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A functional evolution of the Leucobryaceae

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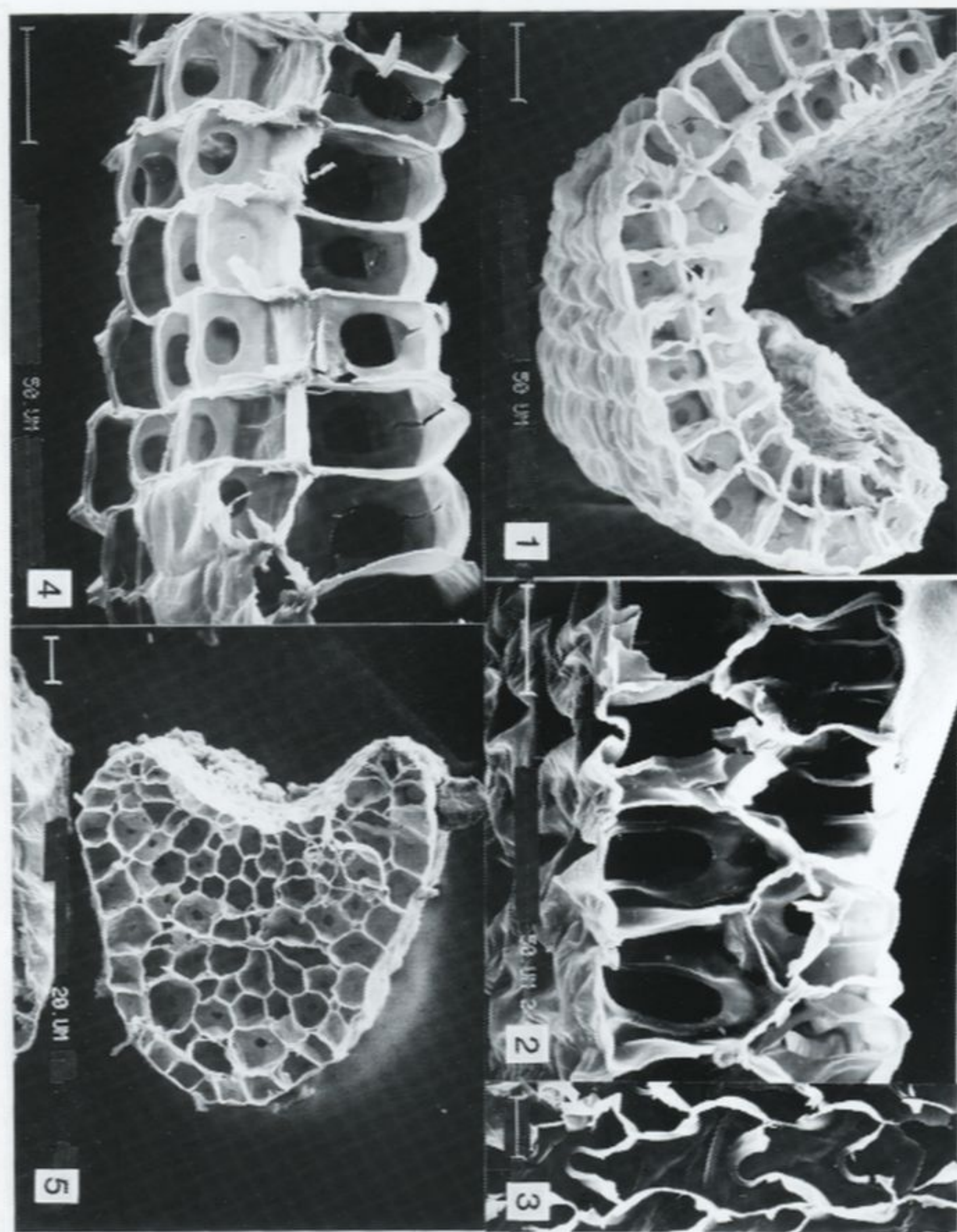
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Abstract. Recent conclusions on the limits of the Leucobryaceae and on the function of the Leucobryaceous leaf are used as basis for further observations on evolution of the group. Eight genera are recognized in the family; 1. *Leucobryum*, 2. *Steyermarkiella*, 3. *Ochrobryum*, 4. *Arthrocormus*, 5. *Schistomitrium*, 6. *Holomitriopsis*, 7. *Cladopodanthus*, and 8. *Octoblepharum*. The leaf form, capsule shape, and peristome substructure of *Leucobryum* seems to derive from a *Campylopus*-type member of the Dicranaceae. Four basic stages are noted in the functional evolution of the family. 1. The stratification of the leaf into leucocysts and chlorocyst layers with leucocysts holding water and internally generated gas; 2. The shift from soil substrates seen mostly in Temperate Zone *Leucobryum* to rotten wood substrates or epiphytism; 3. Increasing reliance on vegetative reproduction with reduction of reliance on sporophytes; 4. Morphogenetic increase of the number of chlorocysts in the leaf. Geographical concentrations of the genera are noted, and distributions between hemispheres are apparently mostly by way of the South Atlantic. The use of functional considerations in evolutionary studies is emphasized. The retention of paraphyletic groups in taxonomy is defended.

Members of the Leucobryaceae are known to all bryologists on the basis of their thick whitish leaves, and most students have sectioned the leaves to see the unique mass of large leucocyst cells surrounding a network of slender green chlorocyst cells (Figs. 1-5). However, most bryologists, after superficially distinguishing the commonly encountered members of the family give no further thought to its evolution. Genera have been distinguished on the basis of capsule form, peristome, calyptra, and details of cell structure in the leaves. The differences involved have caused some bryologists such as Cardot (1900) and Andrews (1947) to assume that different elements of the Leucobryaceae are directly related to two other totally different families of mosses, Dicranaceae and Calymperaceae. The present study extends the study of the

family begun by Robinson (1985), and many of the changes observed in the evolution of the family are seen to correlate with various functional considerations.

For purposes of the present paper a series of separate steps are taken. First, the basic conclusions of Robinson (1985) regarding the limits of the family are briefly revisited. Next, the apparent origin of the family is considered, establishing the evident outgroup. The third step involves a review of the characters by which the genera of the family are distinguished, with a summary of apparent subgroups within the family. Finally, certain anomalous aspects of the results are discussed with a defense of function as a character. The apparent paraphyletic nature of the Dicranaceae in relation to the Leucobryaceae is noted, and the value of



Figures 1-5. SEM views of Leucobryaceae leaves. 1. *Leucobryum scalare* C. Müll. ex Fleisch., *Touw 10293* (US), cross-section. 2, 3. *Steyermarkiella anomalodictya* H. Robins., *Steyermark 92266* (US), 2. Cross-section, 3. Long-section. 4. *Holomitriopsis laevifolia* (Broth.) H. Robins., *Steyermark 92613* (US), cross-section. 5. *Arthrocomus schimperi* (Dozy & Molk.) Dozy & Molk., *Leiberg 122* (US), cross-section. Lines in Figures 1-4 = 50 µm, in Figure 5 = 20 µm.

paraphyletic groups is defended.

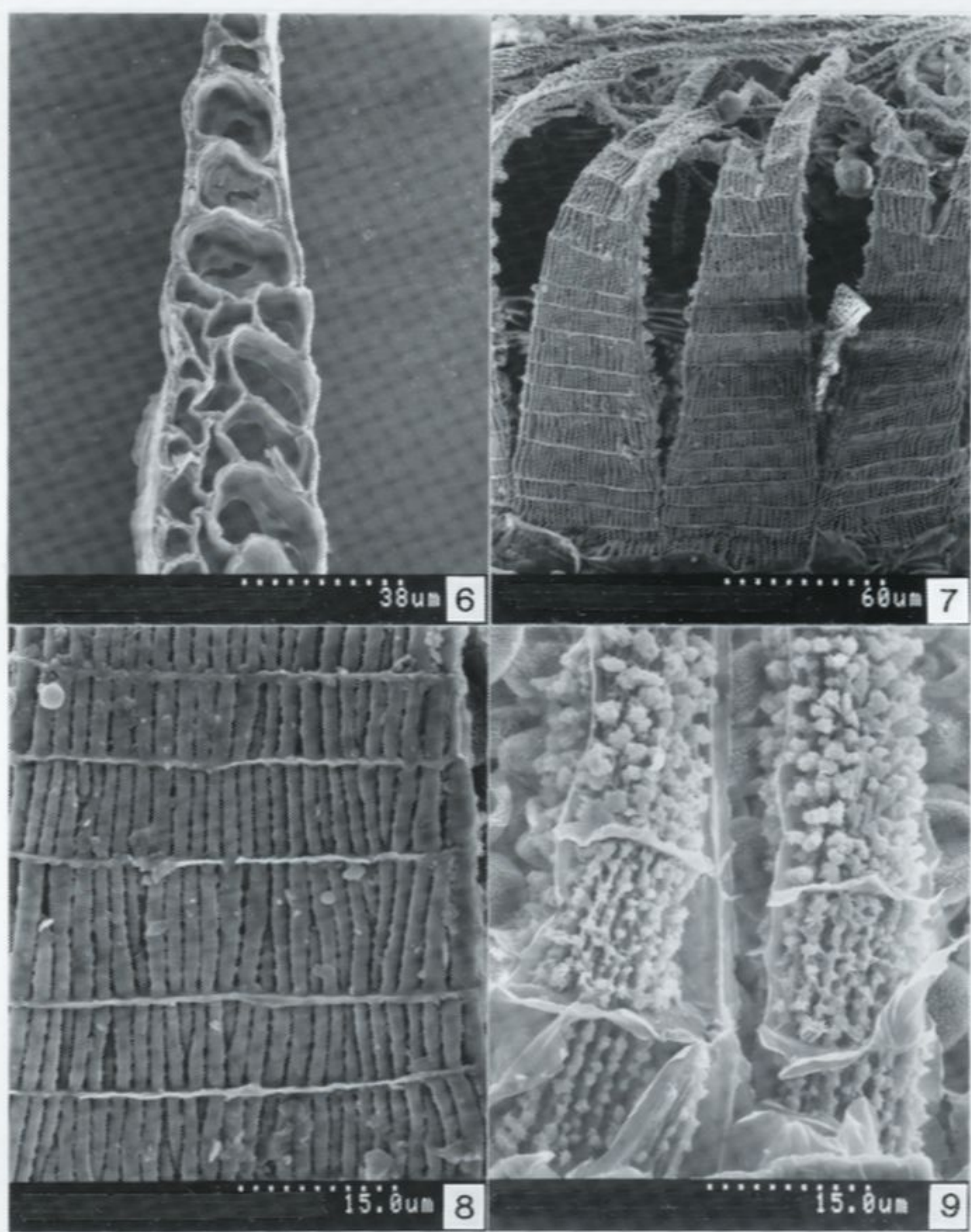
Limits of the Leucobryaceae

Older treatments of the family such as that of Brotherus (1924) have included the standard genera *Leucobryum* Hampe, *Ochrobryum* Mitt., *Schistomitrium* Dozy & Molk., *Cladopodanthus* Dozy & Molk., *Octoblepharum* Hedw. and *Arthrocormus* Dozy & Molk., as well as *Leucophanes* Brid. and *Exodictyon* Card. Two other genera, *Cardotia* Besch. and *Carinafolium* Williams have been synonymized respectively with *Leucobryum* (Andrews 1947) and *Octoblepharum* (Bartram 1960). The only other genera that have been included in the family are *Holomitriopsis* H. Robins. and *Steyermarkiella* H. Robins. The diversity within this series of genera caused some authors to extract at least *Leucophanes* as a separate family Leucophanaceae. Herzog (1926) treated only *Leucophanes* in the latter family while Fleischer (1904) included *Cardotia*, *Octoblepharum*, *Arthrocormus*, and *Exodictyon*. Most, but not all, of the genera included by Fleischer have some irregularity in leucocyst positions that results in some or all the chlorocysts being triangular. The capsules of the latter group, where known, were also erect with variously reduced 'Pottioid' peristomes (Andrews 1947), and the group was considered to be related to the Calymperaceae. The evident relationship of the latter group to the Calymperaceae, the relation of *Leucobryum* to the Dicranaceae, and the apparent basic unity of most of the Leucobryaceae led Cardot (1900) to suggest the Leucobryaceae was primitive and the Dicranaceae and Calymperaceae derived. The latter view was rejected by Andrews (1947) but the unsatisfactory division of the family proposed by Fleischer (1904) was retained with the assumption the Leucobryaceae had two origins.

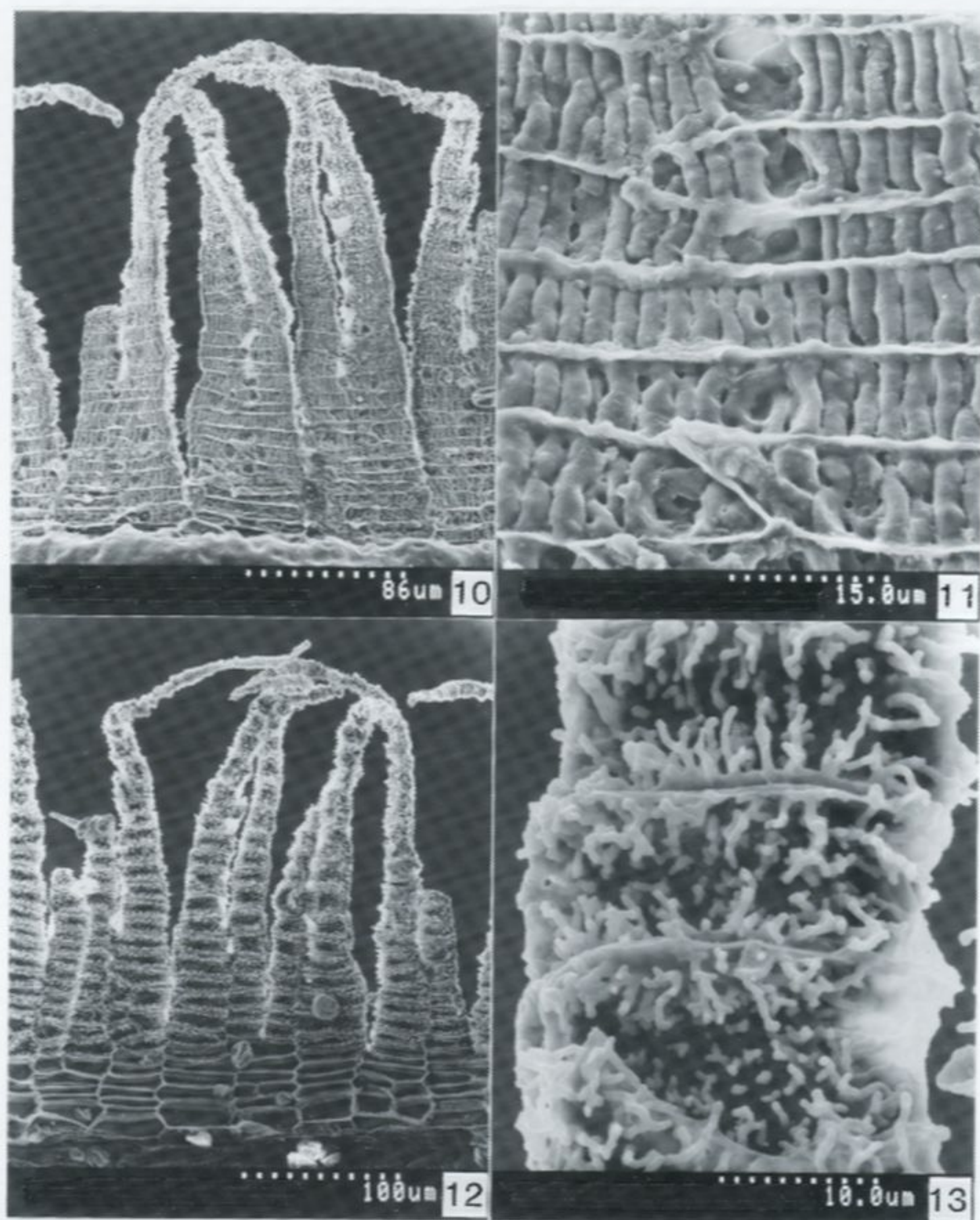
Robinson (1985) approached the study of the Leucobryaceae from a functional

perspective, noting that the leaf structure imposed certain functional limitations. The theoretical approach led to a successful search for evidence of gas in the leucocyst cells of living leucobryaceous leaves. The gas was considered necessary for proper gaseous exchange at the surfaces of the included chlorocysts, even as the leucocyst layers continued to function for water storage. It was further noted that the genera that least needed such gas in the leucocysts were the same genera that departed most from the leaf structure interpreted as a broadened midrib (Lorch 1894), and the same genera were the only ones showing clear indications of relationship to the Calymperaceae. On that basis, *Leucophanes* and *Exodictyon* were excluded from the Leucobryaceae by Robinson (1985) and the two genera were placed within the broad concept of the Calymperaceae although they were not closely related to each other within that family. *Leucophanes* is the one genus outside of the presently defined Leucobryaceae that has a similar pattern of leucocyst layers enclosing a chlorocyst network, but the structure in *Leucophanes* is derived much more from laminal than from costal material. A differentiated costa is present in the middle of the leaf of *Leucophanes*. All the remaining genera that share the Leucobryaceous leaf with internally generated gas were kept together in the Leucobryaceae. The Leucobryaceae are like many other Land Plants in having trapped gas in close proximity to their photosynthetic tissue, but they are distinctive in having the gas trapped inside cells instead of between cells.

Problems in relating such genera as *Leucobryum* and *Octoblepharum* to each other remained after the Robinson (1985) study, but the problem of a Calymperaceous relationship for genera such as *Octoblepharum* was removed. This latter view is retained in this study.



Figures 6-9. Leaf and peristome structures of Dicranaceae. 6. *Campylopus cavifolius* Mitt., Holm-Nielsen, Jaramillo, de Vries 17311 (US), leaf cross-section. 7, 8. *C. caudatus* (C. Müll.) Mont. in Dozy & Molk., Brass 29891 (US), outer surface of peristome teeth. 9. *Pilopogon gracilis* (Hook.) Brid., Norris & Gastony 7520 (US), outer surface of peristome teeth.



Figures 10-13. Peristome teeth of *Leucobryum albidum* (Brid.) Lindb., Harper 38 (US), 10, 11. Outer surfaces, 12, 13. Inner surfaces.

Relationships of the Leucobryaceae

The present perception of the relationships of the family are based almost entirely on the nature of the one genus, *Leucobryum*. That genus shows what are considered unmistakable characters of the Dicranaceae. The usually curved capsules bear a clearly Dicranaceous type peristome (Figs. 10-13) with closely set vertical bars on each external sector of the tooth. The same type of ornamentation is seen in *Dicranum* (Robinson, 1971) and *Campylopus* Brid. (Fig. 7, 8). If the family Leucobryaceae consisted only of *Leucobryum*, there would be ample reason to place the family totally within the Dicranaceae. In the Dicranaceae the structure of the Leucobryaceous leaf is also anticipated in the broadened costa and large leucocyst-like cells of many species of *Campylopus* (Fig. 6). In such species as *Campylopus cavifolius* Mitt. the structure suggests that gas is produced within the leucocysts as in the Leucobryaceae. Frahm in this symposium reports seeing such internally generated gas in the latter genus.

The problem with the Dicranaceous origin of the Leucobryaceae is the need to explain the great diversity within the latter family from a seemingly less variable ancestral group. The topic is further explored below, but it is notable that some of the characters in which the Leucobryaceae vary are found in the Dicranaceae, even within the *Campylopus* relationship. Erect capsules with slender peristomes are found in *Campylopus* and in its close relative *Pilopogon* Brid. (Fig. 9). Erect capsules are even found within *Leucobryum* in *L. incurvifolium* C. Müll. (Robinson 1965a). The peristomes of various Leucobryaceae that do not seem like Dicranaceae such as *Schistomitrium* (Figs. 14, 15) and *Octoblepharum* (Figs. 16, 17) are types that could be derived by reduction from a Dicranaceous peristome, especially that of *Octoblepharum* which in other

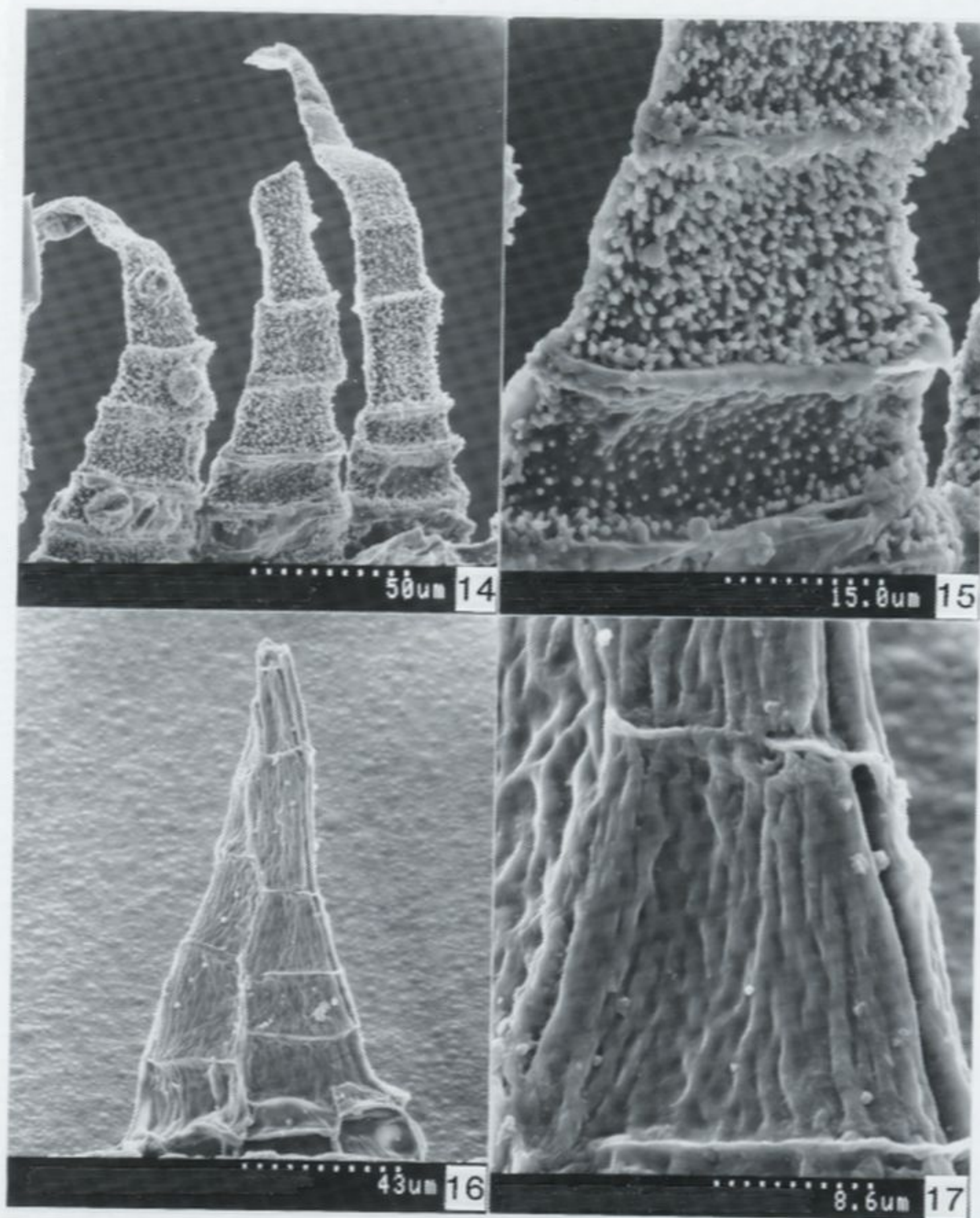
characters is one of the most disparate elements in the family. For capsules like that of *Ochrobryum*, a simple formula must be applied. Anything that is totally freakish is essentially useless for determination of what is or what is not closely related. Nothing has been detected in the redelimited Leucobryaceae of this study that bars possible relationship to the Leucobryaceae or shows reason to relate any of the genera to any other known family.

Characters of the genera of the Leucobryaceae

Capsules, calyptrae, propagula, planation of the leaf, number or relative thickness of the leucocyst layers in the leaf, and the shapes of the leucocyst walls can all be useful indistinguishing and grouping the genera of the Leucobryaceae.

Capsule.—The capsule with its peristome is one of the most obvious features for distinction within the family. Curved capsules with well-developed vertical striations on the outer surface like those of the Dicranaceae are known in the family only in *Leucobryum* and the erect capsule in *L. incurvifolium* is treated here as a minor exception where the peristome remains unchanged. Two elements placed in or close to *Leucobryum* in this study, *Cardotia* of the Indian Ocean and *Steyermarkiella* of eastern Venezuela are placed in the absence of any knowledge of their capsules, and it is suspected that their capsules if found would also be curved with vertically striated peristomes.

The erect symmetrical capsules of all other genera of the family are treated here as derived. It seems notable that they are associated with genera that occur on organic substrates or have become epiphytic. As such, the genera with erect capsules do not necessarily bear those capsules pointed upward from the ground.



Figures 14-17. Peristome teeth of Leucobryaceae. 14, 15. *Schistomitrium nieuwenhuisii* Fleisch., Merrill 6209 (US), outer surface. 16, 17. *Octoblepharum albidum* Hedw., Maxon 750 (US), outer surface.

In such a situation regular curvature of the capsule would serve no purpose.

The capsule of *Ochrobryum* thoroughly distinguishes the genus from all others. The capsule is reduced to the form of an inverted operculum, evidently by some 'morphogenetic trick'. The latter term refers to an abrupt and often unique rearrangement of the developmental process. Such "tricks" do not require intermediates and offer little aid in establishing relationships. The leaves of *Ochrobryum* with their propagula better demonstrate a phyletic distance between the genus and others in the family.

Peristome.—The basic peristome of the family is the Dicranaceous / Fissidentaceous type with vertical striations on the outer surface, the type that is found fully developed in the Leucobryaceae only in *Leucobryum*. Other forms in the family are all considered derived from the type in *Leucobryum*.

The eight peristome teeth, or perhaps more properly eight pairs of teeth, of *Octoblepharum* in some views seem to have essentially identical markings on both the inner and outer surfaces (Figs. 16, 17). They were drawn by Fleischer (1904) with four vertical cell rows on the outer surface on the basis of Indonesian material. Examination of American material that seems to show less rows (Figs. 16, 17) actually shows that two of the rows are reduced to narrow marginal vestiges.

The SEM views of the individual teeth of *Schizomitrium* also seem to lack a vertical median line on either surface (Figs. 14, 15). In this case the Fleischer illustration (1904) agrees. Nevertheless, the closely related *Cladopodanthus* as drawn by Fleischer (1904) and *Holomitriopsis* (Robinson 1965b) have rather ordinary bifid teeth. The *Schizomitrium* teeth are evidently a rather limited reduction within the Leucobryaceae.

Arthrocormus is still another example of reduced teeth in the family. As drawn by Fleischer (1904) they are like reduced *Schizomitrium* teeth.

The reduction of the peristome in the Leucobryaceae reaches its extreme in *Ochrobryum* which has both a reduced capsule and a complete loss of peristome. The trend in the family is for capsule and peristome reduction correlated with increased epiphytism. The new habitat seems to reduce the need for fully formed and fully functional capsules. The general trend for reduction is so strong that the trend toward loss of the vertical division on the outer surface of the teeth in *Octoblepharum*, *Schizomitrium*, and *Arthrocormus* is not regarded as evidence of a particularly close relationship between those genera.

Calyptra.—Most members of the Leucobryaceae have cucullate calyptrae, the condition that is found in most members of proposed outgroup in the Dicranaceae. Genera with cucullate calyptrae include the one considered most like the Dicranaceae, *Leucobryum*, and the ones considered most modified in chlorocyst disposition, *Octoblepharum* and *Arthrocormus*.

Ochrobryum has narrowly mitrate calyptrae that cover the long- rostrate opercula. Fleischer (1904), Brotherus (1924), and Bartram (1949) all characterize the calyptra of *Ochrobryum* as hairy. The American specimens surveyed seem nearly if not completely glabrous. The material from Asia usually has dense spreading hairs at the base similar to those of *Schizomitrium*. Other features of *Ochrobryum* and *Schizomitrium* indicate that they are not close, and provide no support for the idea of common origin of the character.

The three genera, *Schizomitrium*, *Holo-*

mitriopsis, and *Cladopodanthus*, that are related by the cross-sections of the leaves, also all have mitrate calyptrae. The calyptrae of *Holomitriopsis* and *Cladopodanthus* are glabrous while those of *Schistomitrium* have coarse spreading hairs at the base. The hairs of *Schistomitrium* are generally like those of *Ochrobryum* and some Dicranaceae in the relationship of *Campylopus* such as *Mitrobryum* H. Robins. (Robinson 1968), but not sufficiently alike to indicate direct relationship. Instead, hairs on the calyptrae in the Dicranaceae such as *Campylopus* seem to demonstrate the lack of consistency of the character in at least that group. In this study the hairs on the calyptrae are considered a localized apomorphy in *Schistomitrium* since they are lacking in both related genera, and since they are associated with a genus that has a more derived form of peristome tooth. The genera with glabrous calyptrae, *Cladopodanthus* and *Holomitriopsis*, are also the genera with a less modified form of peristome.

Propagula.—The vegetative reproduction of the Leucobryaceae involves various specializations. It consists of specialized deciduous leaves in many species of *Leucobryum*. Many other Leucobryaceae have leaf fragments that seem capable of growing into new plants. Specialized budlike propagula are borne distally on the leaves of some species of *Ochrobryum* such as *O. gardneri* (C. Müll.) Lindb. (Correns 1899), *O. crumii* H. Robins. and *O. obtusifolium* (C. Müll.) Mitt. The character is unlike anything in other Leucobryaceae. Propagulae that have been reported in two species of *Octoblepharum* (Harrington & Égunyomi 1976) and in *Arthrocormus* (Enroth 1988) are monoseriate more like those of the Calymperaceae, and Enroth emphasizes the fact that both genera had been placed in the latter family by Ellis (1985). The propagula in the Leucobryaceae are more commonly found on leaf margins than in

the Calymperaceae, but the margins involved are costal material while the similarly positioned margins of the Calymperaceae are laminal tissue. The propagula in the Calymperaceae are on specialized leaf apices or along the sides of the costa. The presence of monoseriate propagula in *Arthrocormus* and *Octoblepharum* is not accepted by the present author as evidence that those genera belong to the Calymperaceae.

The specialized propagula would seem to serve little purpose in a family where unspecialized leaf fragments are so easily distributed. Such easily distributed leaves are common in the Leucobryaceae, and apparently even in *Ochrobryum*. A specimen, *Kellerman 7397b* (US) determined as *Ochrobryum* from Guatemala by Peterson and *O. propaguliferum* Dix. from Ceylon have deciduous leaves on some stem apices, but the identification of these specimens with *Ochrobryum* needs confirmation.

Such development of vegetative reproduction by whole leaves and leaf fragments might be a factor in reduction of dependence on the sporophyte for reproduction. With most distribution being by vegetative means, the sporophyte would be reduced to its most essential evolutionary role of providing for occasional genetic segregation and recombination. The leucocyst covered chlorocysts of the leaf fragments would seem capable of survival for reasonably long periods of time. Such fragments would reduce the dependence on climatic conditions that are neither too wet or too dry for adequate spore distribution.

The deciduous leaves and leaf fragments of the Leucobryaceae would easily be distributed by animals such as birds. The distribution by birds would be highly beneficial for the epiphytic taxa, and in the present view has been a major factor in evolution of the advanced members of the

Leucobryaceae.

Leaf cell shapes.—The leaf cells vary in two ways that are useful to taxonomists. One is by differentiation of the cell layers, the other is by the shape of the leucocysts at the intersections with the chlorocysts.

Three genera, *Schistomitrium*, *Cladopodanthus*, and *Holomitriopsis* share a marked difference in the depth of the cells in the two layers of leucocysts (Fig. 4). The character was noted by Florschütz (1964) in South American material later named *Holomitriopsis* (Robinson 1965b) when he suggested its relationship to the eastern Hemisphere *Schistomitrium*. The character is regarded here as a marker for the related group of three genera. Robinson (1985) noted in *Holomitriopsis* the tendency for the shallower dorsal series of cells to more easily lose their outer walls thus potentially exposing the chlorocysts to external air (Fig. 4). If this trait is true of the group it would seem a partial reversal of the basic Leucobryaceous leaf strategy in which the advantage of one layer of ventral water-storage cells is retained.

There are examples in diverse elements of the family such as *Leucobryum* and *Octoblepharum* of extra layers of leucocysts in the leaves. The extra layers are evidently minor elaborations of the basic two leucocyst layers during their developmental phase (Ruhland 1924). One genus, *Arthrocnemum*, has a more complex development of many leucocyst layers in which there are two or three layers of chlorocysts (Fig. 5). The character must involve a basic morphogenetic rearrangement. Ruhland (1924) illustrates a leaf apex of *Leucobryum glaucum* (Hedw.) Ångstr. that has some extra chlorocysts outside of the central layer. The latter example is a rarity in *Leucobryum*, but shows how the condition in *Arthrocnemum* could have arisen.

The pattern of leucocyst intersections with

the chlorocysts has been much noted in the previous taxonomic studies of the Leucobryaceae. The alternate (Fig. 2) rather than opposite (Figs. 1, 4) positions of the cells in the two different layers has been used to distinguish genera such as *Cardotia* as well as whole series of genera that Fleischer (1904) and Andrews (1947) seemed willing to relate to totally different sources outside of the family. Andrews (1947) discussed the variation of the character in relation to *Cardotia* as he reduced that genus to the synonymy of *Leucobryum*. Andrews said the Cardot (1900) drawings and material named by Thériot as *Cardotia* from Madagascar had all the appearance of a *Leucobryum* except that the chlorocysts in the upper part of the leaf were triangular in section rather than quadrangular. Andrews noted that in the lower part of the leaf the cells were quadrangular, "Agreeing in both these respects with *Octoblepharum*, though otherwise there is no great resemblance between the two genera." According to Andrews, "This character may be of importance, but that *Cardotia* belongs in close relationship with *Octoblepharum* rather than *Leucobryum* is very questionable indeed." Andrews confirmed Cardot's claim of similar considerable development of triangular chlorocysts in the apical part of the leaf in *L. albidum* (Brid.) Lindb. of North America. Andrews reduced *Cardotia* to the synonymy of *Leucobryum* and also discounted the value of the alternate-celled condition as a division between groups of genera in the family. Nevertheless, the alternate condition of the leucocysts has been used to distinguish another probable close relative of *Leucobryum*, namely *Steyermarkiella* (Figs. 2, 3), but here the alternate condition is throughout the leaf and is reinforced by a highly anomalous modification in the cell shape (Fig. 3).

The alternate leucocyst arrangement is strongly developed in *Octoblepharum*, and alone could normally distinguish that

genus from *Leucobryum*. However, one functional aspect of the alternate versus the opposite pattern of leucocysts has been overlooked in the considerations of the character. The alternate pattern has the net result of approximately doubling the number of chlorocysts in the central plane of the leaf in relation to the number of leucocysts with which they intersect. In this way the alternate leucocyst arrangement is like the *Arthrocnemum* modification where chlorocysts occur in more than one layer. Both mechanisms increase the ratio of chlorocysts to leucocysts. These changes increase the ratio of live functional cells in relation to dead surrounding cells by simple morphogenetic tricks. It would seem to be one trend in the family that represents continuing elaboration of a character instead of degeneration. It would seem to indicate what is comparatively important in the survival strategy of the Leucobryaceae.

Geography of the Leucobryaceae

The distributions of the genera of the family can be summarized with estimates of numbers of species for various regions. The numbers are derived from both herbarium records and some literature such as Brotherus (1924), Bartram (1933, 1939) for Hawaii and the Philippines, Gangulee (1971) for eastern India, Schultze-Motel (1973, 1974, 1975) for Melanesia, Samoa, and West Africa, Crosby et al. (1983) for Madagascar, Enroth (1989) for Borneo, Magill (1981) for South Africa, Scott et al. (1976) for Australia, Sainsbury (1955) for New Zealand, and Florschütz (1955) for American *Octoblepharum*. The high numbers cited for some areas may indicate the need for synonymizations like those of Enroth (1989) dealing with Borneo. Precise limits on distribution are inevitably uncertain, but some limits are assumed on the basis of the general absence in regions of extreme cold or extreme aridity. The family is mostly limited to the tropical

and subtropical zones in the World, but in reality the family seems to occur mostly in areas that are ecologically temperate.

***Leucobryum*.**—The literature indicates 2 species in eastern North America with a third in Florida, 6 in Central America, 4 in northern South America, 1 species south into Argentina, and 4 in southeastern Brazil. Europe has 2 species with one the same as in North America and northern Asia. Nine species are cited for Gabon and 16 for central Africa, 3 reach South Africa, and 19 occur in Madagascar. Eastern India has 9 species, China 14, Japan 9, southeast Asia 16, the Philippines 5. Four species reach Australia with 2 reaching the south, one species is in New Zealand. Hawaii has 3 species. The many species once listed for Indonesia have been reduced to 8 by the work of Enroth (1989) indicating that similar reductions may occur in other areas when studies are complete.

As represented, *Leucobryum* is the most widely distributed genus in the Leucobryaceae. It is the only one with a few species ranging northward into Temperate North America and Europe, and one occurring as far south as southern New Zealand. There are other examples of the most primitive members of groups having the widest distributions of any part of a group, a phenomenon that gave rise to the now largely discredited Age and Area Hypothesis of Willis (1915). In the case of *Leucobryum* this concept might explain the diversity found in both Hemispheres. However, the occurrence of the genus in the Temperate Zones seems correlated with the ability of the species involved to live on a soil substrate, a trait not seen in other genera of the family. In addition, the genus contains a number of specialized species in the tropics which either grow on organic substrates or are sometimes epiphytic.

The species of the genus seem most

numerous in the Paleotropics, but a few distinctive elements such as *L. incurvifolium*, *L. martianum* (Hornsch.) Hampe, and the *L. crispum* C. Müll. group occur in the Neotropics. The synonymized *Cardotia* is in the Madagascar region, a region credited with the largest concentration of species in the genus. The only evidence of direct interchange between hemispheres involves *L. glaucum* in the north between eastern North America, Europe and Asia. The distribution of the genus does not seem to be of recent origin, and the dispersal between the hemispheres may have originally been strictly between tropical regions.

***Steyermarkiella*.**—The genus is known only from the eastern Guayana Highlands of northern South America. It is regarded here as a distinct genus but a close relative of *Leucobryum*. The alternate leucocysts suggest that closest relationship is to the *Cardotia* element of the Madagascar region, and the genus shows no resemblance to any Neotropical elements of *Leucobryum*. *Steyermarkiella* occurs in an area where other bryophytes are found with close Paleotropical relationships (Robinson 1986).

***Ochrobryum*.**—Three species are cited from Central America and northwestern South America, 1 species is from western Mexico, and 5 are cited from southern Brazil. West Africa has 3 cited species and 1 species is cited from each of Central Africa and Madagascar. The Himalayas and Ceylon are credited with 1 species each and 4 are cited from southeast Asia.

The species are apparently concentrated in South America, West Africa, and southeast Asia. The concentrations seem rather evenly distributed, and the Hemisphere of origin is not evident. The only reasonable avenue of dispersal between the Hemispheres is across the South Atlantic. *Ochrobryum* has a geo-

graphical distribution that is completely distinct from that of *Schistomitrium* which is the other member of the family with fringed mitrate calyptrae.

***Arthrocormus*.**—The genus is known only from the Paleotropical region where the one species ranges from Ceylon eastward through Melanesia. The range scarcely overlaps with that of *Ochrobryum* but overlaps rather closely with that of the *Schistomitrium* / *Cladopodanthus* group and with a large number of *Leucobryum* species.

***Schistomitrium*, *Cladopodanthus*, and *Holomitriopsis*.**—The genera are credited respectively with 3, 4, and 1 species. The first two genera are restricted to the area of Malaysia, Indonesia, The Philippines and Melanesia. The presence of the related *Holomitriopsis* in the eastern part of the Guayana Highlands of South America is in an area notable for some Paleotropical elements (Robinson 1986). Distribution of the elements associated floristically with *Holomitriopsis* was evidently across the South Atlantic, but at this time the Paleotropical genera of the *Schistomitrium* group are not known from Africa or India. Species may have been in those areas previously or they might prove to be there at present identified as *Leucobryum*. *Holomitriopsis* was originally described as a *Leucobryum* and its true relationship was not suspected until the study by Florschütz (1964). *Holomitriopsis* is considered here as a comparatively recent extension of the range of this basically Paleotropical group into the Western Hemisphere.

***Octoblepharum*.**—Eleven species occur in the American tropics, 2 species are in West Africa, 4 in central Africa, and only the 1 supposedly pantropical species is cited from India eastward into the Pacific. The latter species is also credited to Hawaii, but it may have been introduced from America rather than Melanesia.

The genus is primarily tropical American in distribution with most of the paleotropical representation apparently consisting of a single nearly pantropical species. As such the genus is regarded as neotropical in origin. The most divergent element in the genus, with a carina near the base of the leaf, is the northern South American *O. tatei* (Williams) Bartr. that was first described as the distinct genus *Carinafolium* (Williams 1931). The genus *Octoblepharum* has been in the neotropics for at least 20–25 million years on the basis of a Hispaniola specimen in amber loaned by Dr. F. Hueber (Robinson 1985). The age of the genus in the area is probably much greater.

General Considerations and Conclusions

The earlier discovery of a basic functional peculiarity in the Leucobryaceous leaf (Robinson 1985) has been enlarged upon to offer a projected functional evolution of the family at both the ecological and morphogenetic levels. Direct experiment has not been attempted, but a number of inevitable conclusions can be derived from the basic continuing experiment found in nature. The functional progression could be presented in a cladistic form, but a review of the characters of the family is too incomplete. Only two synapomorphies are presently known that would unite any of the derived genera into a distinctive subgroup, the closeness of chlorocysts to the ventral surface and the mitrate calyptrae generally unite *Schistomitrium*, *Cladopodanthus* and *Holomitriopsis*. It is also notable that the important functional changes noted in this study often occur within rather than between genera.

A number of stages are recognized in the functional evolution of the Leucobryaceae, some having secondary effects.

1. The stratification of the leaf into inner chlorocyst networks and outer leucocysts.

The leucocysts hold both water and internally generated gas.

2. The shift from soil to rotten wood or adoption of epiphytism with restriction to tropical or subtropical regions. Change of substrates resulting in less consistently vertical sporophytes reducing the reason for curved capsules. The shift of habitats to less persistent substrates increasing evolutionary rates.

3. Increasing reliance on vegetative reproduction and potential bird distribution. Accompanying loss of reliance on sporophytes with reduction of sporophyte structure.

4. Morphogenetic increase of number of chlorocysts in the leaf.

The stages listed above can be elaborated as follows:

1. The functional strategy described for the Leucobryaceae by Robinson (1985) must be of some limited benefit to the mosses involved if their distribution is any guide. The specialization has not conferred the ability to survive in places where other mosses do not occur, but it seems to have left the genera fully competitive within the more moist and less frigid areas where other mosses are found. The Leucobryaceae are successful, but they are not significantly out-competing other mosses in any specific habitat. The specialization involves a reduction in the photosynthetic tissue of the leaf, but it insures a more continuous optimal vapor pressure of both gas and water for gaseous exchange at the surfaces of the chlorocysts in those tissues. The two effects might mostly offset each other. Still, any one species with such leaves could compete in a wider range of habitats than other single species.

The functional change inherent in the structure of the Leucobryaceous leaf seems to have offered only limited advantages

over the function of leaves in the supposed Dicranaceous ancestors, but the change unquestionably set the evolution of the group in a different direction from that of the Dicranaceae. The physiology changed first and structural changes followed later. Thus, *Leucobryum* has the Leucobryaceous strategy but retains most of the form of the ancestral Dicranaceae.

2. The shift of the Leucobryaceae from soil to rotten wood or living plant substrates has a number of important results. It seems at least partly responsible for the limitation of all advanced Leucobryaceae to the tropics and subtropics. The change from soil substrates also reduces the tendency for sporophytes to be borne erect which reduces the value of a curved capsule.

A more profound effect of the change of substrates involves the comparative stabilities of those substrates. Many *Leucobryum* species and many Dicranaceae occur on more stable substrates, a feature correlated with the more conservative evolution of those groups. The more advanced Leucobryaceae occur on less stable substrates which correlates with their apparent accelerated evolution. The less stable environment would impose generally shorter life cycles and could also be more subject to catastrophic change. The greater vulnerability to catastrophic change correlates with greater discontinuities in structural features between various derived genera.

One by-product of unequal rates of evolution is the presence of paraphyletic groups. Certainly, the Dicranaceae is a paraphyletic group without the Leucobryaceae. *Leucobryum* seems technically near enough to the ancestral stock of the Leucobryaceae to be considered paraphyletic in relation to other genera of the family.

I would agree with cladists that a proper

cladistic study should not be limited to a paraphyletic group, that is, failing to include any derived groups in the study. I would totally disagree with cladists that the taxonomic groups should be re delimited to eliminate paraphyly when the recognizeability of the group by ordinary taxonomists would be impaired. Thus, there is no mandate to redefine the Dicranaceae to include the functionally and structurally distinct Leucobryaceae, nor redefine *Leucobryum* to include any derived groups. In the case of *Leucobryum*, the lack of known apomorphies between it and the common ancestor of most other Leucobryaceae does not mean that none exists. In fact, only *Steyermarkiella* of the distinguished genera is suspected here of being derived directly from *Leucobryum*. Finally, experience seems to indicate that attempts to reduce the paraphyletic condition are not accepted by taxonomists when they conflict with marked structural characters (Robinson 1987).

3. Vegetative reproduction is found in many mosses including many Dicranaceae so that the phenomenon is not limited to the Leucobryaceae. Nevertheless, most if not all the Leucobryaceae shed whole leaves or leaf fragments capable of producing new plants. The prevalence of the vegetative reproduction would inevitably reduce reliance on sporophytic reproduction, and is certainly correlated with forms of Leucobryaceae in which the sporophyte is variously reduced. The capsules and peristomes are reduced, sometimes to extremes as in *Ochrobryum*, and sporophytes in some of the genera are rare. Sporophyte reduction is more prevalent and more extreme than in the Dicranaceae. Sexual reproduction would continue to serve the more limited function of genetic segregation and recombination but would be of reduced significance in maintaining or increasing species distribution.

Another factor reducing the importance of the sporophyte in the Leucobryaceae is the wet habitats in which many of the species occur. As noted by Robinson (1986), too much moisture can adversely effect the dispersal function that is highly developed in many sporophytes. The unique capsule design in *Ochrobryum* might circumvent the problem if any of the spores are retained in the cavity of the long-rostrate, deciduous operculum.

Octoblepharum albidum Hedw. commonly has many sporophytes and also has one of the widest distributions of any member of the family, apparently being nearly pantropical. The species has some fragmentation of leaves, and both methods of distribution must contribute to its broad geographical range. It seems notable that the increased presence of sporophytes is found in a species that seems to occur in somewhat drier habitats than most other members of the family.

The deciduous leaves and leaf fragments of the epiphytic Leucobryaceae would easily come in contact with birds and other arboreal animals. Contact with such animals would result in direct transmittal of the reproductive structures to other appropriate habitats.

4. The basic leaf form of the Leucobryaceae has two subsequent modifications of interest, the shift to alternate arrangement of leucocysts in genera such as *Octoblepharum* and *Steyermarkiella*, and the development of more than one layer of chlorocysts in *Arthrocnemum*. Both specializations have in common the increase in relative number of chlorocysts in the leaf. The functional significance of both specializations seems obvious, and the fact that two such modifications occur in the family seems to emphasize the importance of the chlorocysts to the survival strategy of the family.

This review of the Leucobryaceae has demonstrated the value of a functional approach to taxonomy. The importance of function is hard to over-estimate. Organisms that could not function can be found only in theory such as in some cladograms. Taxonomists should not forget physiological or morphogenetic realities as they study their groups.

The final pattern that is revealed in the Leucobryaceae supports many theoretical

