P, Q: *Vernonia divergens*. – E, J, O: *V. elaeagnifolia*. – A–E: Development of anther wall layers. – F: L.s. part of anther lobe showing periplasmodium and one-nucleate pollen grains. – G: Fibrous endothecium. – H, I: Pollen tetrads. – J, K: Mature pollen grains. – L: L.s. ovary showing two ovules. – M: Ovule. – N, O: Megaspore mother cell in meiotic prophase. – P: Megaspore dyad. – Q, R: T-shaped and linear megaspore tetrads respectively.

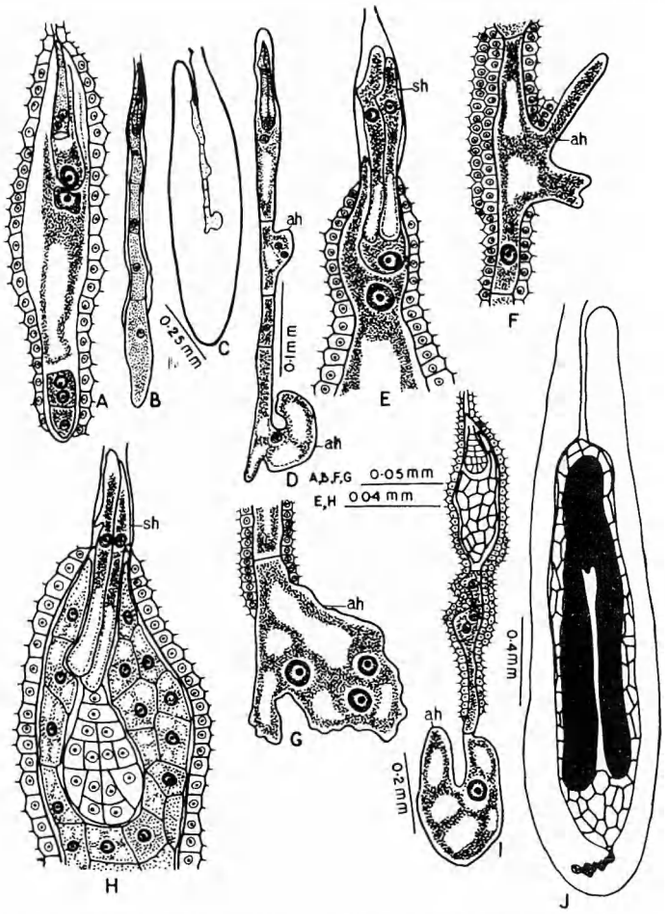

Fig. 2. A: *Vernonia elaeagnifolia*. – B–J: *Elephantopus scaber*. – A: Mature embryo sac before fertilisation. – B: Young embryo sac. – C, D, F, G, I: Antipodal haustoria. – E, H: Synergid haustoria – J: L.s. ovule showing a well developed dicotyledonous embryo and endosperm. Note the persisting antipodal haustorium. – ah antipodal haustorium, sh synergid haustoria.

meristematic cells surrounded by the epidermis. When the anther becomes tetralobate, a row of 4–6 hypodermal archesporial cells are differentiated in each of the four lobes (Figs. 1 A, 4 A). These archesporial cells expand radially and undergo periclinal divisions, which result in the formation of a primary parietal layer towards the outside and a primary sporogenous layer towards the inside. The primary parietal layer divides periclinally to form two layers (Fig. 1 B), of which the inner directly becomes the tapetal layer, while the outer one divides periclinally once more and produces an outer hypodermal layer and an inner middle layer (Fig. 1 C). Thus the wall development follows the Dicotyledonous type (Davis 1966).

The epidermis persists in the mature anther. The subepidermal layer develops fibrous thickenings and forms the fibrous endothecium (Figs. 1 G, 4 E). The middle layer becomes crushed and degenerates during the meiotic divisions in the pollen mother cells. The tapetum shows a dual origin. The peripheral tapetal cells of the anther develop from the parietal layer, while on the side towards the connective they develop from the already extant anther cells. The tapetum is of Periplasmodial type and its cells become binucleate. Simultaneously with the differentiation of the exine of the one-nucleate pollen grains, the walls of the tapetal cells become disorganised and the cytoplasm flows into the anther locule from all sides, forming a true periplasmodium (Figs. 1 F, 4 D). The nuclei of the periplasmodium remain healthy for a long time. In the mature

anther the periplasmodium is completely consumed by the developing pollen grains.

In the two species of *Adenostemma* the primary sporogenous cells divide along all planes, to yield a moderate-sized mass of pollen mother cells (Figs. 4 B, C), while in *Vernonia elaeagnifolia, V. divergens* and *Elephantopus scaber* they undergo only transverse divisions, to yield only a single row (Figs. 1 D, E). The pollen mother cells divide simultaneously and produce tetrahedral and isobilateral pollen tetrads (Figs. 1 H, I, 4 F, G). Cytokinesis takes place by a process of furrowing. The nucleus in the young pollen grain is centrally situated and the cytoplasm is initially not vacuolated. After a short time a large central vacuole develops, which displaces the nucleus out to the periphery of the pollen grain. The nucleus divides mitotically, forming a small lenticular generative cell and a large vegetative cell. In the later stages of development the wall separating the two nuclei rounds off and the generative cell moves in to the cell centre, where it divides to form two male cells. At the shedding stage, the pollen grains are 3-celled and tricolpate, with a thick spinous exine (Figs. 1 J, K, 4 H, I). The sperms are spindle-shaped.

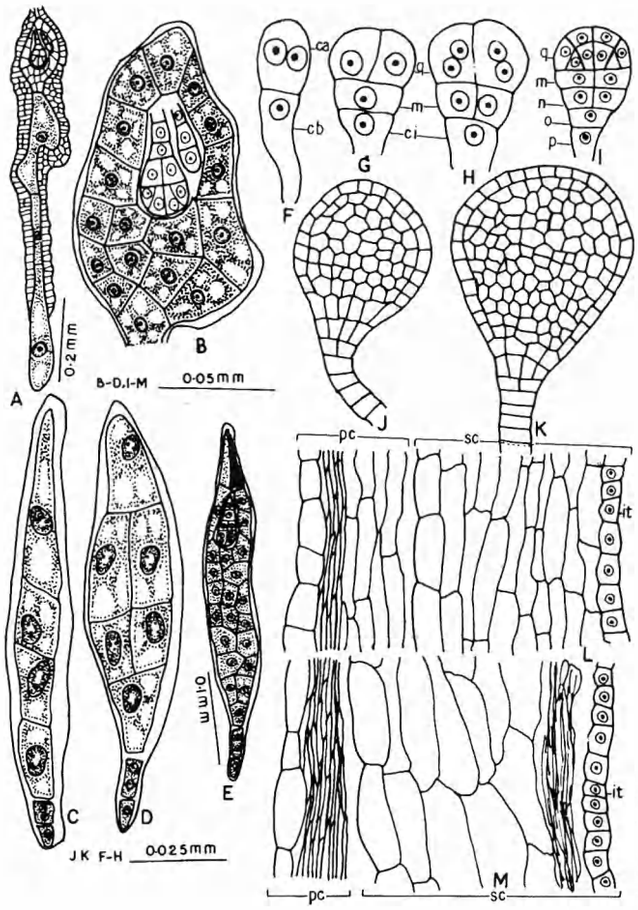

Fig. 3. A, B, I–K: *Elephantopus scaber*. – C–H, L, M: *Vernonia elaeagnifolia*. – A: Embryo sac showing twin embryos, cellular endosperm and twin embryos. – B: Micropylar part of A enlarged showing cellular endosperm and twin embryos. – C–E: Various stages in the development of endosperm. – F–K: Stages in the development of the embryo – L, M: Pericarp and seed coat at organised embryo sac and quadrant embryo stages respectively. – it integumentary tapetum, pc pericarp, sc seed coat.

Ovary and ovule

The ovary is inferior, bicarpellary, syncarpous and unilocular, with a single basal ovule which is anatropous, unitegmic and tenuinucellate. The ovule arises as a papillate outgrowth from the base of the ovary. During its further growth, the ovule, due to anticlinal divisions, becomes inverted and is thus anatropous. An integumentary vascular strand traverses the entire ovule, extending to the very tip of the integument (Fig. 1 M). At the time of megaspore tetrad formation, the cells of the inner epidermis of the integument elongate radially, become glandular and function as the integumentary tapetum (Figs. 1 Q, R, 4 L, M), which remains uniseriate throughout, with uninucleate cells (Figs. 2 A, 4 O, P) except in *Elephantopus scaber* in which it becomes multiseriate (Figs. 2 F, I, 3 A).

A feature of special interest is the exceptional occurrence of two ovules per ovary. This was observed in about 3 % of the ovaries of *Elaphantopus scaber* studied during the course of the investigation (Fig. 1 L). In all cases the ovules were arranged face to face and had a common funicle. The development of the female gametophyte was synchronous in the two ovules and showed normal features.

Megasporogenesis and female gametophyte

The nucellus consists of a single layer of epidermal cells surrounding a single archesporial cell which directly functions as the megaspore mother cell (Figs. 1 N, O, 4 J, K). It enlarges considerably and undergoes meiotic divisions to produce a linear tetrad of megaspores (Figs. 1 P, R, 4 L). In *V. divergens* T-shaped tetrads were also sometimes observed (Fig. 1 Q). The chalazal megaspore of the tetrad becomes

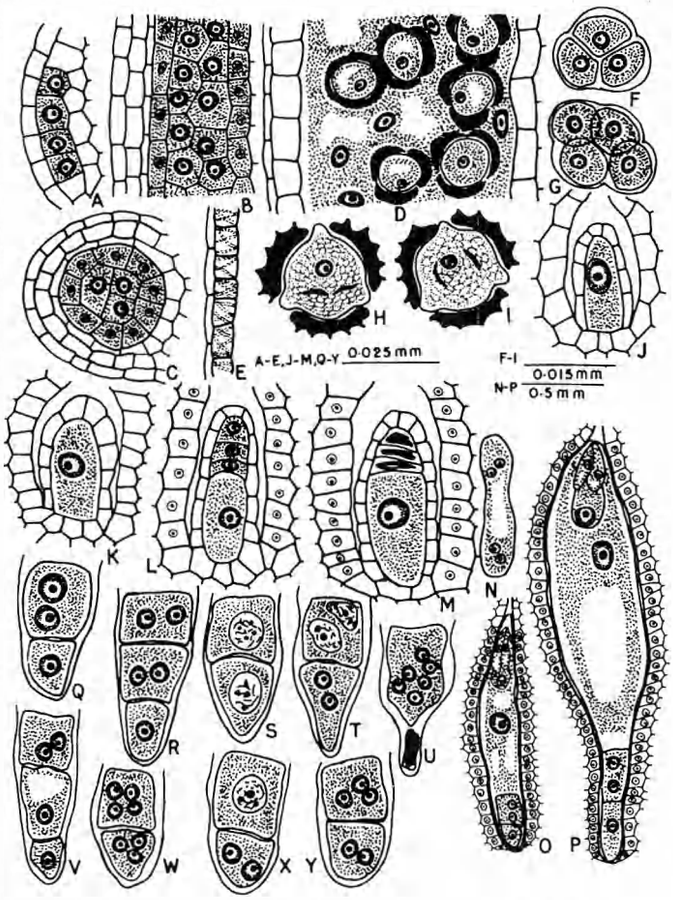

Fig. 4. A, B, D, E, G, H, J, M–O, Q–Y: *Adenostemma rugosum*, – C, F, I, K, L, P: *A lavenia*. – *A*: L.s. part of anther lobe showing archesporium. – B, C: L.s. and T.s. anther lobes, respectively, showing epidermis, wall layers and pollen mother cells. – D: L.s. part of anther lobe showing periplasmodium and one-nucleate pollen grains. – E: Fibrous endothecium. – F, G: Tetrahedral and isobilateral pollen tetrads respectively. – H, I: Mature pollen grains. – J, K: Megaspore mother cells. – L, M: Tetrads. – N: 4-nucleate embryo sac. – O, P: Organised 8-nucleate embryo sacs. – Q–Y: Antipodal cells.

functional and the three micropylar ones degenerate (Fig. 4 M). The functional megaspore undergoes three mitotic divisions, resulting in an eight-nucleate embryo sac of the Polygonum type (Fig. 4 N, O). The newly-formed embryo sac is spindle-shaped except in *E. scaber,* in which it is narrow and elongate (Fig. 2 B). The synergids are hooked (Figs. 2 E, 4 O). In *E. scaber* they elongate, protrude into the micropyle, and function as haustoria (Fig. 2 E). These haustoria persist even after a globular embryo has formed in the embryo sac (Fig. 2 H). In *V. elaeagnifolia* and *V. divergens* the synergids degenerate just prior to fertilization (Fig. 2 A), while in *A. lavenia* and *A. rugosum* they degenerate just after fertilization (Fig. 5 A).

In *E. scaber* three antipodal cells are uninucleate and are arranged in a linear row (Fig. 2 B). Later on they become multinucleate. Simultaneous with the growth of the embryo sac the antipodal cells also increase in size and invade the chalazal tissue of the integument (Fig. 2 C, D). The micropylar and chalazal antipodal cells, later on also the middle one, produce lateral pouch-like extensions which finally develop into haustoria. The micropylar antipodal haustorium becomes branched; the branches ramify and invade the sides of the integument (Fig. 2 F). The chalazal antipodal haustorium, which becomes either a bulbous foot-like structure or a U-shaped structure, crushes and absorbs the chalazal tissue (Fig. 2 G, I). Haustorial remnants persist even after very well-developed cotyledons have been formed in the embryo (Fig. 2 J). The haustorium formed from the middle antipodal cell does not behave so aggressively.

In the other taxa studied there were either two or three antipodal cells. When two, the upper antipodal cell is always binucleate (Figs. 2 A, 4 Q), and when three, all of them are uninucleate. In *A. rugosum* nuclear divisions and fusions of the antipodal cells result in the formation of multinucleate and polyploid antipodal cells (Fig. 4 R–Y). The antipodal cells in all these species persist up to the time of the formation of a globular embryo in the embryo sac (Fig. 5 D).

Fertilization, endosperm and embryo

Fertilization is porogamous. The pollen tube enters the embryo sac without destroying either of the synergids. The pollen tube opens by a circular apical pore and discharges its contents in the vicinity of the egg and the secondary nucleus (Fig. 5 A). In *E. scaber* syngamy and triple fusion occur almost simultaneously while in the other taxa triple fusion was completed before syngamy took place (Fig. 5 A). The pollen tube persists until a few endosperm cells have been formed (Fig. 5 B).

The development of the endosperm is of the Cellular type except in *E. scaber* in which it is of the Nuclear type. In *E. scaber* the primary endosperm nucleus divides before the zygote. The two nuclei thus formed undergo further divisions and produce a number of free nuclei.

Later on, wall formation commences from the micropylar end and proceeds towards the chalazal region, ultimately filling the entire embryo sac with cellular tissue (Fig. 3 A, B).

In *V. elaeagnifolia, A. lavenia* and *A. rugosum* the primary endosperm nucleus divides much earlier than the zygote. Cell plate formation, which is transversely orientated, then occurs. In *V. elaeagnifolia* the aforementioned two cells undergo one more transverse division to produce a linear row of four cells (Fig. 3 C), while in *Adenostemma* they undergo vertical divisions at right angles to one another (Fig. 5 B). These four cells then divide in all directions to form a massive cellular tissue (Figs. 3 D, E, 5 C, D).

In the mature seeds of all the species studied the endosperm, except for one or two layers of cells, gradually becomes absorbed by the growing embryo.

The embryogeny (Figs. 3 F–K, 5 E–M) thus conforms in every detail with that of the Senecio variant of the Asterad type (Johansen 1950).

Polyembryony. In a single instance, in *E. scaber,* twin embryos were observed. The position of the second embryo suggests that it may have originated from one of the synergids (Fig. 3 A, B).

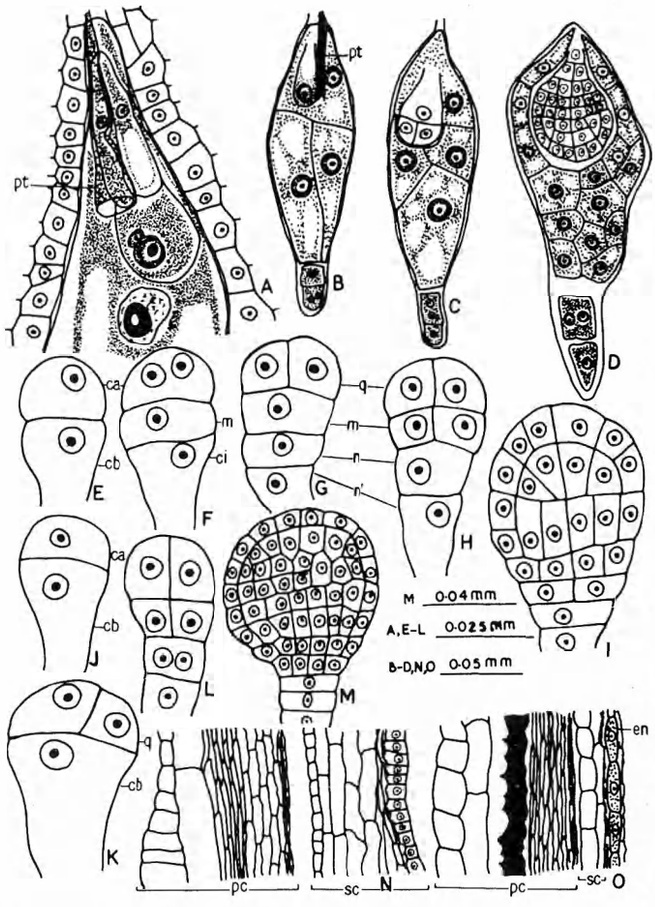

Fig. 5. A, C, D, J–O: *Adenostemma lavenia*. B, E–I: *A. rugosum*. – A: L.s. upper part of embryo sac showing syngamy and primary endosperm nucleus. Note persistent pollen tube. – B–D: Stages in the development of endosperm. – E–M: Various stages in the development of the embryo. – N, O: Seed coat and pericarp at organised embryo sac and mature seed stages, respectively. – en endosperm, pc pericarp, pt pollen tube, sc seed coat.

Seed coat and pericarp

At the fully organised stage of the embryo sac, the integument consists of 10–20 layers of parenchymatous cells in *V. elaeagnifolia* (Fig. 3 L), 18–20 layers of cells in *E. scaber* and 6–10 layers in *A. lavenia* and *A. rugosum,* in addition to the epidermis and the integumentary tapetum (Fig. 5 N). After fertilization the cells around the integumentary tapetum become enlarged and depleted in appearance forming the periendothelial zone. This degeneration extends into the peripheral region and all the integumentary layers except the epidermis have become crushed by the time a well-developed embryo has formed (Fig. 5 O). Meanwhile the integumentary tapetum also becomes crushed. In *E. scaber* the integument becomes crushed in the chalazal region and is absorbed by the antipodal haustoria. The embryo sac increases in size laterally and both crushes and absorbs all the integumentary layers except the epidermis. Thus, in the fully mature seed, it is only the epidermis which becomes thickened and forms the seed coat.

At the megaspore mother cell stage, the ovary wall of *V. elaeagnifolia* and *E. scaber* consists of two zones of subepidermal cells. The outer zone consists of narrow vascular cells and the inner zone consists of loosely-arranged parenchymatous cells, which are radially elongated (Fig. 3 L). At the quadrant stage of the embryo the inner layers of the ovary wall which constitute the inner zone, become completely crushed, while the cells of the outer zone elongate and, together with the epidermis, form the fruit wall (Fig. 3 M). At maturity the pericarp thus consists of the thick-walled cells of the outer zone and the epidermis.

In *A. lavenia* and *A. rugosum* the ovary wall,

at the organised embryo sac stage, consists of an epidermis, a hypodermis and an inner layer of parenchymatous cells traversed by vascular elements (Fig. 5 N). After fertilization schizogenous cavities develop between the hypodermis and the inner layers of the ovary. A brown resinous substance exudes from the hypodermis and accumulates in the schizogenous cavities. At maturity this resinous substance hardens into a dark mass. Meanwhile, the inner layers of the ovary wall, except for a few layers, enlarge and then become obliterated. In the mature achene the pericarp thus consists of the epidermis, the hypodermis, a hardened dark layer and a few inner layers (Fig. 5 O).

Discussion

The taxa studied fit in well in the picture obtained from previous studies of the embryology of other representatives of the respective tribes (see Introduction). However, Tiagi & Taimni's (1963) statement that in *Vernonia cinerea* the seed coat is entirely absent appears questionable, since in *V. anthelmintica* (Misra 1972) and in the species of Vernonieae studied here the outer epidermis of the ovule becomes thickened and forms the seed coat.

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Three new West Indian species of Chionanthus (Oleaceae)

William T. Stearn

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Chionanthus adamsii and *C. proctorii* from Jamaica and *C. caymanensis* from the Cayman Islands, West Indies, are described. A key to the six species of Jamaica and the Cayman Islands is included. *Linociera* is here treated as congeneric with *Chionanthus*.

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The Cayman Islands are three low-lying coral islands in the West Indies, lying S of north-central Cuba and NW of western Jamaica. The smallest, Little Cayman, measures about 9 miles (14.5 km) by 1 mile (1.6 km), and is situated about 60 miles (96.5 km) from the largest, Grand Cayman, measuring about 17 miles (27.4 km) by 7 miles (11.3 km). Several botanists have visited them, notably A. S. Hitchcock in 1891, W. Kings in 1938 and Martin Brunt in 1965 and 1969, but the most thorough investigation of their flora, which includes some 586 species of flowering plants, has been made in recent years by George Proctor from the Institute of Jamaica, Kingston, Jamaica. The islands possess a few endemic taxa, of which *Crossopetalum caymanense, Chamaesyce bruntii, Allophyllus cominia* var. *caymanensis, Cestrum diurnum* var. *marcianum, Agalinis kingsii* and *Verbesina caymanensis* have recently been described by Proctor (1977). To these *Chionanthus caymanensis,* likewise discovered by Proctor, is added here. The occurrence of this species on Little Cayman testifies to its long isolation. The relatively high number of species occurring on these small islands with a total area of 100 sq. miles (25,900 hectares) is evidently due to their position between Cuba and Jamaica, both large islands with very rich and diverse floras, from which over a long period of time miscellaneous species have strayed across at least 150 miles (240 km) of sea to colonize them.

Jamaica, a very hilly and mountainous island, possesses some 3000 species of flowering plants, of which about 27 % are endemic according to C. D. Adams (1972) and, despite intensive collecting, it continues to yield hitherto unnamed species. Two of these are here named *Chionanthus adamsii* and *C. proctorii* as a tribute to the very important contribution that Adams and Proctor have made to our knowledge of Jamaican plants.

Until recently these three species would have been placed in the genus *Linociera*. In preparing an account of the Oleaceae for Fawcett & Rendle's *Flora of Jamaica vol. 6* I could find, however, no characters weighty enough to justify the separation of *Mayepea* Aublet (1775) and *Linociera* Swartz (1791) from *Chionanthus* L. (1753) and have accordingly treated them as congeneric (cf. Stearn 1977).

Key to Jamaican and Cayman Islands species of Chionanthus

1. Petiole 1–3 cm. Calyx divided to 1/3. Ovary pubescent ..... *C. domingensis*
– Petiole 0.3–1.5 cm. Calyx divided to 1/2 or more. Ovary glabrous 2

2. Anthers 5–6.5 mm, linear, equalling the corolla lobes ..... *C. ligustrinus* (Swartz) Pers.
– Anthers 1–3 mm, ellipsoid, much shorter than the corolla lobes 3
3. Leaves glabrous beneath. Inflorescence glabrous 4
– Leaves with minute hair tufts (domatia) in vein axils or pubescent along midrib beneath. Inflorescence pubescent 5
4. Leaves mostly narrowly elliptic; veining prominent above. Corolla lobes 4–6 mm. Jamaica ..... *C. adamsii*
– Leaves mostly obovate; veining obscure above. Corolla lobes 2 mm. Cayman Islands ..... *C. caymanensis*
5. Corolla lobes 10–15 mm. Stigma slightly lobed ..... *C. proctorii*
– Corolla lobes 4–7 mm. Stigma distinctly lobed ..... *C. jamaicensis*

Chionanthus adamsii Stearn, sp. nov. – Fig. 2 A

Holotypus: Jamaica, St. Catherine parish, Hellshire Hills, Lance Wood, Q7, 550 feet, 2.9.1970, P. Scott 242 (BM).

Arbor parva c. 3 m alta; ramuli grisei glabri. *Folia* longe petiolata; lamina plerumque anguste elliptica, apice acuminata, basi attenuata, c. 2–7 cm longa, 0.6–3.4 cm lata, glabra, subtus squamis minutis vel foveolis punctata, domatiis nullis, coriacea, venis primariis 5–7 utroque latere costae sub angulo c. 50° abeuntibus, rete venularum prominulo; petiolus 10–15 mm longus. *Inflorescentia* terminalis vel axillaris laxa pauci- vel multiflora, c. 3–7 cm longa, glabra; pedicelli 1–5 mm longi. *Calyx* c. 1.3–1.5 mm longus, glaber, ad medium in segmenta triangularia glandulo-punctata divisus. *Corollae lobi (Petala)* albi, oblongo-elliptici, per paria basi cum filamento staminis connati, c. 4.5–6 mm longi, 1.0–1.5 mm lati. *Stamina* c. 3 mm longa; antherae ellipsoideae, c. 1.5–1.8 mm longae; filamenta fere 1.5 mm longa. *Pistillum* 2 mm longum; ovarium glabrum, in stylum 1.1 mm longum (stigmate crasso triangulari leviter bilobato c. 0.6 mm longo incluso) contractum. *Fructus* immaturus c. 1 cm longus.

This species is notable for the filaments being almost as long as the anthers. It has been named in honour of C. Dennis Adams, who, after making many contributions to the knowledge of the flora of W tropical Africa, has further earned the gratitude of botanists by his comprehensive *Flowering plants of Jamaica* (1972) together with two smaller, profusely illustrated publications, *The Blue Mahoe and other bush* (1971) and *Caribbean flora* (1976). Adams (1972 p. 580) mentions this as an undescribed species of *Linociera*. His "*L.* sp. A" is here named *C. proctorii*. His "*L.* sp. B" may come within the range of variation of *C. domingensis* and has accordingly been left unnamed.

Additional material. Jamaica, St. Catherine parish: Hellshire Hills, Long Road Track, Q4, 500 feet, 13.8.1970, T. Tulloch 144 (BM).

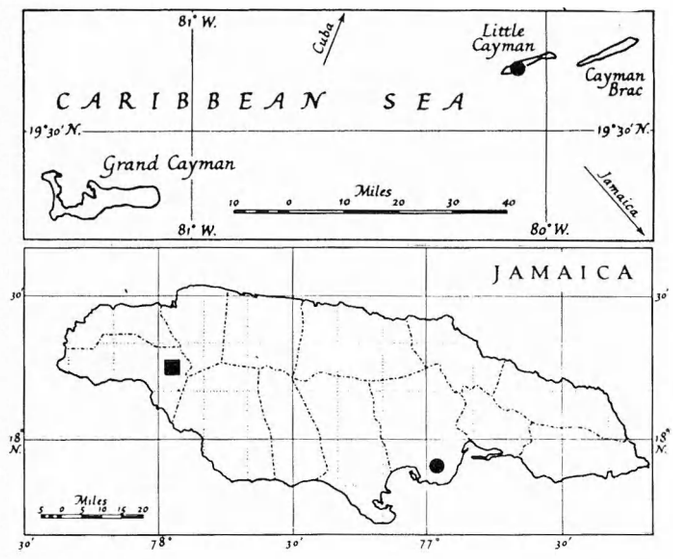

Fig. 1. Distribution of *Chionanthus* species. – Above: *C. caymanensis*. – Below: *C. adamsii* (dot) and *C. proctorii* (square).

Chionanthus caymanensis Stearn, sp. nov. – Fig. 2 C

Holotypus: Little Cayman, 1/2 to 1 mile NNE of airfield terminal, 12.7.1967, Proctor 28183 (BM).

Frutex vel arbor parva 3–5 m alta; ramuli grisei glabri, juventute squamis numerosis minutis ceraceis vestiti. *Folia* breviter petiolata; lamina plerumque obovata, apice acuta vel abrupte breviterque acuminata, basi longe attenuata et in petiolum 0.5–1 cm longum decurrens, 2–5.5 cm long, supra medium 1–2.5(–3) cm lata, glabra, domatiis nullis, venis primariis inconspicuis 6–7 utroque latere costae sub angulo 50–60° abeuntibus. *Inflorescentia* terminalis laxa multiflora, c. 3–6 cm longa, glabra; pedicelli vix 1 mm longi. *Flores* odori. *Calyx* c. 1–1.5 mm longus, glaber, ad medium in segmenta triangularia fissus. *Corollae lobi (Petala)* albi, per paria basi conjuncti, oblongo-obovati, c. 2 mm longi 1 mm lati. *Stamina* c. 1.6 mm longa; antherae ellipsoideae, c. 1–1.4 mm longae; filamenta c. 0.8 mm longa. *Pistillum* c. 1.5–1.8 mm longum; ovarium glabrum; stylus 1 mm longus (stigmate crasso bilobato c. 0.4 mm longo incluso). *Drupae* oblique ellipsoideae, 7–8 mm longae.

This species, remarkable among West Indian members of *Chionanthus* for its very short corolla lobes, is apparently endemic to Little Cayman Island and accordingly merits protection. It is certainly among the most interesting of the discoveries made by George Richardson

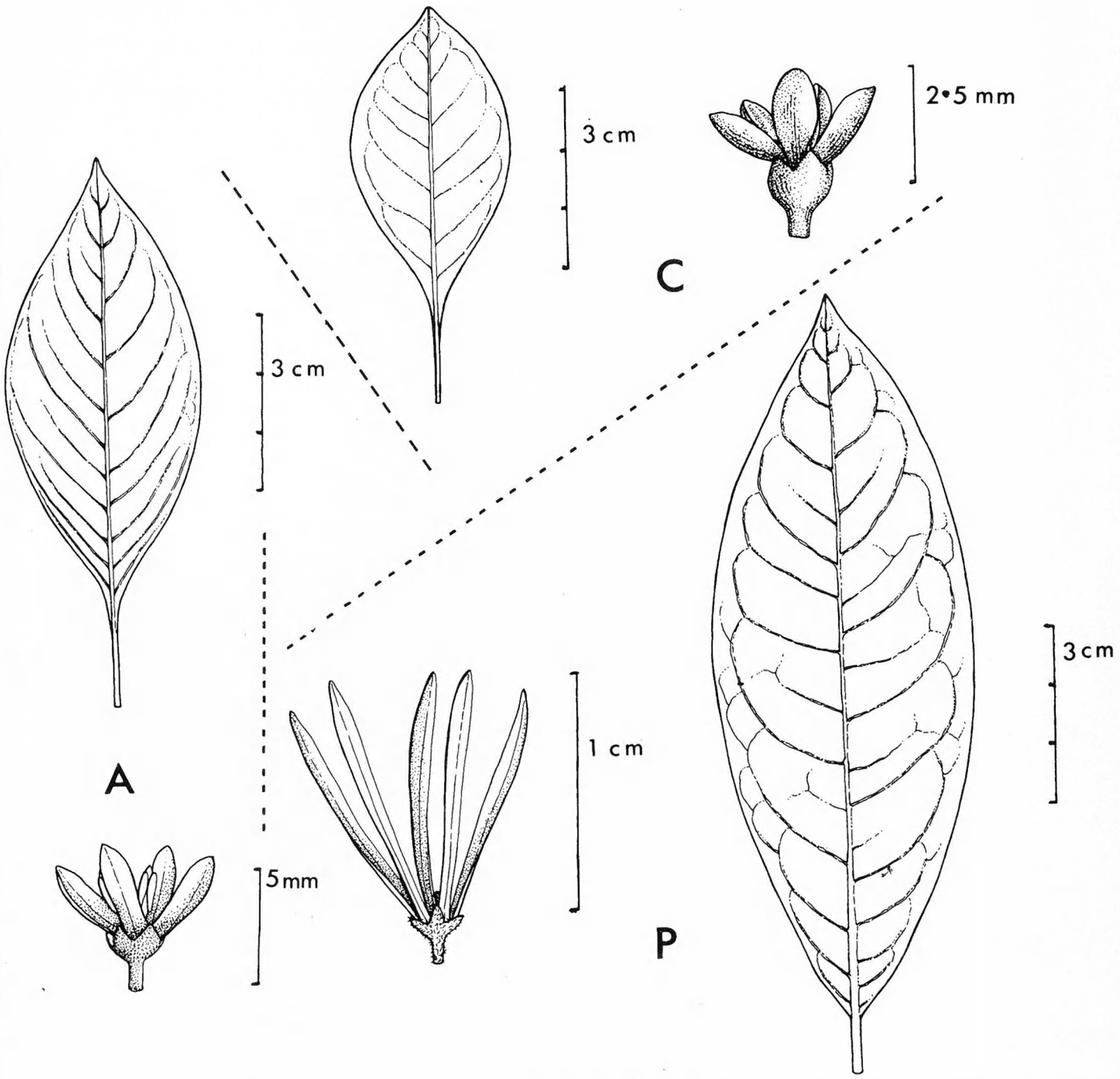

Fig. 2. Leaves and flowers of West Indian *Chionanthus* species. – A: *C. adamsii* (Scott 242 in BM). – C: *C. caymanensis* (Proctor 28138 in BM). – P: *C. proctorii* (Proctor 22206 in BM) – Drawing by Ann Davies.

Proctor during his intensive botanical exploration of the Cayman Islands.

Chionanthus proctorii Stearn, sp. nov. – Fig. 2 P

Holotypus: Jamaica, Westmoreland, Clarks Wood district, 24 April 1961, Proctor 22206 (BM).

Arbor ad 10 m alta; ramuli grisei, juventute pilis brevibus appressis pubescentes. *Folia* breviter petiolata; lamina elliptica vel anguste elliptica, apice breviter acuminata, basi cuneata, c. 6–14 cm longa, 2–6 cm lata, subtus in axillis venarum domatiis parvis albopilosis munita et secus costam sparse pubescentia, cetero glabra, pergamacea, venis primariis 5–7 utroque costae sub angulo 60–70° abeuntibus, rete venularum inconspicuo; petiolus 4–10 mm longus. *Inflorescentia* axillaris laxa pauciflora, c. 3.5–4.5 cm longa, pubescens; pedicelli 1–2.5 mm longi. *Flores* odori. *Calyx* c. 0.8 mm longus, pubescens, fere ad basim in segmenta triangularia partitus. *Corollae lobi (Petala)* albi liberi lineares, c. 10–15 mm longi, 0.6–0.8 mm lati. *Stamina* c. 1.3 mm longa; antherae ellipsoideae, c. 1 mm longae, apiculatae; filamenta c. 0.3 mm longa. *Pistillum* c. 1.5 mm longum; ovarium glabrum, in sty-

lum c. 0.8 mm longum (stigmate capitato vix lobato c. 2 mm longo incluso) contractum.

By its profuse flowers with long linear corolla lobes, this recalls *C. domingensis* Lam. *(Linociera domingensis* (Lam.) Knoblauch) but that species has leaves with much longer petioles, calyx divided only to the upper third, and pubescent ovary. Using Camp & Monachino's (1939) key it comes next to *C. jamaicensis* (Urban) Stearn (*Linociera jamaicensis* Urban) with shorter corolla lobes, longer style and deeply divided stigma, and *C. dussii* (Krug & Urban) Stearn (*Linociera dussii* (Krug & Urban) Knoblauch), a species of Martinique with longer petioles, larger inflorescence and longer and broader corolla lobes. It is named in honour of George Richardson Proctor, indefatigable collector and student of West Indian plants.

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Valantia calva, a new species from Linosa, Sicily

Salvatore Brullo

Brullo, S. 1979 02 15: Valantia calva, a new species from Linosa, Sicily. *Bot. Notiser 132:* 61–64. Stockholm. ISSN 0006-8195.

Valantia calva Brullo, sp. nov. (Rubiaceae) is described. It is a rare therophyte of volcanic lapilli on the mountain summits on the island of Linosa (S of Sicily). The chromosome number is 2n = 18. A key to the species of *Valantia* is provided, together with distribution maps. The new combination *Valantia muralis* var. *intricata* (Lojac.) Brullo is made.

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Valantia calva Brullo, sp. nov. – Fig. 1
Holotype: Italy, Linosa, Monte Vulcano, 20.4.1977 Brullo (CAT).

Planta annua, 2–9(–12) cm longa, glabra aut pilis praesertim adspersis, gracillima, caule e basi ramoso, ramis simplicibus, gracilibus, saepe intricatis, filiformibus, 4-angulato-costatis, nitidis, internodiis inferioribus sterilibus 3–9 mm longis, superioribus approximatis florigeris, spicam interruptam et foliosam formantibus. Folia verticillato-quaterna, spathulata, parvula, 1–2 mm lata, 2–4 mm longa, breviter petiolata, apice rotundata, sine mucrone. Flores hermaphroditi, 1–1,2 mm, viridi-luteoli, lobis obtusis. Corpus fructiferum juvenile erectum, hispidum, ad maturitatem deflexum, glabrum, calvum, laeve, eburneum, 1,5–2,5 mm longum, 1,4–1,8 mm latum, sine cristis fimbriatis nec rostro dorsali, apice tricorni, annulo seminifero tenuiter ciliolato. Mericarpium unicum, nigrum, laeve, ad hilum parce setulosum, 0,8–1 mm longum.

Additional material: Italy, Linosa, Montagna Rossa, 21.4.1977 Brullo (CAT).

Annual prostrate herb, branched from the base. *Stems* highly intertwined, unbranched, slender, glabrous and smooth, 4-ribbed. Lower internodes 3–9 mm, upper ones shorter. *Leaves* in whorls of 4, 1–2 × 2–4 mm, spathulate to ovate, obtuse; petiole short and narrow. *Cymes* axillary in whorls of 4, absent from the lower nodes, 3-flowered. Central flower hermaphrodite, 4-merous, lateral flowers male, 3-merous. *Corolla* yellowish green, 1.0–1.2 mm in diam. in hermaphrodite flowers, less in male ones; corolla lobes obtuse. *Stamens* epipetalous, alternating with corolla lobes; anthers yellow, 2-locular. *Style* 2-fid; stigmas capitate. Peduncles and pedicels deflexed and coalescing after anthesis to form a fructiferous corpus. *Fructiferous corpus* 1.5–2.5 × 1.4–1.8 mm, slightly compressed laterally, ivory white, glabrous (except for ventral cilia), smooth, lacking a dorsal rostrum, apically 3-horned; lateral horns horizontal, stout, central one longer, strongly bent upwards; ventral part of corpus with a cavity, bordered by short and lax cilia; each cavity with only one mericarp. *Mericarp* reniform, black, 0.8–1 mm, with short, yellowish, appressed hairs near hilum.

Distribution and habitat. This species is only known from the island of Linosa S of Sicily. It grows among volcanic lapilli at the top of the Monte Vulcano (195 m) and Montagna Rossa (187 m). The volcanic rock is here partly covered with a layer of dark purple, fine, volcanic scoriae. The habitat is very arid and sterile. *V. calva* grows in association with some other small annuals, the most frequent ones being *Catapodium marinum* (L.) C. E. Hubbard, *C. rigidum* (L.) C. E. Hubbard, *Parietaria cretica* L., *Plantago afra* L., *Rumex bucephalophorus* L., *Sedum litoreum* Guss., *Silene nocturna* L., *Trifolium scabrum* L., *Valantia muralis* L. and *Vulpia membranacea* (L.) Link. This

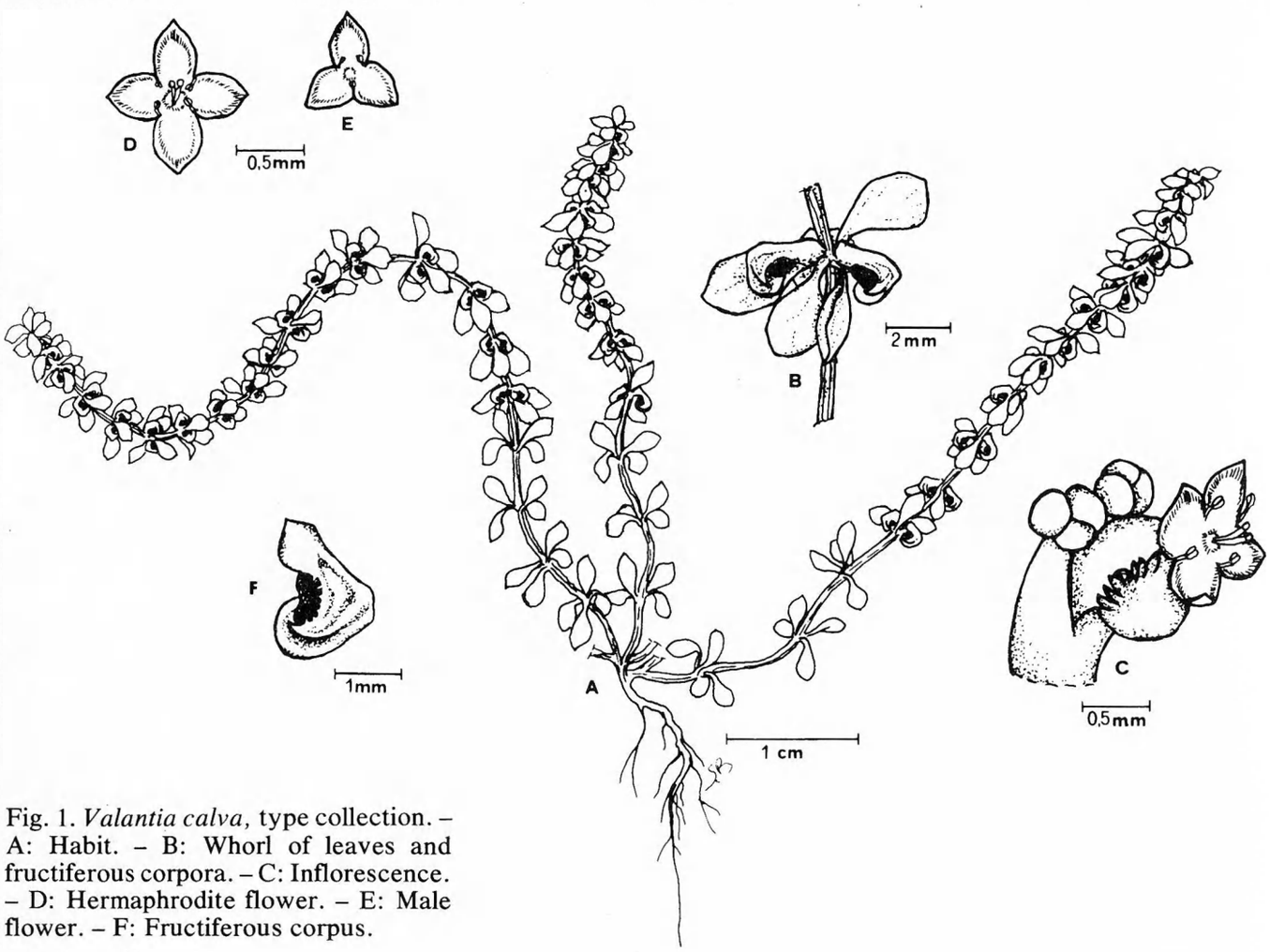

Fig. 1. *Valantia calva,* type collection. – A: Habit. – B: Whorl of leaves and fructiferous corpora. – C: Inflorescence. – D: Hermaphrodite flower. – E: Male flower. – F: Fructiferous corpus.

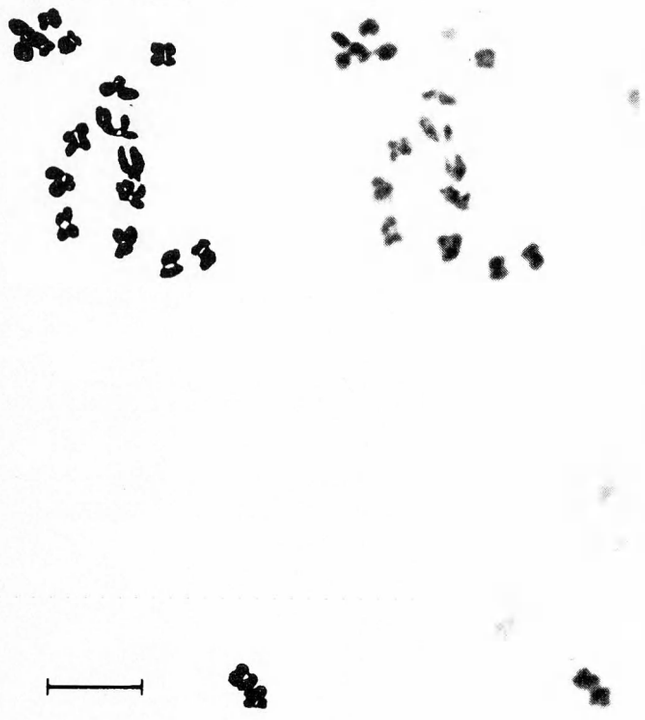

Fig. 2. *Valantia calva,* root-tip mitosis, metaphase plate. Scale 5 μm.

plant community, which must be referred to the class *Thero-Brachypodietea,* is optimally developed in March and April.

Chromosome number. The chromosome number of *Valantia calva* is 2n = 18 (Fig. 2). The counts were made from root tips of cultivated progeny from the type collection; the root tips were pretreated with 0.2 % colchicine, fixed in Carnoy, stained in Feulgen after hydrolysis in HCl, and squashed in 45 % HAc. The number 2n = 18 is known from *V. muralis* and *V. hispida* (Fagerlind 1934, 1937), while *V. aprica* has 2n = 22 (Ehrendorfer 1976).

Taxonomic relationships. The genus *Valantia* comprises five species (including *V. calva*) and is essentially Mediterranean (Fig. 3). The species differences are shown in the key below. *V. calva* seems to have affinities with *V. muralis,* but is very distinct from it (and all other species of *Valantia*) in the morphology of the fructiferous corpus (Fig. 4). Its procumbent habit and delicate, intertwined stems are also unusual

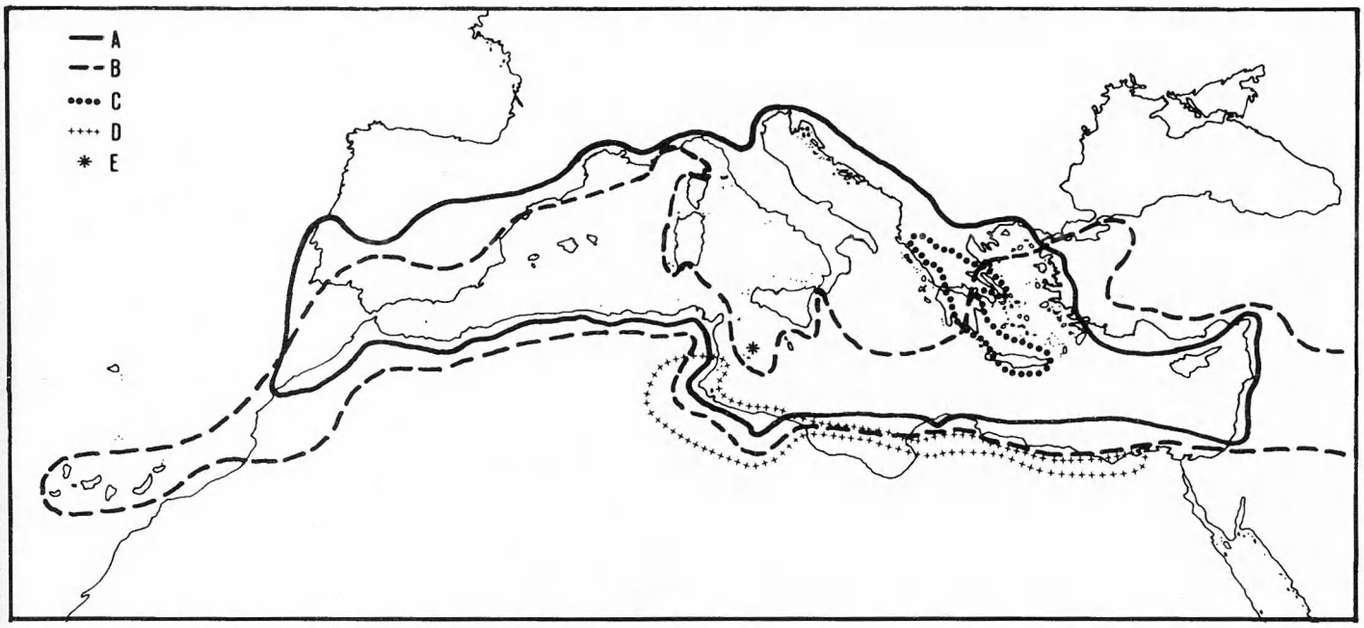

Fig. 3 Distribution of *Valantia* species according to specimens seen (CAT, FI, MPU, NAP, P, PAD, PAL, RO) and literature records. – A: *V. muralis*. – B: *V. hispida*. – C: *V. aprica*. – D: *V. columella*. – E: *V. calva*.

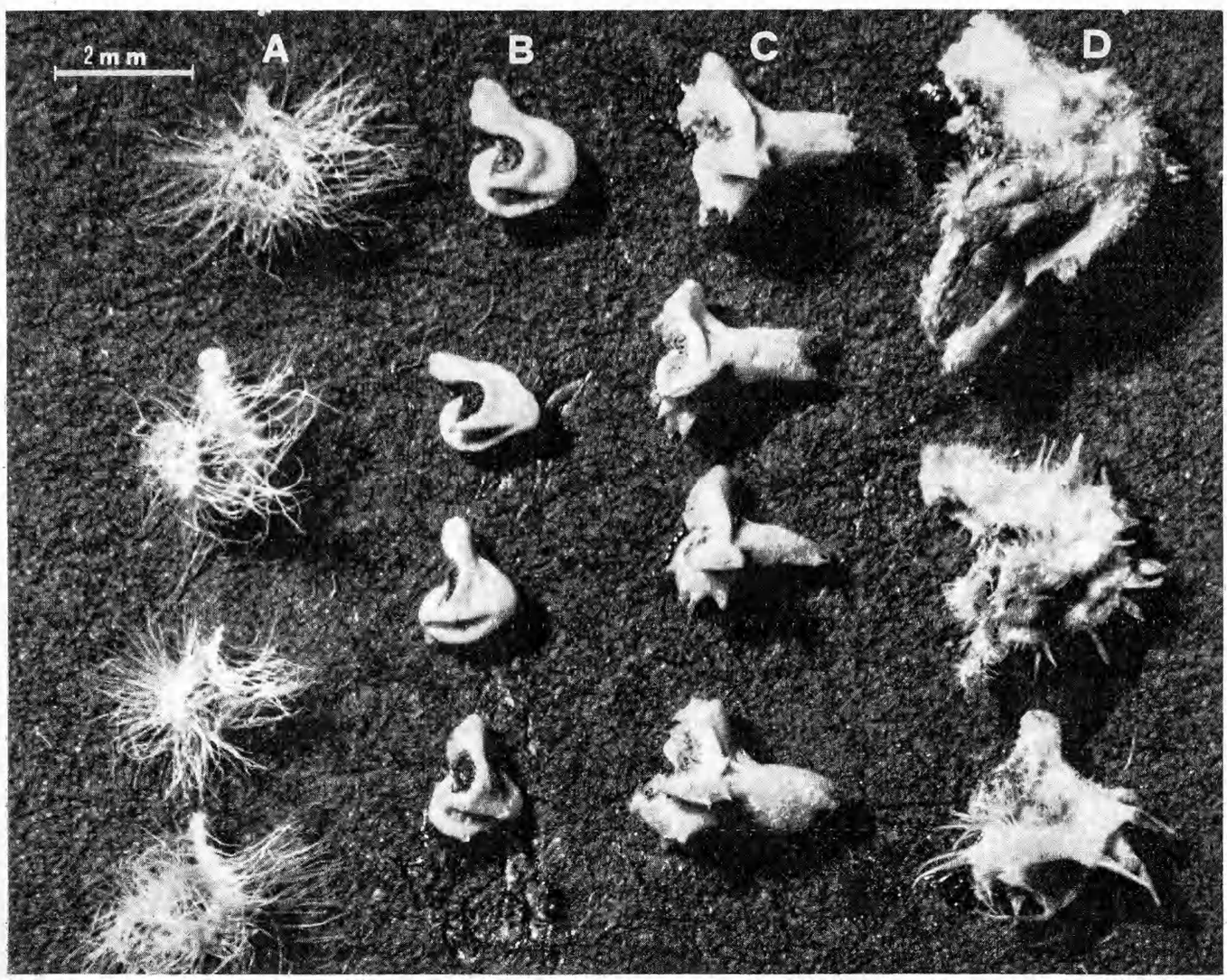

Fig. 4. Fructiferous corpora of annual species of *Valantia*. – A: *V. columella* (Cyrenaica, leg. Brullo). – B: *V. calva* (holotype). – C: *V. muralis* (Sicily, leg. Brullo). – D: *V. hispida* (Cyrenaica, leg. Brullo).

in the genus, otherwise found only in *V. muralis* var. *intricata*. *V. calva* is most likely a neo-endemic, since Linosa is a volcanic island of Quaternary age.

Key to the species of Valantia

1. Perennial. Peduncle and pedicels not incrassate, laxly enveloping the mericarps. Hermaphrodite flower 2.5 mm. Mericarp 1.4–1.6 mm ..... *V. aprica* (Sibth. & Sm.) Boiss. & Heldr.
– Annual. Peduncle and pedicels incrassate, enclosing the fruit. Hermaphrodite flower less than 2 mm. Mericarp less than 1.4 mm. 2
2. The whole plant hispid. Mericarps 2, papillose, with short, white hairs near hilum 3
– Glabrous or only slightly pubescent upwards. Mericarp 1, smooth, with short, golden-yellow hairs near hilum 4
3. Plant scabrid–hispid, 6–20 cm. Lower internodes up to 12 mm. Fructiferous corpus strongly incrassate, up to 5 mm, dorsally with straight, coarse bristles dilated at the base. Mericarp 1.1–1.4 mm ..... *V. hispida* L.
– Plant hispid, covered with setae, 1–4 cm. Lower internodes up to 4 mm. Fructiferous corpus slender, up to 2 mm (excluding setae), covered with slender setae up to 2.5 mm. Mericarp 0.5–0.8 mm ..... *V. columella* (Ehrenb. ex Boiss.) Baldacci (1893)
4. Slender, procumbent plant. Fructiferous corpus 1.5–2.5 × 1.4–1.8 mm, glabrous and smooth, without dorsal horn, ventral cavity enlarged, bordered by short and lax cilia. Mericarp projecting ... *V. calva* Brullo
– Robust plant with erect or procumbent branches. Fructiferous corpus 2–3 × 2–3 mm, with dorsal horn and three terminal crests covered with bristles; ventral cavity narrow, bordered by long and dense cilia. Mericarp entirely enclosed ..... *V. muralis* L.

Valantia muralis L. var. **intricata** (Lojac.) Brullo, comb. nov.

Basionym: *Valantia intricata* Lojacono, Fl. Sic. 2(1): 11 (1902).

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Bellevalia hyacinthoides, a new name for Strangweja spicata (Liliaceae)

Karin Persson and Per Wendelbo

Persson, K. & Wendelbo, P. 1979 02 15: Bellevalia hyacinthoides, a new name for Strangweja spicata, (Liliaceae). *Bot. Notiser 132:* 65–70. Stockholm. ISSN 0006–8195.

The oldest legitimate name for the plant usually referred to as *Strangweja spicata* (Sibth. & Sm.) Bertol. is *Strangweja hyacinthoides* Bertol. Morphological and cytological investigations show that the species is better placed in the genus *Bellevalia* as *B. hyacinthoides* (Bertol.) K. Persson & Wendelbo, forming a section of its own, sect. *Strangweja* (Bertol.) K. Persson & Wendelbo. The species is endemic to Greece.

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During work on the problem of generic delimitations within the *Hyacinthus–Bellevalia* complex, it was natural to take a closer look at the monotypic genus *Strangweja* Bertol., originally a split from *Hyacinthus*. Mostly the validity of the genus has been taken for granted, but Krause (1930) and Airy Shaw in Willis (1973) took a broad view and included it in *Hyacinthus* together with a number of smaller related genera.

An investigation showed that the karyotype of *Strangweja hyacinthoides* was identical with the very characteristic *Bellevalia* type. A reexamination of the morphological characters distinguishing *Strangweja* from *Bellevalia* as well as from other related genera, lead us to the conclusion that the two genera should be merged. Boissier (1846) had come to the same result although he changed his mind later (Boissier 1882) and kept *Strangweja* separate. *Bellevalia hyacinthoides* is separated from the other species of the genus by some characters which make it necessary to keep it in a section of its own.

Bellevalia sect. **Strangweja** (Bertol.) K. Persson & Wendelbo, comb. nov.

Basionym: *Strangweja* Bertol., Mem. Soc. Ital. Sci. Modena 21, parte fisica: 2 (1837) – *Foxia* Parl., Nuov. Gen. Spec. Monocot.: 17 (1854), nomen illeg. – *Hyacinthus* sect. Strangweia (Bertol.) Baker, Journ. Linn. Soc. 11: 424 (1871) – Type species: *B. hyacinthoides* (Bertol.) K. Persson & Wendelbo.

Inflorescence subspicate with pedicels not elongating in the fruiting stage. Bracts comparatively large. Filaments with a tooth on each side. Capsule with transversely broadly elliptic valves, emarginate at apex. Seeds pyriform.

Bellevalia hyacinthoides (Bertol.) K. Persson & Wendelbo, comb. nov. – Fig. 1

Basionym: *Strangweja hyacinthoides* Bertol., Mem. Soc. Ital. Sci. Modena 21, parte fisica: 3 (1837) – Type: Floret in horto Bot. Bononiensi Decembri decedente, et toto Januario, etiam sub dio. Patria hactenus ignota (BOLO? not seen).

Hyacinthus spicatus Sibth. & Sm., Fl. Graecae Prodr. 1: 237 (1809); non Moench (1794), nom. illeg. – *Puschkinia dubia* Kunth, Enum. Pl. 4: 338, 680 (1843) – *Bellevalia spicata* Boiss., Diagn. Pl. Or. Nov., Ser. 1, 7: 110 (1846) – *Foxia spicata* (Boiss.) Parl., Nuov. Gen. Spec. Monocot.: 17 (1854), nom. illeg. – *Strangweja spicata* (Boiss.) Boiss., Fl. Or. 5: 309 (1882), nom. illeg. – Type (syntypes): In insula Zacyntho, et in agro Argolico (OXF, not seen).

Bulb 1–2.5 cm diam., broadly ovoid; outer tunics brownish, contracted into a short neck. *Leaves* 4–8, ± lying on ground, longer than the inflorescence, elongating much during flowering,

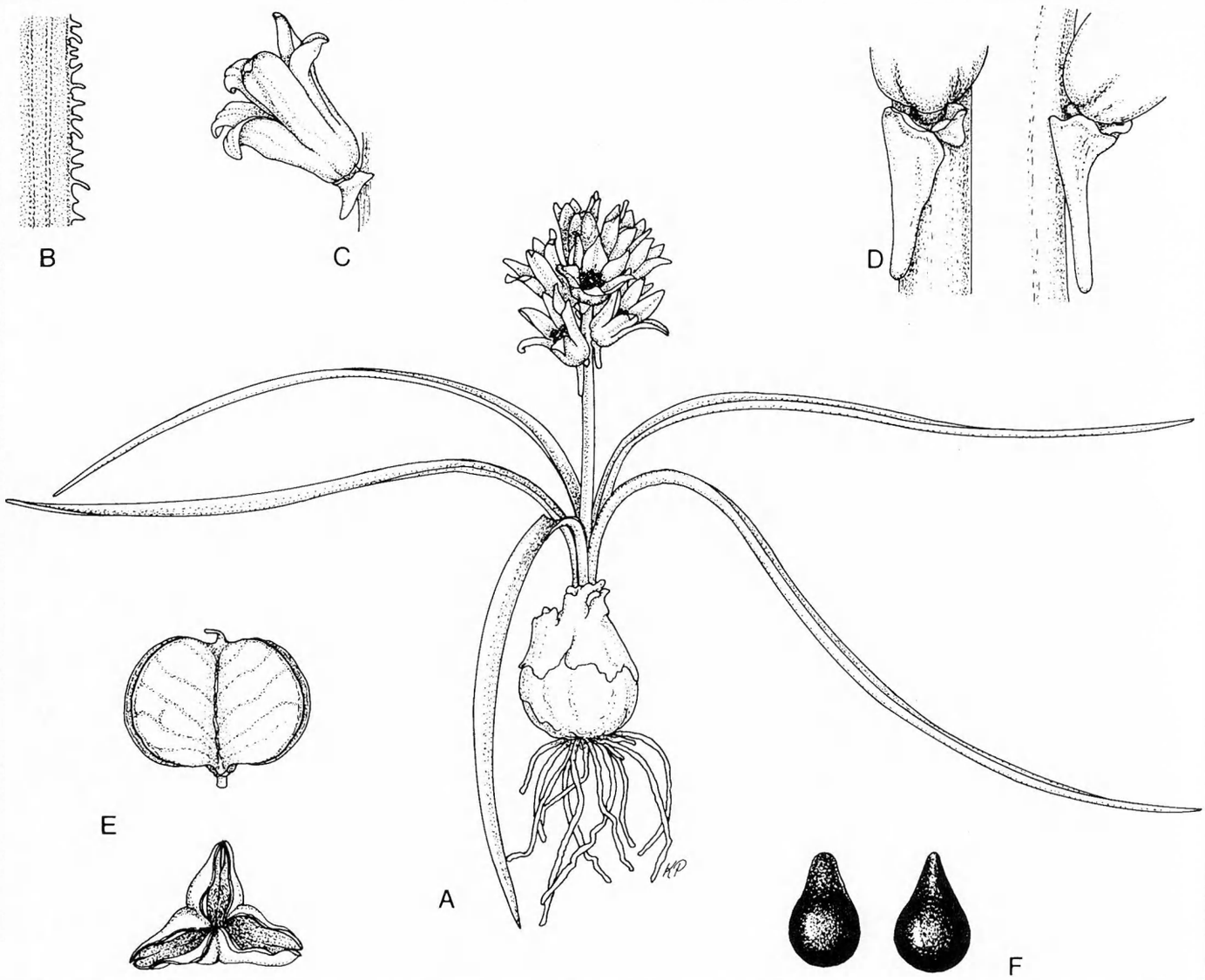

Fig. 1. *Bellevalia hyacinthoides*. – A: Habit, × 1. – B: Leaf margin, × 25. – C: Perianth with bract from middle of inflorescence, × 2. – D: Bracts from base of inflorescence, × 4. – E: Top and lateral view of fruit, × 2. – F: Seeds, ×4. – A–D: Greece, 4 km S Ligourion (Persson s.n.), E–F: Greece, Mt Parnassos (Rix 2180).

sometimes becoming up to 30 cm long, 1–3.5 (–5.5) mm broad, nearly filiform to linear, flat, dark green, margin densely and shortly ciliate, nerves sometimes papillose-scabrid below. *Scapes* 1–3, from bulb to top of rhachis 2.5–17 cm in flowering state, tinted purplish above ground. *Inflorescence* 5–13-flowered, spike-like; flowers ascending, subsessile. *Bracts* up to 5 mm long, shortly bilobed at apex, below attachment with a pinkish-lilac, long, curved spur-like lobe. *Perianth* 7–12 mm long, cylindric-campanulate with lobes somewhat recurved, pale blue; lobes two to three times as long as tube, 2–3 mm broad, narrowly elliptic-oblong, rounded at apex and obliquely mucronate. *Filaments* attached at base of lobes, about 1.5–2 mm, connate for nearly 2/3 of their length, with a 0.5 mm long tooth on each side; anthers 1.5–2 mm, violet-blue. *Ovary* with 4 ovules in each locule. *Style* 2.5 mm, cylindric, stout. *Capsule* 3-winged, chartaceous; valves about 7 mm long, 10 mm broad, transversely elliptic to subreniform, ± truncate at apex. *Seeds* 3–3.5 × 2 mm, pyriform; testa smooth, black, shiny.

Nomenclature

According to articles 63, 64 and 72 of the Code the oldest valid name for our plant will be *Strangweja hyacinthoides* Bertoloni (1837). Possibly the year of printing for this paper was 1835 (cf. Pritzel 1872) whereas the whole volume was

issued in 1837. The name *Hyacinthus spicatus* Sibthorp & Smith (1809) must be rejected as a later homonym of *Hyacinthus spicatus* Moench (1794). Often this plant has been treated as *Strangweja spicata* (Sibth. & Sm.) Bertol. following Index Kewensis vol. 1 (1895), but Bertoloni (1837) never made this combination. He compared his plant *Strangweja hyacinthoides* with *Hyacinthus spicatus* Sibth. & Sm. but could not come to a conclusion because he found the description to be 'imperfetta' and there was no illustration to compare with. The epithet *spicata* is used legitimately for our plant for the first time by Boissier (1846) in the combination *Bellevalia spicata* Boiss. *Puschkinia dubia* Kunth (1843), based on the same type material as *Hyacinthus spicatus* Sibth. & Sm. nom. illeg. and *Bellevalia spicata* Boiss. 1846, cannot be used in *Bellevalia* because of *Bellevalia dubia* (Guss.) Roem. & Schult. with the basionym *Hyacinthus dubius* Gussone 1821.

The spelling *Strangweia* instead of *Strangweja* was adopted by several authors (Boissier 1882, Halácsy 1904, Hayek 1932). But Stafleu (in litt.) is of the opinion that the original spelling of Bertoloni should be kept as he obviously tried to "latinize" the namn and his use of j instead of i was intentional. The genus was named in honour of William Fox-Strangways (1795–1865), English diplomatist and botanist.

Parlatore (1854) considered *Stranvaesia* Lindley 1837 of Rosaceae and *Strangweja* Bertol. as homonyms – both were named after Fox-Strangways. Accordingly he changed the name of the latter to *Foxia*. Post & Kuntze (1904) followed the same line of thought when they changed the spelling of both generic names to *Strangwaysia* and then concluded that they were homonyms.

Morphology

Perhaps the most useful character for recognizing the genus *Bellevalia* on flowering material is the shape of the filaments. These are fused with the perianth tube for more or less its whole length. The free parts are ± triangular, flat and usually connate at the base (Fig. 2). Feinbrun (1938–1940), who published a monograph of the genus, did not realise the importance of this character. Related genera as *Muscari, Hyacinthella, Hyacinthus* and the recently described *Alrawia* (Persson & Wendelbo 1978) all have thread-like filaments. *B. hyacinthoides* agrees with other species of the genus in the general shape of the filaments. However, it differs from most species in having distinctly toothed filaments (Fig. 2 G). Only in species like *B. ciliata* (Cyr.) Nees and *B. dubia* (Guss.) Roem. & Schult. there is a rudiment of a tooth between the free parts of the filaments (Fig. 2 B, C). See also *B. cyanopoda* Wendelbo (1967 Fig. 2 D, F).

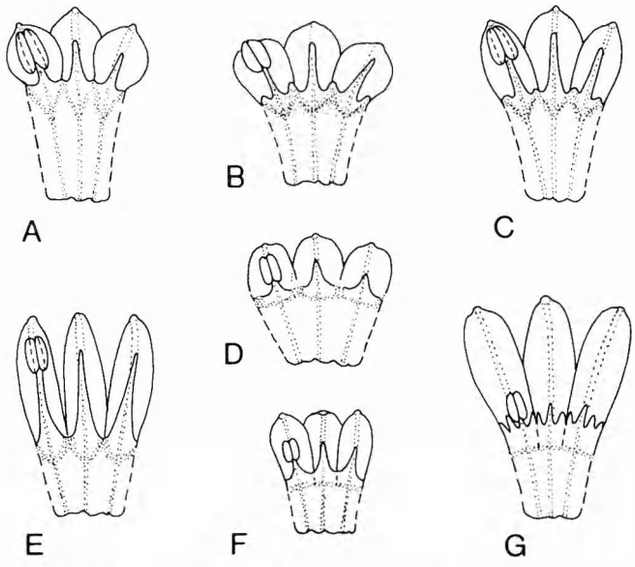

Fig. 2. Parts of dissected perianths. – A: *Bellevalia macrobotrys* Boiss. – B: *B. dubia* (Guss.) Roem. & Schult. – C: *B. ciliata* (Cyr.) Nees – D: *B. pycnantha* (C. Koch) Los. – E: *B. romana* (L.) Reichenb. – F: *B. tabriziana* Turrill – G: *G. hyacinthoides* (Bertol.) K. Persson & Wendelbo, × 2.

The genus *Strangweja* was mainly based on the character of the toothed filaments, but this cannot be considered important enough to be used as a generic character. In the genus *Allium* all species of the section *Allium* have the three inner filaments toothed, whereas most species of the other sections have entire filaments. The similarity between *Bellevalia hyacinthoides* and species of *Puschkinia* in the shape of the filaments pointed out by Kunth (1843) when he treated the former as *Puschkinia dubia,* is certainly superficial. This latter genus is, judged from fruit characters, probably more closely related to sections of *Scilla*.

Other more prominent features of *Bellevalia hyacinthoides* are the subspicate inflorescence, the comparatively large bracts with a long recurved basal lobe, the deeply lobed perianth and the pyriform seeds (Fig. 1).

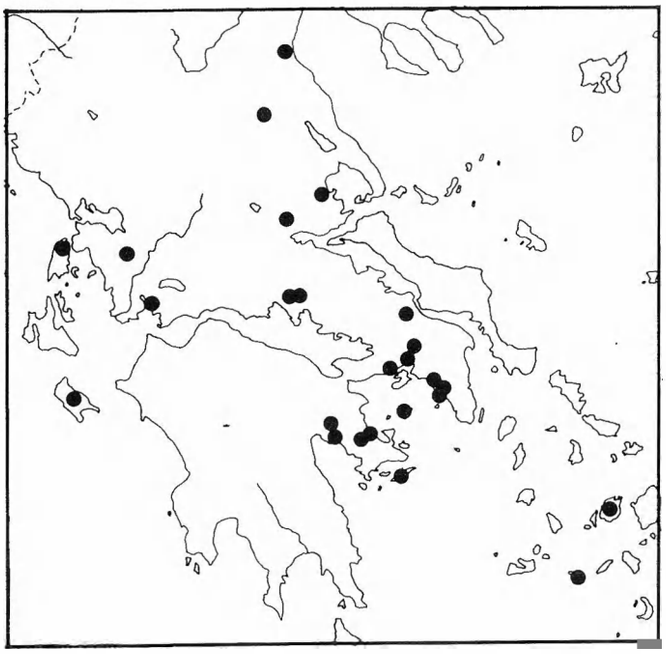

Fig. 3. *Bellevalia hyacinthoides*. Total known distribution (Greece). Based on herbarium material at ATH, ATHU, G, GB, K, LD.

A dense subspicate inflorescense is otherwise found in *B. turkestanica* Franch. of the C Asiatic, monotypic section *Muscarioides,* in *B. desertorum* Eig & Feinbrun and *B. sessiliflora* (Viv.) Kunth of the section *Patens* subsect. *Cavarea,* and in *B. densiflora* Boiss. together with *B. nivalis* Boiss. & Kotschy of subsect. *Romana*.

As regards the bracts the difference between *B. hyacinthoides* and other species of the genus is rather quantitative than qualitative. Also in *B. romana* (L.) Reichenb. the bracts of the lowermost flowers are rather large and coloured like those of *B. hyacinthoides*.

The deeply divided perianth of *B. hyacinthoides* (Fig. 1 C) with spreading and somewhat recurved lobes is characteristic but again in *B. romana* the perianth is split halfway and sometimes more, and the lobes are somewhat recurved. The perianth is in the latter white – sometimes pale bluish as in *B. hyacinthoides* – but turns lurid (cf. Bot. Mag. tab. 939 sub *Scilla romana).* This change of colour is seen in most *Bellevalia* species but does not seem to occur in *B. hyacinthoides*.

The smooth seed testa is, together with the shape of the filaments, the most distinctive character of the genus *Bellevalia*. The pyriform shape of the seed of *B. hyacinthoides* (Fig. 1 F) seems to distinguish this species from the other species of the genus. Feinbrun (1938 p. 134) stated in a general description of seed characters of *Bellevalia* that the seeds may rarely also be pyriform, but we cannot find any reference to this seed shape in the descriptions of any of the species. They all seem to have broadly ellipsoidal or more or less globular seeds (Feinbrun 1940 p. 336). Still we would not attach too much importance to this difference between *B. hyacinthoides* and other species.

B. hyacinthoides has a ciliate leaf margin (Fig. 1 B) as most of the species of *Bellevalia*.

Ecology and distribution

Little information is to be gained from the labels about the ecology of *Bellevalia hyacinthoides*. It is found at altitudes from near sea level up to about 1000 m, on dry, stony slopes and in abandoned fields and may also be seen in olive groves. *B. hyacinthoides* is endemic to Greece where it is reported mainly from the coastal regions of the S and C parts (Fig. 3). In the Kikladhes it is so far only found on the islands of Paros and Folegandros. Due to the early flowering and its small size this species has certainly been overlooked in many places.

The flowering period starts at the end of January and finishes in April or possibly later in localities at higher altitudes.

Cytology

Two collections were investigated, one from Mt Parnassos, 1000 m (Rix 2180), the other from Litochoron near Mt Olympus, 70 m (Persson s.n.). The root tips were pretreated in a mixture of 0.6% colchicine and 2 mM 8-hydroxyquinoline (1:1) and then stained according to the usual Feulgen squash method. The idiogram was based on measurements of ten metaphase plates. The nomenclature for centromeric positions follows Levan et al. (1965).

B. hyacinthoides was found to have 2n=8 (Fig. 4) with one pair of m chromosomes, two pairs of sm and one pair of st chromosomes, thus closely following the general *Bellevalia* scheme as represented in the majority of the species studied (Bentzer, Bothmer & Wendelbo 1972, Bothmer & Bentzer 1973, Feinbrun 1938, Garbari 1968, Levan 1944, Pogosjan 1975). There were no variations in chromosome morphology and no satellites were found, otherwise a common

though variable feature of the *Bellevalia* karyotype.

The genus *Bellevalia* is clearly distinguished from all the related genera in its karyotype: the chromosomes are few, large and have a characteristic morphology.

Conclusions

Summing up one may conclude that *Bellevalia hyacinthoides* cannot be referred to a separate genus. All important caryological and morphological characters agree with those of the genus *Bellevalia*. Such characters are the number, size and morphology of the chromosomes, the general shape of the perianth including the filaments, the shape of the capsule and the smooth seed testa. The distinctly toothed filaments and the pyriform seeds are, however, features that grant this species a somewhat isolated position within the genus as a member of a monotypic section *Strangweja*. There is a considerable similarity between *B. hyacinthoides* and *B. romana*, and this similarity may be more than casual. Crossing experiments between these two species and also others might give a clue to real relationships.

Acknowledgements. We are much indebted to Dr Elisabeth Georgiadou, Goulandris Natural History Museum, Athens, and Dr M. Dittrich, Conservatoire botanique, Genève, for loan of material; to Dr Pauline H. Haritonidou, Botanical Museum, University of Athens, and Mr B. Mathew, Royal Botanic Gardens, Kew, for living bulbs and lists of herbarium material, and to Dr F. Stafleu, Utrecht, for comments on some nomenclatural problems. The present study was supported by grants from the Swedish Natural Science Research Council.

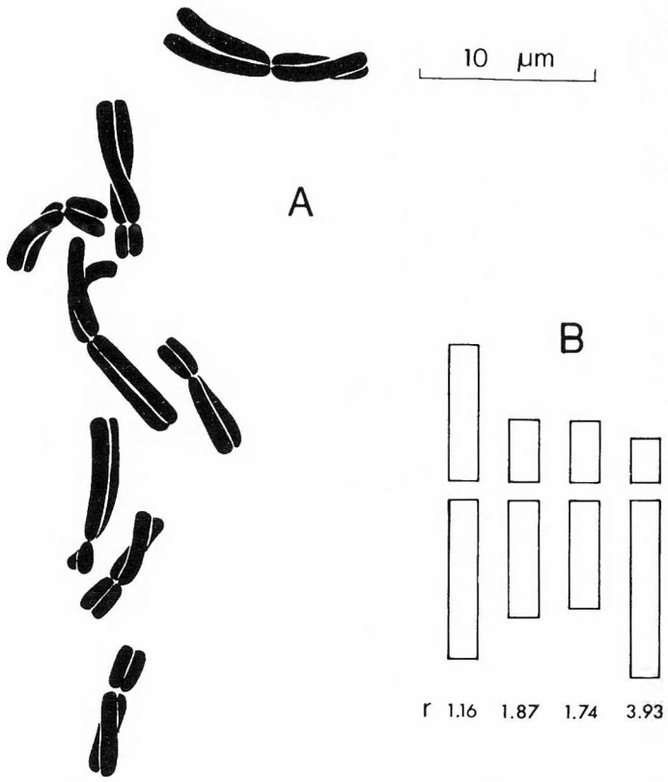

Fig. 4. *Bellevalia hyacinthoides*. – A: Mitotic metaphase (Greece, Litochoron, Persson s.n.). – B: Idiogram (Greece, Mt Parnassos, Rix 2180). r = mean values for arm indices.

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Chrysochromulina cyathophora (Prymnesiophyceae), a new species from Danish coastal waters

Helge Abildhauge Thomsen

Thomsen, H. A. 1979 02 15: Chrysochromulina cyathophora (Prymnesiophyceae), a new species from Danish coastal waters. *Bot Notiser 132:* 71–76. Stockholm. ISSN 0006-8195.

Chrysochromulina cyathophora Thomsen, sp. nov. is described on the basis of electron microscopical examination of shadowcast whole mounts. The water samples yielding this new species originate from the western Baltic, the Great Belt and the southern Kattegat, Denmark, in October 1975 and June 1976. The subspherical cell possesses two smooth flagella and a short coiling haptonema. The cell surface is covered by two layers of scales. The inner scales are circular, flat, with very fine concentric ridges on the distal surfaces. The outer scales are narrow cylinders, without any conspicuous ornamentation but with a characteristic decrease in wall thickness two thirds from the base.

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The present paper is part of a series of investigations on Danish marine nanoplankton based upon material collected during four cruises in the Kattegat and western Baltic in the period October 1975 to June 1976 (cf. Thomsen 1977 a, b, 1978, Thomsen & Oates 1978).

The electron microscopical examination of this material – approximately 500 grids – has shown that independent of season and geographical position within the area, any water sample will hold one or more species of *Chrysochromulina* (Prymnesiophyceae, formerly Haptophyceae). Unfortunately, however, species of *Chrysochromulina* often appear on the preparations as incomplete cells with discarded appendages, or merely as isolated groups of scales, in most cases probably as a result of injuries during the processing for electron microscopy. It thus applies to *C. cyathophora* sp. nov. that isolated groups of scales were recognized long ago and that incomplete cells have been observed repeatedly. Generic authentication was, however, not achieved until quite recently when during the examination of whole mounts prepared from an Arkona Basin water sample, a complete cell turned up showing a coiling haptonema between two smooth flagella.

Chrysochromulina cyathophora Thomsen, sp. nov.

Cellula subsphaerica, exsiccatione complanata circiter 3 (2.9–3.3) μm diam. Flagella bina 10–12 μm longa, haptonema extensum circiter 7 μm longum. Squamae dimorphae, interioribus laminaribus, exterioribus poculiformibus. Squama interior circularis, circiter 0.8 μm diam., in pagina extrorsa carinis concentricis circiter 0.01 μm distantibus ornata. Squama exterior e parte cylindrica, subrecta, 0.5–1.1 μm longa circiter 0.2 μm diam., basi crassa, in parte tertia superiore subito multo tenuiore et lamina basali in pagina introrsa juxta marginem striis radialibus indistinctis ornata composita.

In aqua 11.1 graduum Celsii salinitatis 16.5‰ inventa die 21 Octobris anni 1975 prope pagum danicum Kolby Kaas (lat. bor. 55°48′, long. orient. 10°30′) e summo mari hausta, figuris typificis hic appositis 4 A cum partibus magis magnificatis 3 B, E, 4 B, C monstrata.

Cell subspherical, c. 3.0 μm (2.9–3.3 μm) in diameter when dry; two flagella 10–12 μm long and a haptonema c. 7 μm long when extended. Scales of two kinds. Inner scales plate-like,

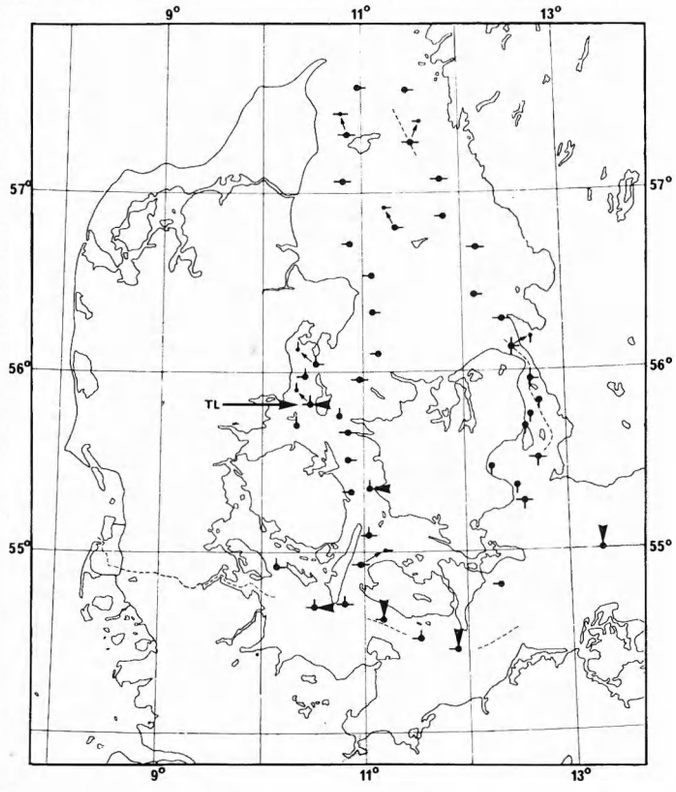


Fig. 1. Map showing all the stations where samples were taken in October 1975 (●–), January 1976 (●), March 1976 (–●) and June 1976 (●). Arrows indicate samples from 10 m depth. The finding places of *C. cyathophora* are indicated by big arrowheads. The type locality is marked with TL and an arrow.

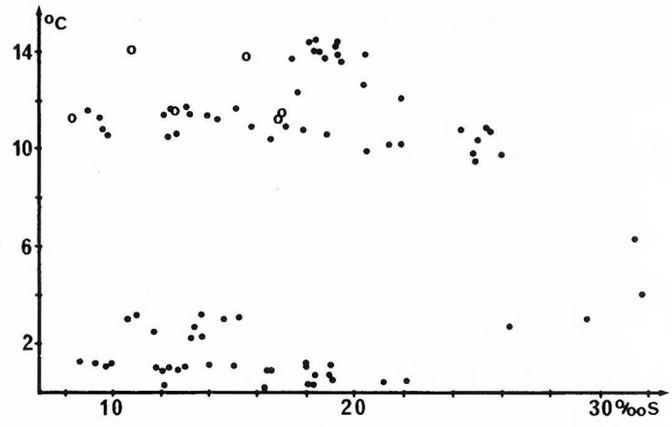


Fig. 2. Temperature/salinity diagram comprising all the water samples examined (cf. Fig. 1). The water samples yielding *C. cyathophora* are marked with open circles.

circular, approximately 0.8 μm in diameter, with a pattern of concentric ridges on the distal surface (c. 10 per 0.1 μm). Outer scales cylindrical, almost straight-sided, diameter c. 0.2 μm, 0.5–1.1 μm long, and proximally attached to a base-plate. The proximal base-plate surface is indistinctly radially striated at the periphery. The thickness of the cylinder wall decreases abruptly about two thirds from the base.

Type specimen, as shown in Fig. 4 A with details in Figs. 3 B, 4 B, C, found in a surface water sample collected near Kolby Kaas (55°48′N, 10°30′E) (Fig. 1) on October 21, 1975 (11.1°C, 16.5 ‰ S).

Material and methods

All the observations presented have been carried out on shadowcast whole mounts prepared from freshly collected sea-water samples. Fig. 1 shows all the localities where *C. cyathophora* was found. The temperature and the salinity of the water samples with *C. cyathophora* are shown diagrammatically in Fig. 2.

Whole mounts were made from filtered (20 μm) surface water samples collected by means of a 5 l non-toxic water bottle. The material was concentrated by gentle centrifugation. Small drops of the re-suspended pellet of material were pipetted onto carbon/formvar coated grids, fixed in osmic vapour for approximately 30 seconds and subsequently left for drying. The grids were washed in redistilled water for about 10 minutes in order to remove salt crystals. When completely dry, the grids were stored in gelatine capsules.

Whereas the above mentioned steps of procedure were accomplished on board "Martin Knudsen", the subsequent handling of the grids took place at the Institut for Sporeplanter, University of Copenhagen. The grids were shadowcast with gold/palladium and examined in the JEM-T8 electron microscope of the institute.

Observations

The description of *C. cyathophora* sp. nov. is based on electron microscopical examination of seven specimens only, four of which are shown in Figs. 3, 4.

Fig. 3. *Chrysochromulina cyathophora*. – A: Part of cell with numerous cylinder-scales. The scale-case formed by the imbricated, circular inner scales is clearly visible (arrowheads). The arrow points to a cylinderscale base-plate on which a very coarse radiating pattern is discernible. Micrograph T 998, × 15,000. – B: Cylinder scale. Note the abrupt change of wall thickness. Micrograph T 1856, × 40,000. – C: Whole cell with numerous cylinder scales. Micrograph T 1730, × 7,500. – D: Whole cell with two flagella and partially coiled haptonema. Micrograph T 1817, × 9,000. – E: Two flattened cylinder scales. Micrograph T 1857, × 50,000.

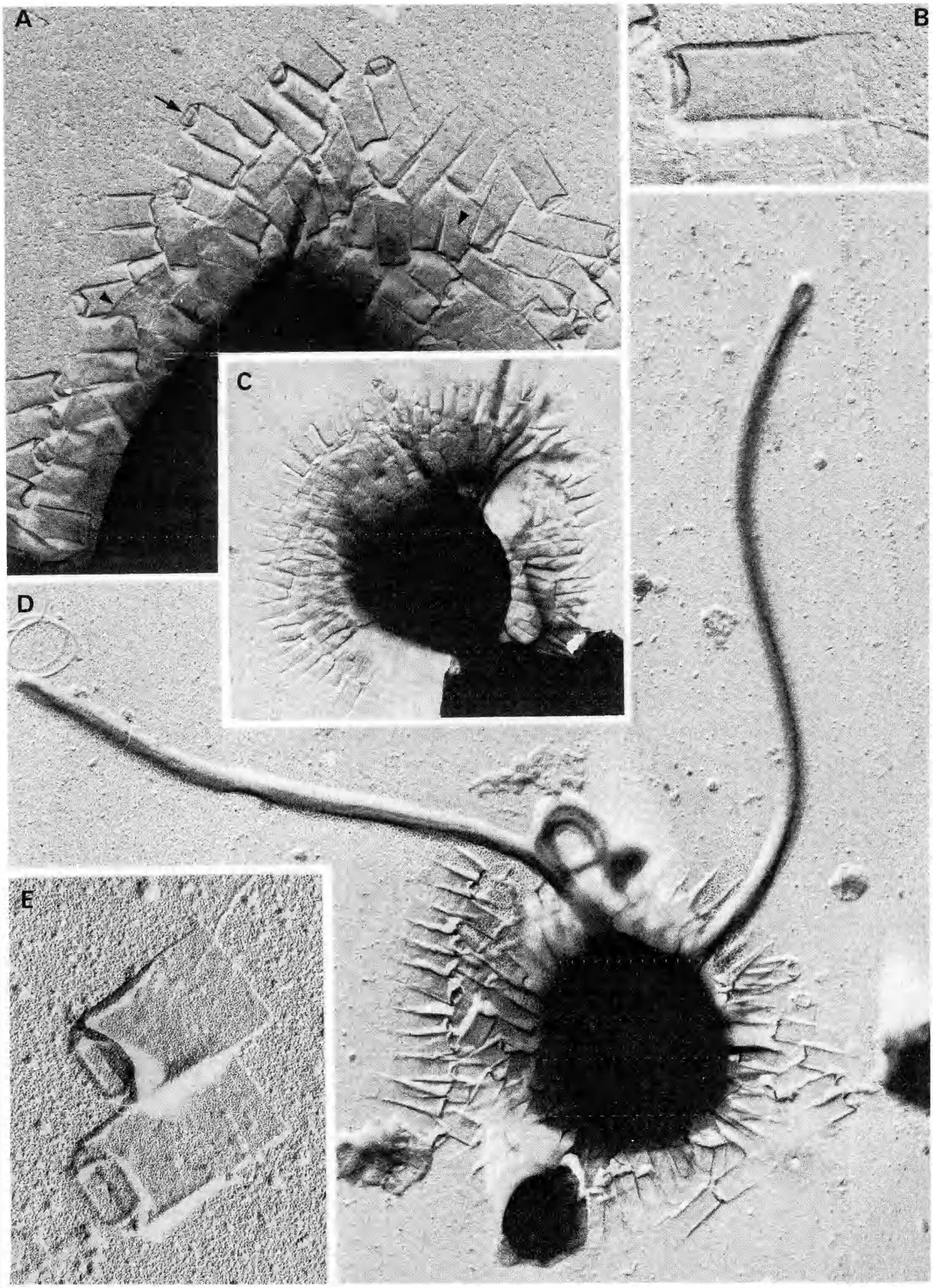

A
B
C
D
E

Fig. 3 D shows the only complete cell observed. Two smooth flagella, 10–12 μm long, and a somewhat shorter coiling haptonema (c. 7 μm long when extended) arise close together from an almost spherical protoplast (c. 3 μm in diameter). It should be remembered that cell measurements based upon whole mounts of cells are almost certainly underestimates (in particular cell diameter).

A closer inspection of e.g. Fig. 4 A shows that the cell is covered by scales of two types. The outer cylindrical scales are so numerous and firmly linked together that the inner circular scales are only rarely visible (Fig. 4 C). Once recognized, however, the scale-case formed by the imbricated plate-scales can be identified from almost any micrograph. This armour of plate-scales appears as a clearly delimited area (cf. Figs. 3 A, 4 A, arrowheads). The conspicuous size difference between the protoplast proper, which appears dark in Fig. 4 A, and the plate-scale casing (Fig. 4 A, arrowheads) is a rough estimate of the protoplast size reduction caused by the preparation technique.

The thin-walled cylindrical outer scales are nearly straight-sided. The diameter of the apparently completely collapsed anterior end is 0.20–0.25 μm, whereas the base-plate – mostly appearing rectangular when dried down on the grid surface – has a diameter ranging from 0.16 μm to 0.19 μm. The wall thickness changes abruptly above the middle of the cylinder (Figs. 3 B, E, 4 C). The proximal surface of the base-plate shows a rather indistinct peripheral pattern of coarse radiating ridges (Figs. 3 A, 4 A, arrows). Attempts have been made to count the number of cylinder scales scattered around the *C. cyathophora* protoplasts. In each case the number was approximately 125. This is certainly an underestimate, the total number probably being more than twice this figure.

Direct evidence that the *C. cyathophora* scales are true cylinders cannot be drawn from whole mounts alone. However, the striking similarity – when comparison is based upon whole mounts – between the outer scales of *C. cyathophora* and the cylinder scales of *C. microcylindra* Leadbeater and *C. megacylindra* Leadbeater (both examined by thin sectioning of embedded material, see Leadbeater 1972 and Manton 1972 a), strongly speaks in favour of the assumption that the outer scales of *C. cyathophora* are also true cylinders.

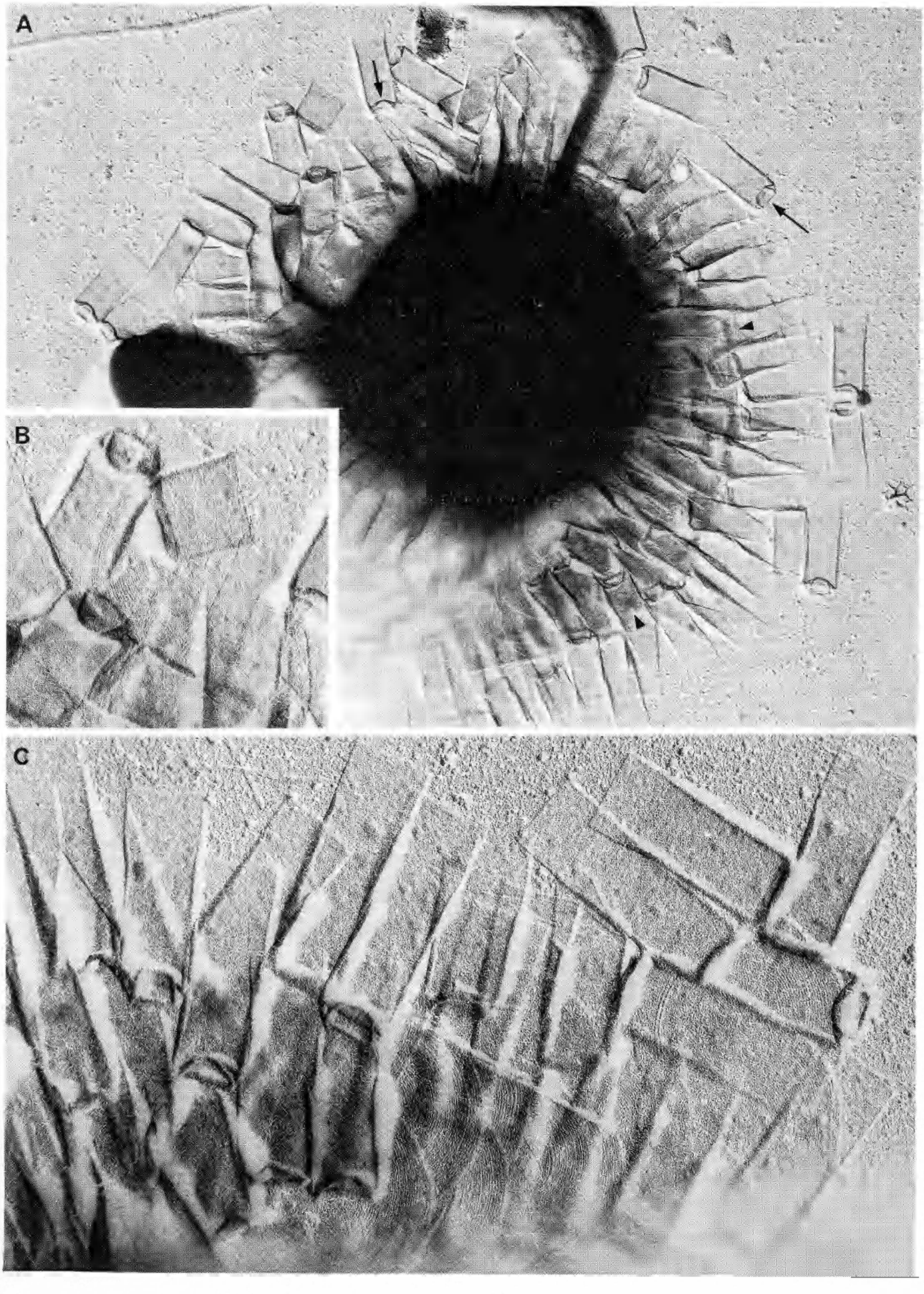
The inner scale layer consists of circular, plate-like scales, approximately 0.8 μm in diameter (0.78–0.83 μm). Due to the relatively weak tendency of the periplast to fracture, only the distal surface of these scales are known. A very delicate arrangement of concentric ridges with a periodicity of c. 10 nm covers the whole plate.

Discussion

Generic authentication of the present species was made possible thanks to the fortunate find of a complete cell carrying two flagella and a coiling haptonema. The latter characteristic is considered by e.g. Manton & Leadbeater (1974) as being a significant taxonomic criterion for separating species of *Chrysochromulina* from species of *Prymnesium* and *Phaeocystis* (it should be emphasized perhaps that the genus *Chrysochromulina* as presently circumscribed comprises species also without the capacity of helical haptonema coiling such as *C. mantoniae* Leadbeater (Manton & Leadbeater 1974) and *C. spinifera* (Fournier) Pienaar & Norris, cf. Parke & Dixon 1976). As furthermore the scale-types associated with *C. cyathophora* are definitely related to those of *C. microcylindra* Leadbeater and *C. megacylindra* Leadbeater it seems fully justified to refer the present species to the genus *Chrysochromulina*.

Whereas the *C. cyathophora* scales – especially the cylinders – are somewhat similar to those known from other species of *Chrysochromulina*, the plate-scales of the present species show characteristics which alone are sufficient to distinguish *C. cyathophora* from all electron microscopically investigated *Chrysochromulina* species. The characteristic pattern of delicate

Fig. 4. *Chrysochromulina cyathophora*. – A: Whole cell with partially discarded appendages. Arrows point to cylinder-scale base-plates showing coarse radiating ridges. The scale-case formed by the circular inner scales is marked with arrowheads. Micrograph T 920, × 15,000. – B: Detail from Fig. 4 A showing two circular scales with fine concentric ridges. Micrograph T 1854, × 40,000. – C: Detail from Fig. 4 A. Several imbricated circular scales with concentric ridges visible at the bottom of the picture. Micrograph T 1855, × 40,000.


A
B
C

concentric ridges on the entire distal scale surface is not parallelled by any known member of this genus. In some species (e.g. *C. microcylindra, C. megacylindra, C. mactra)* somewhat similar concentric ridges are present but only as a peripheral band. Manton (1972 b) interprets the plate-scale of *C. mactra* as a reduced two-layered scale, the main modification being elimination of the central part of the upper concentrically striated layer. Correspondingly, the plate-scales of *C. cyathophora* may be interpreted as representing a "primitive" type of scale where no elimination of upper layer material has taken place. Sections of plate-scales will be needed, however, to clarify this.

C. cyathophora is closely related to *C. megacylindra* and *C. microcylindra*. The cylinder scales from these three species, although basically similar, can be distinguished mainly on the basis of the cylinder diameter and the ornamentation of the proximal base-plate surface.

Whereas *C. cyathophora* is thus easily distinguished from all other *Chrysochromulina* species investigated by electron microscopy, the possibility cannot be excluded that this new species is conspecific with *C. orbiculata* Rouchijainen (Rouchijainen 1972; description based on light microscopy only), as is also a possibility with four other species (*C. minor, C. fragilis, C. adriaticus* and *C. pyramidosa,* cf. Thomsen 1977 p. 152).

From Fig. 2 it appears that *C. cyathophora* has only been observed in 6 out of 86 water samples examined. The water samples yielding *C. cyathophora* all fall within the intervals of 8–17 ‰ S and 11–14°C. The lack of samples from the temperature interval between 5 and 10 °C naturally has to be taken into consideration. In general words *C. cyathophora* seems to be a non-characteristic member of the nanoplankton flora of this area, when appearing confined to relatively warm, brackish water.

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Microfungi on Dryas

Lennart Holm

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The Ascomycete flora on *Dryas* (Rosaceae) has been investigated. An annotated list is given of the 16 species found with publication of the following new names. Discomycetes: *Allophylaria dryadis* Nannf. ex L. Holm, sp. nov., *Hypoderma dryadis* Nannf. ex L. Holm, sp. nov., *Odontotrema alpinum* (Sacc.) L. Holm, comb. nov. – Pyrenomycetes bitunicati: *Epipolaeum absconditum* (Johanson) L. Holm, comb. nov., *Leptosphaerulina dryadis* (Starb.) L. Holm, comb. nov., *Stomiopeltis dryadis* (Rehm) L. Holm, comb. nov.

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Dryas (Rosaceae) is a genus of arctic-montane creeping dwarf shrubs. It comprises a few nearly related taxa; according to Hultén (1959) "three or possibly four species: *D. octopetala, D. integrifolia, D. Drummondii* and (possibly) *D. grandis*". *Dryas octopetala* is the most widely distributed species and the only one occurring in Europe. Its close ally *D. integrifolia* is found from E Siberia through arctic America to Greenland, intergrading freely with *D. octopetala*. *D. drummondii* finally, well characterized by its drooping flowers with yellow petals, is altogether American, mainly confined to the NW. Distribution maps have been published by e.g. Hultén (1959).

Dryas octopetala is a renowned plant, as a zone fossil of Late-glacial clays. Like its congeners it has considerable mycological merits, too, since it is the host of quite a number of interesting microfungi. Apparently these plants offer an attractive substrate; the coriaceous leaves are long persistent (though generally annual) and the tomentum of the leaf underside may reduce evaporation, providing a favourable micro-habitat for fungi.

Most *Dryas* fungi are not known to occur on other hosts; the exceptions are *Gibbera polyspora* and possibly *Leptosphaerulina dryadis*, which might be identical with *L. pulchra* (on *Potentilla*). Apart from this case the mycoflora on *Dryas* has no rosaceous character; it is rather more reminiscent of the fungal flora on Ericaceae, particularly *Cassiope tetragona* (cf. Holm 1975) which is often a companion of *Dryas*. Little is known with certainty about the frequency and distribution of these fungi. No doubt *Mycosphaerella octopetalae* is the most common; it is perhaps a constant companion of *Dryas*. Judging from my experience several other species are also common, or rather common, like *Cainiella johansonii, Isothea rhytismoides, Melanomma dryadis, Stomiopeltis dryadis* and *Wettsteinina dryadis*.

With regard to their ecology these fungi are strikingly specialized, not only being restricted to *Dryas* but generally to some particular part of the host. A conspicuous example is provided by *Melanomma dryadis*, confined to the flowers. Most species are foliicolous, but they are often restricted to one leaf side. *Hypoderma dryadis, Epipolaeum absconditum, Isothea rhytismoides, Mycosphaerella octopetalae* and *Stomiopeltis dryadis* are all epiphyllous, whilst *Allophylaria dryadis* is strictly hypophyllous. Judging from the scanty material available, *Odontotrema alpinum, Gibbera polyspora* and *Sphaerotheca*

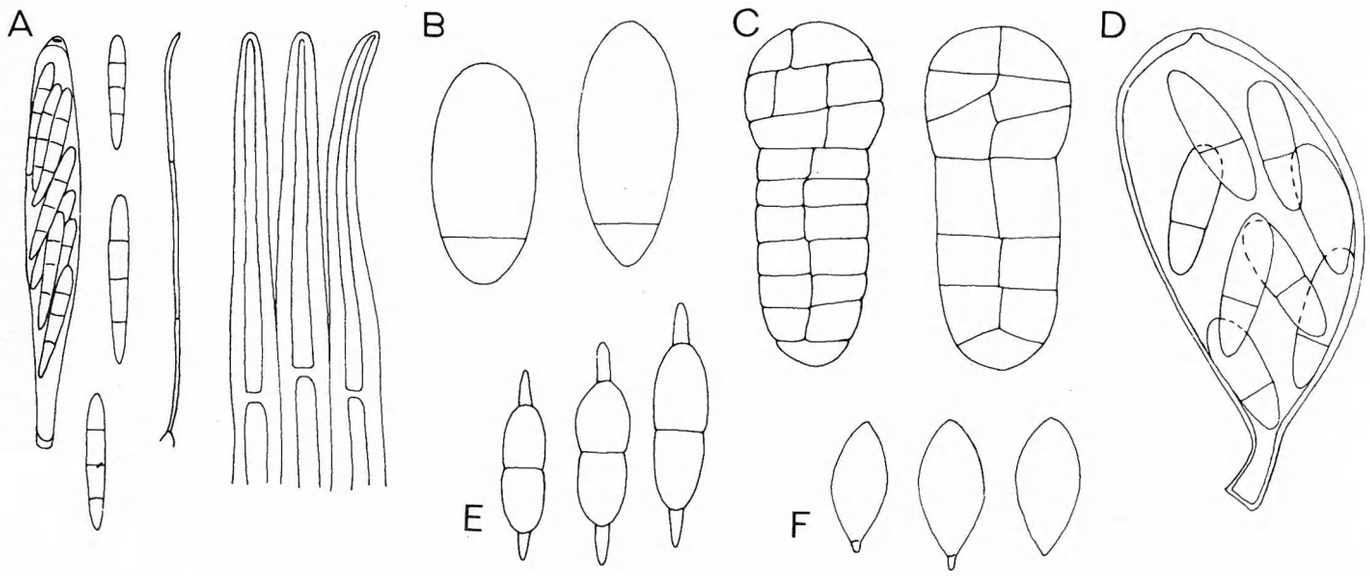


Fig. 1. A: *Allophylaria dryadis,* ascus, spores, paraphysis and hairs. – B: *Pseudomassaria islandica,* spores. – C: *Leptosphaerulina dryadis,* spores. – D: *Epipolaeum absconditum,* ascus. – E: *Gnomonia dryadis,* spores. – F: *Gnomoniella vagans,* spores. – All × 1000.

volkartii are hypophyllous, too. Only a few species occur in both leaf sides, viz. *Cainiella johansonii, Pseudomassaria islandica* and *Wettsteinina dryadis,* the first-mentioned evidently preferring veins and pedicels. As far as is known *Gnomonia dryadis* and *Gnomoniella vagans* are bound to leaf and flower stalks.

Several investigators have paid attention to the *Dryas* fungi, from Babington (1839) to Barr (1959). Especially noteworthy in this field are the contributions of the lynx-eyed Carl Johan Johanson (1884). His premature death in 1888, when trying to save a drowning boy, was a lamentable loss to mycology. Since the 1950'ies professor J. A. Nannfeldt has been engaged in a study of these fungi, and for this purpose has scrutinized numerous sheets of *Dryas octopetala* in UPS from Scandinavia and the Arctic. His studies have been very fruitful and have i.a. resulted in the discovery of two new species, viz. *Allophylaria dryadis* and *Hypoderma dryadis*. Unfortunately Dr Nannfeldt has not found the time to complete the work, and as I got involved in the *Dryas* fungi when working through my fungus collections from Iceland, made in 1971, he asked me to take over the job. It is a pleasant duty to thank him for this interesting task and for much valuable advice and information.

This investigation is based mainly on the collections of *Dryas* fungi in UPS (many of them extracted from the phanerogame herbarium) and if nothing else is stated the material cited is preserved in UPS. Some further collections have been borrowed from C, PAD and S; my sincere thanks are due to the curators of these institutions. I am also very much indebted to my wife, fil. lic. Kerstin Holm, for her assistance.

The present article is a brief survey of the ascomycetes on *Dryas* known to me. I hope that it will be serviceable for the identification of these fungi, and the emphasis is on diagnostic characters, not on lengthy descriptions. Probably additional species can be found, but I believe that most of the common ones are included.

Artificial key

1. Discomycetes 2
– Pyrenomycetes 4
2. Ascocarps opening by a longitudinal slit ..... *Hypoderma dryadis*
– Not so 3
3. Ascocarps superficial, attached to the tomentum ..... *Allophylaria dryadis*
– Ascocarps erumpent ..... *Odontotrema alpinum*
4. Ascocarps shield-like, superficial ..... *Stomiopeltis dryadis*
– Ascocarps ± globose to pyriform 5

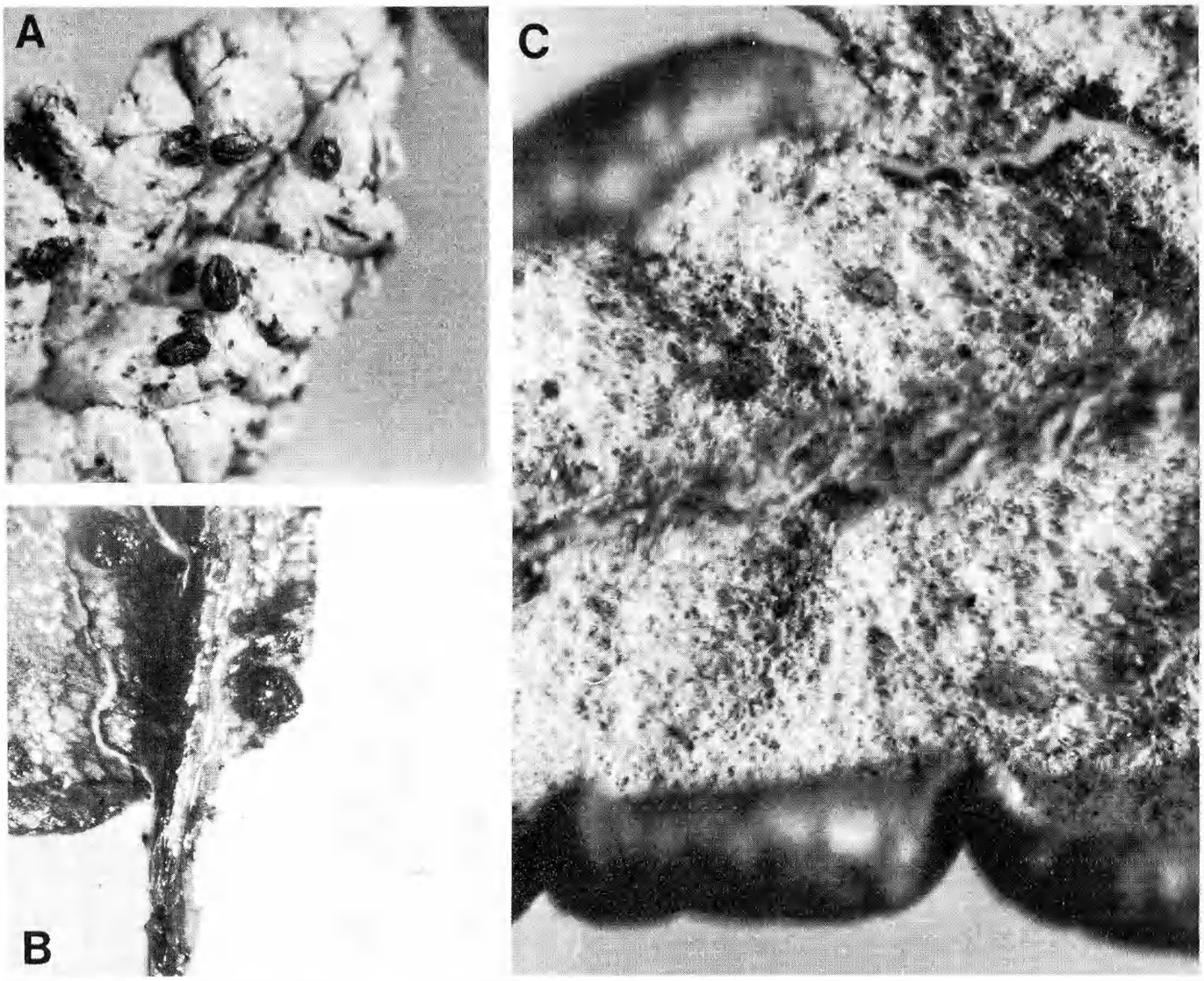


Fig. 2. Ascocarps in surface view. – A: *Hypoderma dryadis*, × 16. – B: *Odontotrema alpinum*, × 16. – C: *Allophylaria dryadis*, × 32.

5. Ascocarps apically setose 6
– Ascocarps glabrous or hairy, not setose 7
6. Ascocarps immersed, asci 8-spored ..... *Pseudomassaria islandica*
– Ascocarps superficial, asci polysporous ..... *Gibbera polyspora*
7. Ascocarps distinctly beaked 8
– Not so 10
8. Spores ± kidney-shaped ..... *Cainiella johansonii*
– Not so 9
9. Spores with a median septum ..... *Gnomonia dryadis*
– Spores with a basal septum (or none) ..... *Gnomoniella vagans*
10. Spores one-celled 11
– Spores septate 12
11. Ascocarps hypophyllous, superficial ..... *Sphaerotheca volkartii*
– Ascocarps epiphyllous, subcuticular ..... *Isothea rhytismoides*
12. Spores with transverse septa only 13
– Spores ± muriform ..... *Leptosphaerulina dryadis*
13. Spores 2-celled 14
– Spores finally 4-celled 15
14. Ascocarps immersed-erumpent ..... *Mycosphaerella octopetalae*
– Ascocarps superficial, in the median foliar groove ..... *Epipolaeum absconditum*
15. Ascocarps in flowers and fruits ..... *Melanomma dryadis*
– Ascocarps in leaves, spores with a gelatinous sheath ..... *Wettsteinina dryadis*

Discomycetes

Allophylaria dryadis Nannf. ex L. Holm, sp. nov.

Typus: Suecia, Jaemtlandia, paroecia Undersåker, in montibus Snasahögarna, N. Tvärådalen, c. 900 m, 22.VII.1946, J. A. Nannfeldt 8564a (UPS).

Fig. 1 A, 2 C, 4.

Species textura excipuli Allophylariae similis sed pilis marginalibus crassitunicatis distincta. In tomento foliorum siccorum Dryadis octopetalae crescit.

Apothecia urceolate–infundibuliform, 150–200 μm diam., first olive brown, darkening with age. Medullary *excipulum* hyaline, of small, ± cubical cells. Ectal excipulum distinct, basally and laterally c. 15 μm broad, of thick-walled, finally pigmented cells: the outermost globose, the inner ones more elongate, up to 10 μm long; upwards the ectal zone changes into a textura oblita, at the margin passing into obtuse, very thick-walled hairs of varying length, up to 40 × 5–6 μm. *Asci* narrowly clavate, briefly stipitate, 40–50 × 6–8 μm, with a minute apical ring, I+. *Spores* hyaline, subclavate–subcylindrical, 12–15(–17) × 2 μm, 3-septate. *Paraphyses* filiform, septate, about 1 μm thick, not inflated at tips.

The true taxonomic place is somewhat uncertain. The marginal hairs are foreign to *Allophylaria* and possibly the species merits a genus of its own. It has a very specialized ecology. It occurs in the tomentum, attached to the hairs, without contact with the foliar tissue. Evidently it is a xerophyte, as is also indicated by the thick-walled hairs. It may be more than a mere accidental occurrence that it so far is known only from areas with a ± oceanic climate.

This inconspicuous fungus was apparently unknown until discovered by Nannfeldt some 30 years ago. It may be rare, as we have not found it in any herbarium sheet of *Dryas* in spite of much search. Up till now it is known from six collections only, besides the type the following ones.

Sweden: Jämtland. Åre, Skurdalshöjden, c. 750 m, 31.VII.1950, Nannfeldt 10949b. – *Torne lappmark.* Jukkasjärvi, Mt Låktatjåkko, NE slope, r. alp. about 900 m, 7.VIII.1928, Nannfeldt 1617a.

Iceland: Árnessýsla. Hrúnamannahreppur, Brúarhlöð, 24.VII.1971, K. & L. Holm 59 c–71. – *Mýrasýsla.* Stafholtstungur, Varmaland, 2.VIII.1971, K. & L. Holm 57 b–71. – *Vestur-Húnavatnssýsla.* Vatnsnes, c. 3 km N of Hvammstangi, 2.VIII.1971, K. & L. Holm 58 c–71.

Hypoderma dryadis Nannf. ex L. Holm, sp. nov.

Typus: Suecia, Jaemtlandia, paroecia Åre, in declive australi montis Skurdalshöjden, c. 750 m, 31.VII.1950, J. A. Nannfeldt 10949 a (UPS).

Fig. 2 A, 5 A.

Ascocarpis longitudine 0.2–0.6 mm, sporisque 13–16 × 4–5 μm, minutis distincta. In pagina superiore foliorum siccorum Dryadis octopetalae.

Ascocarps epiphyllous, subcuticular, scattered, 0.2–0.6 mm in length, the small ones almost circular in outline, the larger ones broadly elliptic, opening by a longitudinal slit. *Asci* clavate, with a long tapering pedicel, c. 100 × 12 μm, I–, 8-spored. *Spores* rod-like, with obtuse ends, hyaline, with rather thick wall but without gelatinous coating, 13–16 × 4–5 μm. *Paraphyses* thread-like, flexuous, overtopping the asci, very narrow, c. 1 μm broad.

This species is similar to *Hypoderma hederae* but seems well characterized by the small ascocarps and spores. It was reported from the Dovre Mountains in Norway by Rostrup (1891 p. 5) as *"Hypoderma commune"*. It might be a rare species, as I have searched for it in vain. Besides the type collection there are so far only four finds, all on *D. octopetala*.

Sweden: Jämtland. Åre, Snasahögarna Mts, c. 750 m, 27.VII.1951, Nannfeldt 11606d. *Lule lappmark.* Gällivare, Mt Paukitjåkko near Sitasjaure, 11.VII.1924, leg. B. Bohlin. – *Torne lappmark.* Jukkasjärvi, Mt Kartimvare, r. alp. 11.VII.1928, Nannfeldt 1203 a.

W. Greenland, Kisengiartak, 8.VIII.1883, A. Berlin.

Odontotrema alpinum (Sacc.) L. Holm, comb. nov.

Basionym: *Heterosphaeria alpina* Saccardo, Michelia 2: 165 (1880) – *Sphaeropezia alpina* (Sacc.) Saccardo, Bot. Cbl. 18: 253 (1884) – *Phacidium alpinum* (Sacc.) Müller & von Arx, Phytopath. Zeitschr. 24: 360 (1955) – Type: Italy, Vette di Feltre, *Dryas octopetala,* in dead leaves (PAD!).

Fig. 2 B, 5 B.

Ascocarps hypopyllous, dark, c. 0.4 mm diam., erumpent–prominent, first closed, then opening by a circular hole with an irregularly scurfy margin. *Asci* about cylindrical, c. 50 × 6 μm (immature), 8-spored. Ascus tip rather thick, membrane turning bluish with Iodine. *Spores* oblong, hyaline, 10–14 × 2 μm, 3-septate. *Paraphyses* filiform, not incrassate at apex.

Saccardo's original description is fairly good. He also published an illustration, *Fungi Italici* tab.

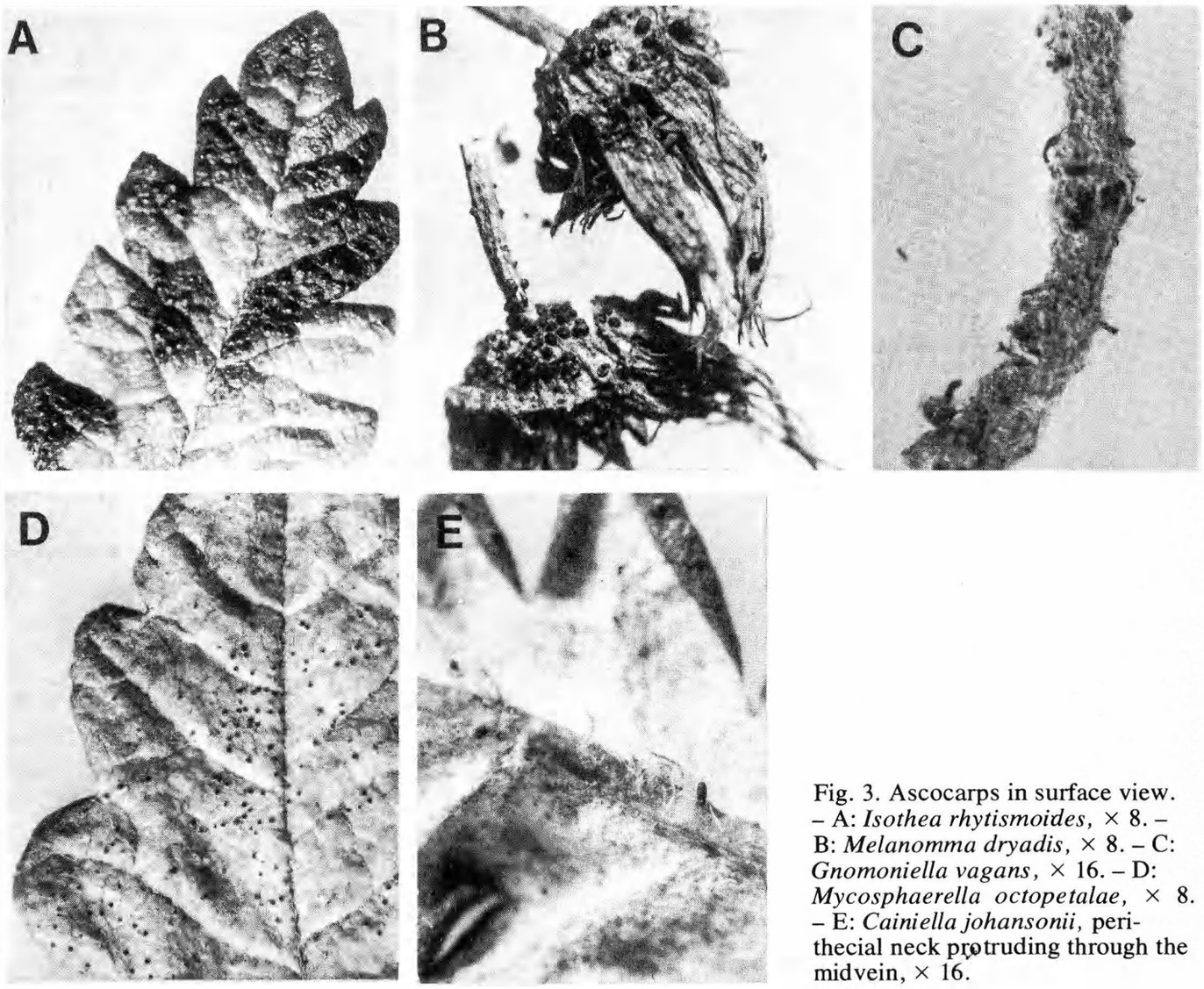


Fig. 3. Ascocarps in surface view. – A: *Isothea rhytismoides*, × 8. – B: *Melanomma dryadis*, × 8. – C: *Gnomoniella vagans*, × 16. – D: *Mycosphaerella octopetalae*, × 8. – E: *Cainiella johansonii*, perithecial neck protruding through the midvein, × 16.

1366. This species is the type of *Sphaeropezia* Sacc., cf Müller & von Arx (1955). It is, however, in every respect a typical *Odontotrema*, and obviously closely akin to *O. cassiopes* on *Cassiope tetragona* (Holm 1975). It differs from *O. cassiopes* i.a. by narrower spores.

It is rather surprising that this conspicuous fungus so far is known from the type collection only, (which is not fully mature). The species should be sought for in the Alps.

Pyrenomycetes unitunicati

Cainiella johansonii (Rehm) E. Müller

Müller, Sydowia 10: 121 (1957) – *Lizonia Johansonii* Rehm, Österr. Bot. Zeitschr. 1904: 86 – Type: Germany, Bavaria, Herzogenstand, in dead leaves of *Dryas octopetala*, 4.XI.1900, leg. Rehm (S!).

Fig. 3 E, 6 A.

Perithecia scattered, immersed, c. 0.2 mm diam., 0.3–0.45 mm high, with a long protruding neck, 0.2–0.3 mm long and 0.1 mm wide. *Asci* ± oblong, almost sessile, c. 150 × 35 μm, with an apical refractive apparatus, I−, generally 8-spored but abortive spores are common. Mature *spores* very distinctive, almost kidney-shaped, bicellular, 35–40 × 23–27 μm, long, hyaline (finally brown with terminal germ pores, fide Müller).

A very peculiar fungus, easily recognized at low magnification by the long protruding neck, which is rather light brown, especially at the tip. The perithecia are found in both sides of the leaves, but are particularly often seen in the petioles and the midveins.

Müller published some interesting details which I have not been able to verify, however. According to him the spores get finally dark

brown and have terminal germ pores. The apical ascus apparatus was said to consist of a perforated globe, partly I+. My material agrees better with Barr's (1959) description: "apical apparatus consisting of a circular pore at tip of cytoplasm, with a refractive area above the pore extending to the wall, no blue coloration in Melzer's."

It is amazing that this species, one of the most common and conspicuous microfungi on *Dryas*, was virtually unknown until described by Müller. As a matter of fact, the identification with Rehm's *Lizonia johansonii* seems very hazardous: little in Rehm's description is indicative of this species, it rather suggests immature *Wettsteinina dryadis*, which moreover is present in the (very poor) type material.

Cainiella johansonii seems to be rather common in the Scandes. Müller reported two finds from the Alps, and Barr (1959) listed four from the Canadian Arctic, on *Dryas drummondii* and *D. integrifolia*. Scrutiny of the *Dryas* collections in UPS has extended the known distribution to the Faroe Islands (Österö pr. Ejde, 17.VIII.1895, H. G. Simmons), Spitzbergen (Green Harbour, 8.VII.1913, E. Asplund) and Novaya Zemlya (Matotschkin Scharr, Aagaard).

Gnomonia dryadis Auersw.

Auerswald, Mycol. Europ. 5/6: 26 (1869). – Type: "Auf abgestorbenen Zweigen von *Dryas octopetala*" (n.v.).

Fig. 1 E.

Perithecia immersed, c. 0.2 mm diam. (according to Barr (1959) they can attain 540 μm in diam. and are provided with a beak up to 385 μm long). *Asci* very numerous, cylindrical, c. 65 × 8 μm, with a refractive apical ring. *Spores* ellipsoid–fusiform, 2-celled, 14–18 × 5–6 μm, with terminal gelatinous appendages c. 3–4 μm long.

I have seen only one, very scanty collection, with old beakless perithecia, apparently broken. Barr's figures (1959) for the asci are rather deviating from mine, viz. 80–90 × 13–16 μm, thus ellipsoid rather than cylindrical. Auerswald's spore measurements are remarkably large, 27 × 6 μm, but it can hardly be doubted that my fungus is conspecific with his. The spore appendages are difficult to discern in our material but are present, as evident in Indian ink.

Barr indicated that *Gnomonia dryadis* may be rare as she had found it only once (Canada, Labrador, Hebron, on overwintered stalks of *D. integrifolia*), though searching for it in numerous collections.

Sweden: Torne lappmark. Jukkasjärvi, Kerkevagge, r. alp., in petioles of *D. octopetala*, 31.VII.1952, L. Holm 1085b.

Gnomoniella vagans Johanson

Johanson, Öfv. K. Sv. Vet.-Akad. Förhandl. 1884 (9): 163 (1884) – Type: Iceland, Eskifjörður, *Dryas octopetala*, 9.VI.1883, H. Strömfelt (UPS!).

Fig. 1 F, 3 C.

Perithecia densely scattered in petioles and peduncles, immersed, with a long protruding neck, c. 0.2 mm long. *Asci* numerous, clavate, c. 60 × 12 μm, with an apical refractive ring, I–, 8-spored. *Spores* ± obovoid, hyaline, 13–15 × 6–7 μm, one-celled, often with a basal appendage c. 2 μm long and 1 μm broad.

A conspicuous species, recognizable by the long protruding perithecial necks, which are thinner than in *Cainiella johansonii* and apparently generally ± bent. Johanson's description of the spore is somewhat misleading as he states that "the spores membrane is apically thickened, sometimes forming a small colourless papilla" (translated from the Swedish original). This "papilla" is basal, at least according to our experience, and Barr, too, depicts them that way (1959 Fig. 137). Moreover it is delimited from the spore wall, and very probably represents a small basal cell. *Gnomoniella vagans* is thus in fact apiosporous, and the spores are rather similar to those of e.g. *Apiognomonia carpinea*.

Barr (1959) suggested that *G. vagans* is a rare species, which seems to hold true. We have not found it, in spite of much search. Johanson (1884) mentioned that he had collected it himself, too, in Sweden, Jämtland, Åre, Renfjället, in 1884. Barr reported one find from Canada, Baffin Island, Clyde Inlet, on *Dryas integrifolia*. Nannfeldt succeeded in picking out a fragmentary sample from another collection of Strömfelt's, from the same locality as the type, 21.VI.1883 (UPS).

Isothea rhytismoides (Bab. ex Berk.) Fr.

Fries, Summa Veg. Scand. 421 (1849) – *Sphaeria Rhytismoides* Babington ex Berkeley, Ann. Mag. Nat. Hist. ser. 1. 6: 361 – *Laestadia rhytismoides* Saccardo,

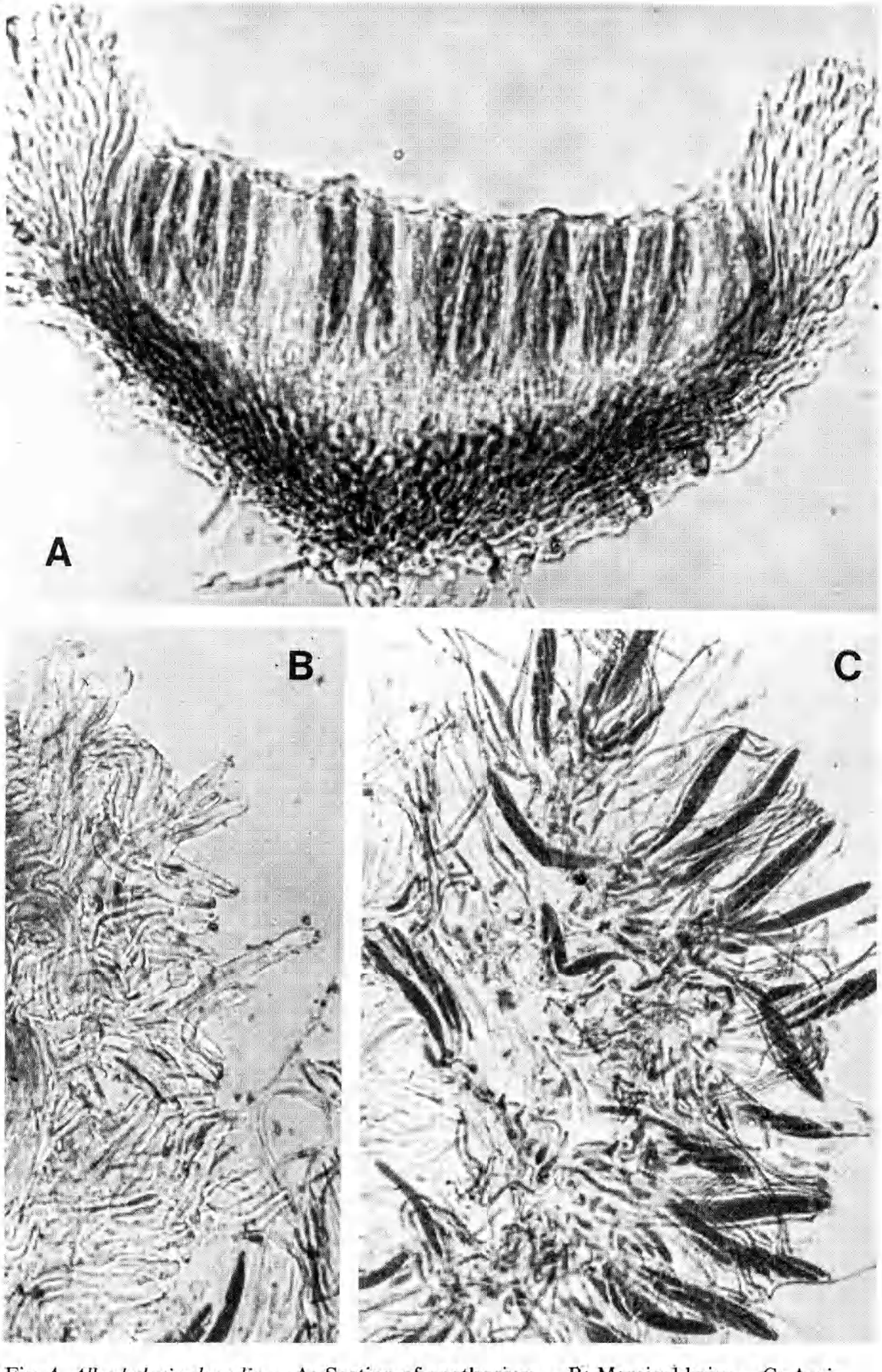


Fig. 4. *Allophylaria dryadis*. – A: Section of apothecium. – B: Marginal hairs. – C: Asci and paraphyses. – All in Lactic Blue, × 530.

Syll. Fung. 1: 424 (1882) – *Hypospila rhytismoides* (Bab. ex Berk.) Niessl. in Rabenhorst-Winter, F. eur. 3261 (1885) – Type: Scotland, Sutherland, Inchnadamff, IX.1838, C. Babington (UPS isotype!).

Sphaeria Dryadis Fuckel, Symb. Myc. 108 (1870) – *Didymella Dryadis* (Fckl.) Spegazzini, Dec. Mycol. Ital. No. 89 (1879) – Type: Germany, Bavarian Alps (n.v.).

Exs.: Berk., Brit. Fungi 324 (UPS) – Doassans & Pat., Champ. 23 (UPS) – Fuckel, F. rhen. 2161 – Herb. Myc. Rom. 2487 (UPS) – Rbh., F. eur. 1343 (UPS), 3261 (UPS) – Rehm, Asc. 843 – Speg., Dec. Mycol. Ital. 89 (UPS) – Vgr, Micr. rar. sel. 405 (UPS), 917 (UPS) – Weese, Eumyc. sel. 635 (UPS) – Wien, Krypt. exs. 618 (UPS).

Fig. 3 A, 6 D.

The most conspicuous of all the *Dryas* fungi. The fruit-bodies are densely gregarious, together forming shining black foliar spots catching the eye, particularly when the leaves are still green. It is a true parasite, infesting living leaves. *Ascocarps* subcuticular, about 0.2 mm diam., apparently to be regarded as perithecia coalesced with a surrounding blackened stroma. *Asci* clavate, c. 125 × 20 μm, with a remarkably long tapering pedicel, apically broadly rounded with a small refractive ring, I–. *Spores* oblong, often slightly broader upwards, one-celled, hyaline, 12–15 × 5–6 μm. The nucleus is stained by Cotton Blue.

A very good description was published already by Winter (1886 p. 566) and it has been fully treated by several authors, e.g. Müller & von Arx (1954) and Barr (1959). Spegazzini (Decad. Mycol. Ital. 89, in sched.) claimed that the spores finally became two-celled. I have only seen one-celled spores, also in the material cited by Spegazzini.

Isothea rhytismoides is common and widespread, and may be coextensive with its hosts.

Pseudomassaria islandica (Johanson) Barr

Barr, Mycologia 56: 854 (1964) – *Venturia islandica* Johanson, Öfv. K. Sv. Vet. Akad. Förhandl. 1884 (9): 168 (1884) – *Chaetapiospora islandica* (Johanson) Petrak, Sydowia 1: 87 (1947) – Type: Iceland, Eskifjörður, *D. octopetala,* 21.VI.1883, H. Strömfelt (UPS isotype!).

Trichosphaeria dryadea Rehm, Hedwigia 42, Beiblatt: 292 (1903) – Type: Austria, Tyrol, Kaisertal, *D. octopetala* (= Rehm, Asc. 1484; S!).

Venturia tiroliensis von Höhnel, Ann. Mycol. 1: 395 (1903) – Type: Austria, Tyrol, Sulden, 1899, *D. octopetala* (n.v.).

Exs. Rehm, Asc. 1484 (S).

Fig. 1 B, 7 C, D.

Ascocarps immersed, scattered, 0.1–0.2 mm diam., subglobose with an erumpent apex which is generally clad by a few stiff dark setae, up to 0.2 mm long. *Asci* ± oblong, c. 100 × 25 μm, with an apical ring which is I+, 8-spored. *Spores* ellipsoid, 20–25 × 10–12 μm, hyaline–yellowish, with a septum near the base.

Detailed descriptions have been published by Petrak (1947) and Barr (1964).

The synonymy indicated above was first pointed out by Petrak (1964). Barr's transfer of the species to *Pseudomassaria* seems fully justified.

Pseudomassaria islandica is a very characteristic species, easily recognized by the setose ascocarps and the pronounced apiospory. It occurs in both sides of the leaves, underneath often in the midvein. There are conflicting statements about this in the literature: "plerumque hypophyllis" (Johanson), "superiori pagina immersa" (Rehm), "in pagina superiore" (von Höhnel), "epiphyll" (Petrak; Müller & von Arx 1962 p. 701), "usually epiphyllous" (Barr).

A related species, *Pseudomassaria minor,* also on *Dryas,* has been described by Barr from Arctic Canada. It is said to differ by smaller spores, 12–16 × 4.5–6.5 μm with a nearly median septum. I have not found it.

In spite of being rather common *P. islandica* has not been reported from Sweden before. The following finds have been made.

Sweden: Härjedalen. Tännäs, Mt Hamrafjället, r. alp., 21.VII. & 30.VII.1933, Nannfeldt 4589b & 4802b. – *Jämtland.* Undersåker, Snasahögarna Mts, r. alp., c. 900 m, 22.VII.1946, Nannfeldt 8564b. Åre, Mt Skurdalshöjden, 750 m, 31.VII.1950, Nannfeldt 10949 c. – *Torne lappmark.* Jukkasjärvi, Mt Nuolja, r. alp., 23.VIII.1946, L. Holm 501b.

Sphaerotheca volkartii Blumer

Blumer, Beitr. Krypt.-Fl. Schweiz 7 (1): 115 (1933) – Type: Switzerland, Graubünden, Fürstenalp 1800 m, *D. octopetala,* leg. A. Volkart (n.v.).

Exs.: Lundell & Nannf., F. exs. suec. 1500.

This inconspicuous mildew, with a poorly developed conidial state, easily escapes notice. However, it may be rare, and is so far known from a few localities in Europe only. There are two Swedish finds, from Jämtland, Snasahögarna Mts, and Torne lappmark, Mt Nuolja. See further Junell (1967).

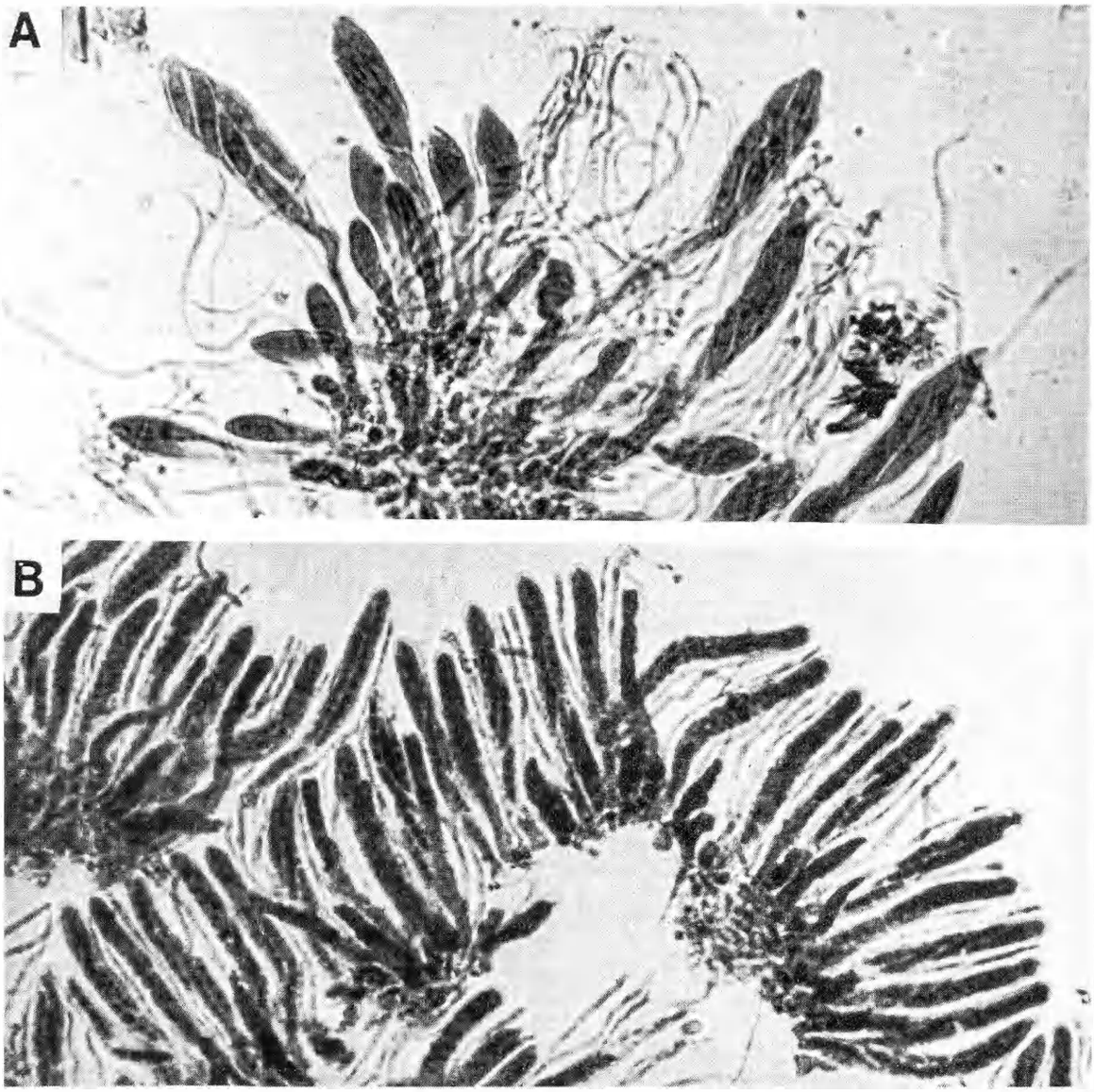


Fig. 5. A: *Hypoderma dryadis,* asci and paraphyses. – B: *Odontotrema alpinum,* asci and paraphyses. – Lactic Blue, × 530.

Pyrenomycetes bitunicati

Epipolaeum absconditum (Johanson) L. Holm, comb. nov.

Basionym: *Lizonia abscondita* Johanson, Öfv. K. Sv. Vet.-Akad. Förhandl. 1884 (9): 167 (1884) – Type: Iceland, Eskifjörður, *Dryas octopetala,* 21.VI.1883, H. Strömfelt (UPS isotype!).

Fig. 1 D, 6 B, C.

Ascocarps superficial, ± pyriform–obtusely conical, c. 100 μm diam., 150 μm high, with a rather distinct neck, c. 50 μm high and wide; at the base with a profuse, superficial, brown mycelium. *Asci* few, c. 10, about saccate, 50–55 × 18–20 μm, 8-spored. *Spores* obovate, with a submedian septum, 14–17 × 7.5–9 μm, rather thick-walled, finally faintly brownish. *Interthecial threads* sparse, septate.

Johanson's description is very good. It is truly admirable that he discovered this fungus with his simple optical equipment. It has a very specialized way of life, hidden in the median furrow of the upper leaf surface; biologically it recalls *Epipolaeum sulcicola* B. Eriksson, which is found exclusively in the leaf furrow of *Empetrum nigrum*.

The true systematic position of this species seems rather problematic. It is certainly not related to the bryophilous *Lizonia emperigonia,* the type and sole member of *Lizonia*. On the other hand a kinship with *Epipolaeum* seems possible; in many regards it fits well in this

genus, though the ascocarp form is deviating. In *Epipolaeum* the ascocarps are generally globose.

Epipolaeum absconditum is certainly apt to be overlooked but it may in fact be rather rare. It has not been recorded since the original publication, where Johanson also mentioned a find from Sweden, Jämtland, Mt Renfjället. I have seen it in a few samples only besides the type.

Sweden: Härjedalen. Tännäs, Mt Hamrafjället, r. alp., c. 1050 m, 21.VII.1933, Nannfeldt 4589 c. – *Jämtland.* Undersåker, Snasahögarna Mts, N. Tvärådalen, 900 m, 22.VII.1946, Nannfeldt 8564 e. Åre, Skurdalshöjden, 750 m, 31.VII.1950, Nannfeldt 10949 f. – *Torne lappmark.* Jukkasjärvi, Björkliden, 1.VIII.1951, L. Holm.

Gibbera polyspora B. Eriksson

B. Eriksson, Svensk Bot. Tidskr. 68: 207 (1974) – Type: Sweden, Torne lappmark, Abisko, *Arctostaphylos alpina,* 30.VI.1923, Nannfeldt 302 b (UPS holotype!).

Fig. 7 A, B.

Ascocarps scattered, superficial, hypophyllous, more or less pyriform, c. 100 μm diam., apically with a few dark setae, up to 50 × 5 μm, tapering towards the apex, basally inflated. *Asci* few, saccate, shortly stipitate, c. 75 × 20 μm, with numerous (c. 32?) spores. *Spores* bicellular, hyaline, very variable in size and shape, cf. below.

The above description is based on a very fragmentary material, viz. two samples where the fungus occurs sparsely intermixed. As far as I can see it agrees well with the so-called *Gibbera polyspora,* so far known only from four Scandinavian collections, all on *Arctostaphylos alpina*. It is easily recognized by the polysporous asci, a unique feature among the *Dryas* fungi. The apical bristles also provide a good microscopic character; they are much shorter than in *Pseudomassaria islandica,* hardly visible under the binocular.

The material on *Arctostaphylos alpina* seen by me has very narrow spores, almost needle-shaped; according to the original description they are (14–)18–22(–25) × 2(–3) μm. The species may in fact be characterized by a remarkable spore variability; anyway the two collections on *Dryas* differ widely in spore appearance. The fungus in Bohlin's sample (Fig. 7 B) has fusiform spores with rather acute ends, 15–18 × 4 μm, whilst Nannfeldt 1203 (Fig. 7 A) has much shorter and more ellipsoid spores, c. 8 × 3 μm; perhaps they are immature.

The taxonomic position of the species is very doubtful, and the alignment to *Gibbera* may be an expedient for the time being.

Sweden: Lule lappmark. Gällivare, Mt Paukitjåkko near Sitasjaure, 11.VII.1924, B. Bohlin. – *Torne lappmark.* Jukkasjärvi, Kartimvare, r. alp. 11.VII. 1928, Nannfeldt 1203.

Leptosphaerulina dryadis (Starb.) L. Holm, comb. nov.

Basionym: *Sphaerulina Dryadis* Starbäck, Bihang K. Sv. Vet.-Akad. Handl. 16(3):3:10 (1890) – Type: Sweden, Jämtland, Åre, Skurdalsporten, in dead leaves of *Dryas octopetala,* A. Y. Grevillius (n.v.).

Fig. 1 C, 8 A.

The dwarf among the *Dryas* fungi! *Ascocarps* c. 50 μm diam., about pyriform, immersed and rather light brown except for the somewhat protruding apex. *Asci* very few, saccate, 8-spored. *Spores* hyaline, 30–38 × 12–15 μm, about "slipper-shaped", upper part rounded, cylindrical below, long, with 5 transverse septa and one, ± incomplete, longitudinal septum; several additional transverse and longitudinal walls are formed at maturity, at least often. A good description was provided by Starbäck (1890).

This species is no doubt closely akin to *Leptosphaerulina pulchra,* on *Potentilla* spp., and possibly they are conspecific. However, there are some differences. The spores seem to be less septate in *L. pulchra*. According to Barr (1959 p. 7) the latter species has finally brown spores, something which I have not observed in *L. dryadis*. And as the *Dryas* fungi in general are host-specific, I do not feel it justified to lump the two taxa.

Leptosphaerulina dryadis may be rare; anyway, it escapes notice very easily. Starbäck stated it to be epiphyllous, but I have seen it only in the underside of dead leaves, particularly in the veins. It has not been reported since the original description. I have found it in the following samples.

Sweden: Lule lappmark. Gällivare, Paukitjåkko pr. Sitasjaure, 11.VII.1924, B. Bohlin. – *Torne lappmark.* Jukkasjärvi, Kartimvare, r. alp., 11.VII.1928, Nann-

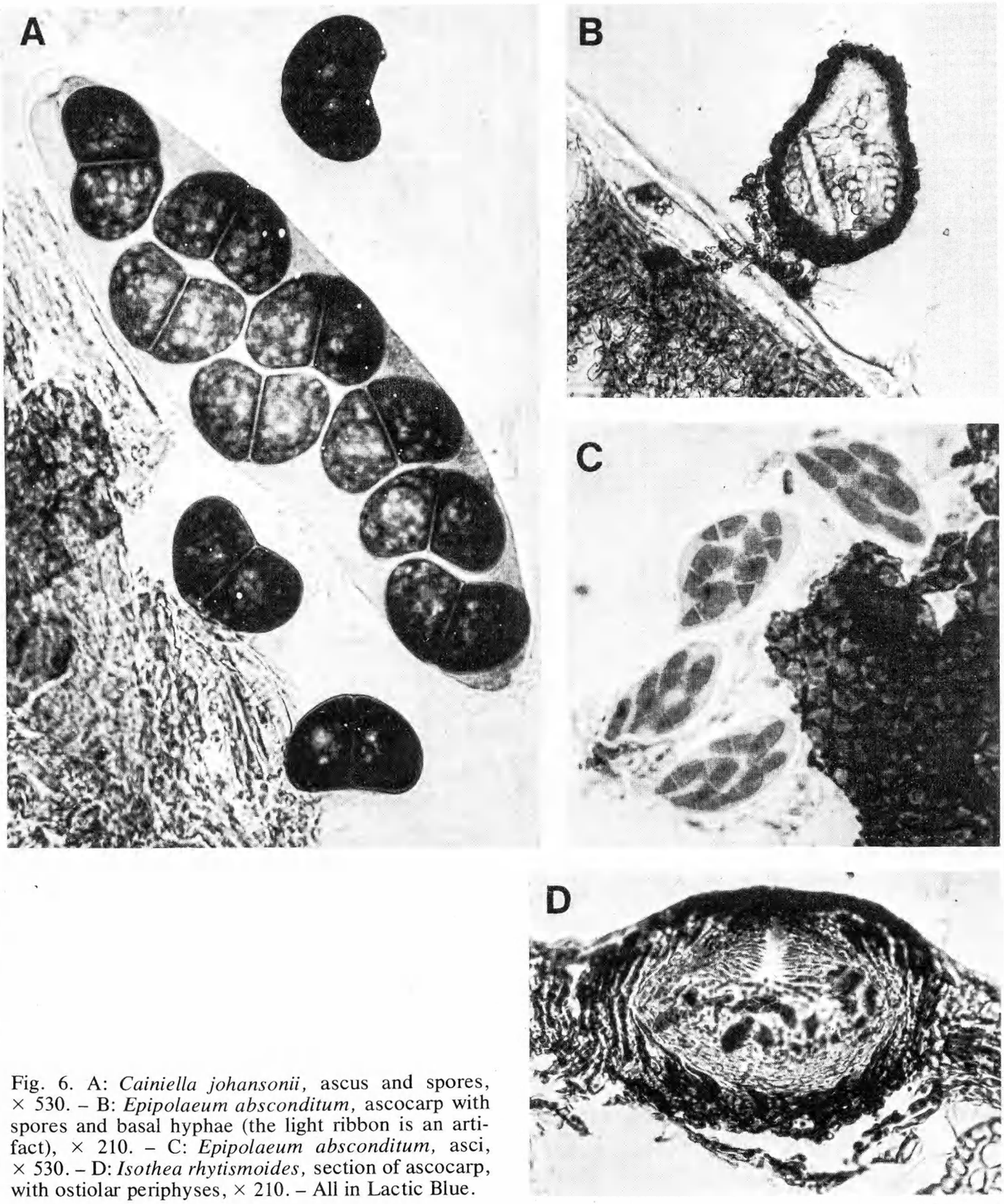


Fig. 6. A: *Cainiella johansonii,* ascus and spores, × 530. – B: *Epipolaeum absconditum,* ascocarp with spores and basal hyphae (the light ribbon is an artifact), × 210. – C: *Epipolaeum absconditum,* asci, × 530. – D: *Isothea rhytismoides,* section of ascocarp, with ostiolar periphyses, × 210. – All in Lactic Blue.

feldt 1203. Kerkevagge, r. alp., 31.VII.1952, L. Holm 1085 a.

East Siberia: St. Lawrence Bay, *D. octopetala,* 20–21.VII.1879, Vega exped.

Melanomma dryadis Johanson

Johanson in Rabenhorst, F. europaei no. 3659 (1890) – Type: Sweden, Jämtland, Renfjället, c. 900 m, *D. octopetala,* 13.VII.1884, leg. Johanson (UPS isotype!).

Leptosphaeria Dryadis Rostrup, Bot. Tidsskr. 25: 305 (1903) p.p., vide Holm 1957 p. 69.

Exs.: Rbh., F. eur. 3659 (UPS) – Rehm, Asc. 1438 (S) – Vgr., Micr. rar. sel. 105 (UPS).

Fig. 3 B.

A species well characterized by its peculiar biology, occurring in and on the flowers; the ascocarps are aggregated on carpels and sepals. *Spores* broadly ellipsoid, 20–27 × 6.5–8 μm, 3-septate, yellowish brown. A full description was given by Holm (1957 p. 69). The species is hardly a *Melanomma* but its true affinities are doubtful to me.

M. dryadis seems to be fairly common in Scandinavia, and it has also been reported from Iceland and the Alps (Holm 1957). It is certainly widespread, and I can communicate a find from Novaya Zemlya: sinus Besimannaja, *D. octopetala,* 2–6.VII.1875, Kjellman & Lundström (UPS).

Mycosphaerella octopetalae (Oud.) Lind

Lind, Rep. Sci. Res. Norw. Exp. Nov. Zemlya 1921. 19: 12 – *Sphaerella octopetalae* Oudemans, Versl. Meded. K. Akad. Wet. Naturk. ser. 3 (2): 159 (1885) – Type: Novaya Zemlya, *Dryas octopetala,* VII.1881, M. Weber (UPS isotype!).

Fig. 3 D, 8 B.

Ascocarps ± densely scattered in the upper leaf side, globose, immersed–somewhat erumpent, up to 100 μm diam. *Asci* saccate, 60–65 × 30–35 μm, almost sessile. *Spores* about ellipsoid, with a supramedian septum, 20–25 × 8–10(–11) μm, hyaline to faintly brownish.

This is the most common of all the *Dryas* fungi, virtually present in all dead leaves, where it seems to be confined to the upper leaf surface. It was included in *M. tassiana* by von Arx (1949 p. 51), an opinion apparently shared by Barr (1959). I cannot approve of this lumping. *M. octopetalae* surely is a separate taxon, confined to *Dryas,* which should not be merged with the polyphagous saprophyte *M. tassiana.* It is not very variable; the spores are characteristically large and thick.

Mycosphaerella octopetalae is probably co-extensive with the genus *Dryas.*

Three other *Sphaerellae,* said to have considerably smaller spores, have been reported to occur on *Dryas,* viz. *Sphaerella dryadis* Auersw., *S. dryadicola* Rostr. and *S. ootheca* Sacc. I have not seen any trace of those.

Stomiopeltis dryadis (Rehm) L. Holm, comb. nov.

Basionym: *Microthyrium microscopicum* var. *Dryadis* Rehm, Ann. Mycol. 2: 520 (1904) – *Trichothyrium Dryadis* (Rehm) Rehm, Ann. Mycol. 7: 414 (1909) – *Calothyrium Dryadis* (Rehm) von Höhnel, Ber. Deutsch. Bot. Ges. 37: 111 (1919) – Type: Germany, Bavarian Alps, Valepp, *Dryas octopetala,* 880 m, VI.1904 (= Rehm, Asc. 1571, S!).

Exs.: Rehm, Asc. 1571 (S).

Fig. 9 A.

An inconspicuous fungus, in all respects a typical member of *Stomiopeltis,* i.e. ascocarps superficial, scutate, with a shield composed of sinuous, irregularly lobed cells, at the margin passing into coarse supracuticular hyphae. The ascocarps are epiphyllous, sometimes growing already on living leaves. It is probably closely allied to e.g. *S. callunae* B. Eriksson, but seems to be distinct by larger spores, 10–12 × 3–4 μm. Rehm stated that the spores are provided with a mucous sheath. I have not seen this, nor is it mentioned in Barr's detailed description (1959). The spores in her illustrations (Fig. 107–108) are more ellipsoidal than those seen by me.

Stomiopeltis dryadis is probably not rare but has been little noticed. It was described from the Alps and has since been reported from Arctic Canada by Barr (1959) who listed 3 samples, all on *Dryas integrifolia.* Nannfeldt has found it in 8 collections.

Sweden: Härjedalen. Tännäs, Mt Hamrafjället, r. alp. c. 1050 m, 21.VII.1933, Nannfeldt 4589 a. – *Jämtland:* Undersåker, Snasahögarna Mts, r. alp. c. 900 m, 22.VII.1946, Nannfeldt 8564 c. Åre, Mt Skurdalshöjden, c. 750 m, 31.VII.1950, Nannfeldt 10949 d. – *Torne lappmark:* Jukkasjärvi, Mt Låktatjåkko, NE slope, r. alp. c. 900 m, 7.VIII.1928, Nannfeldt 1617 c. Mt Nuolja, slope towards Björkliden, r. alp. inf., 23.VIII. 1946, L. Holm 501.

Iceland: Husavik, 25.VI.1903, O. Paulsen. Mark (Holt), Bildudalur, 15.VII.1937, G. Thorlaksson.

The Faeroes: Österö, Mt Kodlen, 300 m, 17.VIII. 1895, H. G. Simmons 438 Fung.

Wettsteinina dryadis (Rostr.) Petrak

Petrak, Sydowia 1: 322 (1947) – *Massarina Dryadis* Rostrup, Meddel. Grønland 3: 560 (1888) – *Pleospora Dryadis* Petrak, Hedwigia 68: 221 (1928), non *P. Dryadis* Fuckel – Type: Greenland, Shannon Island, *Dryas octopetala,* coll. 2nd German North Pole Exp. (C).

Fig. 9 B–D.

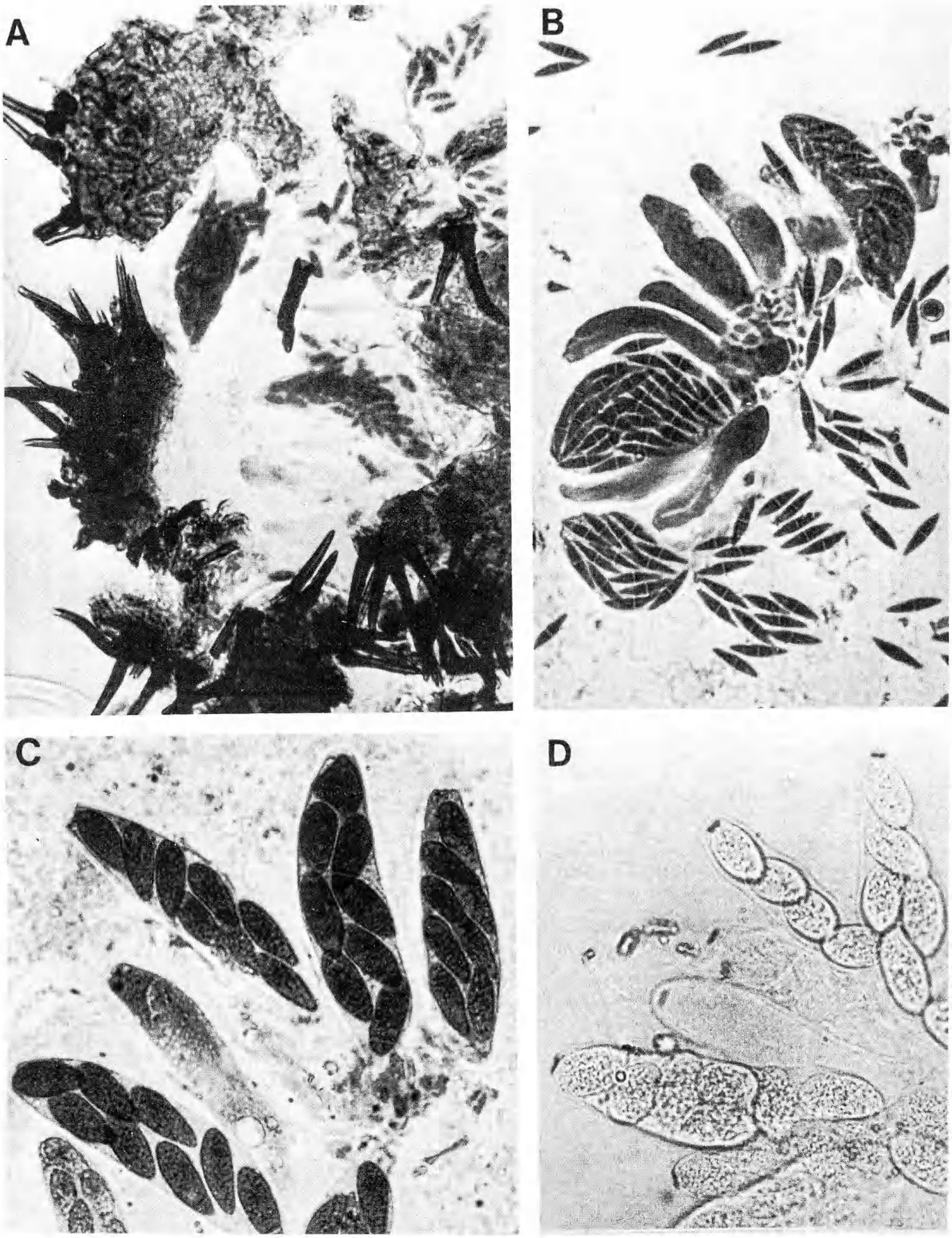


Fig. 7. A: *Gibbera polyspora*. Nannfeldt 1203, crushed perithecium with setae, asci and spores. – B: *Gibbera polyspora*, leg. Bohlin, asci and spores. – C: *Pseudomassaria islandica*, asci. – D: Ditto in Iodine with stained apical annulus. – All × 530, A–C in Lactic Blue.

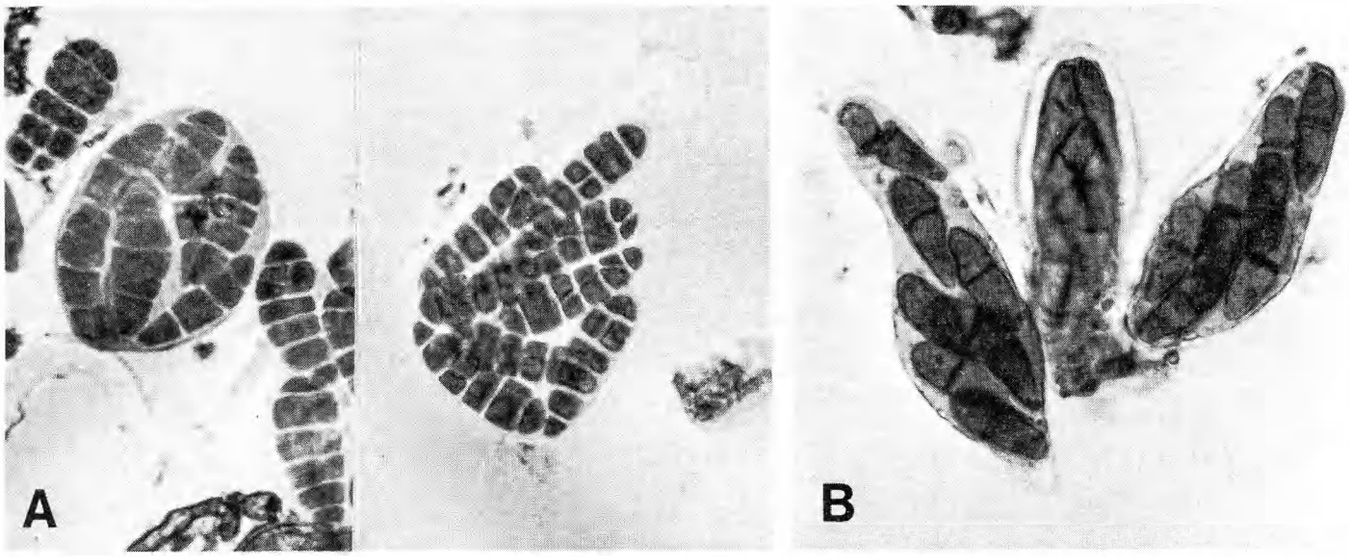


Fig. 8. A: *Leptosphaerulina dryadis*, asci and spores. – B: *Mycosphaerella octopetalae*, asci with spores. – Lactic Blue, × 530.

Ascocarps scattered, often numerous, immersed but for the rather coarse protruding neck, pyriform, c. 150 μm diam. *Asci* saccate, up to 150 × 50 μm, 8-spored. *Spores* ellipsoidal, long hyaline and bicellular, with a gelatinous coating, finally 3-septate, brownish, verrucose, 33–40 × 15–16 μm. The young spores are characterized by the two annular "borders", which eventually develop into the secondary septa.

A lengthy description was given by Petrak (1928). He was in error, however, when stating "Fruchtgehäuse nur epiphyll"; the ascocarps are also common in the leaf underside and the pedicels. As a rule it can be recognized under the binocular by its general appearance. It may be confounded with *Mycosphaerella octopetalae* which, however, has almost globose ascocarps.

Wettsteinina dryadis seems to be widespread. Barr (1959 p. 10) gave it as "common and widely distributed in arctic and alpine regions of the world". It seems to be common in the Scandes, too, though it has not been reported from Sweden before, whereas Rostrup (1891 p. 9) published a find from Norway, Kongsvold. Five Swedish collections in UPS, from Jämtland, Lule lappmark and Torne lappmark. I have also seen it in *Dryas* samples from Iceland, Greenland and Novaya Zemlya.

Species dubiae

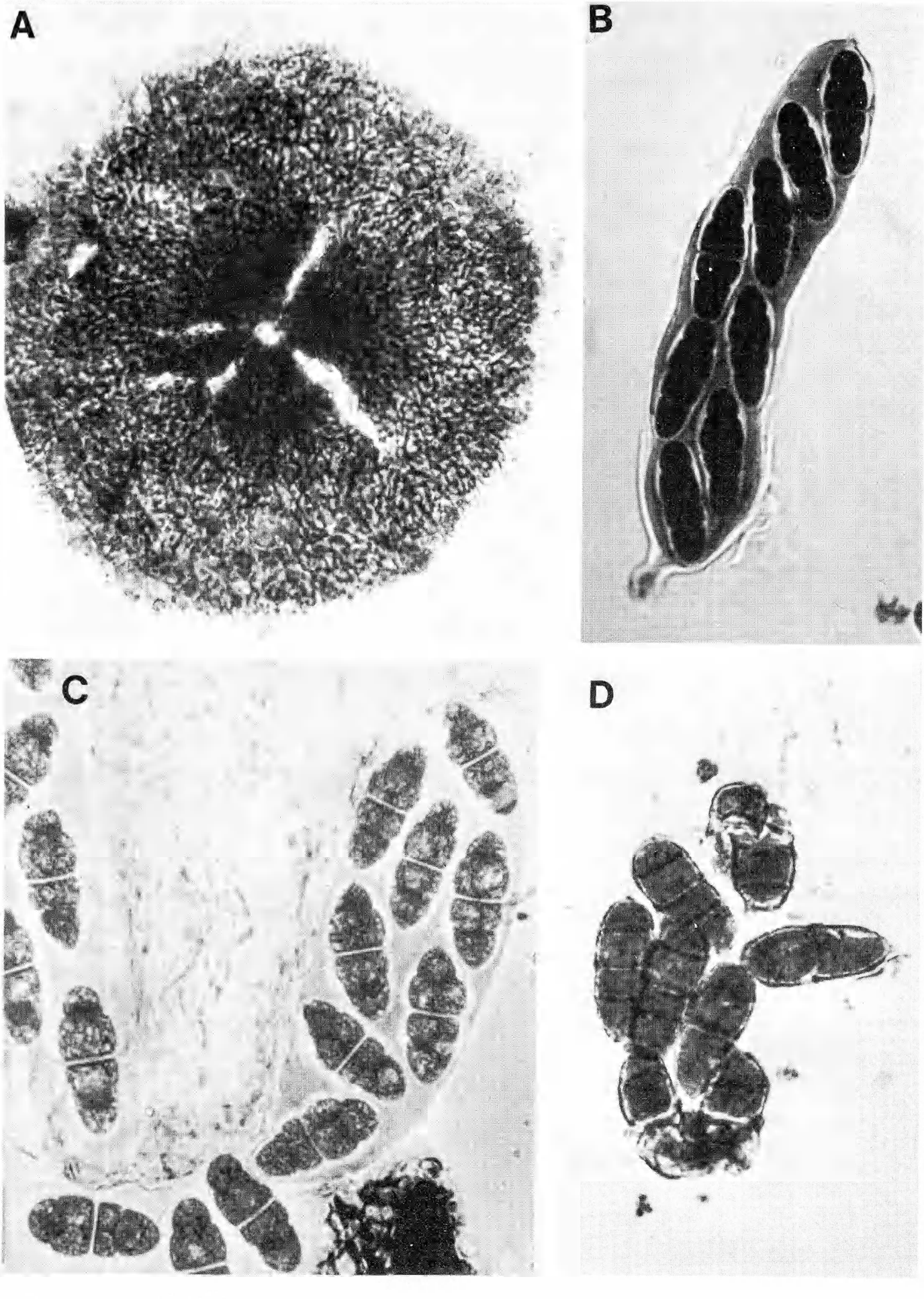
Didymosphaeria dryadis (Fuckel) Berl. & Vogl.

Berlese & Voglino in Sacc., Add. Syll. Fung. 114 (1886) – *Pleospora Dryadis* Fuckel 1874 p. 93 – Type: East Greenland, Clavering Isl. & Sabine Isl. (2. Deutsche Nordpolfahrt) (n.v.).

Fuckel's description of *Pleospora dryadis* is suggestive of *Wettsteinina dryadis*, but for one important detail: the spores were said to be two-celled and finally yellowish brown. As already mentioned the fully mature spores of *W. dryadis* are brownish, but as far as I have seen they are always 4-celled at the late stage. Fuckel's illustration (Fuckel 1874 Fig. 4) of asci and spores is not very indicative of *Wettsteinina* either. However, I am inclined to believe that his fungus was in fact an aberrant form of *Wettsteinina dryadis*. His descriptions are well known for their accuracy.

"Didymosphaeria dryadis" has been reported several times from the Arctic (Rostrup 1894 p. 22, Lind 1910 a p. 153, 1910 b p. 7, 1928 p. 22, 1934 p. 18). The fungus referred to by these authors was apparently immature *Wettsteinina dryadis*. There are two collections in C under the name of *Didymosphaeria dryadis*, both from E Greenland: (1) Danmarks Ö, 1892, leg. N. Hartz, det. E. Rostrup (1894 p. 64); (2) Dan-

Fig. 9. A: *Stomiopeltis dryadis*, scutellum. – B–D: *Wettsteinina dryadis*, asci and spores in Lactic Blue; in D fully mature spores with verruculose wall. – All × 530.


A
B
C
D

marks Havn, 1908, A. Lundager, det. J. Lind. *Wettsteinina dryadis* is abundant in this material. The identity is moreover indicated by the descriptions given by the mentioned authors, particularly Lind (1910 b p. 7): "Ascis crasse tunicatis 100–120 $\mu \times 36$–40 μ, sporidiis 28–32 $\mu \times 12$–16 μ strato hyalino obvolutis".

Leptosphaeria rostrupii Sacc. & D. Sacc.

Saccardo & D. Saccardo, Syll. Fung. 17: 721 (1905) – *Leptosphaeria Dryadis* Rostrup, Christiania Vidensk-Selskabs Skr. I, 1904 (4): 24 (1904), non *Leptosphaeria Dryadis* Rostrup, Bot. Tidsskr. 25: 305 (1903) – Type: Norway, Kongsvold, VIII.1881, A. Blytt (O).

According to Rostrup's description this fungus was found in the upper leaf-side of dry *Dryas* leaves, and characterized i.a. by 4-celled yellow spores, 25–30 × 8–10 μm. No fungus corresponding to the description could be found in the type collection (cf. Holm 1957 p. 70) nor have I seen one elsewhere. Rostrup's report is so far the only one of this doubtful taxon.

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The genus Ramaricium (Gomphaceae)

James Ginns

Ginns, J. 1979 02 15: The genus Ramaricium (Gomphaceae). *Bot. Notiser 132:* 93–102. Stockholm. ISSN 0006-8195.

Three species are added to *Ramaricium* Eriksss. *R. alboflavescens* is from E North America. Synonyms are *Serpula illudens, S. imperfectus* and *Coniophora corticola. R. polyporoideum* (type species of *Phlyctibasidium* Jül.) is known from the same region and Brazil. *R. flavomarginatum* is known from the *Quercus* forests of the pacific region of Washington, USA and Vancouver Island, Canada. The other two species of *Ramaricium* are contrasted with these. *R. occultum* (type of the generic name) is a rare species from Sweden. *R. albo-ochraceum* is known from C Europe, NE North America and Colombia. The genus is compared with *Kavinia* and *Ramaria.* Ferrous sulphate applied to dried basidiomes of *Ramaricium* and *Kavinia* species gave a reaction similar to that seen on specimens of *Gomphus* species.

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The genus *Ramaricium* Eriksss. (1954) was proposed for *R. occultum* Eriksss., which has microscopic characters similar to *Kavinia* Pilát and some species of *Ramaria* S. F. Gray em. Donk. The three genera are readily distinguished on the basis of gross morphology, *Ramaricium* with corticioid basidiomes, *Kavinia* with effused-hydnoid and in *Ramaria* they are clavarioid. The microscopic features which they share are the size, shape and occasional pleurobasidial habit of the basidia, the shape and cyanophily (typically both spore wall and the wall ornamentation are cyanophilous) of the spores, and the diameter, wall thickening, septation and ampullate swellings of the hyphae.

Following Eriksson's (1954) discussion, Donk (1961) included the three genera in the Gomphaceae and he (Donk 1964 p. 268) added another three genera to the family. Basidiomes of these genera range from corticioid and hydnaceous (both effused and pileate) to clavarioid (both simple and branched) and cantharelloid.

My special interest in the group arose during the preparation of a monograph of the genus *Coniophora* DC. ex Merát. Several species, transferred decades ago to *Coniophora,* do not conform to the limits of the genus acceptable to me. In searching for a more appropriate generic disposition, Dr John Eriksson of Göteborg and I concluded that three of the species are congeneric with *R. occultum;* and *Trechispora albo-ochraceum* (Bres.) Liberta (1973), also studied during our search, fits into *Ramaricium* as well.

The addition of these species to *Ramaricium* requires a minor emendation of the genus and I have combined with this a key to the species, some scanning electron microscope photographs of spores and hyphae, a comment on each species, notes on the ferrous sulphate test and descriptions of *R. alboflavescens* and *R. flavomarginatum.*

Ramaricium Eriksss.

Eriksson, Svensk Bot. Tidskr. 48 p. 189 (1954) – Type species: *R. occultum* Eriksss.

Phlyctibasidium Jülich, Proc. K. Nederl. Akad. Wet., Amsterdam (C) 77 p. 154 (1974) – Type species: *P. polyporoideum* (Berk. & Curt.) Jülich.

Corticioid with an olivaceous tinted hymenial

surface which contrasts with a pure white subiculum and hyphal strands; hymenium smooth, pale ochraceous to pale olivaceous, rather fragile, rather thick, crustose; subiculum cottony, rather thick (up to 1 mm); hyphal strands scattered, to 0.1 mm diam.; hyphae distinct, narrow (1.5–3 μm diam.) with clamp connections and infrequent ampullaceous swellings; pleurobasidia present but infrequent; basidia typically pedicellate, 30–50(–100) × 7–9 μm, sterigmata four.

Other features, typically found in combinations, but some not occurring in all species, are: thickened hyphal walls (*R. albo-ochraceum* and *R. occultum* have hyphae with thin walls), warts on the hyphae (found in *R. polyporoideum, R. flavomarginatum* and *R. alboflavescens*), and spores which are broadly ellipsoid with an elongated apiculus, with a thickened, pale yellow, cyanophilous wall, ornamented with cyanophilous warts (occurring in *R. occultum, R. polyporoideum* and *R. albo-ochraceum; R. alboflavescens* has similar spores but they are globose to broadly ovoid and lack definite ornamentation).

Key to the species of Ramaricium

1. Spores practically smooth, subglobose, 5–6 μm diam. ..... *R. alboflavescens*
– Spores practically smooth, broadly cylindrical, 10–16.5 μm long ..... *R. flavomarginatum*
– Spores warted, broadly ellipsoid, 6.5–8 μm long with an elongated, distinct apiculus 2
2. Spores 5–6 μm broad; subicular hyphae typically with thickened walls and many with small warts on the surface ..... *R. polyporoideum*
– Spores 3.5–4.5 μm broad; hyphae thin-walled and lacking warts 3
3. Growing on wood ..... *R. albo-ochraceum*
– Growing within mats of mosses ..... *R. occultum*

Ramaricium alboflavescens (Ell. & Ev.) Ginns, comb. nov.

Basionym: *Corticium alboflavescens* Ell. & Ev., Acad. Nat. Sci., Proc., Phila. 1894 p. 324 (1894) – *Coniophora alboflavescens* (Ell. & Ev.) Hoehnel & Litsch., K. Acad. Wiss. Wien, Math.-Nat. Kl. Sitzungsber. 116 p. 791 (1907) – Orig. coll.: USA, West Virginia, Fayette Co., Short Creek, Nuttall 365, "on dead standing trunk of *Kalmia latifolia*?" ex Ellis Collection (NY lectotype, designated here), and according to Burt (1917 p. 249) parts in Ell. & Ev., Fungi Coll. Exs. 403 (NY) and N. Amer. Fungi Exs. 3005 (NY, S).

Coniophora corticola Overh., Mycologia 30 p. 274 (1938) – Orig. coll.: USA, Pennsylvania, Hunt Co., Charter Oak, Overholts Hb. 17936 (cited in orig. descr. as 17036) (TRTC isotype).

Serpula illudens Overh. ex W. B. Cooke, Mycologia 49 p. 214 (1957) – Orig. coll.: USA, Tennessee, Mt LeConte, 11.IX.1935, Sharp, Overholts Hb. 19127 (PAC holotype).

Serpula imperfectus Overh. ex W. B. Cooke, Mycologia 49 p. 215 (1957) – Orig. coll.: USA, Pennsylvania, Center Co., Roetz Gap, 10.X.1939, Overholts Hb. 22178 (PAC holotype).

Basidiomes effused, small, circular (5 mm diam.) to elongated (2 × 9 cm), to 0.5 mm thick; margin distinct, white, cottony, raised, rather thick, 1(–2) mm wide; hymenium pale olive drab, olive-buff, tan, olive-tan, pale olive brown, even, fragile, crustose, often randomly fissured, finely pruinose, readily separating from the subiculum; subiculum white, cottony, thin, homogeneous.

Subicular hyphae woven, flexuous, frequently branched, with clamp connections, 1.6–3.5 μm diam., rarely swollen at a septum to 7 μm; hyphal walls hyaline, thin-walled or occasionally rather thick-walled, surface mostly covered with minute projections which are apparently remnants of a mucilaginous, acyanophilous coating (Fig. 1 D–E), with scattered granules and crystals on some segments; subhymenium composed of frequently branched hyphae with smooth walls, vertically oriented, the zone impregnated with a gelatinous substance; hyphoid cystidia (perhaps only aborted basidia) scattered, filiform, 1.5 μm diam. or with the apex clavate and swollen to 3.5 μm; basidia basically clavate with a weak to pronounced median constriction, usually with an abrupt taper about two-thirds of the length below the apex to 3.5 μm diam., 33–45 × 8–10 μm; sterigmata four, each up to 7 μm long; spores (Figs. 1 B, C, 3 D) globose, some subglobose to very broadly ovoid, surface outline slightly undulating, 5.9–7.8 × 5.5–7.3 μm, with a distinct truncated apiculus; spore wall hyaline or pale yellow, neither amyloid or dextrinoid, cyanophilous, thickened (0.8 μm).

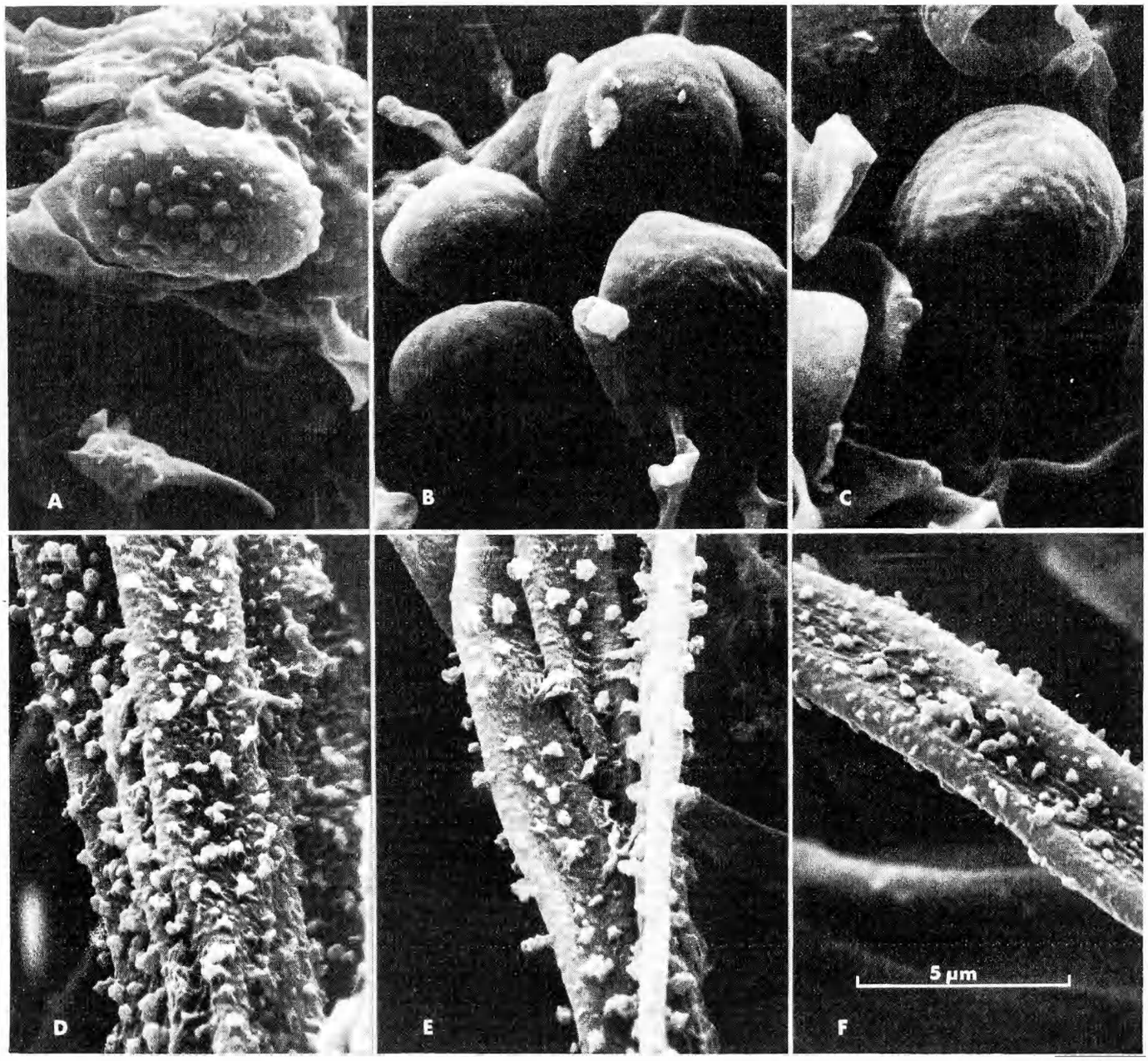


Fig. 1. *Ramaricium* spores and hyphae. – A: *R. albo-ochraceum,* TRTC 15251. – B–E: *R. alboflavescens,* TRTC 21380. – F: *R. polyporoideum,* DAOM F 7127. – Photos: L. Ryvarden, Oslo.

Saprophytic on dry, decaying wood often raised off the ground, of *Tsuga canadensis, Thuja occidentalis* and *Kalmia latifolia,* associated with a white rot. Known only from North America where its range extends from Ontario (the southern peninsula near Lakes Erie and Ontario) and New York through the Appalachian Mountains in Pennsylvania, Virginia, West Virginia and Tennessee. Collected in September and October, except the type which is labelled, perhaps in error, February.

Culture. In culture, following Nobles's (1965) procedures, the growth rate slow, in 6 weeks the mat 7 cm radius and not covering the plate; mat white to greyish, raised nearly 1 mm, at 2 weeks pure white around the inoculum plug, felty to woolly but the mycelium less dense toward the margin, at 5 weeks mat homogeneous, downy, densely-downy, to downy-woolly and tough; margin even, about 2 mm wide, submerged, sparse, translucent. Reverse at 4 weeks showing a faint yellowish color around the

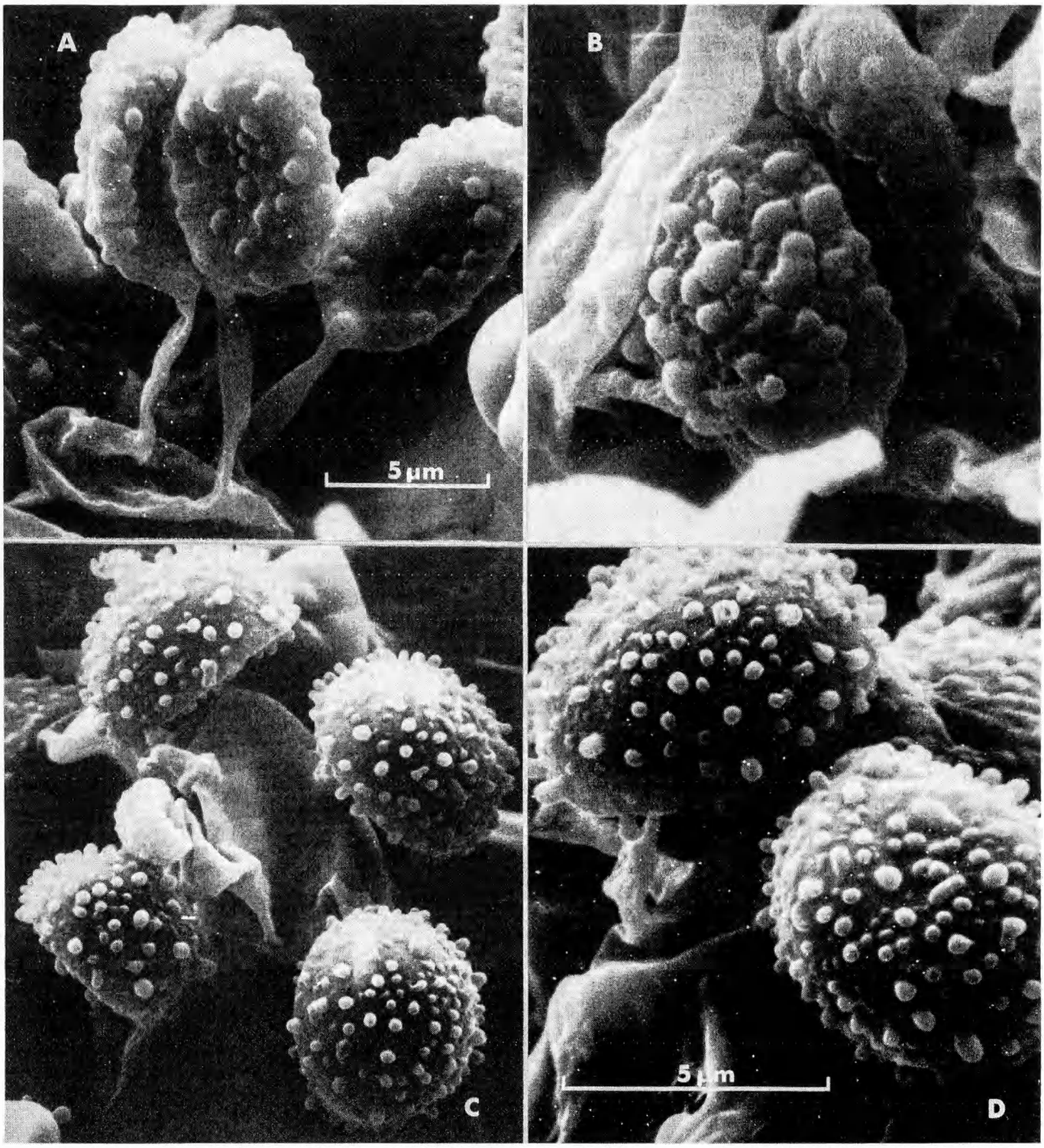


Fig. 2. *Ramaricium* spores. – A, B: *R. occultum*, holotype. – C, D: *R. polyporoideum*, DAOM 7127. – Bar in A applies also to C, and bar in D applies also to B. – Photos: L. Ryvarden, Oslo.

inoculum, at 5 weeks egg-yellow in the zone beneath the older part of the mat. Odor none or slightly sweet. Ferrous sulphate (1 g $FeSO_4 \cdot 7H_2O$ in 100 ml distilled water) did not stain a 6 week-old mat green. On gallic acid agar the oxidase reaction intense, the discoloration zone 4 cm diam.; no mycelial growth. On tannic acid agar at 2 weeks the oxidase reaction weak to moderate, the discoloration zone 15 mm diam.; no mycelial growth. Laccase test with gum guaiac reagent negative.

Advancing zone hyphae hyaline, thin-walled, 2.8–4.4 µm diam., with clamp connections; hyphae in older portions of the mat modified to:

(1) some rather broad (3.6 μm diam., occasionally swollen to 9 μm) with slightly thickened walls, widely scattered clamps and some retraction septa; (2) some narrow (up to 1.6 μm diam.) with a ramifying habit, thin-walled; and (3) some which produce short branches which proliferate by producing many short, dichotomous, aseptate branches about 1.2 μm diam., up to 70 μm long, typically interwoven into a knot. At 6 weeks no warts on the hyphae and all elements acyanophilous.

Culture studied: DAOM 17712 (TRTC 21380).

Key code: (1).2.3.7.11.26.32.36.39a.47.(54). 55. (Nobles 1965). In the code the symbol 39a is used to represent a reverse discoloration that is yellow, at least in part.

Material studied (in addition to types, see above). *Canada:* Ontario, Brant Co., Oakland Swamp, Cain, TRTC 21380 (DAOM, GB, NY), TRTC 15065 (FH); Nashville, Cain, TRTC 24932 (DAOM, NY, S, UPS) and c. 15 collections from Brant and nearby York County (TRTC). – *USA:* New York, Copake, Peck, MBG 54580 (BPI) – Virginia, Blacksburg, Shear 71203 (BPI).

Ramaricium albo-ochraceum (Bres.) Jülich

Jülich, Persoonia 9 p. 417 (1977) – *Corticium albo-ochraceum* Bres., Ann. Mycol. 1 p. 96 (1903) – *Trechispora albo-ochraceum* (Bres.) Liberta, Can. J. Bot. 51 p. 1888 (1973) – Orig. coll.: Poland, Sept., Eichler 37 (S holotype).

A detailed description is found in Liberta (1973). *R. albo-ochraceum* grows on dry, partially decayed wood of *Alnus* (Europe) or *Abies, Picea, Pinus, Populus* and *Tsuga* (Canada).

Material studied. Poland: type, see above. – *Austria:* Tirol, Ruzbachtal im Stubai, 28.III.1923, Litschauer (S) – *Canada:* New Brunswick, St. Andrews, 26.VIII. 1933, Mounce (DAOM F6555) – Ontario, Campbellville, near Guelph, 1.V.1941, Cain, TRTC 17770 (DAOM); Petawawa, N of Pembroke, 13.VII.1951, White (DAOM 31119); Oxbow Lake, W of Algonquin Park, 16.VIII.1941, Cain, TRTC 17929 (DAOM), TRTC 17935 (DAOM); North Bay, Marion Lake, 18. IX.1951, Quirke (DAOM 31120); Lake Timagami, 31. VII.1939, Cain, TRTC 15251 (GB); Kenora, 25.IX. 1932, Mounce (DAOM F6412) – Manitoba, Victoria Beach, near Winnipeg, 22.VI.1935, Bisby & Mounce (DAOM F6413). – Also known from USA and Colombia (Liberta 1973).

Ramaricium flavomarginatum (Burt) Ginns, comb. nov.

Basionym: *Coniophora flavomarginata* Burt, Ann. Missouri Bot. Gard. 13 p. 311 (1926) – Orig. coll.: USA, Washington, W Klickitat Co., 11.XII.1902, Suksdorf 888 (FH holotype).

Basidiomes effused, typically in clusters, each up to 3 × 3 cm and to 1 mm thick; margin distinct, white, coarsely fimbriate, typically of short (up to 5 mm long) strands; hymenium when fresh "avellaneous" (Burt), when dried more nearly pinkish buff (Munsell Colors 2.5Y8/4–10YR7/4), smooth to tuberculose, each tubercle to 0.7 mm diam., rather firm, crustose, dry, dull, finely pruinose, thickening and becoming stratose; context pure white, cottony, up to 1 mm thick, homogeneous.

Subicular hyphae rather loosely woven, flexuous, infrequently branched, with clamp connections, rarely swollen at a septum to 7.5 μm diam. (Fig. 3 F), walls hyaline, thin-walled or more typically rather thin-walled (up to 0.7 μm thick), the surface of a few segments coated with small acyanophilous warts (up to 0.8 μm diam.), also with scattered, roughened crystals (up to 4 μm diam.) on the surface of some segments; hyphoid cystidia (Fig. 3 F) scattered in the hymenium, clavate to cylindrical, some with papillate or forked apices, 2–4 μm diam.; basidia (Fig. 3 F) basically clavate with a slight median constriction and typically with an abrupt taper, about 30 μm below the sterigmata, to a long stem-like base, wall often slightly thickened, 60–100 × 8–10 μm; sterigmata four, occasionally abnormally positioned, each up to 9 μm long; pleurobasidia occasional near the margin; spores (Fig. 3 E) broadly cylindrical, often with the apex excentric, i.e. nearly sigmoid, in face view ellipsoid, 10–16.5 × 4.6–4.8 μm, with a blunt apiculus; spore wall pale yellow, neither amyloid nor dextrinoid, acyanophilous, thin, essentially smooth.

Fruiting on the bark of large, dead branches of *Quercus garryana,* associated with a white rot. Known only from the *Quercus* zone of coastal Vancouver Island, Canada and Washington State, USA.

This is the only species of *Ramaricium* in which the basidiomes become stratified as a result of hymenial thickening.

The microscopic features of *R. flavomarginatum* are similar to those of *Kavinia himantia* (Schw.) Erikss. *K. himantia* (see Eriksson & Ryvarden 1976) differs in having smaller basidia, 25–35(–45) × 6–8 μm, smaller spores, 8–10(–12)

× 4–5 μm, hyphae with cyanophilous warts and, macroscopically, a hydnoid hymenial surface. Thus, I reject the synonymy of *R. flavomarginatum* with *K. himantia* proposed by Miller & Boyle (1943 p. 44) and Rogers & Jackson (1943 p. 278).

Material studied. Canada: Vancouver Island, Cobble Hill, 21.IX.1940, Bier (DAOM F10115) – *USA:* Washington, W Klickitat Co., type, see above; W Kl. Co., Bingen, 8.III.1903, Suksdorf 912, 913 (FH).

Ramaricium occultum Erikss.

Eriksson, Svensk Bot. Tidskr. 48 p. 196 (1954) – Orig. coll.: Sweden, Uppland, Djurö par., between Södersunda and Skogsberga, 3.XI.1949, Haglund & Eriksson (UPS holotype).

A detailed description is found in Eriksson (1954). *R. occultum* is known from two collections only. It is very similar to *R. albo-ochraceum* but it grows in quite a different habitat, viz. deep in moist mats of moss (*Hylocomium*) under shrubs of *Juniperus communis*.

Material studied. Sweden: type, see above.

Ramaricium polyporoideum (Berk. & Curt.) Ginns, comb. nov.

Basionym: *Corticium polyporoideum* Berk. & Curt., Grevillea 1 p. 177 (1873) – *Coniophora polyporoidea* (Berk. & Curt.) Burt, Ann. Missouri Bot. Gard. 4 p. 247 (1917) – *Phlyctibasidium polyporoideum* (Berk. & Curt.) Jülich, Proc. K. Nederl. Akad. Wet., Amsterdam (C) 77 p. 154 (1974) – Orig. coll. not seen because this species seems to be one whose concept is agreed upon by everyone.

Detailed descriptions have been published in Burdsall (1971), Liberta (1973) and Jülich (1974). The principal habitat of the species is wood, but it also grows over needles, twigs, woody debris and live plant parts. It is not restricted to dry sites.

Material studied. Canada: Quebec, Mt Burnet, near Ottawa, 19.VIII.1936, Macrae (DAOM F7127) – *USA:* Vermont, Middlebury, Huntswamp, 28.III.1897, Burt (FH, S) – Connecticut, N. Bloomfield, 28.VIII. 1938, Eno, FP 84053 (DAOM) – New York, East Galway, 24.VII.1898, Burt (FH) – Ohio, Champaign Co., Cedar Swamp, 11.X.1959, Cooke 31803 (DAOM) – Michigan, Ann Arbor, 9.XI.1907, Kauffman 3[illegible](FH) – Kentucky, Mammoth Cave, 6.VII.1897, Lloyd 2561 (FH) – Tennessee, Blount Co., Mountvale Springs, 21.IV.1934, Hesler, UTenn 6752 (DAOM) – Georgia, near Tallulah Falls, 24.VIII.1901, Seymour (FH) – Arkansas, Fordyce, 6.IX.1909, Humphrey 5828 (FH) – *Brazil:* Rio Grande do Sul, Parey, 1931, Rick, MBG 150744 (BPI); RGS, 7.IV.1893, Malme (S).

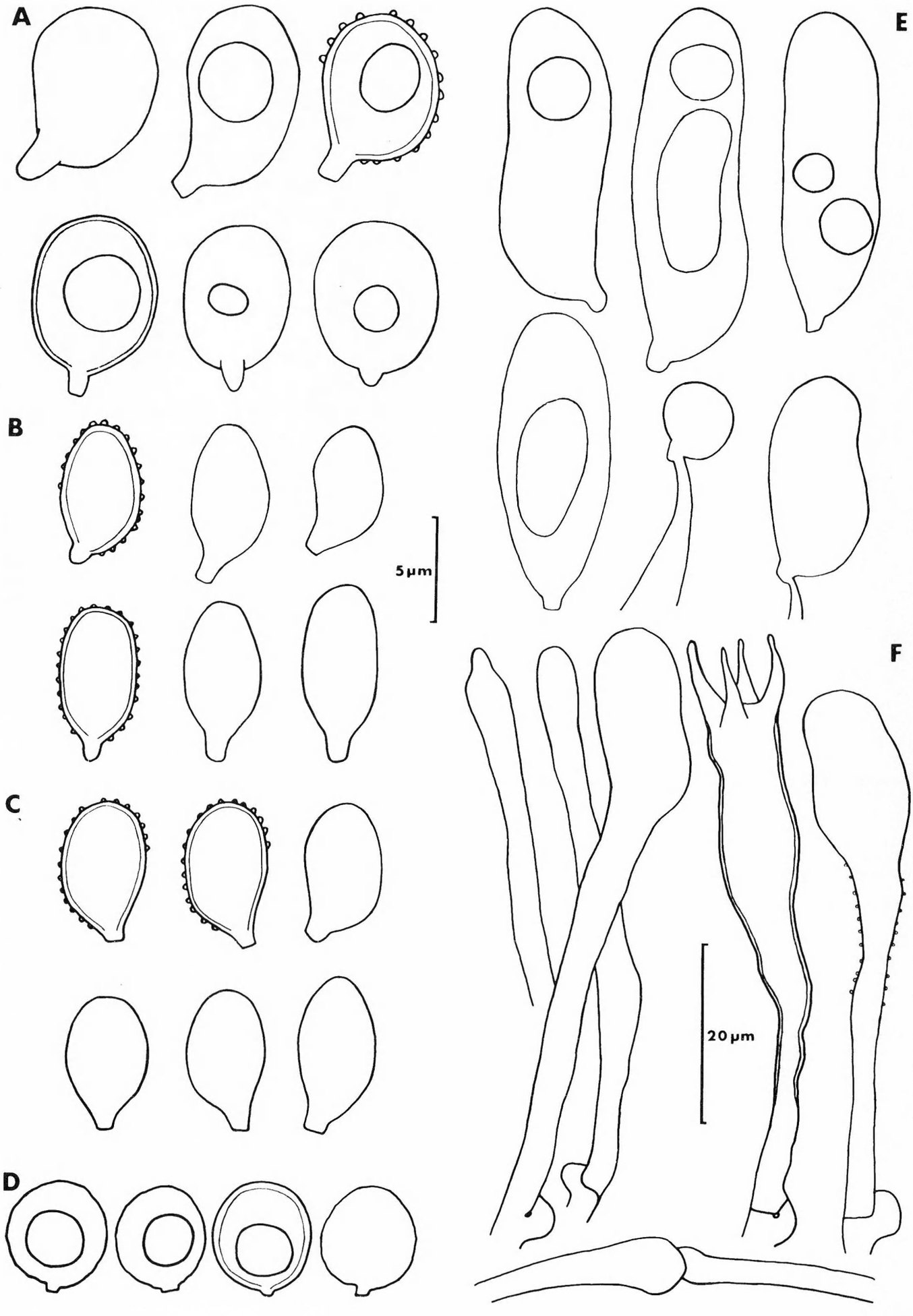
Ferrous sulphate tests

One of the principal characters (Donk 1964) of the Gomphaceae is the dark green discoloration of fresh basidiome tissues following the application of a drop of ferrous sulphate solution. However, the reaction of the basidiomes of *Ramaricium* species is unknown (Donk 964). In the absence of fresh basidiomes I tested dried specimens of *R. alboflavescens, R. albo-ochraceum, R. flavomarginatum* and *R. polyporoideum,* and a live mycelial mat of *R. alboflavescens*. Watling (1971 p. 585) reported that "carefully preserved dried material" showed the typical reaction; thus a comparison was made with dried basidiomes of species of *Gonphus* and *Kavinia*. Both genera are members of the Gomphaceae and *Kavinia* is the genus most closely allied to *Ramaricium*. Finally, several species of *Trechispora* Karst., which have spore ornamentation similar to that found in some species of *Ramaricium,* were tested because *R. albo-ochraceum* has been included in *Trechispora* by Liberta (1973).

The tests were conducted by first wetting the basidiome tissue with a drop of methanol, and then applying a drop of ferrous sulphate soution (1 g $FeSO_4 \cdot 7H_2O$ in 100 ml distilled water). When the living mycelial mat of *R. alboflavescens* was tested the methanol was not used.

The reaction of the species to the ferrous sulphate was of two types, a distinct darkening of the tissue or no discoloration. The tissues of the dried basidiomes of all species of the Gomphaceae tested darkened, including those of the four species of *Ramaricium* which were

Fig. 3. *Ramaricium* species. – A: *R. polyporoideum,* DAOM F 7127, spores. – B: *R. albo-ochraceum,* holotype, spores. – C: *R. occultum,* holotype, spores. – D: *R. alboflavescens,* DAOM 22178, spores. – E, F: *R. flavomarginatum,* DAOM 10115. E shows spores and F shows hyphoid cystidia, on left, two immature basidia, in center and one at right with scattered warts along the midsection, one mature basidium with slightly thickened wall, and below a swollen hyphal septum. Del.: J. Ginns.


A
B
C
D
E
F
5 µm
20 µm

tested. In *R. albo-ochraceum* (DAOM 30184) and *R. polyporoideum* (DAOM 154328, 155731), the hymenial surface stained pale olive grey and grey green, respectively; in *R. flavomarginatum* (Suksdorf 888, 912, 913, DAOM F10115), the discoloration was a rapid change to dark green or blackish purple with an olivaceous tint or green margin on the reagent spot on the hymenial surface. In *R. alboflavescens* (DAOM 154322, 154325) the discoloration was either blackish with a weak grey green color around the margin of the drop or the tissue became olive-black. The live mycelial mat gave no reaction. *Kavinia alboviridis* (Morg.) Gilbertson & Bud. (DAOM F6746, 69842, 72668) showed an immediate darkening of the tissue which after several minutes was dark greenish black. *K. himantia* (DAOM 30208, 72179, 122942) also reacted by showing a very transitory dark green as the tissue became dark purple black.

In *Gomphus floccosus* (Schw.) Sing. (DAOM 107351, 112200, 11830), the hymenial surface stained grey-green, and then darkened to purplish. In *G. clavatus* S. F. Gray (DAOM 113730, 128480), the hymenial surface became blackish and the flesh a pale olive color. In *G. bonarii* (Morse) Sing. (DAOM 89680), the hymenium is blackened in the test.

Five species of *Trechispora* were tested: *T. alnicola* (Bourd. & Galz.) Liberta (TRTC 30200, 18113), *T. farinacea* (Fr.) Liberta (DAOM 100463, TRTC 12247), *T. fastidiosa* (Fr.) Liberta (DAOM 162534), *T. mollusca* (Fr.) Liberta (DAOM 146464) and *T. vaga* (Fr.) Liberta (TRTC 6519, 20080). None of the basidiomes stained with ferric sulphate.

To summarize, the dried basidiomes of the *Ramaricium, Kavinia* and *Gomphus* species tested with ferrous sulphate show similar staining reactions, a darkening usually accompanied by some shade of green. Whether the reaction is similar to that of fresh basidiomes I do not know for I have not seen it.

Discussion

The corticioid basidiomes of the five species are so distinctive macroscopically that the genus is recognizable in the field. The combination of a hymenial surface with an olivaceous tint, and contrasting pure white, tough cottony subiculum and hyphal strands is the principal feature. The dry, rather thick, firm, crustose hymenium separates the group from the athelioid species.

The principal microscopic features of *Ramaricium* are shared by the two species of *Kavinia* (see Eriksson & Ryvarden 1976). The two genera are maintained as distinct primarily on the basis of the configuration and development of the hymenial surface. If taxonomic emphasis were placed, instead, on spore features, the four species with warty spores, i.e. *occultum, alboochraceum, polyporoideum* and *alboviridis,* would be grouped in *Kavinia* and the species with spores lacking warts, i.e. *alboflavescens, flavomarginatum* and *himantia,* would be generically distinct, perhaps under the name *Hydnocristella* Peters. Such an arrangement would accept as congeneric species which are corticioid and hydnoid. I have no strong objection to such a scheme but, in this instance, there is more than just a difference in hymenial configuration. In *Ramaricium* the hymenial surface is continuous initially and continues to be so throughout the expansion of the basidiome. In *Kavinia* a hymenium is initiated on each of the developing spines so that even at maturity the spines are separated by a sterile subiculum. Only occasionally in *K. himantia* does a hymenial surface eventually become continuous between some spines (e.g. TRTC 30207 and DAOM 167548).

Corner (1970 pp. 11, 226) and Petersen (1971) were not convinced that the two *Kavinias* were congeneric. Corner, noting the similarities in spore and hyphal features, suggested that *K. himantia* was allied with *Lentaria soluta* (Karst.) Pilát, whereas the "ochraceous, rough or verruculose spores of *K. bourdotii* (= *K. alboviridis*) may relate it with *Ramaria* or the hydnoid *Beenackia.*" Petersen segregated *K. himantia* by placing it in *Hydnocristella* and distinguished it from *Kavinia* by the spores which are "smooth, thin-walled, cylindrical and without cyanophilous reaction to speak of (although the wall itself is weakly so)," the hyphae which lack "ampulliform or onion-shaped swellings," and lastly the "small, cyanophilous, densely distributed spines" on some hyphal segments. However, I found occasional ampullate swellings on the hyphae of *K. himantia* and so did Eriksson & Ryvarden (1976 Fig. 376 d). The other features given to distinguish *Hydnocristella* from *Kavinia* are not, when compared with the distribution of these features in *Ramaricium,* of sufficient

importance to be used at the generic level. I accept *K. alboviride* and *K. himantia* as congeneric.

The principal microscopic features of *Ramaricium, Kavinia* and some species of *Ramaria* are (in no particular order of importance for it is the combination of several in a species that is taxonomically significant): cyanophilous, warty spores; broadly ellipsoid to broadly cylindrical spores; pale yellow, thickened, cyanophilous spore wall; narrow, warty hyphae with thickened walls; ampullate swellings; broad basidia with a stem-like base; and pleurobasidial habit.

The spores of three species of *Ramaricium* are broadly ellipsoid with an elongated base and have cyanophilous walls and warts (Figs. 1 A, 2 A–D, 3 A–C). The same spore characters occur in *Kavinia alboviride* (Eriksson & Ryvarden 1976 Fig. 374 b). *R. alboflavescens* has subglobose spores which lack warts but the outline is not actually smooth (Fig. 1 B–C). The spore surface is a series of low, broad mounds which may be very appressed warts. It resembles closely the surface of spores of *K. himantia* (Eriksson & Ryvarden 1976 Fig. 377 b). The spores of *R. flavomarginatum* (Fig. 3 E) appear smooth but the wall may be slightly undulating, as in *K. himantia*.

The hyphae of the five *Ramaricium* species are similar in type of septation with clamp connections and diameter, 1.5–3 μm. *R. alboflavescens* (Fig. 1 D–E), *R. flavomarginatum* and *R. polyporoideum* (Fig. 1 F) have characteristic warts on the surface of the hyphae which are like those in *K. himantia* (Eriksson & Ryvarden 1976, Fig. 377 c). Hyphae in other species have a smooth outline. The warty ornamentation on the spores and hyphae (Figs. 1, 2, 3 A–C) may be the remains of a watery-gelatinous layer which upon drying has contracted to leave scattered deposits. In some collections of *R. alboflavescens,* there are what appears to be remnants of a mucilaginous layer on the surface of some hyphae whereas other hyphae have the characteristic warts on the surface. In *K. himantia* the warts are cyanophilous, in *R. polyporoideum* some hyphal segments have cyanophilous warts (most are acyanophilous) and in *R. alboflavescens* and *R. flavomarginatum* the warts are acyanophilous.

Corticium polyporoideum is the type species for the genus *Phlyctibasidium*. By transferring *C. polyporoideum* to *Ramaricium,* proposed 1954, the name *Phlyctibasidium,* proposed 1974, becomes a synonym of *Ramaricium*. The generic diagnosis (Jülich 1974) of *Phlyctibasidium* differs from that of *Ramaricium* by characters here taken to distinguish *R. polyporoideum* from the other species placed in *Ramaricium*. The principal feature is the presence of basidia "often with cyanophilous warts on the surface." In *R. polyporoideum* the spores, hyphae and basidia are typically covered with cyanophilous warts. In *R. alboflavescens* most of the hyphae (Fig. 1 D–E) are covered with similar warts, and in *R. albo-ochraceum* (Fig. 1 A, 3 B) and *R. occultum* (Fig. 2 A–B, 3 C) the spores are typically covered with cyanophilous warts. The point is that some species of *Ramaricium* have cyanophilous warts on several types of cells. Their occurrence on the basidia of *R. polyporoideum* does not warrant its segregation into a separate genus.

Acknowledgements. Professor Gunnar Harling and Dr John Eriksson were most hospitable and provided a work area and other facilities during my four months of study at the Department of Systematic Botany, University of Göteborg. Dr Leif Ryvarden, Oslo, kindly furnished the scanning electron microscope pictures in this paper.

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Appraisal and definition of Cyathus triplex (Nidulariaceae)

Harold J. Brodie

Brodie, H. J. 1979 02 15: Appraisal and definition of Cyathus triplex (Nidulariaceae). *Bot. Notiser 132:* 103–108. Stockholm. ISSN 0006-8195.

Cyathus triplex Lloyd (Nidulariaceae) has been poorly understood due to lack of critical detail in the original description. Study of the type material of *C. triplex* indicates that it is a valid species belonging to the group with a two-layered cortex and moderately large spores. An expanded description is given, emphasizing the distinctive light-olive colour, faint but distinct plication and conspicuous firm emplacement. Macro-and microphotographs of the type material are presented.

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The taxonomy of the Nidulariaceae is still far from being in a satisfactory state. One example of the kind of problem that remains is this study of herbarium material identified as *Cyathus triplex* Lloyd. Examination of 18 collections from K, two from C and the revision of 24 packets in my personal herbarium revealed the fact that very few of the fungi mentioned compare closely with the type material.

The principal cause of confusion appears to have been the fact that Lloyd's (1906) description is not sufficiently detailed to facilitate separation of *C. triplex* from similar species. After careful study of Lloyd's type material, I feel that *C. triplex* is a valid species; a full description and photographs of the type material are given in this paper. In addition, several minor complicating details are discussed and appraised.

Lloyd's description and type

In his monograph, Lloyd (1906) described *Cyathus triplex* as follows:

"*CYATHUS TRIPLEX* (Plate 109) – Cups 5–6 × 5, even within and without, with connivent, spreading, somewhat scabrous hairs. Inner surface even, silvery white. Peridiole 2 mm with a very thin adnate tunica. On soaking in water the tunica swells and becomes white and loosens up. Cortex thick, evidently double, but subhomogeneous and the fibrils slender. Spores elliptical, 12–14 × 16–22.

These specimens are from Mauritius, and grew caespitose, attached to twigs and roots. It is a doubtful species to me, being too close to both the preceding (*C. pallidus* and *C. intermedius*). The cups are those of *pallidus,* but darker and the hairs more scabrous. The spores are close to *intermedius,* but the tomentum of the young cups is quite different. Mauritius, Chas. A. O'Connor."

The above description was presumably based mainly, if not exclusively, on a collection bearing Lloyd's label "*Cyathus triplex, Type,* No. 05804; Chas. O'Connor, Mauritius", undated (Fig. 1). It contains c. 70 specimens. The material is now no. 34528 of the Lloyd Mycological Collection in USDA.

Detailed description of the type

Fruit-bodies commonly caespitose, 3–8 in a cluster (Fig. 1 A), *light olive brown* (close to Isabelline), slender, crucibuliform, with *slightly curving sides* (Fig. 1 B), narrowly attached at base, 5–6 mm wide at the mouth, 6–7 mm high exclusive of emplacement. Basal *emplacement very conspicuous* (Fig. 1 B), a firm globose mass almost as wide as the mouth. Outer surface of fruit-body a mat of fine hyphae overlaid with

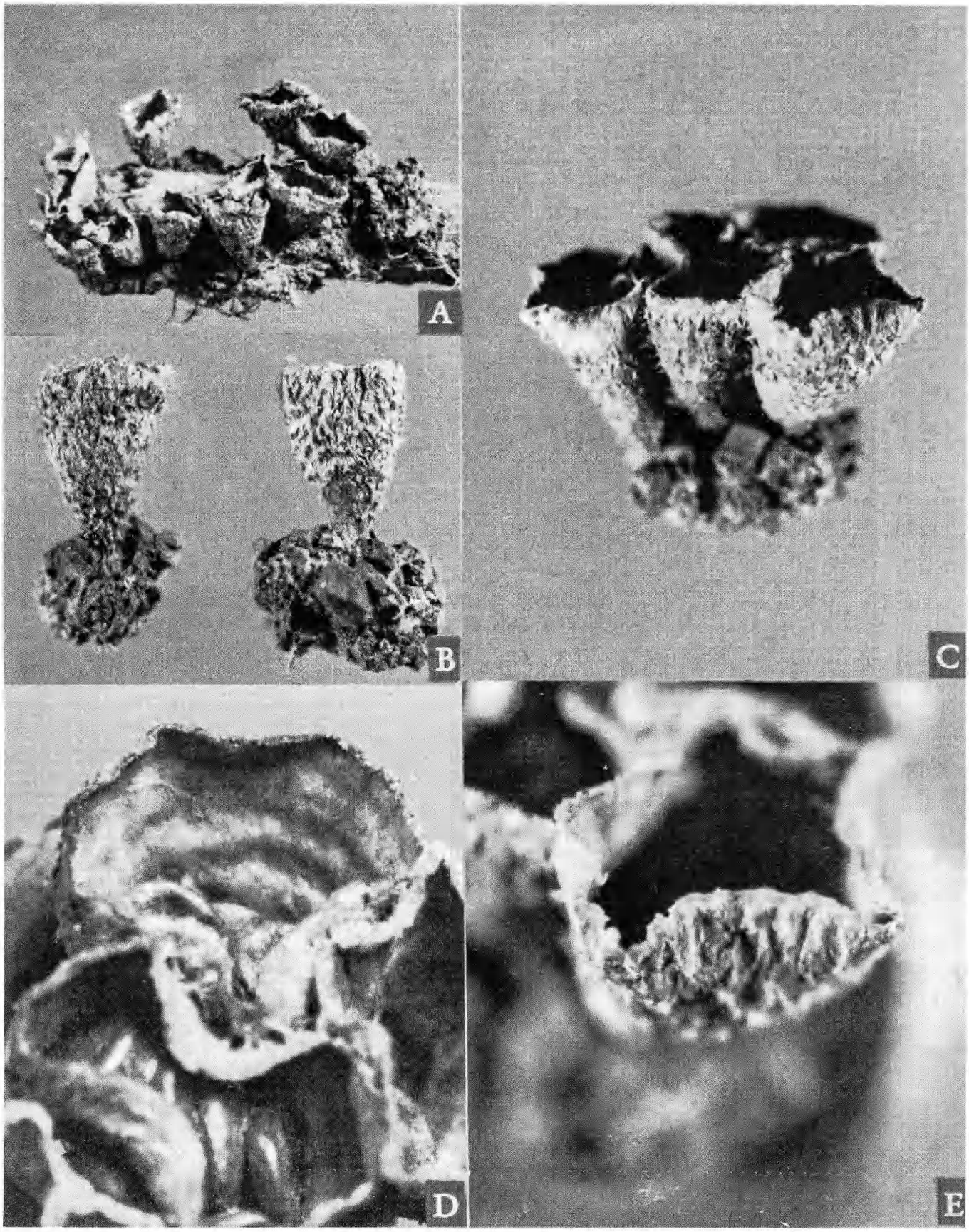

Fig. 1. *Cyathus triplex,* type collection. – A: Group on dead wood showing caespitose habit, ×2. – B: Two single specimens each showing solid and conspicuous emplacement, tall conical form and shaggy exterior, ×3. – C: Cluster of fruit-bodies, central and right-hand specimens show broad external plication and cones of tufted hairs, ×4. – D: Inner surface of peridium (upper specimen) shows faint internal plication at right; note broad transverse ridges and relatively smooth or non-fimbriate lip; shiny, smooth peridioles are seen in lower specimen, ×9. – E: Lip and outer surface of peridium showing smooth lip and coarse irregular plication, ×9.

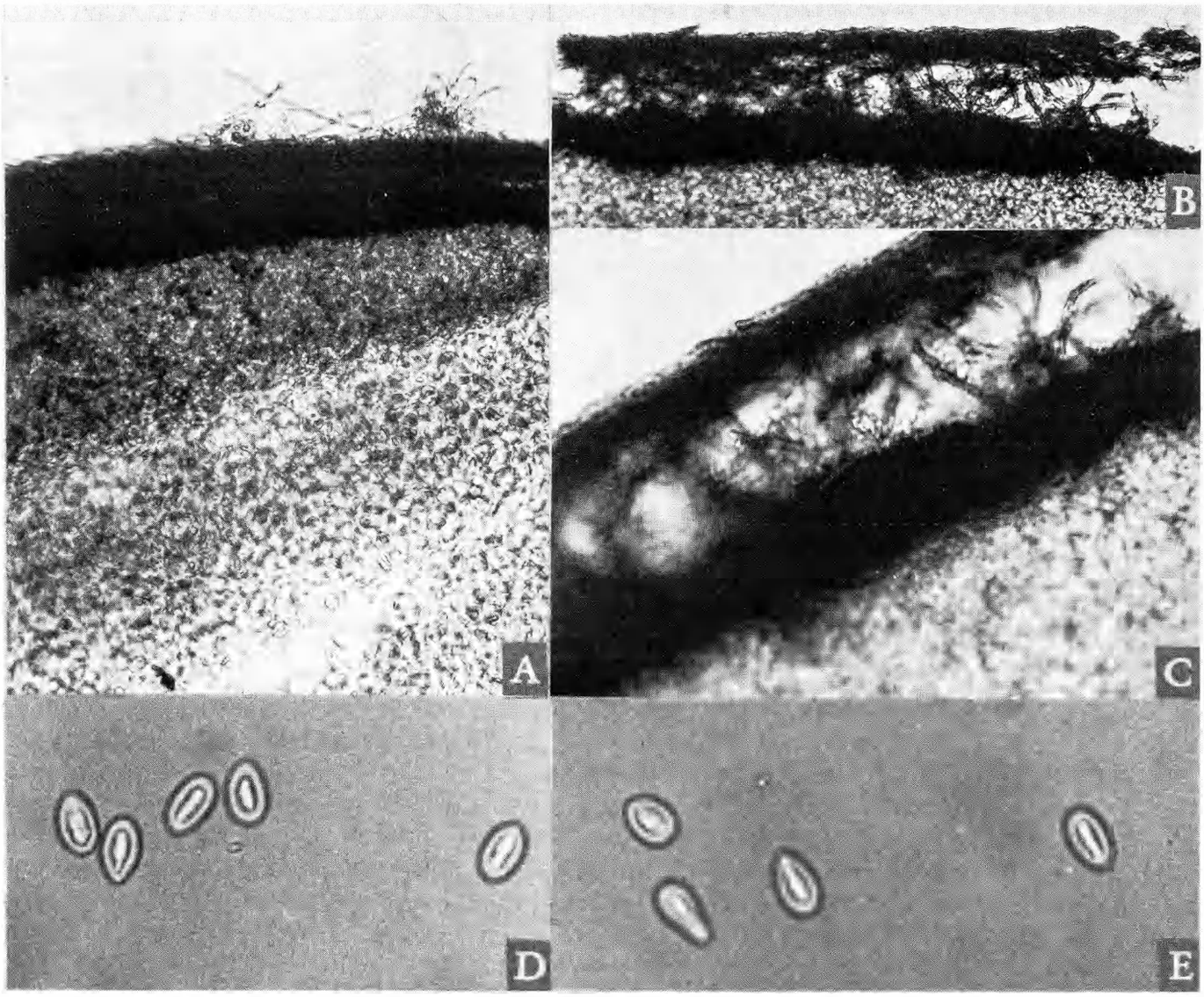

Fig. 2. *Cyathus triplex,* type collection. – A: Section of peridiole from outside to center; on outside, remnants of tunica; dark cortex, section is too thick to show detail but separation of two layers barely evident at right and less so at left; free spores seen in center, ×c. 150. – B: Thin section of cortex showing two dark layers of cortex separated by lighter-coloured loosely-interwoven hyphae, ×c. 150. – C: Exterior of peridiole at higher magnification; only a few of the light-coloured hyphae of the tunica remain attached in this section, ×c. 400. – D, E: Basidiospores showing thick spore wall and ovoid outline, ×700.

conspicuous, conical, occasionally curled, *tufts of down-pointing hyphae* (Fig. 1 B, C). Outer surface *plicate, though faintly* (Fig. 1 C, E) *or not at all* in some specimens. Inner surface *very light buff, shiny* (especially when moistened), *distinctly plicate* in smooth folds (Fig. 1 D, E) c. 1 mm wide. In about 10 % of the specimens no plication is evident. In many specimens there are also broad shallow transverse troughs (Fig. 1 D). *Lip* or mouth of fruit-body *appearing smooth* (Fig. 1 D) but actually *minutely fimbriate* at 30 × magnification. Hyphae of fimbriate lip slightly darker than hyphae of peridium elsewhere. *Peridioles* distinctly *light grey-brown,* externally *shiny,* mostly 2 mm in diameter; outline mostly circular, occasionally angular. *Tunica* usually obvious under 10 × magnification, especially when moistened, but *flimsy* and easily detached, though in places as much as 30 μm thick. *Cortex* clearly *two-layered* in most specimens (Fig. 2 B, C), subhomogeneous in some; each dark layer 20–25 μm thick; separating layer c. 6 μm. *Basidiospores* mostly *ellipsoid* but *frequently ovoid* (Fig. 2 D, E), a small proportion subglobose, 12–15 × 18–21 μm; *thick-walled,* the wall 2.5–3.0 μm.

At first glance, the light colour, curving sides (Fig. 1 B, right) and conspicuous downward-pointing hairs of the type specimens suggest *Cyathus pallidus*. The colour of dry specimens, however, is different from the pale straw colour of *C. pallidus;* it is a distinctive light ochraceous brown. The colour of most specimens is close to Isabelline (65) or Hazel (88) in Rayner's Mycological Colour Chart (Rayner 1970). The colour of moistened specimens is close to Rayner's umber. In brief, the type specimens are light olive brown and there is no trace of the reddish or chocolate shade of such tropical species as *C. poeppigii* Tul. or *C. setosus* Brodie.

The mouth of the fruit-body is minutely fimbriate seen at a magnification of 30×. However, at less magnification (Fig. 1 D) the mouth appears unusually smooth in comparison with many common tropical species and would normally be described as smooth.

The inner wall of the fruit-body is marked by a shallow broad plication which is not conspicuous and even not present in some specimens. The inner surface itself is smooth and strikingly shiny though, in most specimens, not "silvery" as Lloyd described it.

Two impressive characteristics of the type material were not mentioned by Lloyd. The first of these is the very firm and rather large emplacement (Fig. 1 B); in clustered specimens, emplacements may be fused and so be somewhat less conspicuous. The second feature is the faint but definite plication of a large proportion of the fruit-bodies (Fig. 1 C, E) on the outside and also on the inside. In a few specimens, however, no fluting or plication can be seen on either outer or inner surfaces.

The conical tufts of hairs (Fig. 1 B, C) are obvious on all but a few older, rubbed specimens.

The thick-walled spores are by no means all elliptical as Lloyd stated. In many spore samples the predominant spore shape is ovoid (Fig. 2 E) and globose spores are not uncommon.

Other specimens in the Lloyd herbarium

Second O'Connor collection. In addition to the specimens labeled "type", there is a second collection (c. 36 specimens) in the Lloyd herbarium (no. 34527) also from Chas. O'Connor, Mauritius, and undated as well. Presumably it is not a duplicate for it bears a separate label number: "08 + 280 *Cyathus triplex* (*c.f.* Nidulariaceae p. 23). Spores 12 × 20, abundant; Chas. A. O'Connor, Mauritius".

Lloyd did not refer to this in his description, and he may have received it after the publication of his monograph. This possibility is suggested by the note "*c.f.* Nidulariaceae p. 23" on the label. Specimens of this collection differ from the type as follows: they are mostly smaller and many are immature; they are somewhat paler; the inner surface of the peridium is lighter in colour than in the type and closer to Lloyd's adjective "silvery"; fewer specimens are clearly plicate. These differences are minor and do not affect my description above.

Two Ceylon collections. Although not cited by Lloyd, two collections from Ceylon were labeled by him as *C. triplex,* viz. no. 34529 and 34530. Both are ascribed to "T. Petch, Peradeniya, Ceylon, Oct. 06". They are very similar to one another but strikingly different from the type in the following important respects: fruit-bodies considerably larger (max. 7 mm high, 8 mm at mouth); colour much darker, some a deep chocolate brown; peridioles plumper, darker and larger (up to 2.5 mm); emplacements much less conspicuous; peridium not plicate. I cannot identify the Ceylon fungi at present with certainty, but I suggest they may be old weathered specimens of *C. setosus* Brodie. Moreover there is a collection at Kew labeled "Peradeniya, 3854, Nov. 1913" which seems very similar and which is probably *C. setosus*. Why Lloyd named the Ceylon specimens *C. triplex* remains a puzzle.

Other records

Although I have made no attempt to assemble all available records of specimens that have been identified as *C. triplex,* an account of some fairly recent records may be of value.

Palmer (1961) published some notes about the Nidulariaceae in Persoon's herbarium and included a fairly full description of a specimen which had been labeled *Nidularia laevigata* and which he (Palmer) identified as *Cyathus triplex*. Although I have not examined the material studied by Palmer, his description makes it seem likely that the determination is correct. Palmer (1961

pp. 440 and 442–443) refers to the presence of a proximal notch on the basidiospores but I was unable to detect this structure in basidiospores of Lloyd's type material.

Dissing (1963) published a brief description of what he believed to be *C. triplex* from Thailand, and included an excellent photograph of a section of a peridiole. Through the courtesy of Dr Dissing, I was able to examine his two collections and I can confirm that both correspond very closely with Lloyd's type, more closely in fact than most other material labeled *C. triplex* which I have studied.

Pavlich (1976), in reporting *C. triplex* from Peru, included a seven-line description (in Spanish) which seems to refer to this species but I have not seen the material.

Reid (1976) listed *C. triplex* from Puerto Rico, Sri Lanka, Mauritius, Africa, Guyana and Venezuela, based on some 18 collections at Kew. Reid also gave a description of *C. triplex* based on a collection from Tobago.

Dr Reid kindly arranged the loan of his Tobago collection as well as the 18 Kew collections which he cited. His Tobago collection differs markedly from the type of *C. triplex* in the following respects: fruit-bodies dark brown, almost chocolate colour, wider and higher; emplacement not solid and conspicuous but more nearly byssoid; peridioles considerably larger and plump (2.5–3 mm); the mouth is setose. The latter characters would indicate that Reid's collection is probably *C. setosus* Brodie.

As to the 18 Kew collections, only two or possibly three correspond well with Lloyd's type material. These bear the following labels: Warriapola 5556, Jan. 1918 – Sri Lanka, Middlemarch, Oct. 1906, det. Lloyd, 2135 – Ryvarden 10699, Tanzania, Tanga, Usambara Mts., Feb. 1973 (no peridioles, identification not certain).

Reid (1976 p. 686) also refers to a collection from Guyana (Holmia, Potaro, River, Dec. 1908, Bartlett 8709) which had been identified by myself as *C. triplex*. Recent re-examination of these specimens reveals that they do not correspond at all to the type of *C. triplex*. They are very probably *C. intermedius* (Mont.) Tul.

Brodie (1968). In 1968 I reported that I had obtained cultures of dikaryon mycelium of *C. triplex* and drew attention to the fact that it was dark brown whereas dikaryon mycelium of *C. pallidus* and *C. intermedius* is essentially unpigmented. This difference, I felt, suggested that *C. triplex* may not be closely related to these two species. I now believe that my identification of the cultured material (cultures obtained from no. 1266 Herb. H. J. Brodie) was incorrect. Re-examination of my no. 1266 (Jamaica, 1954) indicates with reasonable certainty that it is *C. setosus* Brodie. Unfortunately, all peridioles in the specimen were used in the endeavour to obtain cultures; a revision of peridiole and spore features therefore cannot be made. My note on the packet regarding the spores is "thick-walled, elliptical, 13–4 × 19–23 μm". Spore shape and spore size are both closer to *C. setosus* than to those features in the type of *C. triplex*.

Brodie (1975). An identification error of more serious consequence concerns the actual specimen used for the photograph representing *C. triplex* in my monograph (Brodie 1975 p. 163). Collection no. 6645 of my herbarium is clearly a mixture of *C. triplex* and *C. intermedius*. The specimen shown as Fig. 47 a (left) is *C. intermedius,* the one on the right is very probably correctly named, though it differs somewhat from the type material.

Specimens in Herb. Brodie. In all, of 24 collections in my own herbarium which I had identified as *C. triplex* prior to the present study, only 14 correspond well or reasonably well with Lloyd's type. Many of the others are *C. setosus,* a species which I described (Brodie 1975) long after I had made the identifications; a few are *C. intermedius*. The following specimens are, as far as I am able to tell at present, absolutely identical to Lloyd's type material (my herbarium numbers): 1221, C. B. Heiser, Turrialba, Costa Rica, 18.7.1953; 1423, J. Winston, Bengal, 1.1918; 78006, H. Dissing 8127, Rachabury, Thailand, 10.11.1961. Several other collections which I believe to be correctly determined differ from Lloyd's type in rather minor details.

Cyathus triplex, according to the present concept, is known from Costa Rica, Dominica, Florida, Guam, India, Jamaica, Mauritius, Peru, Sri Lanka, Tanzania, Thailand and Venezuela.

Comparison with other species

To the unaided eye, *C. triplex* is most liable to be mistaken for some of the darker forms of *C. pallidus* (Brodie 1975 p. 161). The faint plication and conspicuous solid emplacement of *C. triplex,* however, are not present in *C. pallidus*. As to microscopic characters, the spores of *C. triplex* are so much larger than those of *C. pallidus* that confusion is impossible and the cortex of *C. triplex* is two-layered whereas that of *C. pallidus* is one-layered.

Again superficially, especially as to colour, size and faint plication, *C. triplex* could be confused with *C. berkeleyanus*. The latter species, however, is distinctly plicate and lacks the tufts of long hairs and the solid emplacement of *C. triplex*. *C. berkeleyanus* has unusually small spores (Brodie 1975 p. 178) and a one-layered cortex.

It is not appropriate in a paper such as this to discuss at length the problem as to which of the morphological features of *Cyathus* do (or may eventually) provide the best indices (taken singly or collectively) of taxonomic relationships. From my own limited knowledge at present, it is not possible to make positive assertions. *C. triplex* certainly does seem to resemble *C. pallidus* and *C. intermedius,* particularly in spore size but also in the crucible-like shape of peridia which have thin curved sides and in the presence of tufts of down-pointing hairs. However, *C. triplex* has a clearly two-layered cortex whereas that of the other two species is one-layered. Moreover, whereas the peridium of *C. triplex* is distinctly (though faintly) plicate, neither of the other species possesses that feature. My opinion (Brodie 1975 p. 163) that *C. triplex* is not closely related to *C. pallidus* and *C. intermedius* based on comparison of cultures is invalidated due to erroneous determination of the material (see above). A fresh comparison of cultures derived from correctly identified specimens might help to solve the problem of their taxonomic relationship.

In identifying *C. triplex,* the most serious hazard is undoubtedly the matter of plication. It is certainly present in many specimens of the type but not sufficiently striking to obviate its being overlooked; moreover, not all specimens of the type are plicate. The colour, two-layered cortex (Fig. 2 B, C) and conspicuous globose emplacement (Fig. 1 B), however, are reliable characters when considered along with others as described herein.

Acknowledgements. For the loan of Lloyd's type material I am indebted to the courtesy of Dr David Farr. Dr Derek Reid kindly arranged for the loan of materials from Kew. Dr H. Dissing's collections from Thailand were obtained through the courtesy of Dr Bert Fredskild, Copenhagen. Photographs reproduced herewith were taken by Mr H. F. Dietrich, University of Victoria, B. C.

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Embryology of Arctoteae-Arctotinae (Compositae)

Lennart Ahlstrand

Ahlstrand, L. 1979 02 15: Embryology of Arctoteae-Arctotinae (Compositae). *Bot. Notiser 132:* 109–116. Stockholm. ISSN 0006-8195.

Megasporogenesis and embryo sac development of five species of *Arctotis* L. and one each of *Haplocarpha* Less. and *Arctotheca* Wendl. were studied. A preliminary report for the monotypic genus *Cymbonotus* Gaud. is also given. The archespore is usually 1-celled, rarely 2-celled. After meiotic divisions a linear tetrad is always formed. The embryo sac is formed from the chalazal megaspore while the other three megaspores degenerate. Embryo sac development is monosporic of the 8-nucleate Polygonum type. Although degenerating, both synergids and antipodes endure even during endosperm formation. The three antipodes remain 1-nucleate and undivided. In mature embryo sacs remnants of the synergids persist, as a dark-staining and very conspicuous structure lying above the developing egg-cell. There are no haustoria. The integumentary tapetum, one cell-layer thick, remains unchanged even in mature embryo sacs possessing endosperm. The endosperm formation of the *Arctotis* species is Cellular. The chromosome number n = 9 is given for *Arctotis acaulis* L., *A. venusta* T. Norl., *A. gumbletoni* Hook. fil. and *A. fastuosa* Jacq.

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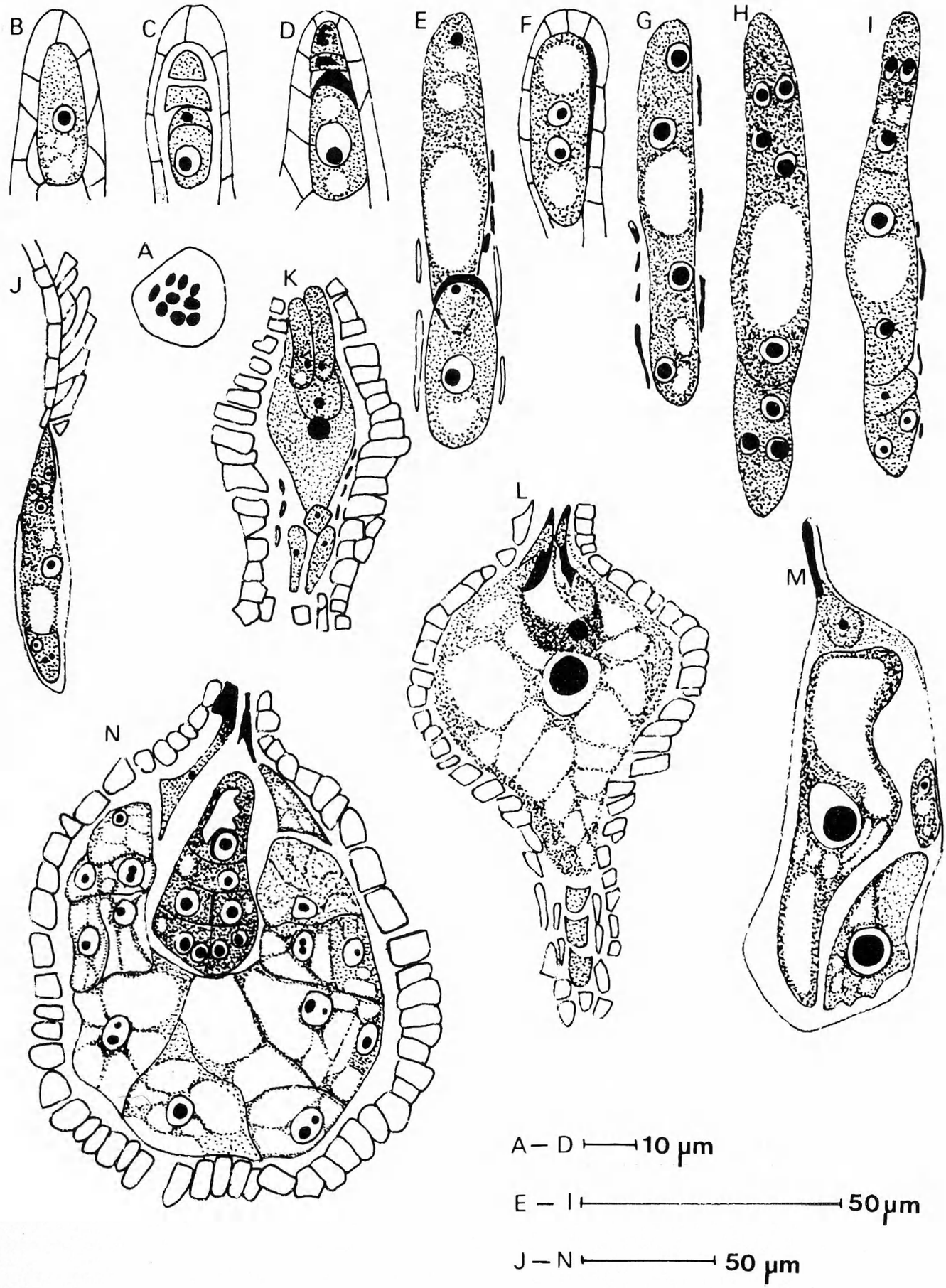
The subtribes Arctotinae, Gorteriinae and Gundeliinae of the tribe Arctoteae were established by Bentham (1873). He considered that the tribe Arctoteae forms a link between the tribes Anthemideae and Calenduleae on the one hand and the Cynareae on the other. Hoffmann (1894) placed the Calenduleae and the Cynareae close to the Arctoteae. He included *Ursinia* Gaertn. and *Arctotis* L. in the subtribe Arctotinae and regarded the latter genus as being the furthest removed from the Cynareae in the subtribes of Arctoteae. Most modern authors are of the opinion that *Ursinia* is better removed from the Arctoteae (Ahlstrand 1978). Hoffmann (1894) divided *Arctotis* into nine sections, which correspond with the four genera of Arctotinae recognized by Levin (1922), viz. *Arctotis, Haplocarpha* Less., *Arctotheca* Wendl. and *Cymbonotus* Gaud. Lewin believed that *Cymbonotus* is closely related to *Arctotis*, but he kept it separate because of its geographical restriction to Australia. Small (1919) linked the Arctoteae with the Senecioneae. Cronquist (1955) considered the Arctoteae to be related to both the Anthemideae and the Cynareae; all three of them are stated to have originated independently from the Heliantheae. Carlquist (1976) incorporated the Arctoteae into his discoid subfamily Cichorioideae, because he thought it had developed from a cichorioid-carduaead ancestral complex. Both Wagenitz's (1976) and Jeffrey's (1977) views on the evolution of Arctoteae coincide rather well with Carlquist's; Turner's (1977) views, however, are more in line with Cronquist's. Norlindh (1977), in his review of Arctoteae, retains the tribal subdivision unchanged and includes the genera *Arctotis, Cymbonotus, Arctotheca, Haplocarpha* and *Dymondia* Compton in the subtribe Arctotinae while excluding *Ursinia*.

Nearly all the genera of Arctotinae have their main distribution in S Africa. The only exception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is *Cymbonotus*, which is restricted to Australia. *Haplocarpha* also occurs in the E African Highlands and in Ethiopia. A few species of *Arctotis* and *Arctotheca* are recorded from Australia (Phillips 1951, Norlindh 1977).

Dahlgren (1924) found that the embryo sacs of *Arctotis stoechadifolia* (probably = *A. venusta* T. Norl.) and *A. calendulacea* (= *Arctotheca calendula* (L.) Levyns) are comparatively small. Their antipodes are diminutive and they degenerate early. In two instances one of the antipodes in *A. stoechadifolia* was observed to increase in size and take on the appearance of an egg cell. None of the species has a synergid haustorium. Endosperm formation in both is Cellular, as found for "*A. stoechadifolia*" by Schürhoff (1926).

The aim of the present investigation was to decide whether the embryological data agree with the taxonomic treatment of the genera concerned. Macrosporogenesis, development of the embryo sac and, in certain species, endosperm formation are dealt with here.

Material and methods

The material was grown in Göteborg in 1967 from achenes received from the Botanical Garden of Uppsala (*Arctotis breviscapa*) and from the National Botanic Garden, Kirstenbosch (*Arctotis venusta*). Fixations were also made of material from flowering plants in the Botanical Garden of Lund (*Arctotis venusta*, 1964; *A. acaulis, Arctotheca calendula*, 1967), in the Botanical Garden of Copenhagen (*Arctotis gumbletoni, Haplocarpha lyrata*, 1967; *Arctotheca calendula*, 1966) and in the Royal Botanic Gardens, Kew (*Arctotis fastuosa*, 1966). The *Cymbonotus* material originates from a visit to Australia by Professor N. A. Sørensen, Trondheim. Regrettably the voucher specimens of this material have been lost, and the report on the embryology of *Cymbonotus* must therefore be regarded as preliminary. Nevertheless, Professor Sørensen is convinced (pers. comm.) that the investigated material was correctly identified.

The identification of the other specimens was made by Professor T. Norlindh, Stockholm. Voucher specimens, and the slides studied, are deposited at the Department of Systematic Botany, University of Göteborg.

The cytological technique used is that described by Ahlstrand (1978).

Results

Arctotis fastuosa Jacq. Chromosome number n = 9 (Fig. 1 A). The archespore is usually 1-celled (Fig. 1 B). The meiotic divisions give rise to a linear tetrad of megaspores (Fig. 1 C), of which the lowermost germinates to produce an embryo sac (Fig. 1 D) and the others degenerate. Fig. 1 E shows an unusual case, with two competing embryo sacs developing. The nutrient supplies are almost certainly only sufficient to sustain one mature embryo sac and so it is probable that only one will attain the 8-nucleate stage. The cells of the nucellus have degenerated by the time the 4-nucleate stage is reached (Fig. 1 G). One side of the micropylar canal nearly always possesses slender cells, inclined at an oblique angle to the extension of the embryo sac (Fig. 1 J). In organized embryo sacs the synergids do not reach the micropyle (Fig. 1 J, K). The synergids always have a vacuole below the nucleus (Fig. 1 K). There are three antipodes (Fig. 1 K, L); no secondary division of these cells has been noticed. Sometimes they lie in a row (Fig. 1 L), sometimes irregularly (Fig. 1 K). When nearing maturity the embryo sac grows markedly in breadth; the central part becomes rather globose (Fig. 1 L). The integumentary tapetum survives, even during endosperm stages, without showing any sign of disintegrating (Fig. 1 N). The tapetum seems to represent a very firm envelope, inside which the embryo sac must develop. The synergids begin to degenerate when the embryo sac has become fertilized (Fig. 1 L). Very often they acquire a hooked appearance (Fig. 1 N). In fertilized embryo sacs the endosperm chamber becomes repeatedly vacuolated. Probably a successive formation of endosperm cells occurs, which is synchronous

Fig. 1. Megasporogenesis and embryo sac development in *Arctotis fastuosa*. – A: PMC, metaphase plate n = 9. – B: EMC. – C: Tetrad stage. – D: Germination of ES. – E: Two megaspores of the same tetrad trying to form embryo sacs contemporaneously. – F: 2-nucleate ES. – G: 4-nucleate ES. – H: 8-nucleate ES. – I: Organized ES. – J: Organized ES; the synergids do not reach into the micropyle canal. – K: Organized ES with integumentary tapetum. – L: Old, pear-shaped ES with degenerating synergids and antipodes. – M: ES with endosperm cells. – N: ES with proembryo and endosperm cells, hook-shaped synergids in degeneration and persistent integumentary tapetum. – EMC embryo sac mother cell, ES embryo sac, PMC pollen mother cell.

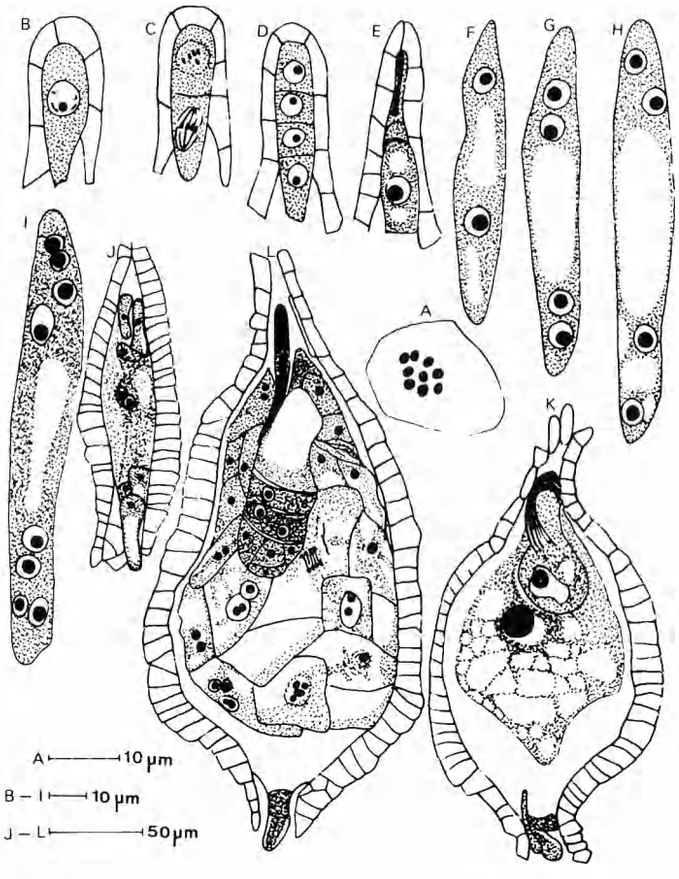

Fig. 2. Megasporogenesis and embryo sac development in *Arctotis venusta*. – A: PMC, metaphase plate n = 9. – B: EMC. – C: Dyad stage. – D: Tetrad stage. – E: Germination of ES. – F: 2-nucleate ES. – G: Young 4-nucleate ES. – H: 4-nucleate ES. – I: 8-nucleate ES. – J: Organized ES with integumentary tapetum. – K: Old ES with curved synergids and antipodes in degeneration stages. – L: ES with proembryo and endosperm cells; synergids and antipodes in degeneration stages.

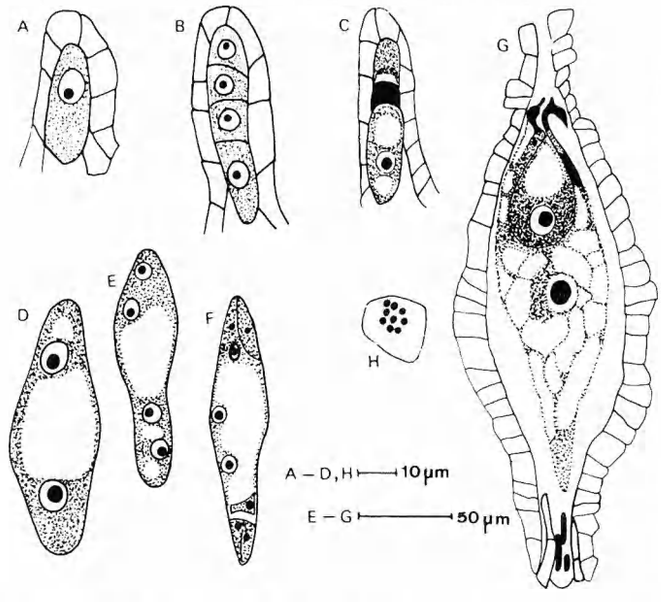

Fig. 3. Megasporogenesis and embryo sac development in *Arctotis acaulis*. – A: EMC. – B: Tetrad stage. – C: Germination of ES; degenerating tetrad cells. – D: 2-nucleate ES. – E: 4-nucleate ES. – F: Organized ES. – G: Old ES; degenerating curved synergids with hooks. – H: PMC, metaphase plate n = 9.

with the divisions of the endosperm nuclei (Fig. 1 M, N). Free secondary endosperm nuclei in the plasma have not been observed, and the initial endosperm formation is thus Cellular.

Other Arctotis species. In *Arctotis venusta* T. Norl. (Fig. 2), *A. acaulis* L. (Fig. 3), *A. breviscapa* Thunb. (Fig. 4), and *A. gumbletoni* Hook. fil. (Fig. 5) the embryology is very uniform and similar to that of *A. fastuosa* (for further information, see the corresponding figures and texts).

Haplocarpha lyrata Harv. The archespore is 1-celled (Fig. 6 A). Megasporogenesis results, via a dyad stage (Fig. 6 B), in the formation of a linear tetrad (Fig. 6 C). The lowermost megaspore develops into an embryo sac (Fig. 6 D). Embryo sac development is monosporic of the Polygonum type (Fig. 6 D–H). The vacuolated synergids do not extend into the micropylar canal (Fig. 6 H). The nuclei of the three antipodes disappear early on (Fig. 6 H), although the cells themselves remain intact (Fig. 6 H, I). The shape of the embryo sac changes with age, becoming pronouncedly spherical (Fig. 6 I), the integumentary tapetum meanwhile usually remaining unchanged (Fig. 6 I). Old synergids often have a bowed shape and sometimes the course of the pollen tube at the time of fertilization is visible. Endosperm development could not be followed in this material.

Arctotheca calendula (L.) Levyns. The archespore is 1-celled (Fig. 7 A). Megasporogenesis results in four megaspores linearly arranged (Fig. 7 B). The lowermost one is the most vigorous and develops into an embryo sac (Fig. 7 C). Embryo sac development is monosporic and follows the Polygonum type (Fig. 7 B–F). The synergids do not extend into the micropylar canal. In the later stages of the embryo sac the synergids may be very broad and their upper ends may become slightly hooked (Fig. 7 G). The embryo sac becomes more globose at the time of fertilization (Fig. 7 G). The integumen-

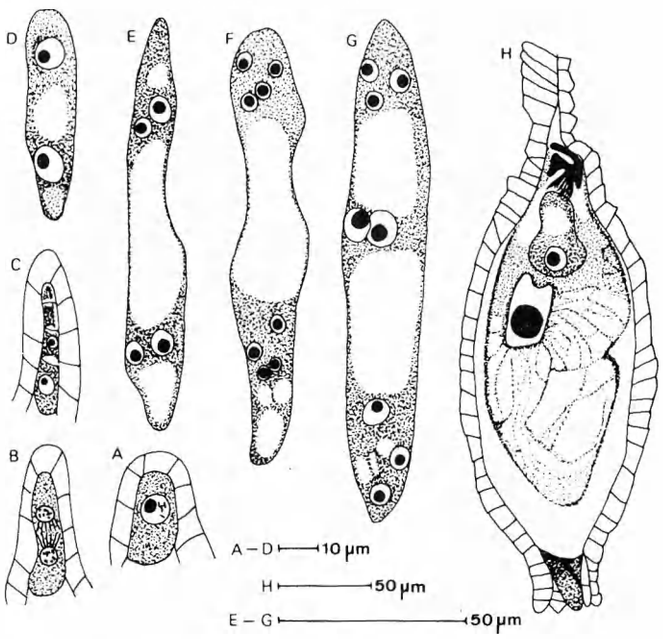

Fig. 4. Megasporogenesis and embryo sac development in *Arctotis breviscapa*. – A: EMC. – B: EMC in division. – C: Tetrad stage. – D: 2-nucleate ES. – E: 4-nucleate ES. – F: Young 8-nucleate ES. – G: Older 8-nucleate ES. – H: Old ES with degenerating, curved, hooked synergids and antipodes.

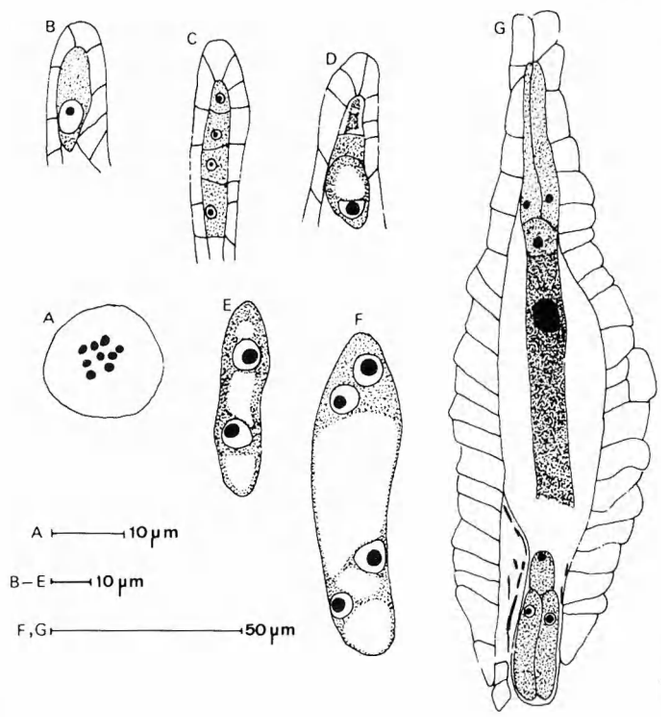

Fig. 5. Megasporogenesis and embryo sac development in *Arctotis gumbletoni*. – A: PMC, metaphase plate n = 9. – B: EMC. – C: Tetrad stage. – D: Germination of ES. – E: 2-nucleate ES. – F: 4-nucleate ES. – G: Young organized ES with integumentary tapetum.

tary tapetum remains unchanged. The nuclei of the three antipodes degenerate (Fig. 7 G).

The *Cymbonotus* material revealed an 8-nucleate embryo sac, in shape and organization similar to that of *Arctotis fastuosa* (Fig. 1 L). In the later stages the synergids sometimes lie curved on top of the egg cell. Initially there are three antipodal cells; however, I am uncertain whether they undergo secondary division or not.

Discussion

The archespore is 1-celled, very rarely 2-celled (in *Arctotis acaulis* and *A. fastuosa*). A monosporic embryo sac development of Polygonum type is characteristic for all the genera investigated. Neither synergid nor antipode haustoria are developed.

In the fertilized embryo sacs of the *Arctotis* and *Haplocarpha* species, the synergids stain very densely; they become displaced by the growing, vacuolized, egg cell; the distal parts of the synergids curve around the top of the egg cell. This is a general and conspicuous character, unique for the Arctotinae. At times these old and degenerate synergids display some sort of indentations (Figs. 1 N, 3 G) which resemble the hook-shaped synergids discussed by Dahlgren (1928, 1938) and Fagerlind (1943).

The three antipodes are 1-nucleate and remain so until they degenerate during the early endosperm stages. Like Dahlgren (1924) found egg-like, vacuolized, antipodes in "*Arctotis stoechadifolia*", I also, but more rarely, find such ones in *A. venusta*.

The shape of the embryo sac represents a second common character in all the genera investigated. From being comparatively small and thin in the early stages, the embryo sac increases in volume at the time of fertilization and afterwards; it increases in breadth especially and the central part become more or less spherical. This character is most evident in *Arctotis fastuosa* and *Haplocarpha lyrata*.

The integumentary tapetum consists of a single layer of cells and seems to remain unchanged, even during the endosperm stages. Schnarf (1929 pp. 61–65) deals with the functions of the integumentary tapetum. My own findings,

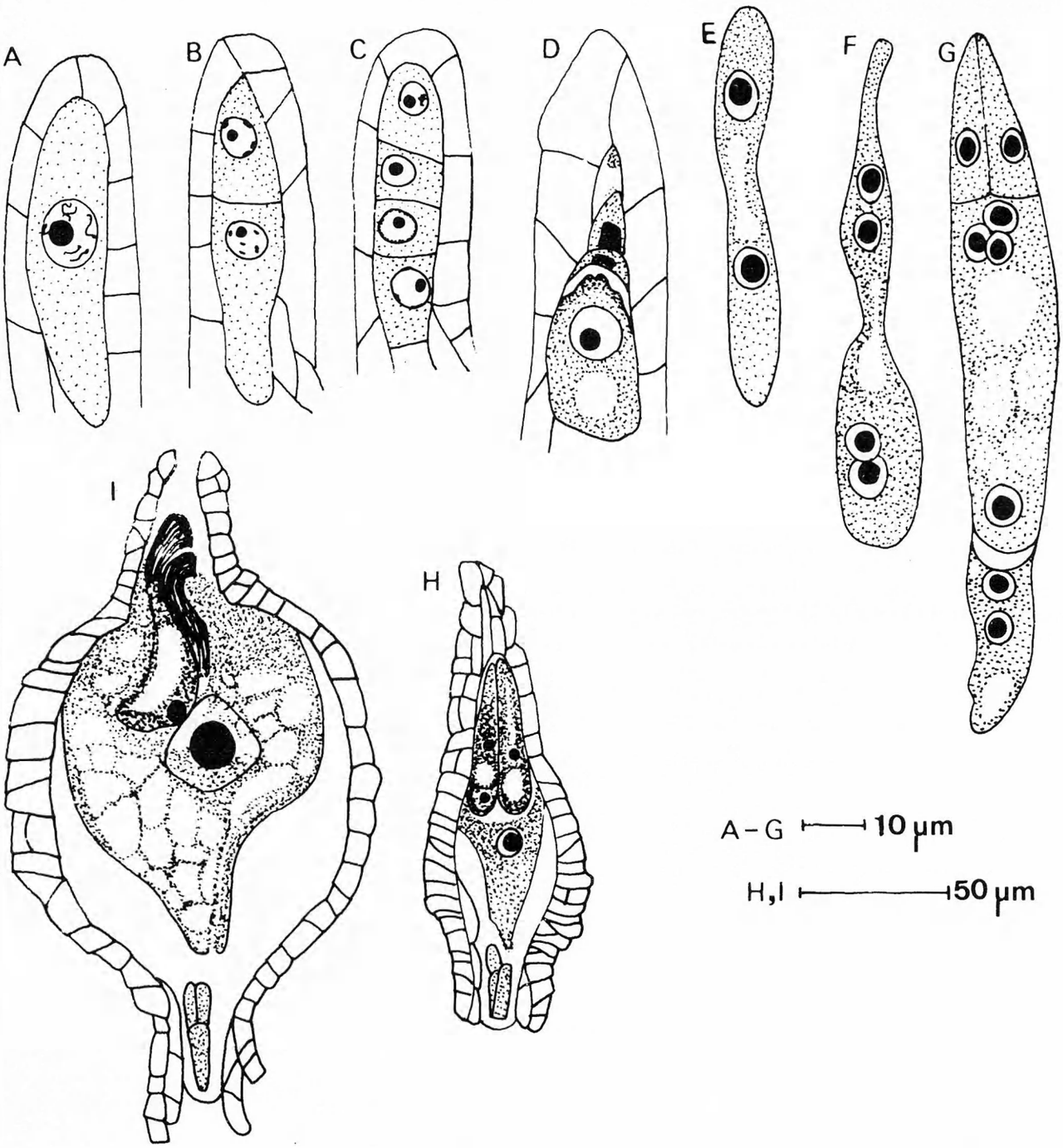

Fig. 6. Megasporogenesis and embryo sac development in *Haplocarpha lyrata*. – A: EMC. – B: Dyad stage. – C: Tetrad stage. – D: Germination of ES. – E: 2-nucleate ES. – F: 4-nucleate ES. – G: 8-nucleate ES. – H: Organized ES. – I: Old ES with curved synergids and antipodes in degeneration.

that endosperm formation in *Arctotis* is of the Cellular type, are in line with those of Dahlgren (1924) and Schürhoff (1926).

The exine structures of the pollen grains of *Arctotis, Cymbonotus, Arctotheca* and *Haplocarpha* are so uniform and unique that Skvarla et al. (1977) described them as an 'Arctotoid pattern'. Furthermore, Norlindh (1977 p. 947) reported a distinct affinity of *Dymondia* pollen with *Arctotis* pollen. It would therefore appear that a great similarity in pollen form exists between all the genera of the Arctotinae.

Few chromosome numbers have been published for the Arctotinae. Generally speaking, species of *Arctotis, Haplocarpha* and *Arctotheca* have n = 9 and 2n = 18 (Norlindh 1977). However, the E African alpine *Haplocarpha*

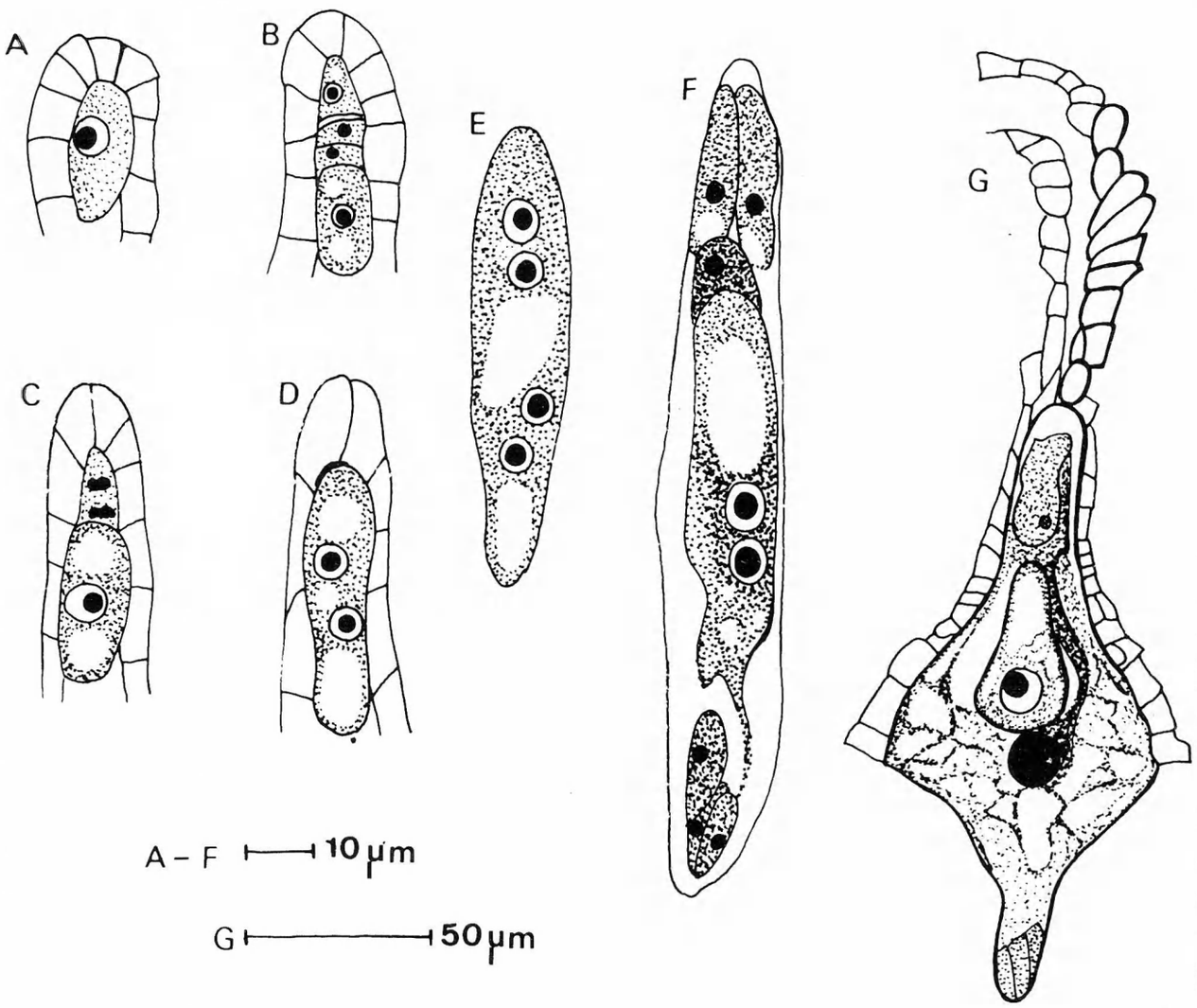

Fig. 7. Megasporogenesis and embryo sac development in *Arctotheca calendula*. – A: EMC. – B: Tetrad. – C: Germination of ES. – D: 2-nucleate ES. – E: 4-nucleate ES. – F: Organized ES. – G: ES with the micropyle canal, part of the integumentary tapetum; the course of the pollen tube to the diploid nucleus is visible.

rueppelli (Sch. Bip.) Beauverd has 2n = 30 (Hedberg & Hedberg 1977).

Norlindh (1977) gives an account of the morphological and anatomical characters of the genera in the Arctoteae. The Arctotinae differ from the subtribe Gorteriinae in having free involucral bracts. Since these bracts tend to accrete in a few species of *Arctotis* and *Haplocarpha*, the boundaries between the two subtribes become rather vague.

Baagøe (1977) found that the ligules of some *Arctotis* species had an epidermis of Mutisioid type. Her findings thus support the views expressed by Carlquist (1976) and other authors concerning the origin and relationships of the Arctoteae.

The results of the present embryological investigation reveal a great degree of uniformity, with a few unique specializations. It would seem that the genera of the Arctotinae form a natural group, a view supported by the palynological and cytological data.

Acknowledgements. I am greatly indebted to Professor Tycho Norlindh, Stockholm, for help in identifying my voucher material and for criticising an earlier draft of the manuscript, to Professor Nils Andreas Sørensen, Trondheim, for information about the *Cymbonotus* material, and to Professor Gunnar Harling, Göteborg, for valuable help and advice.

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Botanical literature

Bliss, L. C. (ed.) 1977: *Truelove lowland, Devon Island, Canada: a high arctic ecosystem.* XXII + 714 pp., numerous pictures and diagrams, one map in colours. University of Alberta Press, Edmonton. ISBN 0-88864-014-5. Price Can. $ 20.

Although the environment has at last been recognized as something even politically important, it is remarkable when an ecological study of a small area far from dense habitation involves 84.4 man-years of work, or that of an average 45 ecologists per year, at the cost of almost $ 1.5 million. Such an investigation was organized and performed on Devon Island in arctic Canada during the summers of 1970 to 1974 as a part of the International Biological Program under the direction of L. C. Bliss, who also has edited its report. The impressive volume contains more than 700 pages written by 45 authors. Although extensive studies of arctic biology have been made by large expeditions in Greenland and the Soviet Arctic in the past, this certainly is the most immense investigation ever completed in the cold northlands.

Since the volume reviews more or less intensive studies of various conditions that concern ecological productivity in an area of 43 km², almost every biologist with ecological leanings will find in it something of interest. A list only of the papers is formidable, but they discuss phenomena as diverse as permafrost, soils, bedrock geology, hydrology, micrometeorology, and various kinds of vegetation. Other chapters describe processes as evapotranspiration, nitrogen fixation, or photosynthesis, whereas still others review the invertebrate and vertebrate consumers, decomposition and microbiology, ecosystem modelling, the Inuits or Eskimoes, and industrial development.

In several appendices are listed the entire observed flora and fauna of the area, which includes 181 species of lichens, about 90 species of fungi, 132 species of mosses, 96 species of vascular plants, numerous invertebrates, 35 species of birds, and 7 species of mammals, a truly impressive number for a small area in the high Arctic. The book concludes with an index which unfortunately is so incomplete that its value for retrieval of even basic data is very limited.

Although the ecological coverage of the book is impressive, the opposite is true for its taxonomical background, at least for the higher plants, because taxonomy has been neglected as in most other IBP projects. The species list in Appendix 6 is a hodgepodge of exactly defined taxa and units so collective that even those familiar with arctic plants may become confused. One-fifth of the names used are either misapplied or seriously inexact, reaching the peak of phytogeographical ignorance by identifying the high arctic plants of *Silene acaulis* with the local endemic variety *exscapa* from the Alps! That is certainly unfortunate in an ecological investigation, even one emphasizing productivity.

This book is a remarkable achievement by Canadian scientists that certainly will long remain among the most valuable reference works on arctic biology.

Áskell Löve

Brodie, H. J. 1975: *The bird's nest fungi.* XV + 199 pp., 64 figs., 11 tables. University of Toronto Press. Toronto and Buffalo. Price (bound) $ 25.

In relation to their moderately small size and rarity, few fungi have received more attention

from botanists than the odd-looking bird's nest fungi. The explanation, naturally, lies in their exotic appearance, which has stimulated their collection and investigation since the beginning of the 17th century. The secrets of their spore dispersal, in particular, baffled scientists for a long time.

The foremost authority on these fungi is H. J. Brodie, formerly Professor of Botany at the University of Alberta, Edmonton, who has devoted a lifetime to their study. The present monograph forms a logical culmination to his numerous publications on the subject. It is not strictly speaking a taxonomic revision, but brings together what is known about all aspects of the bird's nest fungi. For example, there are chapters on their history, morphology, cytology, genetics, spore dispersal, ecology, distribution, and systematics. All accepted species are described and discussed and the book finishes with a selective bibliography, glossary, and index. The numerous illustrations are of high quality. There is also an amusing chapter, headed "Nidulariana", which contains various odd items of information, including a comic strip illustrating the spore dispersal mechanism. How typically Anglo-Saxon!

The bird's nest fungi are a small and sharply defined group. The order Nidulariales comprises the family Nidulariaceae, with the genera *Mycocalia* (5 accepted species), *Nidularia* (2–3), *Nidula* (4), *Crucibulum* (3), and *Cyathus* (42), and the monotypic family Sphaerobolaceae, with *Sphaerobolus* only (not dealt with here). The genera are also fairly well delimited, and are usually recognizable to the naked eye, or with the aid of a hand-lens. All have more or less cup- or vase-shaped fruit-bodies, but are mainly distinguished by the presence or absence of an epiphragm and a funiculus, or by differences in the structures of the latter and of the wall of the fruit-body.

As is often the case with clear-cut genera, the species may be difficult to separate. The fruit-bodies of most bird's nest fungi are extremely variable in form, size, and colour, which has resulted in unnecessarily many descriptions of new species and lower taxa. Spore size also varies markedly in some species, since the spores increase in size after their detachment from the basidia. This has led to much confusion about spore measurements in the past. Among Brodie's prime interests have been the unravelling of such modifications and of the sterility barriers. The results of his crossing experiments and work with pure cultures are basic for our understanding of the nature of many species. Numerous names have been brought into synonymy and new taxa have been established. Of the c. 57 accepted species, Brodie himself has described 13, mainly in *Cyathus*.

The remarkable splash cup mechanism receives full treatment. Although some early authors suspected that rain drops could be the agent responsible for the initial phase of diaspore dispersal, it was not until 1927 that G. W. Martin found experimental evidence for it. Later, A. H. R. Buller, Brodie, and other researchers have completed these investigations. In consequence we are now fully aware of the intimate connections between form and function in the bird's nest fungi; how the shapes and sizes of the fruit-bodies are optimally adapted for peridiole dispersion, and how the sticky funiculus, when present, is a tool for anchoring the peridioles either to the growing site, or to the vegetation for later endozoic transport.

The Nidulariaceae are largely a tropical to warm-temperate group, growing preferably on old angiospermous wood. Nevertheless, their choice of substrate can be exceedingly diversified (dung, plant fibres, herbaceous stems, nutshells, pine needles, etc.). Parasitism and mycorrhizal associations, however, have not been demonstrated with certainty. It is more difficult to get an accurate picture of the distribution of the fungi. Too little is at present known and the author's judgements are quite rightly cautious. For example, it is fairly well established that *Crucibulum laeve* and *Cyathus poeppigii* are circumpolar and tropical respectively, but it remains to be seen whether the supposed endemism of *Cyathus novae-zeelandiae* and *C. annulatus* (Alberta) really holds true.

The taxonomic part constitutes only a quarter of the book, but is not the least in importance, since it forms a guide to the identification of the taxa. Oddly enough, there is no key to the many *Cyathi* (only to the species groups), on the grounds that long keys are difficult to use and too frequently "used as a substitute for a careful comparison of specimen with the full descrip-

tion''. This is to underestimate the reader's capability and his needs and Brodie later found it appropriate to construct such a key (*Bot. Notiser 130,* 1977). The author also has the idea that lists of complete synonymity are superfluous. Only a few synonyms are mentioned under each species, some more in the index, and for the rest literature references are given. But the first place most people expect to find a full synonymity is precisely in such a monograph! It would have been very convenient to have at least all the taxonomic synonyms listed under the species.

Among further points in this chapter worthy of comment, I will only mention one more. It is true that *Cyathus fimicola* Lloyd in Stevenson & Cash is an invalid name and a later homonym of *C. fimicola* Berk., but the reader ought to be informed that the latter is a superfluous name for *Crucibulum laeve*. It may be added that Lloyd also created the alternative name ''*Cyathus annictaris* McGinty'', which is etymological nonsense and was meant as a joke. Nevertheless, it has recently been taken seriously by Stevenson (*Contrib. Reed Herb. 23,* 1975), although still being invalid. It is a pity that Brodie did not settle this nomenclatural matter once and for all in his monograph. This also applies to the invalid *Cyathus costatus* Lloyd in [sic!] Stevenson & Cash.

Monographs of the type reviewed here sometimes receive the hallmark of being considered the terminus of a particular field of research. Nothing could be less true. Instead they mark the start of a new epoch. No doubt Brodie's fine work will act as a beacon and incite a steady stream of investigations on the bird's nest fungi in the future.

Nils Lundqvist

Brücher, H. 1977: *Tropische Nutzpflanzen. Ursprung, Evolution und Domestikation.* XI + 529 pp., 245 figs. Springer Verlag, Berlin–Heidelberg–New York. ISBN 3-540-08185-2. Price DM 248.

This pleasantly written and thoroughly illustrated volume fills a long felt need for a modern and exhaustive review of the plants cultivated in the tropical regions. Its author is one of the leading specialists in the variability and genetics of economic plants, particularly in the tropics and mainly in S America, where he has spent a lifetime in teaching, research, travelling and even farming. He has written this text with the thoroughness typical of his German heritage so that no similar review is available in any language.

The book commences with four concentrated chapters with discussions of the special conditions for cultivated plants that predominate in the tropics, the beginning of domestication of plants, the principles, methods and mistakes in the study of cultivated plants, and the prerequisites and courses of selection of plants cultivated in the tropics. These chapters include a wealth of basic observations, among which are evaluations of the theories of Vavilov and more recent authors.

The bulk of the volume comprises a thorough and well illustrated review of each of the hundreds of plants that are cultivated in the warm regions, with details on their history, distribution, cultivation, agricultural importance and yield, botanical and genetical characteristics, and the possibilities of present and future domestication. Plants of similar use are grouped together, e.g. starch plants, protein plants, plants of technical importance, tropical fruits and vegetables, root plants and stimulants, oil plants and palms. The extention of the coverage is reflected by the nine pages of a three-tiers register.

The volume will be enjoyed by every botanist working with or interested in cultivated plants because the principles of their domestication are similar in all climatical zones. It is a book that is warmly recommended to all botanical libraries, to botanists of tropical regions interested in practical plant science, and to those from less equitable areas who want to know more about the economic flora of the exotic regions and about its immense variability.

Áskell Löve

Muller, F. M. 1978: *Seedlings of the North-Western European lowland.* 654 pp., 1211 figs. ISBN 90-6193-588-1. W. Junk Publishers. The Hague, Boston.

The publication of a seedling flora of NW Europe will be welcomed by agriculturists, foresters,

ecologists and all botanists concerned with field studies. In this work the seedlings of 1211 native and adventive species are illustrated with clear line drawings sufficiently enlarged for a wealth of detail on venation and indumentum to be clearly visible. For each species there is also a brief and strictly comparable description of the hypocotyl, seed leaves (cotyledons), epicotyl and first formed plumular leaves. The season of germination is also recorded. There is a series of diagnostic keys. When tested these were mostly successful. The usage of terms is defined in footnotes throughout the keys. To allow for the variation likely to be encountered amongst seedlings of the same species, several taxa are keyed out more than once.

Because many of the species of the area encompassed are now widespread in temperate regions, the seedling flora will be of considerable value outside the area for which it was prepared. Though the keys may not be particularly useful outside NW Europe the drawings and descriptions are invaluable to the would-be seedling identifier. It is anticipated that the work will serve as a model and a stimulus for other local seedling floras.

Both Dr Muller and the artists are to be congratulated in producing such an excellent book in so short a time.

Trevor H. Clifford

White, M. J. D. 1978: *Modes of speciation.* 464 pp., 31 ill. W. H. Freeman & Co., San Francisco. ISBN 0-7167-0284-3. Price $ 27.50.

No biological problem is more perennial than that of speciation, which often may seem to be too complex and extensive for comprehension by a single scientist. Therefore, it has long been and will long remain the most burning and most challenging of all biological questions. Many scientists wrestle constantly with its solution in numerous technical papers on studies of various details that may seem important for the ultimate answer, and a few of the brilliant minds of every generation have attempted to review the problem in general from various vantage points. Several such texts have been added during the last decade, in various languages, but although each has strived to clarify the issue from new points of view, the apparently irrefutable questions continue to mount.

The most recent, and perhaps also the most penetrating, of these texts is based on extensive studies of the chromosomes of grasshoppers by a leading entomologist-cytogeneticist, who has previously contributed the most stimulating book on the cytogenetics of animals in general. The result is a comprehensive review that reaches far outside the original field of the author so the book is of the greatest interest to every biologist with connections to speciation, whether in animals or plants, fungi or micro-organisms.

White directs his attention mainly towards the significance of chromosomal changes, a phenomenon believed to play a paramount role as at least the first step in most speciation processes. This leads to extensive and detailed discussions of the role of allopatry and sympatry and what he calls stasipatry. Numerous examples are given in support of the conclusion that the perhaps most common course may be stasipatry, or chromosomal rearrangement that reduces fertility when heterozygous and originates somewhere within the area occupied by the ancestral species. This is a view distinctly contrary to the commonly held neodarwinian opinion of allopatry as the essential evolutionary stimulation at all levels, and a corroboration of the old and often snubbed at ideas of evolution commencing sympatrically, as expressed by Darlington, Goldschmidt and several other cytogeneticists not mentioned in this connection. The new reasoning is very logical, highly sophisticated, and convincing, although some of the details brought forward may seem to require some mastication before being swallowed.

Apparently for the sake of completeness, the author allots special chapters to asexual reproduction and to polyploidy that always begins sympatrically. Neither of these chapters add anything new and could have been omitted without detriment.

It is likely that posterity will regard this book as the most important step towards the understanding of speciation presented during this decade. It can be warmly recommended to every student of evolution.

Áskell Löve