

Nova Hedwigia

Beiheft 120

Rudolf M. Schuster

Austral Hepaticae

Part III

Edited by

Matt von Konrat, David Glenney, Anders Hagborg,
Judith Dean Godfrey



J. Cramer

in Borntraeger Science Publishers
Stuttgart 2021

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With 225 figures



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Editors' preface

This volume was made available to us by the publisher to review and make corrections to the text. We have done so, but have avoided giving our own opinions or using new knowledge gained since the author completed the manuscript in about 2006, other than where nomenclatural issues are involved. Our editing changes are of two types: firstly, the usual corrections that need to be made to such things as author and journal abbreviations. Secondly, we have added editorial footnotes to help the reader by pointing out nomina nuda, illegitimate names, invalid names, and where the name meant is ambiguous.

We have also added letters following the year of publication for references where there is more than one publication with the same author and year. The Bibliography contains all references in the previous two volumes plus those in the present volume. Because a consistent referencing scheme was not in place for those two earlier volumes, the Bibliography contains inconsistencies. For instance, Austral Hepaticae I referred to Grolle (1966a) in discussion of *Telaranea lawesii*, while Austral Hepaticae II referred to Grolle (1966a) in discussion of *Gymnomitrium*. The result is that the Bibliography has a few inconsistencies in the lettering scheme.

Matt von Konrat, Anders Hagborg, David Glenny, and John Engel

Preface

The first volume of this work, Austral Hepaticae, Part I (Schuster 2000), includes the introduction to the hepatic flora of Austral regions; brief descriptions of the geographical area covered, and the methodology and approaches used; and acknowledgements. The information in the above sections should cover Part III, for the most part, though an addendum is needed for some additional acknowledgements.

A Note and Acknowledgements for Part III

This work represents a condensation and distillation of research, in the field and in the laboratory, over a fifty-year period. I was fortunate in my life to have been blessed with a healthy constitution, aside from miserable eyes (glaucoma and progressive nearsightedness). Through most of this period, I was also fortunate to have the support of my wife, Olga Marguerite, who both polished my manuscripts and corrected countless typographical errors, which became more abundant with the combination of my increasing arthritis and myopia. The delay in completing this volume arose in no small part from her passing, which brought to a halt a decades-long collaboration from which not only I, but also the users of my books and publications, have greatly benefited. I have missed her observation: "Rudy, you can't say that!" for comments which she asserted fringed on defamation. And I missed more deeply than I can say a wife, loyal, indulgent, and loving. This volume is dedicated, in part, to her memory.

I have been more than fortunate in my life, in my second marriage to my wife, Marlene. She has generously given me her loving support, for my work, and in our life together. She has created a delightful home for us, wherever we have been — in Massachusetts, the Arizona desert, and on the coast in Washington State, and has graciously tolerated my stacks of manuscripts,

journals, and books around our house(s). Marlene's daughter, Joan Waale, has joined her in supporting me, and my work. I am profoundly grateful to both Marlene and Joan for making these last few years most enjoyable.

Finally, I am deeply indebted to Drs. Judith Dean Godfrey and Geoffrey A. Godfrey for their aid — over several years — on my *Austral Hepaticae* manuscripts. Since my deteriorating eyesight, arthritis, and disintegrating musculature have precluded completing this work at an acceptable level on my own, they have been of enormous help. Judy and Geoff have been good friends for many years, and, have known me so well, and for so long, that they could cope without a “Rosetta Stone”. For their generously stepping in to help, my gratitude knows no bounds!

Rudolf M. Schuster (1921–2012)

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Introduction to Part III

With *Austral Hepaticae, Part III*, the approach — but not the methodology — for the taxonomic treatment has had to undergo some significant changes as compared with Parts I and II. Firstly, Parts I and II largely dealt with stenotypic genera and/or families that generally had relatively “clean” perimeters. To a large extent, these sharp perimeters are the result of extinction: particularly in the cool/cold Antipodes, we deal with a remnant or relict flora. Presumably, the large majority of genera (and some families) that once inhabited present-day Antarctica underwent extinction. The fascination of the present-day cool/cold Austral flora is that we find here the remnants or residue of a once much richer flora. The residue of this flora largely exists in present-day Tasmania and the belt of islands extending from New Zealand to New Caledonia.

In these volumes, I dealt with a wide array of mono- or stenotypic genera/families virtually none of which exist (and probably never did exist) in Laurasia. Among them are: *Grollea* R.M.Schust. (monotypic; only *G. antheliopsis* R.M.Schust., the sole species of the Grolleaceae R.M.Schust.); *Trichotemnoma* R.M.Schust. (monotypic; one relict species left in the family Trichotemnaceae R.M.Schust.); *Neogrollea* E.A.Hodgs. (monotypic; placed by Schuster in Lepidoziaceae subfam. Neogrolleioideae, by Engel and Braggins in a monotypic family Neogrolleaceae); and *Brevianthus* J.J.Engel & R.M.Schust. (monotypic; a single relict species in the family Brevianthaceae J.J.Engel & R.M.Schust.). The bulk of these mono- or stenotypic families/genera are Australasian. They almost all agree in: (a) being unisexual; (b) lacking asexually reproductive devices (gemmae, etc.); and (c) being representative of monotypic genera (and often families).

In Part III, we now also deal progressively with modern groups that have undergone massive speciation, e.g., Plagiochilaceae [and, if there had been time to complete the work for a Part IV, the Lejeuneaceae]. In the case of *Plagiochila*, we are overwhelmed by some 1200 supposed binomials, thus the genus can only be treated superficially here. Keys to all species, unlike those for groups in previous volumes, are often impossible to provide; I content myself with presenting a conspectus of sections and treat only isolated representatives of most of these sections. Even such a limited account is now forbiddingly long.

These volumes are *not* intended as a usual taxonomic treatise. My general aim has been to provide a distillation of some four to five decades of study of a large sample of Austral taxa — mostly of living plants. I have devoted my entire career to the process of cleansing perimeters and sharply defining group (family, genus, subgenus) perimeters in a critical fashion. In Part I, p. 2, of this work, I emphasized, “I regard myself as, basically, a student of phylogeny and not primarily as a taxonomist”. To me, the “relationships of organisms are infinitely more interesting than putting species names on ‘unknowns’... The primary emphasis, however, is not on taxonomy at the species level, but on the phylogenetic orientation”.

In these volumes, I have retained a relatively conservative attitude to the size of taxonomic groups. Thus I retain the now old division of leafy hepatics (Jungermanniales) into some 15 suborders, as in Schuster (1966), and *Austral Hepaticae Part I* (Schuster 2000, table p. 37). In that table (p. 37), an alternative arrangement is also shown, where these 15 suborders are organized into 10 orders. Recent studies suggest that this once-radical classification perhaps should undergo relatively minor “inflation”. Thus Lepidoziaceae subfam. Neogrolleioideae R.M.Schust. has been elevated to the rank of a family, Neogrolleaceae (R.M.Schust.) J.J.Engel, and the family Trichotemnaceae R.M.Schust. has been elevated to an order, Trichotemnomales

J.J.Engel¹, on the basis of the gynoeceal apparatus and sporophyte. (Previously, the monotypic genus *Trichotemnoma* R.M.Schust. had been known only from ♂ plants.)

The sequences adopted, and usually explained in some detail, in this volume (i.e., of suborders, families, and the genera within them) reflect the simple (and perhaps wrong) assumption that ancestral Jungermanniales were erect and isophyllous. Thus in the first suborders (Geocalycineae, Balantiopsidineae), we deal with taxa which, with few exceptions, preserve ventral merophytes that develop large underleaves — only exceptional “end taxa” such as *Plagiochila*, *Evansianthus*, and *Pseudolophocolea* have strongly reduced or (*Plagiochila* spp.) vestigial underleaves. I do not mean to imply that isophylly, or an approach to it, automatically means that a genus is “primitive” — *Pachyglossa* is far from that. But there is a general pattern: taxa with highly reduced ventral merophytes always exhibit other signs of specialization.

In this volume, as in the others, I have attempted to provide keys to species wherever feasible. The reader is reminded that, as clearly stated in the preface to Part I, this work deals, basically, with classification and phylogeny. The keys are usually not artificial keys designed for simple identification of taxa — they rather are phylogenetic constructs that try to arrange the taxa in key form, in such a way that an overview of the group is presented. Although labeled “keys”, these are more nearly to be regarded as devices to graphically present the taxa in such a way that allied groups key out together. If these outlines work as keys, good; if not, they should serve to orient the student — which is a more relevant objective.

In these volumes, I have continued to try to describe, discuss, analyze, and illustrate one or more taxa per genus/subgenus in detail, though I have had to greatly limit this. I have tried to abbreviate diagnoses as much as possible. Not only has the need to save space been a factor here, but the extensive and detailed illustrations preclude, in my opinion, the need for long species diagnoses. Some genera (i.a., *Chiloscyphus*, *Leptoscyphus*) have received disproportionately extended treatments. This reflects two factors: their size and difficulty, and especially, the recent appearance of much “microliterature”, often expressing taxonomic opinions that are seriously at odds (cf. the treatment of *Leptoscyphus*). In this present work, I have tried to thread the way between these divergent opinions; I have, surely, been less than successful, perhaps owing to spatial constraints.

Because of spatial limitations, I have continued to embrace the concept of treating, in detail, “type” species — not necessarily nomenclatural types, but taxa I regard as *typical* of the genus. For example, when a taxon has been very poorly known (e.g., *Lethocolea squamata*) and I have abundant new data, in part derived from living plants, I have included this. This also reflects my attempt to lend some life to these taxa; they each are fascinating, with ecological and reproductive biologies that lend them an interest not visible in herbarium packets. For the monster genus *Plagiochila*, I have had to practice ruthless condensation for purposes of this volume, and have excluded half of the manuscript and figures originally prepared.

The scope of this work necessarily required more truncation than would be desirable. It thus fails to do justice to the fascinating African flora, now deteriorating owing to human activity and development. The completion of this work involved repeated condensation and/or rewriting of work, some parts initiated two or more decades ago. It was impossible to rework or rewrite much of this. Parts, therefore, are “dated”, whereas other parts may seem elaborated beyond need. The numerous journal papers cited in the Bibliography serve to complement and flesh out the abbreviated treatments included in these three *Austral Hepaticae* volumes.

¹ Editors' note: *Trichotemnoma* is a *nomen nudum*.

Suborder VII. Geocalycineae R.M.Schust.

[J. Hattori. Bot. Lab. 36:397, 1972; New Man. Bryol. 2:986, 1984]

Plants with growth via a tetrahedral apical cell; with well-developed ventral merophytes (nearly always producing distinct, rarely vestigial underleaves). Plants green [sometimes pale to yellowish green], secondary pigments, if any, brownish [except in *Rhodoplagiochila*]. Stems without a hyaloderm; cortical cells like medullary or smaller, then thick-walled; usually no fungal associates. Usually anisophyllous (only *Pachyglossa* isophyllous). Branching mostly sparing and irregular; primitively with terminal branches [*Frullania* type; virtually never *Acromastigum* or *Microlepidozia* type] and intercalary branches (ventral and/or lateral); with or without development of microphyllous, plagio- and geo-tropic axes. Leaves never conduplicate, basically 2- to 0-lobed, never 3–4-lobed, alternate ranging to opposite, \pm succubous and usually obliquely oriented, dorsally usually inserted to stem midline [rarely not so, leaving a leaf-free dorsal strip; in *Rhodoplagiochila* narrowly interlocking dorsally], edentate to variously toothed. Underleaves from very large to small; rarely with lamina vestigial. Rhizoids primitively in fascicles from bases of underleaves [if these vestigial, then from ventral leaf base], secondarily spreading to ventral face of stem. Cells various: rarely very large and hyaline; cuticle smooth to roughened; oil-bodies always present, normally (1)2–12 rarely more, usually granular [tiny, numerous and homogeneous only in *Leptophyllopsis*] often opaque. Asexual reproduction either absent or via fragmenting or caducous leaves (chains of 1–2-celled gemmae only in some Geocalycoideae).

Unisexual, less often bisexual. Androecia usually bilateral; bracteoles, if any, normally lacking antheridia. Antheridia usually 1–2, rarely (*Tylimanthus*) more, with stalk \pm short, 1-, 2-, rarely 4-seriate; body with cells irregular, rarely elongated, never tiered. Gynoecia often isophyllous even if vegetative areas are bilateral. Usually with a perianth, wide at the unlobed or shallowly lobed mouth, either trigonous or ventral face narrowed (then bilabiate), or perianth reduced or lacking, then with a \pm distinct marsupium developed. Sporophyte with seta usually massive [reduced to an 8–9 + 4-seriate condition only in *Anomylia*], of the general type. Capsules ovoid to ellipsoidal, with straight, fusiform-elliptical valves; wall usually 3–6-, rarely 2 or to 8–9-layered; epidermal cells not tiered, not or moderately elongated, usually clearly one-phase; all or most longer walls, mostly some or many transverse walls, with nodular thickenings [or all walls hyaline, devoid of thickenings]; inner strata usually with semiannular bands, sometimes (e.g., in *Anomylia*) reduced to short spurs on tangential walls. Spores normally 1-celled at time of release and with exosporous germination [precociously pluricellular in some taxa of *Plagiochila*]. Elaters free, usually 2-spiral.

The Geocalycineae include a limited suite of families (Geocalycaceae *s. lat.*, to include Harpanthaceae; Plagiochilaceae, Acrobolbaceae, Arnelliaceae) in the classification in Schuster (1984). The western American Gyrothyraeaceae R.M.Schust. are sometimes included here but differ in two crucial features: (a) they have cylindrical capsules; valves are spirally twisted; and (b) they develop reddish pigmentation, at least in sun forms. Notoscyphaceae probably fit here (p. 228).

As here delimited, the group seems somewhat heterogeneous but a series of tendencies (rather than sharply defined criteria) seem to unite them: (1) Perianths, unless lost, are never contracted to the apex; even in the rather primitive *Harpanthus* the mouth is relatively wide (fig. 536:4 in Schuster 1980) and are, unless strongly laterally compressed, basically trigonous. (2) Leaves show no tendency toward formation of supplementary lobes; they are either bilobed or unlobed; they show repeated tendencies to becoming opposite. (3) There is a strong tendency for retention of isophylly or moderate anisophylly in the gynoecium; in groups preserving a perianth, bracteoles are rarely wholly suppressed. (4) Plants are mostly \pm opaque and rather firm; cells are rarely large and hyaline (and are never devoid of oil-bodies) and stems never develop a distinct hyaloderm. (5) Rhizoids tend to occur in fascicles, mostly at underleaf bases or (Acrobolbaceae; some Plagiochilaceae) sometimes at ventral leaf bases; only in apomorphic taxa are rhizoids scattered. (6) Mycorrhizal associates are lacking or (*Pedinophyllum*) rarely present. (7) Capsules range from ovoid to slenderly ellipsoidal and have straight valves [weakly spiral in a few *Plagiochila* spp.]; their walls are mostly polystratose, sometimes 4–8 (9–10)-

layered; they almost uniformly show a one-phase ontogeny. (8) Except for in the dwarfed *Anomylia*, the seta is always massive, with an indeterminate number of cell rows.

No single one of these phylogenetically significant “tendencies” serves to definitively circumscribe a suborder Geocalycineae. Collectively they seem to lend some reality to the group. Among recurrent tendencies, two stand out: (1) The repeated development of opposite or subopposite leaves (as, e.g., in *Plagiochilion*, *Leptoscyphus*, some *Chiloscyphus* spp., *Syzygiella*, all Arnelliaceae). Development of opposed leaves is such an unusual feature — it fails to recur in any other suborder of Jungermanniales — that one is tempted to invoke the hypothetical “floating gene” to account for it. (2) The repeated narrowing of the ventral member of the basically trigonous perianth, with the consequence that the perianth becomes bilabiate. This occurs several times, presumably independently, in Geocalycaceae; it is the “norm” in Plagiochilaceae. (3) There are repeated tendencies for standardization of branching modes. In no taxa is the ability to form *Microlepidozia*- or *Acromastigum*-type branches retained.² In all generalized taxa (almost all of Lophocoleoideae) the capacity to form terminal, *Frullania*-type branches (aside from in *Amphilophocolea*) is retained; in many advanced taxa (virtually all Geocalycoidae except for *Harpanthus flotovianus*), the capacity to form terminal branches is lost. Lateral- intercalary branching is only sporadically developed. (4) Although primitively a trigonous, prominent perianth is developed (as in *Chiloscyphus* spp.), there are repeated tendencies to augment or supplant this by fleshy, shoot-derived structures. Although this is typical of Geocalycoidae (cf. figs. 537:6–8; 538:2; 540:9; 541:1–6, *Harpanthus*, and 544:8, *Geocalyx* in Schuster 1980) the beginnings of it are apparent in Lophocoleoideae. Thus in *Chiloscyphus patulistipus* (Steph.) J.J.Engel & R.M.Schust. there is a distinct, if low, coelocaul-precursor, as also in *C. austrigenus* (Hook.f. & Taylor) J.J.Engel & R.M.Schust. and *C. otiphyllus* (Hook.f. & Taylor) J.J.Engel & R.M.Schust. (cf. Hässel 1995, figs. 18, 34, 53). [In these taxa the sporophyte superficially “bores” into the shoot apex; the foot is situated 2–3 gyres below the distalmost leaf-derived structures, e.g., perianth and bract bases.]³

The following key to families is unsatisfactory for the simple reason that no “simple” and “reliable” synopsis is possible: intragroup variation defeats any attempt at a satisfactory key. As will become evident, in the large families Geocalycaceae and Plagiochilaceae not only are family limits ill defined, but generic limits (and in many cases, species limits) are frustratingly tenuous.

Key to Families

[Derived from Schuster 1980]

1. Capsule wall normally 3–9(10)-stratose.⁴ Leaves alternate or subopposed, rarely strictly opposite, with abaxial faces never armed. Asexual reproduction (if present) mostly via fragmenting or caducous leaves (or several-celled gemmae, individually produced from margins of leaves). [Most taxa able to produce *Frullania*-type branches; usually retaining large underleaves, at least in gynoeccial region.] 2.
2. Perianth usually retained, wide at mouth [lost in most Geocalycoidae; these have large, bifid underleaves]. *Frullania*-type terminal branches retained in many taxa. Leaves often opposite to subopposite. Capsules rounded at summit 3.
3. Perianth [lost in some Geocalycoidae; there with a marsupium] trigonous (when inflated, obscurely so), the third ventral face sometimes narrow. Gynoeccial region usually isophyllous to anisophyllous; distinct or large bracteoles retained. Vegetative shoots usually anisophyllous; small to very large, mostly bifid underleaves usually retained. [Perianth, if retained, often subtended by a stem-derived coelocaul-precursor, or perigynium.] Family 1. Geocalycaceae H.Klinggr. (p. 6)
3. Perianth, always well preserved, laterally compressed and normally bilabiate at mouth, with

2 Engel reports *Acromastigum*-type branching in one taxon of *Clasmatocolea*; there is no supporting figure.

3 Hässel (1995a) fortunately had the acuity to illustrate longisections of the gynoeccial apparatus for each of the taxa she treated. Apparently the identical (and sometimes more marked) tendency to elaborate a coelocaul-precursor exists in *Clasmatocolea* (cf. p. 146).

4 Only 2-stratose in *Geocalyx*.

- dorsal and ventral keels, usually without a perceptible ventral face; never with a stem-derived component to the perigynoeical structure. Gynoeical region always bilateral like vegetative region; both with vestigial underleaves [if at all lamellate, not simply bifid; mostly ciliate or resolved into cilia] and bracteoles. Plants mostly erect or suberect in growth
 Family 2. Plagiochilaceae (Jörg.) K.Müll.
2. A recognizable perianth never retained; gynoeical shoot apex producing a pendent marsupium at whose summit are paired (often reduced) bracts. Terminal branches never present; branches lateral- and/or ventral-intercalary. Capsules beaked. [Leaves always alternate, usually with papillose or asperulate cuticle; usually with one to few very large (or more numerous but large), opaque, greyish to brownish oil-bodies, the cells usually opaque. Underleaves none or minute (then not bifid). Rhizoids mostly at ventral leaf bases and/or scattered.]
 Family 3. Acrobolbaceae E.A.Hodgs. (p. 443)
1. Capsule wall 2-stratose; capsule not beaked. Leaves alternate or opposed, unlobed, edentate, with abaxial faces smooth or often spurred (spurs sometimes producing gemmae). Branches all intercalary; ventral, or ventral + lateral. Gynoeica producing pendent marsupia; with or without a reduced perianth at their summits. [Many taxa with gemmae of abaxial leaf surfaces and/or tubers.] 4.
4. Leaves opposed, with abaxial faces often spurred (spurs sometimes forming gemmae). Branching ventral or ventral-lateral. Underleaves lacking or filiform, unlobed
 Family 4. Arnelliaceae Nakai (p. 541)
4. Leaves alternate, unarmed on abaxial faces; never gemmiparous. Branching only ventral-intercalary. Underleaves distinct, bifid.
 Family 5. Notoscyphaceae (R.M.Schust.) R.M.Schust.⁵

5 The group probably deserves treatment as an autonomous family. It was treated as Jungermanniaceae subfam. Notoscyphoideae on p. 445 in Vol. II. It is not further treated here.

Family 1. Geocalyceae H.Klinggr.

[Die höheren Cryptogamen Preussens, p. 34, 1858]

Plants highly variable but without anthocyanin-derived pigments, usually relatively soft-textured, whitish or yellowish green and often subhyaline, sometimes brown or fuscous, irregularly branched. Branching in most taxa in part terminal, *Frullania*-type + ventral-intercalary + (often) lateral-intercalary (mixture of branching states variable from taxon to taxon). Stems usually lacking a rigid cortex of thick-walled, elongated cells [except in *Platycaulis*; Fig. 480:10, 13], never with a well-differentiated hyaloderm; mycorrhizal infection lacking, the medullary cells remaining hyaline. Rhizoids usually fasciculate and from underleaf bases, their tips often (sometimes copiously) ramified. Rarely isophyllous (*Pachyglossa*), usually weakly to strongly anisophyllous; underleaves mostly distinct throughout, usually bifid (lanceolate in *Harpanthus*), tending to be approximated on one, less often both, side[s] to ventral base of lateral leaves and sometimes connate with them. Leaves usually clearly succubous, insertion lines usually attaining antical stem midline (not in *Pseudolophocolea*) but not crossing it, alternate but sometimes subopposed, unlobed and edentate to 2(3)-lobed or -dentate, infrequently pluridentate, never folded (canaliculate) or complicate-bilobed. Cells typically thin-walled and with small to distinct trigones, mostly with smooth cuticle; oil-bodies usually 2-many per cell, colorless, usually granular or granular-botryoidal (minute and many in *Leptophyllopsis*; there homogeneous). Asexual reproduction scattered in occurrence (usually none), diverse (cf. discussion).

Dioecious, autoecious or (rarely) paroecious. Usually monandrous; rarely with paraphyses; antheridial body cells tiered or not; stalk moderate in length, less than that of body, 1–2(4)-seriate. Gynoecia isophyllous to anisophyllous; a bracteole always retained, rarely small. Perianth trigonous, with third keel antical (except in *Harpanthus*), or (in *Geocalyx*, *Saccogynidium*) lost, replaced by a marsupium; ventral face of perianth sometimes narrowed; rarely, if ever, lost. Seta of the “general” type, many-seriate. Capsule ellipsoidal to ellipsoidal-cylindrical, with straight valves; wall 2– to 3–6(8)-stratose; epidermal cells with one-phase ontogeny; all longitudinal and many/most transverse walls with radial (“nodular”) thickenings; innermost layer usually with complete/incomplete semiannular bands (occasionally reduced to short, lingulate thickenings). Spores small, 1-celled at release, with exogenous germination; sporeling usually of the filamentous type. Elaters 2-spiral, spirals narrow, ends usually little tapered and blunt.

Type Genus. *Geocalyx* Nees

A large, complex family, with some 25–26 genera in 3 subfamilies. All but two (*Harpanthus*, *Saccogyna*) occur regionally. It was once traditional to place the genera united here in the Geocalyceae (= Harpanthaceae) into two families (Müller 1951–1958, pp. 197–198), Harpanthaceae [including, teste Müller, *Harpanthus*, *Geocalyx* and *Saccogyna* (and, in error, *Hypogastranthus*)] and Lophocoleaceae (including *Lophocolea*, *Chiloscyphus*, *Heteroscyphus* and *Conoscyphus*). Evans (1939) had treated these genera as representing a single family, Harpanthaceae, but attributed there also genera (*Mylia*, *Pedinophyllum*, *Apotomanthus*) now placed in other families. *Mylia*, *sensu* Evans, was shown (Schuster 1959a, 1959b, 1960) to include three genera, *Mylia s. str.* (Jungermanniaceae), and *Leptoscyphus* Mitt. and *Anomylia* R.M.Schust. (both in Geocalyceae *s. lat.*); *Pedinophyllum* is today, perhaps wrongly, placed in the Plagiochilaceae. Including genera that perhaps do not fit into the Geocalyceae, the family has “grown” in the last 3–4 decades into a large, complex, very difficult group with a minimum of 25–26 genera.

The Geocalyceae were divided (Schuster 1973, 1979, 1980, 1984) into three subfamilies: Geocalycoideae, Lophocoleoideae and (for taxa with bilateral gynoecia) Leptoscyphoideae. A detailed review of this division is in Schuster & Engel (1982). In essence, it is shown (cf. Schuster 1980, pp. 283–284; cf. table) that some six relevant criteria separate Geocalycoideae from the Lophocoleoideae + Leptoscyphoideae. In Schuster & Engel (l.c., p. 66) the

wisdom of separating the last two groups into two units is stated to “remain open and unresolved.” For reasons detailed on p. 12, I have concluded that division of the genera in this last “complex” into two subfamilies is, practically speaking, almost impossible.

Broadly defined, the Geocalycaceae appear to show some remote affinities to the Plagiochilaceae and, perhaps less so, to the Arnelliaceae (Southbyaceae). They are defined not only by the criteria in the family key (p. 4) and by the above diagnosis, but by a series of phylogenetic tendencies, some of which recur in scattered fashion, others that are negative in the sense that their absence seems relevant. Among them are: (1) Almost universal lack of 1–few-celled gemmae produced in branched chains (exception: *Geocalyx* and *Harpanthus*; cf. below), and only very scattered asexual reproduction, in general: by caducous leaves, fragmenting leaf tips, etc. — methods of asexual reproduction widespread, if scattered in occurrence as in Plagiochilaceae. (2) A marked tendency for rhizoids to become ramified distally, sometimes elaborately so, as in *Platycaulis* (Fig. 480:11, 13) and their almost universal restriction to fascicles at the underleaf bases (Fig. 480:1, *Platycaulis*). (3) The wide open perianth, formed [except, again, in *Harpanthus*; cf. below] by fusion of three flat components, thus with the third face postical, derived from a ventral merophyte, flat, and the lines along which these elements fused often distinctly winged. (4) The universal lack of vinaceous or reddish pigments, of leaves and rhizoids. [*Clasmatocolea tjivideiensis*, on the basis of the vinaceous rhizoids, is obviously misplaced on that sole basis.] (5) Recurrent tendencies to adopt a growth pattern involving erect/ascending leafy axes + geotropic leafless/microphyllous axes (the latter often originating at bases of leafy branches) — a tendency seen again in many Plagiochilaceae. (6) The universal retention of distinct appendages of ventral merophytes, both on vegetative shoots and in gynoecea. Generally, in both Lophocoleoideae and Geocalycoidae underleaves are conspicuous and usually bifid (by contrast in Plagiochilaceae they are usually reduced, have no or a vestigial basal lamina, and bear several laciniae/cilia ending in slime papillae). In general, rhizoids remain restricted to underleaf bases (in Plagiochilaceae usually scattered). However, in *Pedinophyllopsis* underleaves and ♀ bracteoles are reduced (and the latter copiously bear cilia ending in slime papillae; cf. Fig. 488:2). Underleaves are even more reduced, to a few cilia ending in slime papillae, but rhizoids are “virtually” restricted to underleaf bases in *Pseudolophocolea*. In underleaf form and in the reduced bracteoles these two genera very closely approach the Plagiochilaceae.

The diagnosis and several of the six “tendencies” outlined above, fail to fit *Harpanthus* Nees, with three Holarctic taxa. The position of this genus in the Geocalycaceae is questionable. The family is divisible into three units, as per the key, p. 8. [*Harpanthus* is not again treated; see the detailed account in Schuster 1980, pp. 285–308, figs. 536–542.]

The taxonomy of the Geocalycaceae — especially of the Lophocoleoideae — remains unresolved. Several factors are at play: (1) Species are, in general, very malleable so that some workers (Herzog; Stephani) sometimes described the same taxon 2–3, or even 4–6, times. In particular, juveniles (or weak forms developed under marginal conditions) of apomorphic taxa may simulate “mature” forms of relatively plesiomorphic taxa. (2) Genera and subgenera are often not sharply separated. Thus *Hepatostolonophora* is separated from *Clasmatocolea* chiefly on the basis of growth form: the former develops microphyllous rhizomes and stolons, the latter not. Yet *Xenocephalozia*, placed by Grolle in *Clasmatocolea*, is stoloniferous, at least sporadically. *Chiloscyphus* and *Lophocolea*, still often regarded as “good” genera, merge so almost imperceptibly that there seems no way to “save” the latter as an autonomous genus. Where others see two genera, I see an amoeba-shaped genus with some 7 ill-demarcated arms, or subgenera. In general — with the exception of Hässel (1996) who adopts an exceedingly broad genus concept, generic limits have been drawn ever more narrowly. [Thus *Leptoscyphus*, *sensu* Grolle (1963) today includes three genera; *Clasmatocolea sensu* Grolle (1960) includes 3–4 genera, one (*Austrosyphus*) belonging to a different family and suborder.]

The Geocalycaceae are here broadly treated to include as well the “Lophocoleaceae” of Jørgensen (1934) and Müller (1951–58, p. 593). As previously noted, Müller treated the Geocalycoidae and Lophocoleoideae as autonomous families and treated them very far apart. The lophocoleoids, here treated as a subfamily of Geocalycaceae, were circumscribed — in part — on the basis of the presence of terminal branching, with only a dorsal half-leaf produced associated with the terminal branch (cf. p. 593 in Müller, l.c.). By contrast, Müller diagnosed the “Harpanthaceae” as with ventral-intercalary branching from the axil of underleaves (Müller, l.c., p. 1062).

However, branching modalities fail to allow a certain separation into two families: (1) In *Harpanthus flotovianus*, branches, although usually ventral-intercalary, are at least occasionally terminal-lateral and *Frullania*-type (Evans 1912; Schuster 1980, fig. 542:2). In *Amphilophocolea* of New Zealand we have the typically convex leaves of subg. *Lophocolea*, and the bifid underleaves connate on one side with lateral leaves of *Lophocolea*, yet branching is uniformly ventral-intercalary. (2) *Harpanthus*, shows much variation from extremes with the ventral-intercalary gynoeceal branches forming a distinct perianth at least as high as the fleshy perigynium at its base (fig. 538:2 in Schuster, l.c.) to extremes with a reduced perianth at the apex of a perigynium that is from 1–2X as high as the reduced perianth (fig. 541:1–6 in Schuster, l.c.). Thus the gynoeceal apparatus of

Harpanthus combines elements of the lophocoleoids (the distinct perianth) and elements of *Geocalyx* (the fleshy tube surrounding the base of the sporophyte).⁶

I here recognize two principal subfamilies, Geocalycoideae and Lophocoleoideae (inclusive of Leptoscyphoideae), which seem very strongly separated by a wide array of criteria (cf. infra and diagnoses). The two seem very distinct yet the enigmatic *Amphilophocolea* R.M.Schust. (cf. Schuster 2001) exhibits such a mix of criteria of lophocoleoid and geocalycoid nature that it seems to preclude separating the two groups as autonomous families. The salient criteria separating the two groups are summarized as follows:

	Lophocoleoideae	Geocalycoideae
Branching	Malleable, almost always with lateral branching retained, usually at least in part terminal, Frullania-type	Restricted; usually only ventral-intercalary
Cuticle	Smooth, or cells each raised as a tubercle; plants usually \pm nitid	Smooth (<i>Harpanthus</i>) or finely papillose; the plants dull textured
Underleaves	Often connate on one, rarely on both sides with leaves	Free (<i>Geocalyx</i>) or weakly connate with leaves on one side (<i>Harpanthus</i>)
Rhizoids	In fascicles at underleaf bases	Scattered
Gametangia	Usually on leafy axes of diverse length, sporadically on abbreviated intercalary branches.	Normally on weak, short, ventral-intercalary branches
Gynoecea	Always forming a trigonous perianth which has the third keel dorsal; no marsupium developed	Perianth lacking, or \pm short, with third keel postical; a fleshy, stem-derived perigynium or marsupium distinct
Asexual reproduction	Lacking, or via pluricellular gemmae individually formed, or via caducous or fragmenting leaves	Sometimes lacking, but often via 2-celled gemmae formed in chains
Capsule wall	Usually 4–5(6)-layered	Usually 2-stratose

Although, in general, these eight criteria suggest we deal with strongly isolated groups, the existence of intermediate genera like *Amphilophocolea* suggests that the two groups cannot always be sharply separated.⁷

Key to Subfamilies

1. Stem perigynium (*Isotachis*-type) and/or marsupium lacking; with a well-developed perianth, trigonous (third keel dorsal) at least near mouth [ventral “third” sometimes reduced or vestigial; perianth then

6 The perianth type casts doubt upon *Harpanthus* as a member of the Geocalycoideae (and even of the Geocalyceae). The scattered rhizoids occur, admittedly in *Geocalyx*. Adding to the extant taxonomic confusion is *Arctoscyphus fuegiensis* (C.Massal.) Hässel (1996), described as *Leioscyphus fuegiensis* (C.Massal.) Besch. & C.Massal. This plant, judging from Figures in Hässel (fig. 1:1–6), has the laterally compressed wide-mouthed perianth with a stalked ?fleshy base, seen in the generic type, *A. ronsmithii* (cf. fig. 362:3), tentatively treated in the Jungermanniaceae (cf. *Austral Hepaticae Part II*, 2002, p. 393). This species appears to belong in or near *Pseudolophocolea* (cf. *Austral Hepaticae Part II*, 2002, p. 393). Its placement in three genera illuminates the problem of the intrafamilial classification of the family.

7 The puzzle of the position of “*Leioscyphus repens* var. *fuegiensis*” of Massalongo (1885) is touched upon on p. 394, *Austral Hepaticae Part II*. This plant, superficially like a lophocoleoid, is placed within *Arctoscyphus* by Hässel (1996), whose type species has been treated as, probably, a member of Jungermanniaceae (*Austral Hepaticae Part II*, p. 393). It has scattered rhizoids, which is difficult to equate with the Lophocoleoideae.

bilabiate], the mouth wide open. Branching, vegetative and sexual, normally malleable; nearly all taxa with some, many, or most branches lateral (*Frullania*-type and/or lateral-intercalary) but ventral-intercalary branches in many taxa; sexual branches not consistently reduced and ventral-intercalary [except in *Heteroscyphus*]. Rhizoids usually fasciculate. Capsule wall normally 3–6(7)-stratose. Antheridia with body of numerous cells, not clearly elongated, not tiered 2.

2. ♀ Bracts + bracteoles free from each other; perianth conspicuous. Rhizoids from base of underleaf, from cells at juncture of underleaf and stem Subfamily Lophocoleoideae (p. 12)

2. ♀ Bracts + bracteoles connate, jointly forming a tubular structure that encloses and obscures the reduced perianth. Rhizoids arising from lamina of underleaves, ca. 0.25–0.5 above the underleaf base Subfamily Conoscyphoideae (p. 208)

1. Stem perigynium and/or marsupium developed; perianth if present (mostly then abbreviated), with third keel ventral, not dorsal, and mouth constricted. Branching usually all ventral-intercalary [rarely *Frullania*-type; never lateral-intercalary]; sexual branches normally all short, ventral-intercalary. Capsule wall ± 2-stratose. Rhizoids usually (at least in part) scattered. Antheridial jacket cells ± elongated, tiered Subfamily Geocalycoideae (p. 214)

Classification And Evolutionary Progressions: Parallelisms And Problems

The “explosive” nature of evolution in the Geocalycaceae has “bedeviled” all attempts at evolving a satisfactory classification. Unlike groups dealt with in *Austral Hepaticae Parts I and II*, the Geocalycineae appear to have undergone high levels of parallel evolution, possibly since the start of the Cretaceous when immense numbers of new microhabitats were created by the explosive diversification of the Angiosperms.

Arguably, the basic morphological “model” has undergone both parallel modification [end result: taxa with a long distinct history that mimic each other] and bewildering diversification.⁸ Complicating matters visibly is that with the explosive diversification so many taxa evolved, often in parallel fashion, that the taxonomy of the group has become hopelessly muddled.⁹

Parallelisms: A recurrent problem is that the basic morphological model of the Geocalycineae has been modified in exactly parallel fashion, again and again.

The basic model involved a taxon with the following ensemble of features: (a) shoots, ± anisophyllous, retaining large, usually bifid underleaves; (b) succubous, bilobed/bifid lateral leaves, inserted across the entire merophyte; (c) as gynoecia are approached, ventral merophytes produce larger and larger underleaves and, eventually bracts that are isophyllous and identical in all three merophyte rows; (d) the gynoecial isophylly extends to the perianth, which has three keels and a flat ventral face as wide as the lateral; (e) gametangia form on unspecialized leafy axes; and (f) branching remains malleable.

The underleaf has been repeatedly reduced (within *Plagiochila* there is a wide range of reduction — the end result is a mere vestige). The two leaf lobes have been repeatedly reduced/lost and accessory dentition repeatedly evolved. The leaf insertion has been narrowed so that antical stem surfaces are widely exposed (as in *Pedinophyllopsis* and *Pedinophyllum*). Anisophylly in the gynoecium has been repeatedly evolved — the triseriate bracts of *Chiloscyphus* have been modified and a reduced bracteole evolved, again and again (i.e., in *Pseudolophocolea* and *Chiloscyphus* subg. *Lamellocolea*) or the bracteole been nearly or quite lost (*Plagiochila*). The trigonous perianth (isophylly retained) becomes laterally flattened with narrowed ventral face (*Chiloscyphus* subg. *Lamellocolea*; *Leptoscyphus*; even in *Plagiochila tricarinata* Carl) or with the ventral component “lost” (Plagiochilaceae).

In numerous taxa there is no visible pattern as regards sex organ position: both ♂ and ♀ organs form on unspecialized axes of diverse length. The ♂ eventually become intercalary; the ♀ usually form subfloral innovations. From this model we see parallel evolution, again and again, of abbreviation/condensation of gametangial axes. Both ♂ and ♀ become terminal and restricted to weak, short (usually intercalary; sometimes terminal) branches which fail to innovate apically. In the “base” genus, *Chiloscyphus*, this has happened again and again.¹⁰ Thus the genus *Heteroscyphus* is intimately connected to *Chiloscyphus* and differs principally

8 To the point where taxa of *Plagiochila* have evolved which fail to look like *Plagiochila*, and which have in recent years been assigned to genera (*Szweykowskia*, *Steeerochila*, *Acrobolbus* subg. *Xenopsis*) which represent mere extremes of the base genus, *Plagiochila*; cf. p. 233, 242.

9 One result is the creation of hundreds of “new” species, especially in *Plagiochila*, whose claims to validity are weak at best; recent revisions all include very long lists of synonyms.

10 As a consequence the traditional distinction drawn between a “narrow” genus *Chiloscyphus* and a “narrow” genus *Lophocolea* is meaningless as soon as the extra-European flora is studied.

in constantly relegating gametangia to weak intercalary branches, which lack ordinary leaves — the ♂ branches often highly reduced (as in subg. *Tetracymbaliella*).

Branching. In the basic model, both ventral- and lateral-intercalary and *Frullania*-type terminal branching are retained. In some cases, one or another branch type is lost, as in, i.a., *Chiloscyphus* s. lat. and *Plagiochila*. In some advanced taxa only ventral-intercalary branching is retained (as, e.g., in *Campanocolea*). The criterion is more useful in evaluating evolutionary progressions than in fashioning a “mechanical” taxonomy.

Problems. However fascinating the study of these parallelisms may be, the end result is a continuing taxonomic muddle. The parallelisms almost preclude the development of the “usual” mechanical key that traditional taxonomists rely on. We thus “live with” a situation where end taxa, in which all or most of criteria (a) through (f), above, are in the derivative state: these end taxa can be astoundingly similar. Thus it is virtually impossible to consistently separate taxa of *Chiloscyphus* from those of *Heteroscyphus*, when only sterile gametophytes are at hand.

Adding to the problems is another major one: many taxa (especially of *Chiloscyphus* et al.) show bewildering phenotypic responses to varying environments. Juveniles of *Plagiochila* often mimic each other as also in *Chiloscyphus*. As a consequence, any herbarium-derived taxonomy will never be wholly satisfactory.

Subfamily 1. **Lophocoleoideae** Rodway emend. R.M.Schust.¹¹

Plants green to brownish to (infrequently) fuscous, prostrate to erect, irregularly branched; branches terminal, *Frullania*-type and/or lateral-intercalary and/or ventral-intercalary; without *Acromastigum*- and *Microlepidozia*-type branching.¹² Stem lacking a hyalodermis, usually lacking a well-defined thick-walled cortex [a weak, 1-layered, brown cortex in *Platycaulis*], devoid of mycorrhizal infection. Anisophyllous [*Pachyglossa* isophyllous]; always with distinct underleaves. Leaves, alternate to subopposite, ± succubous, usually strongly so [transverse or subtransverse in *Pachyglossa*; transverse to feebly incubous in *Xenocephalozia*], bilobed or unlobed, 1-layered [except in *Pachyglossa*], not folded. Underleaves from large to very small; mostly bifid or bidentate, the lobes often toothed laterally, often connate at base with leaf bases. Rhizoids almost exclusively in fascicles from underleaf bases, the apices often lobed, occasionally (in *Platycaulis*) copiously dendritic. Cells medium-large; mostly 20–36 µm occasionally larger, thin-walled, with minute to large, occasionally coarsely nodose trigones; cuticle usually smooth¹³; oil-bodies (sometimes absent from scattered cells) usually 2–16 per cell and ± granular or granular-botryoidal, rarely numerous (20–40), minute and homogeneous (*Leptophyllopsis*). Asexual reproduction usually lacking, but with gemmae, irregular and several-celled (in *Chiloscyphus* spp.), caducous teeth/lobes of leaves (in *Leptophyllopsis*) or caducous leaves (*Paramocolea*¹⁴, *Anomylia*); never with catenate 1–2-celled gemmae.

Dioecious or autoecious [except for *Chiloscyphus* nearly uniformly dioecious]. Gametangia usually on unspecialized axes of diverse length (on abbreviated branches in some *Chiloscyphus* spp.; always on specialized intercalary leafless branches in *Heteroscyphus*). ♂ Bracts concave at least in a basal pocket; monandrous; antheridial stalk 2-seriate or (*Chiloscyphus* spp.) sometimes 1-seriate. Gynoecia tending to remain tristichous even when sterile regions have strongly reduced underleaves, but sometimes bracteoles reduced. Perianth distinct, basically trigonous but with narrowing of ventral face sometimes bilabiate; mouth basically trilobed (ventral member often narrowed), the mouth wide open. Marsupia never formed; a few taxa (*Clasmatocolea*) with an *Isotachis*-type perigynium. Seta usually massive [except in *Anomylia*]; capsule wall usually 4–5-layered (3-layered in *Anomylia*).

Type Genus. *Lophocolea* (Dumort.) Dumort. = *Chiloscyphus* subg. *Lophocolea*.

I have here broadened the concept of a group Lophocoleoideae to include the Leptoscyphoideae R.M.Schust. (Schuster 1980, p. 267). Basically, it has become almost customary to distinguish between (1) a plesiomorphic group in which anisophylly, no matter how advanced, is limited to vegetative areas, with ♀ bracts + bracteoles mostly similar or identical, and perianths basically with 3 equal/subequal faces (= Lophocoleoideae s. str.), and (2) a group in which, to varying degrees, gynoecia acquire the bilaterality or anisophylly of vegetative regions: bracteoles are shorter and/or smaller — mostly much smaller — than bracts; perianths become 2-lipped because the ventral, third face becomes progressively narrower (= Leptoscyphoideae). I have arrived at the conclusion that the transition from (1) to (2) had occurred several times.¹⁵

11 Jungermanniaceae subfam. Lophocoleoideae Rodway, Tasm. Bryoph. 2:22, 1916. Geocalyceae subfam. Lophocoleoideae R.M.Schust., Hep. Anth. N. Amer. 4:176, 1980.

12 But see *Clasmatocolea* (p. 146). Only *Amphilophocolea* has constantly ventral-intercalary branching.

13 Except in *Amphilophocolea* where minutely verruculose.

14 Editors' note: The genus *Paramocolea* is a *nomen nudum*. See also p. 14.

15 This has led to taxa assigned to *Leptoscyphus* by Grolle being transferred to *Chiloscyphus* (as by Hässel 2001b); cf. p. 119.

Thus *Lamellocolea* J.J.Engel (1991) is basically a *Chiloscyphus* — but with the perianth distally laterally compressed, the ventral face narrowed and mostly (but not always) considerably abbreviated. It is here treated as an outlier subgenus of *Chiloscyphus*. In *Leptoscyphus* subg. *Pseudoleptoscyphus* (p. 124), we also see linkage of an inflated perianth with the open mouth subequally trifid, with a ventral face shorter and little narrower (thus intermediate between a chiloscyphoid and leptoscyphoid perianth), weak and local brownish pigmentation, and clearly *Leptoscyphus*-like oil-bodies (Fig. 466B:6). This plant is clearly intermediate in significant ways and renders a distinction between Lophocoleoideae and Leptoscyphoideae difficult to carry through.

Similarly, *Evansthanthus* with a laterally compressed leptoscyphoid perianth, has much the aspect of a *Clasmatocolea* (Lophocoleoideae) and was placed by Grolle (1972b, p. 86) in that genus. In this genus bilaterality of vegetative regions is marked (underleaves are under 0.12 the area of lateral leaves) and gynoecia have bracteoles that are “underleaf-like, 0.15–0.2 [the] bract in area” (Schuster & Engel 1973, p. 519). Changes in symmetry in the Lophocoleoids thus appear to go from the extreme of *Chiloscyphus* subg. *Notholophocolea*, where radial symmetry is sometimes strongly expressed (Fig. 436:1, 8–9) to that seen in *Evansthanthus*, where underleaves and bracteoles are strikingly reduced in size.¹⁶ Hässel (1996) strongly stressed that in a central group of Lophocoleoids, including *Chiloscyphus s. lat.*, *Clasmatocolea*, and *Xenocephalozia*, cells tend to have 2–3 granular or finely granular oil-bodies. The actual situation is much more complex, as the following examples show.

(1) In *Chiloscyphus s. amplo* (*C. “mucronatus”*; RMS 59599) cells constantly bear one oil-body that appears biconcentric, with a firm outer “pellicle” that is exceedingly obscurely granular vs. the homogeneous interior. (2) In *C. aff. aculeatus*, (2)3–4(5–6) rather small clearly botryoidal oil-bodies occur (Fig. 435a). (3) In *C. (Lophocolea) trispinosus* (RMS 84-926a) some 5–10(12) rather large, ellipsoidal, smooth, very transparent oil-bodies occur; they are not at all granular or botryoidal. (4) In *Cyanolophocolea echinella* there is 1 large or 2–3 large to smaller oil-bodies in most cells; others lack oil-bodies. Oil-bodies here are deep blue, clearly, if finely, botryoidal and rough-surfaced. (5) In *Chiloscyphus (Microlophocolea) muricatus* 1 or 2 large, finely granular, ellipsoidal to paramecium-shaped oil-bodies occur in most cells; some lack oil-bodies. Oil-bodies are colorless and very finely granular (RMS 67-1609a; fig. 12; also RMS 84-541; Lake Gault, N.Z.). (6) *Chiloscyphus (Lophocolea) “opacifolius”* (RMS 55549d; Milford Sd., N.Z.) has (3)4–6(7) large oil-bodies to 11–12 × 20–21 μm, ellipsoidal to fusiform-ellipsoidal, very opaque and brownish, granular. (7) In the *Chiloscyphus (Lophocolea) aculeatus* “complex” oil-bodies go from 2–3(4) to 2–4(5) per cell (RMS 50321a; Tasmania) to (1–2)3–4(5–7) per cell (RMS 48297, N.Z.) to (2–4)5–8(9–10) per cell (RMS 48482; N.Z.) to with 3–4 or 5–8 or even 8–10 oil-bodies per cell (RMS 48927; N.Z.). The variation in size, number and internal “structure” of the oil-bodies is documented at length in the accompanying figures and annotations. They clearly demonstrate that a similar 2–3 oil-body number in *Clasmatocolea*, some taxa of *Chiloscyphus*, and in *Xenocephalozia* has no taxonomic meaning.

Perhaps meaningful, taxonomically, is the coarsely botryoidal nature of oil-bodies in nearly all investigated taxa of *Leptoscyphus* (Fig. 466B:6); in *L. australis* they occur mostly 5–6 per cell and are rather large (6 × 8 to 6–7 × 16 to 7–8 × 15 μm). By contrast, in the allied genus *Anomylia* there are 2–3, occasionally 4–5 small (4.5–6 to 4 × 5–6.5 up to 6 × 9 μm) oil-bodies formed of small, slightly protuberant spherules (Fig. 478:12).

The relationship of Lophocoleoideae *s. amplo* to Geocalycoideae is unresolved; only the existence of the stenotypic Laurasian genus *Harpanthus* Nees has restrained me from separating the two as distinct families. In *Harpanthus*, as in *Clasmatocolea* spp., developing sporophytes are largely immersed in a “perigynium” that is stem-derived. *Harpanthus* has an *Isotachis*-type perigynium combined with an incipient marsupium (figs. 537:6–8; 538:2; 540:9; 541:1–6 in Schuster 1980); in this the distalmost gyre of bracts + bracteole (fig. 536:2–3, l.c.) often exhibits clear anisophylly; and in sterile sectors underleaves are connate on one side with ventral leaf bases (fig. 537:2, 12). Although the ontogeny of the “perigynium” in *Harpanthus* and *Clasmatocolea* is rather different, other criteria are similar to what one can find in both genera.

The taxonomy of the Lophocoleoideae is — and will long remain — bedeviled by two interrelated facts: (1) Most taxa are highly plastic and either show striking responses to different sites; and/or (2) generic/subgeneric boundaries are ill-defined so that the same species may be assigned to 2 or even 3 genera — sometimes by the same author. Out of countless examples the following make my point: (1) *Hepatostolonophora* is treated here as formed of two species; Engel treats them as varieties of one species. Grolle (1960) placed one, *H. abnormis*, into *Clasmatocolea* and (1972b) placed the other (*H. perssonii*) also into *Clasmatocolea*. (2) Grolle (1960a) and Engel (1991) placed *Lophocolea fiordlandiae* E.A.Hodgs. into, respectively, *Clasmatocolea* and *Stolonivector*. (3) I (Schuster 1965) placed *Lophocolea navicularis*

¹⁶ The persistence of bilaterality from vegetative areas into gynoecial ones occurs within *Chiloscyphus* as well. In subg. *Notoscyphus* (*C. brunneorhizus*; RMS 84-1683a; N.Z.) the large, bilobed ♀ bracts are accompanied by a small bracteole, underleaf-like in size and form.

Steph. into *Xenocephalozia*; Grolle (1966a) into *Clasmatocolea* [this plant had also been described as *Microlejeunea chilensis* Steph., *Cephalozia tristosa* Steph. and *Drepanolejeunea stephaniana* C.Massal.]. (4) Engel (1973, 1990) placed *Lophocolea irregularis* Steph. into *Leptophyllopsis* R.M.Schust., a genus based on *L. laxa* (Mitt.) R.M.Schust. ex Hamlin. Fulford (1976) placed in synonymy of *L. irregularis* the *Lophocolea subaromatica* of Herzog, whereas Engel (1980, p. 49) placed it as a synonym of *Clasmatocolea rigens*. As noted on p. 193, this species bears (*teste* Hässel 1995b) pluricellular gemmae, much as in *Chiloscyphus minor*. It cannot, if Hässel's interpretation is correct, be referred to either *Clasmatocolea* or *Leptophyllopsis*. (5) As noted under *Leptoscyphus*, Grolle placed *Jungermannia horizontalis* Hook. (Musci Exot., pl. 96, 1818) into *Leptoscyphus*, as *L. horizontalis* (Hook.) Kühnem., Hässel (1999, 2001) assigned it to *Chiloscyphus*, where Dumortier (1835, p. 19) had earlier placed it — but into a subgenus *Eurychiloscyphus*. (6) The monotypic *Xenocephalozia* (*X. navicularis*) has been described as a *Cephalozia*; as a *Clasmatocolea*; as a *Drepanolejeunea* and a *Microlejeunea* and as subg. *Schusterella* of *Clasmatocolea*; it was originally described as a *Lophocolea* (cf. p. 164) — thus has been assigned to six supposedly distinct genera. (7) Grolle (1960) placed a sterile plant into *Clasmatocolea* as *C. tjivideiensis*, now assigned to *Austrosyphus* (Balantiopsidaceae); Engel (1980, p. 135) regarded the same species as “related” to *Clasmatocolea stronglylophylla*. Indeed, plants belonging to *Stolonivector*, *Leptoscyphus*, *Hepatosolonophora*, *Cylindrococlea* (Cephaloziellaceae), *Pedinophyllum* (Plagiochilaceae) and even *Miriocoleopsis* (Lejeuneaceae) have been described as taxa of *Clasmatocolea*;¹⁷ more examples would be redundant.

The systematics of the Lophocoleoideae thus remain controversial. I have limited myself to trying to clarify the generic boundaries and have segregated a number of new genera from the “main” genera, *Chiloscyphus s. lat.*, *Clasmatocolea s. lat.*, and *Leptoscyphus s. lat.*: (1) *Amphilophocolea*, *Campanocolea*, *Leptophyllopsis*, *Pseudolophocolea*, *Hepatosolonophora*, *Xenocephalozia*, *Evansianthus* from the *Chiloscyphus-Clasmatocolea* complex; (2) *Anomylia*, *Platycaulis*, and *Pedinophyllopsis* from the *Leptoscyphus* complex. The segregate genera, in general, are mono- or stenotypic “outliers” whose segregation has allowed us to draw sharper perimeters about the “classical” genera. In addition, Engel has segregated *Stolonivector*. Thus some 15–16 genera are currently accepted. However, one must note that two current workers in the group (Engel, Hässel) quite disagree as to generic — and often species — boundaries (cf. Annotation 2, under *Leptophyllopsis*, p. 193).

These disagreements foot largely on two facts: (1) Most Lophocoleoids show a very wide range of phenotypic responses to varying environmental conditions. Hence, based solely on study of the often inadequate types, non-reconcilable differences in interpretation may arise. (2) Inadequate attention has been directed to fundamental criteria: branching differences; development of a coelocaulis-precursor vs. its absence; insertion of leaves, to, or not to stem midline; and form, number and size of the oil-bodies. Figs. 435, 435A show a wide range of cells, with form, size and number of the oil-bodies carefully noted (sometimes in the figure legends). They show, indubitably, that cytological characters must be given much more weight in future taxonomic studies (cf. p. 25, above). No group of hepatics is less likely to be understood if only or chiefly herbarium material is relied on.

Most Lophocoleoideae are mesophytes (a few are hygro- or even hydrophytes); they occur mostly on the ground, on both mineral and peaty soils. However, some taxa undergo ecesis on decaying logs, or on peat, and a few (e.g., *Chiloscyphus* Corda) regularly invade tree trunks. Although most occur in sheltered sites (and a few, e.g. *Cyanolophocolea*, occur only in very deeply shaded, constantly humid or damp loci), a few taxa occur in well-illuminated loci in the mountains (e.g., *Pachyglossa*). A few taxa of *Clasmatocolea* may be found on bark or (*C. cucullistipulus*) even, in hyperhumid areas, may invade branches and twigs, often those of *Pernettya* or *Berberis*, or even branches of *Nothofagus*, *Fitzroya* or *Saxegothaea*.

The Lophocoleoideae, as here broadly defined, include very largely dioecious taxa (a few of *Chiloscyphus* and *Heteroscyphus* are autoecious; 1–2 of *Chiloscyphus* subg. *Lophocolea* are actually paroecious; cf. Schuster 1980) and asexual reproduction is rarely present. If it occurs, it is scattered and diverse; mostly via caducous leaves (*Anomylia*, *Paramocolea*; both monotypic) or caducous teeth of leaves (*Leptophyllopsis*; apparently monotypic), or in a few taxa of *Chiloscyphus* subg. *Lophocolea* via gemmae. These are never catenate, are usually irregularly several-celled, and

17 The taxonomic muddle surrounding *Clasmatocolea inflexispina* (= ? *C. amplexans*) and its position in *Clasmatocolea* vs. *Chiloscyphus* epitomizes the problem surrounding any attempt at sharply defining genera in the *Chiloscyphus-Lophocolea-Clasmatocolea-Heteroscyphus* complex; cf. p. 151, under *Clasmatocolea*. Equally, the perimeters of *Clasmatocolea heterostipa* vs. *C. vermicularis* (and the attribution of various synonyms) remain controversial (p. 157). There is an additional problem with the separation of *Heteroscyphus* and *Clasmatocolea*. Taxa like *H. rotundifolius* (Fig. 459; p. 111) have large, reniform underleaves connate on both sides with lateral leaves. *Clasmatocolea* subg. *Squamicalyx*: J.J.Engel approaches *H. rotundifolius* also in the conspicuous to coarse trigones. With sterile plants (as, e.g., of *H. rotundifolius*) one can remain in doubt as to how to separate *Clasmatocolea* and *Heteroscyphus*.

physiologically seem “descendants” of ordinary regenerants. The lack of catenate, 1–2-celled gemmae (such as occur in *Harpanthus* and *Geocalyx*) isolate the Lophocoloideae from the Geocalycoideae.

Taxonomic Sequence: In the following taxonomic treatment I have placed first a series of genera (from *Chiloscyphus* through *Leptoscyphus* and *Anomylia* et al.) in which we find, basically, large and bifid underleaves (and gynoeical bracteoles) which lack conspicuous slime papillae. *Evansianthus*, with conspicuous but unlobed underleaves, represents a second category. Last are treated genera such as *Pseudolophocollea* and *Pedinophyllopsis* in which we have reduced underleaves and bracteoles, typically formed from several slender laciniae and/or cilia, whose filiform segments are largely uniseriate and end in slime papillae. Underleaves of this type are characteristic of many, if not most species of *Plagiochila*. It is the existence of this last group of genera which form a distinct bridge from Geocalyceae to Plagiochilaceae. In this last complex there is a marked tendency for rhizoids to become dispersed (as in *Pedinophyllopsis* — and in *Pseudolophocollea fuegiensis*; cf. p. 188).

Synopsis of Genera¹⁸

1. Plants light to whitish to yellowish green, usually lacking wall pigments when living [if ± brownish, with caducous leaves]. Gynoeica (few exceptions) with bracteole large, from 0.2–0.95 × area of bracts; perianth basically trigonous [in a few cases with ventral lobe shorter and/or narrower; then perianth bilabiate and laterally compressed]. Oil-bodies always feebly to clearly granular [or, in *Leptophyllopsis*, minute, homogeneous] 2.
2. Plants, often fertile, lacking asexual reproduction or (*Chiloscyphus* spp.) with marginal, 1–several-celled, “clumplike” irregular gemmae 3.
3. Leaves unistratose [except in *Evansianthus*, medially/basally] 4.
4. Plants lacking a clear distinction between leafy and microphyllous plagio- and/or geotropic axes 5.
5. Gynoeica with bracts + bracteoles [where distinct] free, not forming a tube. Rhizoids at underleaf bases 6.
6. Gynoeica isophyllous or virtually so; bracteoles large; perianth open at mouth, trilobed 7.
7. Leaves clearly succubous, inserted on an oblique line, the dorsal ends often juxtaposed and/or connate. Cells unarmed, or with papillae that overlie the cell lumina 8.
8. Gametangial branches usually unspecialized; at least some ♀ branches usually ± elongated, usually leafy;¹⁹ androecia not forming slender, determinate, leafless branches. Cells usually thin- or firm-walled, or (*Clasmatocollea* spp.) with coarse trigones 9.
9. Leaves ± abaxially concave; dorsal and often ventral margins, at least, decurved. Leaf cells usually large (25–40 μm on average), thin-walled, with trigones none or small 10.
10. Branching malleable: a few to many branches terminal, *Frullania*-type. Leaf cells usually thin-walled, smooth. Leaves opposite or alternate, inserted to stem midline antically *Chiloscyphus* Corda (p. 23)
10. Branches consistently ventral-intercalary, axillary in underleaves. Leaf cells firm-walled, lacking trigones, finely granulate-verruculose. Leaves

¹⁸ Several genera are still known only from sterile gametophytes. Hence asexual reproductive modalities are arbitrarily used as a primary criterion, a second key (p. 30) utilizes reproductive criteria.

¹⁹ *Cyanolophocollea* R.M.Schust. (p. 90) fails to clearly fit into either the first half, or the second half, of couplet 8. It has gynoeica almost all rare exceptions] on short ventral-intercalary branches; androecia are terminal (eventually intercalary) on leafy axes of diverse length. It differs from all genera keying to couplet 8 in: (a) the leaf surfaces armed with sharp, cellular processes; (b) the wide strip of antical stem surface that is leaf-free; and (c) the deep blue oil-bodies.