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A memoir on the family Blepharostomataceae, I[1]

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A *Summary*, together with a bibliographical index, will follow in the final instalment of this paper.

1. Introduction

The family *Blepharostomataceae* K. Müll. emend. Schust. is here defined to include nine relatively primitive genera with ca. 26 species, having the following basic ensemble of characters: (1) a distinct, well-developed and unistratose perianth, 3-4-5 plicate above; (2) no coelocaule per se, although a coelocaule precursor may be present; (3) development of a shoot-calyptra; (4) irregular, sparing and largely unrestricted branching, usually of both the terminal and intercalary types and rarely restricted to any specific row or rows of merophytes; (5) isophylly or only moderate anisophylly, with both leaves and underleaves basically deeply quadrifid, bifid only in *Isophyllaria*; (6) androecia with flat bracteoles, lacking antheridia; (7) stolons

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or flagella very rarely or never produced; (8) stem without a well-defined cortex, the relatively soft, subhyaline cortical cells being distinctly rectangulate, thin-walled or usually only moderately thick-walled; (9) rhizoids at or near underleaf bases; (10) spores small, 1-2 times the 1-2 spiral elaters in diameter.

A series of other criteria usually holds, but individual genera show exceptions: gynoecia terminal on main stems; androecia becoming intercalary on ordinary stems or branches; cells non-collenchymatous, in the disk (and usually in the lobes) largely rectangulate and often conspicuously elongated; cuticle distinctly but not coarsely papillose to verrucose.

The family, as thus defined, includes the following genera: *Temnoma* Mitt., *Trichotemnoma* Schust., *Blepharostoma* Dumort., *Lophochaete* Schust., *Archeochaete* Schust., *Archeophylla* Schust., *Herzogiaria* Fulf., *Isophyllaria* Hodgs. et Allis. and, in all probability, *Chaetocolea* Spruce. As I have circumscribed the *Blepharostomataceae*, the families *Herzogiariaceae* Fulf. (Fulford 1960), *Pseudolepicoleaceae* Fulf. et Tayl. (Fulford and Taylor 1960) and *Chaetocoleaceae* Fulf. (Fulford 1963) are considered synonyms of the *Blepharostomataceae*. My reasons for such a relatively broad definition of this family, which almost exactly corresponds to the family as originally circumscribed (Schuster 1957), have already been given in part (Schuster 1961, 1963 1963a); the accumulation of additional evidence necessitates some repetition in the present memoir, in order that the naturalness of the family *Blepharostomataceae*, as here defined, can be adequately documented. However defined, the family *Blepharostomataceae* has been accepted by MÜLLER (1951-58), SCHUSTER (1953, 1958, 1959), ARNELL (1956, 1963), FULFORD (1963), INOUE (1963), GROLLE (1964) and others.

The present paper is intended as a summary of a series of previous studies in this family, which involved almost one-half of the taxa here assigned to the *Blepharostomataceae*. Previous papers have dealt with some taxa of *Temnoma* (Schuster 1959, 1963), of *Lophochaete* (Schuster 1957, 1958, 1961, 1963, 1963a), *Archeochaete* and *Archeophylla* (Schuster 1963a, 1965) and *Trichotemnoma* (Schuster 1964). These papers were, in general, attempts at defining and orienting the genera and, where recognized, subgenera. The present memoir is intended to carry the study to the species level.

The family *Blepharostomataceae*, a segregate from the old family *Ptilidiaceae*, is of particular interest in that, although in some respects very primitive, it shows the beginnings of evolution of certain interesting, advanced traits. Among these are: (1) restriction of the sexual organs (or, at least, the antheridia) to short, intercalary, ventral branches: *Trichotemnoma*; (2) evolution of purely lateral, terminal, Frullania-type branching: *Temnoma pulchellum* and *Lophochaete fryei*; (3) evolution of gemmae: *Blepharostoma trichophyllum*; (4) reduction of the seta to a finite series of cell rows: *Blepharostoma*; (5) reduction of the underleaves, with evolution of conspicuous anisophylly: *Archeochaete*; (6) occasional development of a few scattered rhizoids, away from the underleaf bases: *Blepharostoma*; (7) development of purely bifid appendages: *Isophyllaria*. These deviations, even though complicating the derivation of a diagnosis for the family and its orientation in a key or conspectus, are nonetheless a majoritem of interest, since they point to evolutionary pathways exploited more fully in other phylogenetic lines. In spite of these slight attempts at progressive evolution, the family must be considered a very primitive one.

HISTORY:

To understand the circumscription of the *Blepharostomataceae*, we must examine the group in its historical context. The taxa here placed into this family were initially partly placed in the single genus *Blepharostoma* Dumort., while certain species were erroneously assigned to *Lepicolea* Dumort. of the *Lepicoleaceae* Schust. Of the approximately 17-18 species which have been assigned to *Blepharostoma* in this century (by Stephani 1909; Gola 1922; Herzog 1935, 1939; Fulford 1951), only three, *B. trichophyllum*, *B. minus* and *B. arachnoideum*, actually belong there. The other taxa belong to the following genera and families: *Lophochaete*, *Trichotemnoma* and *Archeochaete (Blepharostomataceae); Chandonanthus (Lophoziaceae); Telaranea (Lepidoziaceae); Chaetophyllopsis* and *Herzogianthus (Chaetophyllopsidaceae); Vetaforma (Vetaformaceae)*. Thus the species referred until recently to *Blepharostoma* (specifically until the papers of Schuster, 1957, 1959, 1961a), belong in a minimum of eight genera and five families!

It is thus evident that, until recently, there had been a high level of confusion as to family and generic limits in this complex. Part of the basis for this confusion lies in the fact that the *Blepharostomataceae* were placed in a group *Ptilidioideae* (Spruce 1885; Müller 1905-16; Macvicar 1926; Schiffner 1893-95) or *Ptilidiaceae* (Evans 1939; Buch, Evans and Verdoorn 1938; Verdoorn 1932). This group, in my opinion, is a developmental level rather than a monophyletic taxon; hence it is artificial and should be abandoned. Initial but unsatisfactory attempts at subdivision of the *Ptilidiaceae* s. l. into smaller, more monophyletic units were made by MÜLLER 1948, 1951-58) and NAKAI (1943). The treatments of both of these workers suffer from a bias induced by their study of only the limited flora known from the cooler portions of the Northern Hemisphere. Thus the disposition of genera and the diagnoses and delimitations of families in MÜLLER (1951-58) are in several instances arbitrary and untenable. The lack of any emphasis on branching modes in these treatments is notable.

Although, while concerned with only the few holarctic taxa, I followed MÜLLER (Schuster 1953), it soon became apparent that the form of the male and female reproductive system and modes of branching represented major criteria in any attempt at subdivision of the old *Ptilidiaceae*. When introducing these major criteria, I attempted to refine and redefine the families of *Ptilidiaceae* s. l. (Schuster 1957, 1959), founding two new families, the *Lepicoleaceae* and *Isotachaceae*. This treatment still suffers from a reluctance to place isolated genera into monotypic or stenotypic groups of their own—when the morphological facts so dictate. In essence, my paper (Schuster 1957) is too conservative. I soon found it necessary to restrict more narrowly both the *Trichocoleaceae* and *Ptilidiaceae*—families I had attempted to take over " bodily " from the treatment of MÜLLER (1951-58). The description of the new family *Chaetophyllopsidaceae* (Schuster 1961a), with two new genera, *Herzogianthus* and *Chaetophyllopsis*, simultaneously served to some extent to " purify " both the *Ptilidiaceae* and *Blepharostomataceae*. The description of the genus *Lophochaete* (Schuster 1957, 1958, 1961) for elements previously included erroneously partly in the *Lepicoleaceae*, partly in the *Blepharostomataceae*, served in turn to define more sharply these families.

Subsequent to this initial paper (Schuster 1957), in which the gynoecial system, leaf type and branching were given primary emphasis in family redefinition, these criteria have also been utilized by others. FULFORD and HATCHER (1958), FULFORD (1960) and FULFORD and TAYLOR (1960) described as new the following ptilidioid genera: *Triandrophyllum*, *Herzogiaria*, *Vetaforma* and *Pseudolepicolea*. The first of these four genera was correctly placed in the *Herbertaceae* (as defined by Müller 1951-58 and Schuster 1957). *Vetaforma* was placed into a new family, the *Vetaformaceae*, apparently correctly so. Although the initial data presented on sterile gametophytes (Fulford and Taylor 1960) left the status of the latter genus very much in question, more recent discovery of a coelocaule (Fulford 1962) suggests that the *Vetaformaceae* are a natural group. By contrast, *Herzogiaria*, for which a new family *Herzogiariaceae* was proposed, is, in my opinion, a bona-fide member of the *Blepharostomataceae* (as redefined by Schuster 1957, 1959, 1961). *Pseudolepicolea*, also placed in a new family, the *Pseudolepicoleaceae*, is, as I stated, a synonym of *Lophochaete* (Schuster 1963), a genus whose position in the *Blepharostomataceae* seems secure (Schuster 1957, 1961, 1963).

The recent history of the nearly isophyllous, primitive *Jungermanniales* is thus one of considerable change. There appear to be four distinct extant positions: (1) that epitomized by EVANS (1939), who would " lump " all of the discordant elements into one family; (2) that of MÜLLER (1951-58), who created several additional families but failed to circumscribe these naturally; (3) that of SCHUSTER (1957, as amplified in 1959, 1961, 1963, 1963a), who attempted to redefine the families accepted by MÜLLER, usually on a somewhat narrower basis, in part by segregation of additional families *(Isotachaceae, Lepicoleaceae, Chaetophyllopsidaceae)*; and (4) that of FULFORD (1960, 1963) and FULFORD and TAYLOR (1960), who described four additional families *(Pseudolepicoleaceae, Herzogiariaceae, Vetaformaceae, Chaetocoleaceae)* for other discordant elements.

Of these approaches, it seems to me, that of EVANS (1939) is unquestionably inutile today, as well as unnatural. At the opposite extreme, the attempts by FULFORD (1960, 1963) and FULFORD and TAYLOR (1960) to found new families purely on gametophytic criteria—in large part, on criteria of the sterile gametophyte only—are equally untenable. I am convinced that families must be based on characters other than those simply derived from sterile gametophytes. The extreme emphasis placed on branching as a family criterion has already been discussed (Schuster 1963). In essence, it may be stated that in primitive, erect-growing groups with little morphological differentiation between lateral and ventral merophytes, restriction of branching (and variations in branching modes) must be interpreted in a sophisticated, not in a mechanical manner. In primitive groups such criteria—and others—are not " fixed " to the extent we find in the more derivative families. The demonstration of radical differences in branching modes, i.a. within the *Isotachaceae* (to which HATCHER erroneously attempted to assign a most highly restricted and derivative branching pattern) and in *Lophochaete* (see Schuster 1963, 1963a), as well as in *Temnoma* (see the following pages), adequately attests, in my opinion, to the fallacy of placing too high a value on such criteria, if unsupported by other major characters.

Since the preceding account was prepared, the initial section of FULFORD'S " Manual of the Leafy Hepaticae of Latin America " has appeared (1963). In this

Temnoma is referred to the *Trichocoleaceae*, on apparently inadequate bases; this problem will be subsequently discussed. Also, a new family is founded for *Chaetocolea*, for the singular reason that " since the detail of the structures (shoot-sporophyte relationship and surrounding structures) is not known [sic !], this taxon has been set apart as a separate family ". If we accept the broad definition of the *Trichocoleaceae* in FULFORD to include plants such as *Temnoma*, with predominantly terminal branching and succubous quadrifid leaves, *Chaetocolea* could go into that group, as thus constituted. I prefer, in the absence of conclusive data, to leave it as a genus of *Blepharostomataceae*.

DELIMITATION:

As I have pointed out (Schuster 1959), the family *Blepharostomataceae* of MÜLLER was initially (Müller 1948, 1948a, 1951-58) described chiefly with *Blepharostoma trichophyllum* and its immediate allies in mind. The diagnosis in MÜLLER (1951-58) is clearly inadequate, and for that reason I gave new and emended diagnoses of the group (Schuster 1959, 1961). A sharply defined diagnosis of the family is also present in the conspectus of ptilidiine families and genera (Schuster 1957).

Subsequently, FULFORD (1960) and FULFORD and TAYLOR (1960) proposed as new the families *Herzogiariaceae* (for *Herzogiaria*) and *Pseudolepicoleaceae* (for *Pseudolepicolea*). The first of these represents a valid genus, allied to *Lophochaete*, and hence is to be placed in the *Blepharostomataceae*. *Pseudolepicolea* is a synonym of *Lophochaete*, thus also belongs in the *Blepharostomataceae*. The reasons for such a conservative treatment emerge from study of *Temnoma* and the stenotypic genera *Archeophylla*, *Isophyllaria* and *Archeochaete*. In *Temnoma* we find a fantastic array of branching modes, and also variation from taxa with simply quadrifid leaves (subgen. *Temnoma*) to those with bisbifid leaves (subgen. *Eotemnoma*). In *Archeophylla* we find pronounced specializations involving elaters, a large-celled cortex and development of coarse trigones. In *Archeochaete*, on the other hand, occur thoroughly synthetic features—involving characters found in, respectively, *Blepharostoma*, *Archeophylla*, *Temnoma* and *Lophochaete*. *Isophyllaria*, in turn, has the pigmentation, branching and cell type of *Herzogiaria*, the facies of *Lophochaete*—but has only half as many leaf lobes as these genera. In essence, my researches over the last decade have clearly shown that many more types exist in the *Blepharostomataceae* than previously recognized. With only " *Pseudolepicolea* " and *Blepharostoma* in view, treatment of these as distinct families might have a certain spurious validity. However, it must be recalled that FULFORD and TAYLOR paid no attention to the characters of the antheridium or to those of the sporophyte. Thus their treatment was necessarily artificial, insofar as their conclusions were based on study of only a small part of the evidence. The detailed treatment of the various taxa in this memoir, particularly the treatment of the sporophyte generation, shows that a variety of evolutionary pathways exists, not treated by FULFORD and TAYLOR. If the *Pseudolepicoleaceae* and *Herzogiariaceae* were to be admitted as distinct families, then new families would also have to be established for *Temnoma* s. str., for *Archeophylla*—and perhaps even for *Isophyllaria* !

Subsequent to the preparation of this account, FULFORD (1963) placed *Temnoma* into the *Trichocoleaceae*, although—in obvious contradiction—restricting this

family to plants with branching only of the terminal type (Frullania-type). This treatment leans directly on the demonstration (Schuster 1959) that the capsule-wall anatomy as well as the spore-elater diameter ratio of *Temnoma* was " exceedingly similar to that of *Trichocolea* ". The suggestion has already been made that, in spite of obvious differences, " one is therefore strongly tempted to suggest a close affinity between the two genera " and that " the persistent idea intrudes itself that perhaps the derivative *Trichocoleaceae* may have evolved from Temnoma-like ancestral forms. Surely the almost unique capsule-wall anatomy must be regarded as very suggestive ". (Schuster 1959). Other similarities were cited (Schuster 1959 : 239). With the demonstration that *Temnoma* possesses a wide diversity of branching types, any close affinity to *Trichocoleaceae* becomes doubtful, although my original suggestion of evolution of the *Trichocoleaceae* from temnomoid types remains an attractive possibility. Branching types, the well-developed perianth of *Temnoma* and other criteria all suggest that *Temnoma* is more closely allied to the *Blepharostomataceae*, although forming (as I noted in 1959) an isolated element in that family. Thus the delimitation by FULFORD of a family *Trichocoleaceae* to include the *Temnoma* complex seems untenable. The arbitrary nature of such a delimitation is abundantly clear from the study of *Archeochaete*, which has the quadrifid (but not bisbifid) leaves and underleaves of *Temnoma* and *Blepharostoma*, the trigonous perianth of these genera, the polymorphic branching, and somewhat the facies, of *Archeophylla* and *Lophochaete (Pseudolepicolea)*. Thus *Archeochaete* possesses traits which FULFORD would use to " distribute " the aforementioned generic elements—here all retained in the *Blepharostomataceae*—in three families (*Trichocoleaceae*, *Blepharostomataceae* and *Pseudolepicoleaceae*).

RELATIONSHIPS:

Immediate affinities of the *Blepharostomataceae* appear to be with two other families in which branching patterns also remain plastic: the *Herbertaceae* and *Vetaformaceae*. Both of these families differ from the *Blepharostomataceae* in that the leaf insertion is distincly incubous and the androecia retain antheridia in the bracteoles. In other respects, seeming or real transitions occur. For example, *Isophyllaria* has the bifid leaves, underleaves and bracts typical of many of the *Herbertaceae*, yet leaf insertion (and the slight antical displacement of the leaves), stem anatomy and cell type are blepharostomatoid. Similarly, in *Temnoma palmatum* and several other *Blepharostomataceae* a coelocaule precursor is well developed, associated with which the perianth has undergone considerable reduction. In this respect—and in the very plastic branching of such taxa—an approach exists to the *Vetaformaceae*. It is possible that future discoveries of yet unknown types will necessitate amalgamation of these families. Currently, however, they remain adequately separated, obvious bridges between them not existing.

The *Blepharostomataceae*, through *Temnoma*, may show some affinity to *Trichocolea* and the *Trichocoleaceae*, as suggested earlier (Schuster 1959). However, the development of rather regular, usually pinnate branching, purely of the Frullania-type, in the entire trichocoleoid developmental sequence, represents a major deviation from the blepharostomatoid pattern. Also, the drastic reduction or loss of the perianth and calyptra likewise suggests that the *Trichocoleaceae* have initiated a major departure

from the blepharostomatoid organization. Hence, I believe that a sharp break between these families exists, and that the obvious similarities in leaf form, insertion and cell types are partly homoplastic.

2. Conspectus of genera and subfamilies of Blepharostomataceae

1. Leaves and underleaves divided to base into 2-4 uniseriate segments; no lamina retained; rhizoids (sometimes) in part scattered; with gemmae from leaf-lobe apices; ♀ bracts with lobes irregularly branched and ciliate. Seta with 8 epidermal, 4 inner cell rows; capsule wall 2-layered, epidermal layer with strong, nodular thickenings (chiefly of both faces of alternating longitudinal walls) . . . . . subfam. *Blepharostomatoideae*
Blepharostoma Dumort.

1*. Leaves and underleaves not divided to base: a distinct lamina 2 or more cells high retained; without asexual reproduction (except by fragmentation of leaves); ♀ bracts 2- or 3-4(5)-lobed, the lobes themselves never ramified. (Seta, where known, massive, with many cell rows; capsule wall, where known, 2-5-stratose) 2

2. Perianth urn-shaped, wide at mouth, the external surface and the mouth with finger-like cilia or outgrowths; leaves quite succubous, palmately 2-3-4-lobed, without cilia, the lobes entire, but freely fragmenting; gynoecia on main axes; plants brownish but delicate, with collenchymatous cells. (With intercalary and terminal branching of the Frullania- and Microlepidozia-type)
subfam. *Chaetocoleoideae*
Chaetocolea Spruce

2*. Perianth with external surface smooth, lacking outgrowths; leaves (except in *Archeophylla*) predominantly or exclusively 4-lobed or all 2-lobed, persistent, non-fragmenting 3

3. Androecia (and presumably gynoecia) on highly reduced, short, determinate ventral branches; leaves strongly asymmetrically 4-lobed, the lobes (on mature leaves at least) again developing small, secondary lobes, copiously ciliate with opposed stiff, often arched cilia; plants light to yellow-green, spongy and very soft, even in sun forms. (Cells with distinct but not coarsely bulging trigones; cuticle roughened) . . . . subfam. *Trichotemnomoideae*
Trichotemnoma Schust.

3*. Androecia (and gynoecia) on leading or ± long, normally leafy branches (androecia becoming intercalary); leaves 2- or 3-4-lobed, the lobes sometimes toothed or ciliate, but not developing accessory lobes; leaves usually symmetric or feebly asymmetrical; plants, in exposed sites at least, developing a brown color, rigid to reasonably firm in texture subfam. *Temnomoideae* 4

4. Cells with walls thin to ± thick, with conspicuous to coarse, often nodular trigones; elaters with one very wide spiral; leaves (2)3-4-lobed, irregular, when 4-lobed not bisbifid; stem with cortical cells relatively few, larger than medullary on an average; medullary cells collenchymatous; ♀ bracts

spinose-dentate or spinose-ciliate, with alternate teeth; capsule wall 4-stratose, the cortical cells with few but strong nodular thickenings, the innermost layer with weak nodular thickenings; branches largely postical-intercalary, rarely terminal, Frullania- and Microlepidozia-type; leaf never with cilia (but bract bases toothed) . . . . . *Archeophylla* Schust.

4*. Cells of leaves non-collenchymatous or with small trigones; elaters 2-spiral (where known), the spirals narrow; leaves normally consistently 2- or 4-lobed (3-lobed leaves usually sporadic and rare); cortical cells smaller or ± equal to medullary in diameter, non-collenchymatous; bracts, if toothed, with opposed teeth 5

5. Leaves, underleaves, bracts and bracteole consistently bifid, cuneiform in shape, subvittate (the small, quadrate marginal cells contrasted to the elongated cells of disk middle and middle of lobes); leaves and underleaves unistratose; bracts and bracteoles, leaves and underleaves edentate; perianth longly trigonous, rather sharply so, little or hardly contracted to mouth. *Isophyllaria* Hodgs. et Allis.

5*. Leaves, underleaves, bracts and bracteole normally nearly consistently 4-lobed (on weak axes here and there isolated leaves trifid) 6

6. Lobes of mature leaves armed with opposed teeth or cilia (at least in and near gynoecia); capsule wall 3-5-stratose, with epidermal cells hyaline and lacking thickenings (exc. along dehiscence lines, and sometimes along midline of valve); cuticle clearly papillose to striolate; leaves normally not bisbifid, the sinuses subequal; perianth trigonous, normally very wide at the open mouth, which is ± ciliate. No differentiated, small-celled cortex *Temnoma* Mitt.

6*. Lobes of leaves never ciliate or dentate (the bracts usually without teeth on the lobes); capsule wall (where known) 2-stratose, the epidermal cells with thickenings. (Perianth contracted to the narrow mouth, the mouth denticulate-lobulate to short-ciliolate). 7

7. Branches all intercalary, lateral and postical; leaves and underleaves identical in size and shape, both deeply bisbifid, the rigid, horny, sectaceous, narrow lobes and the disk polystratose; leaves otherwise not toothed or ciliate; cells non-collenchymatous, very thick-walled . . . . *Herzogiaria* Fulf.

7*. Branches at least in part terminal, lateral, of the Frullania-type; leaves relatively short, translucent, not polystratose 8

8. Leaves and underleaves subequal in size and form, clearly bisbifid (rarely with accessory lobes); the median sinus always much deeper; without subfloral innovations (at least if fertile); perianth 4-5-6-plicate distally; stem with a more or less discernible 1-stratose cortex of smaller cells *Lophochaete* Schust.

8*. Leaves and underleaves differing in size, underleaves at most 0.5 area of leaves, often 3-fid; leaves and underleaves when 4-fid with sinuses subequal,

the median only exceptionally slightly deeper, thus not bisbifid; 3-fid leaves occasional; infra-axillary postical subfloral innovations frequent; perianth bluntly 3-plicate distally; stem with cortex not at all differentiated, cortical cells not distinctly smaller than medullary . . . . *Archeochaete* Schust.

3. Artificial key to genera

1. Leaves and underleaves bifid or bisbifid, the lobes always entire and several cells broad (even of subfloral leaves and bracts); perfectly isophyllous 2

1*. Leaves of mature shoots equally quadrifid, or a few trifid (in *Temnoma quadrifidum* leaves weakly bisbifid; here bracts and subfloral leaves are toothed) 4

2. Leaves and underleaves bifid; bracts bifid; leaves unistratose *Isophyllaria* Hodgs. et Allis.

2*. Leaves and underleaves (except on juvenile shoot-sectors) normally bisbifid 3

3. Leaves unistratose, with flat, thin lobes; branching all or predominantly terminal, of the Frullania-type . . . . . *Lophochaete* Schust.

3*. Leaves polystratose, with rigid, horny segments; branching exclusively intercalary, axillary . . . . . *Herzogiaria* Fulf.

4. Leaves and underleaves (3)4-fid nearly to the very base, the segments completely uniseriate; often with gemmae . . *Blepharostoma* Dumort.

4*. Leaves and underleaves never divided to base: an obvious disk present; no gemmae 5

5. Cells of disk with elongated, thin- to equally thick-walled cells 6

5*. Cells of disk with well-developed trigones (usually coarse; sometimes, through the development of thickened walls, not very sharply defined, but nevertheless coarse) 7

6. Leaves and underleaves (usually of vegetative shoot-sectors; at least in and below gynoecia) with opposed, sharp teeth or cilia, usually of both disk margins and of lobes, rarely of one only; perichaetial bracts freely spinose-dentate to copiously ciliate; perianth at mouth ± wide open *Temnoma* Mitt.

6*. Leaves and underleaves quadrifid, without cilia or teeth (or, rarely, with an isolated tooth on one or both margins of the disk); perichaetial bracts quadrifid, without trace of teeth or cilia; perianth mouth closely contracted at apex . . . . . *Archeochaete* Schust.

7. Leaves and underleaves copiously ciliate with opposed, long cilia; plants when moist spongy, yellow-green; leaves asymmetrically 4(5)-fid; androecia on small ventral branches . . . . . *Trichotemnoma* Schust.

7*. Leaves and underleaves edentate; plants usually with brownish pigmentation; leaves symmetrical or almost so, 3- to 4-fid; sex organs usually on leading axes 8

8. Leaves (3)4-lobed to the middle, fragile, the lobes never setaceous; ♀ bracts ± ciliate on margins and on abaxial face; perianth short, urn-shaped, ciliate on external surface . . . . . *Chaetocolea* Spruce

8*. Leaves 3-4-lobed for 0.6-0.75 their length, the lobes acuminate, uniseriate for much of their length, setaceous, rigid; bracts without cilia, or with a few, irregular, non-opposed, setaceous ones; perianth long, contracted to mouth, smooth externally. . . . . *Archeophylla* Schust.

4. Systematic treatment [1]

SUBFAMILY TEMNOMOIDEAE

Subfam. **Temnomoideae** Schust., subfam. nova.

Androecea gynoeceaque in axibus foliatis longis nata; folia 2- vel 3-4-lobata, lobis integris ciliatisve, ad basin latitudinem duarum vel plurium cellularum habentibus, sine lobulis secundariis; formae apricae pigmentationem secundariam praebentes; cellulae tunicae antheridii isodiametricae, non in stratis ordinatae.

TYPUS. *Temnoma* Mitt.

Plants typically brownish to fuscous (in exposed sites), small to vigorous, isophyllous to moderately anisophyllous. *Leaves* typically (3)4-, more rarely 2-lobed, usually symmetrical, lobes arising from a distinct lamina 2 or more cells high; lobes simple (lacking well-developed accessory lobing), entire or dentate to ciliate marginally, at least 2 cells broad at base. *Cells* with walls becoming equally thickened or with distinct collenchyma. No *asexual reproduction* (or perhaps, rarely, with fragmenting leaf lobes serving as propagula). *Androecia* and *gynoecia* on leafy, more or less elongate or leading axes, the androecia becoming intercalary, proliferating distally; gynoecia often with a well developed coelocaule-precursor. *Bracts* 2- or 4-fid, the external surface lacking outgrowths. *Seta* massive, formed of many cell rows (12-15 or more rows forming the epidermal layer). *Capsule* wall, where known, 2-5-stratose.

The *Temnomoideae* include, besides *Temnoma*, the genera *Isophyllaria* Hodgs. et Allis., *Herzogiaria* Fulf., *Lophochaete* Schust., *Archeochaete* Schust. and *Archeophylla* Schust. The entire complex is characterized, primarily, by the combination of: (1) multicellular leaves, with a distinct lamina, from which the lobes arise; (2) sex organs on axes of normal vigor, rather than on reduced ventral-intercalary branches; (3) perianth unarmed on the abaxial face, well-developed, even if marked tendencies occur towards formation of a coelocaule-precursor that elevates the perianth well above the perichaetial bracts.

The subfamily is a complex and variable one, as is evident from the variations in branching. For example, the allied *Herzogiaria-Isophyllaria* complex bears,

[1] Collection numbers of the author are preceded by the initials *RMS*.

apparently, only intercalary branches; *Lophochaete fryei* bears only terminal, Frullania-type branches; *Temnoma*, in various species, bears Frullania-, Microlepidozia- and Acromastigum-type terminal branches and ventral-intercalary (rarely also lateral-intercalary) axillary branches. Yet the six genera I class here are sufficiently interconnected that no clear additional segregation appears possible. For example, even though the bisbifid leaves and underleaves of *Lophochaete* and *Herzogiaria* suggest these genera are closely allied, the closest affinities of *Herzogiaria* appear to be with *Isophyllaria*, which has consistently bifid leaves and underleaves. For these reasons, justified in fuller detail under the various genera, I assign to the single subfamily *Temnomoideae* genera which have been recently assigned by FULFORD (1963) to three families, the *Trichocoleaceae*, *Pseudolepicoleaceae* and *Herzogiariaceae*.

ISOPHYLLARIA

Isophyllaria Hodgs. et Allis., Trans. Roy. Soc. N. Z., Bot. 3: 68. 1965.

TYPUS. *Isophyllaria murrayana* Hodgs. et Allis.

A full discussion and description of this genus is given under its only known species.

Isophyllaria murrayana Hodgs. et Allis., Trans. Roy. Soc. N. Z., Bot. 3: 68. 1965.

Plants fuscous to almost black *, 500-1000 μ wide, at least 7-12 mm long, apparently suberect or erect in growth, probably aquatic *, sparingly branched; branches (all?) postical-intercalary; some branches microphyllous *, flagelliform *. *Stem* black, rather wiry, 100-120 (140) μ in diam., with ca. 18-20 (or more?) rows of cortical cells, which are deeply brownish-tinged and have thick walls (particularly externally, where they are feebly striolate), and are usually much larger * than the medullary cells, ca. (17)18-22(23) μ wide and (21)24-32 μ long; in surface view the cortical cells range from subquadrate to short-oblong to oblong-hexagonal, never twice as long as wide; medullary cells in ca. 5-6 tiers only, small * (ca. 10-14 μ in diam.), with thin, hyaline walls but (in cross-section) sharply defined, conspicuous, pigmented trigones. *Rhizoids* absent from most leafy axes, occasionally present in fascicles from underleaf bases. *Leaves* in three seemingly identical ranks—thus isophyllous *—transversely inserted or almost so, ranging to weakly succubous *, suberect to obliquely spreading, moderately imbricate, black or blackish-brown *, opaque *, but everywhere unistratose *, cuneiform *, narrow-based *, on lower sectors of fertile stem ca. 275-330 μ wide distally and 550-650 μ long, gradually larger upward and to 470-600 μ wide above and 950-1100 μ long on ♀ plants, alternate, bifid * for (0.5)0.55-0.7 their length; disk narrowly obtrapezoidal, cuneately narrowed * basally, almost straight-sided, entire-margined * to sinuous; lobes divergent *, but not strongly so, narrowly lanceolate to linear-lanceolate, gradually acuminate, their tips not strongly attenuated (terminated usually by 2-4 single cells that are essentially isodiametric), usually twisted *, distinctly canaliculate * on mature leaves—except terminally—from (7)9-12 cells wide at base; sinus V-shaped but with rounded * base, which is reflexed * and gibbose; leaf margins everywhere entire * to—locally—sinuous, distinctly, if narrowly and gently reflexed, the lobes usually canaliculate.

* Characters marked with an asterisk are all considered to be generic in nature.

Underleaves exactly like leaves, on sterile sectors ca. 400-460 μ wide and 600-650 μ long, progressively larger upward on fertile plants. *Cells* very thick-walled *, firm *, opaque, the walls light brown (except for the conspicuous *, deep-brown * middle lamella); marginal cells of lobes and almost all of disk diagnostically quadrate or subquadrate * and quite small (ca. 12-15 μ), in 1-2 rows, the interior cells gradually larger and more elongate, the leaf thus Herberta-like * and subvittate *, the narrow cells running well up into the lobes (along lobe midline ca. (12)13-15 × 24-36 μ in and above lobe middle); median cells of disk 14-18(20) × (22)24-34(36) μ; basal cells variable, (14)15-22(24) × (28)36-50(60) μ, at least locally narrowly rectangulate; cuticle, at least in lobes, perceptibly papillose-striolate, in disk roughened in a diagnostic but almost indescribable fashion—appearing almost as if with a thick, roughened cutin layer. No * *asexual reproduction* evident. Plants dioecious; *androecia* intercalary on main axes. *Bracts* in 2-6 pairs, subequal to leaves in size, contiguous to imbricate, to 0.65-0.7 bifid, the entire discal area strongly ventricose, the lanceolate, entire lobes erect, less acuminate than lobes of vegetative leaves; ♂ bracteoles often much smaller than bracts, ± flat and appressed, bifid 0.7 or more (♂ plants often quite strongly anisophyllous even in non-androecial regions); monandrous (always ?). *Bracts* (and subfloral leaves) imbricate, suberect, the subfloral leaves gradually larger upward and grading imperceptibly into the undifferentiated bracts and bracteole; bracts leaf-like in all respects but somewhat larger (to 1200-1250 μ long), cuneiform and narrow-based, with linear-lanceolate, tapering, twisted, canaliculate and entire-margined * lobes, bilobed * ca. 0.6-0.7 their length; disk also entire-margined *, obtrapezoidal. *Bracteole* identical to bracts. *Perianth* rather elongated; no conspicuous coelocaule precursor seen (even though sporophyte had been produced; old seta visible), the bracts and bracteole and adjoining leaves not becoming widely spaced; perianth sheathed in at least basal half by the bracts, ca. 1400-1500 μ long and 550 μ in diam., subterete below but trigonous * for at least 0.5-0.6 * its length, rather weakly and very gradually narrowed in distal 0.5-0.6 or more towards the rather wide open * mouth; apex truncate, not or shallowly lobulate; apical cells largely destroyed, with no evidence of elongated cilia. Otherwise unknown (a fuller description could hardly be prepared without destruction of the brittle and ill-preserved plants).

TYPE. Mt. Allen, Stewart Island, New Zealand — *J. Murray 2193 p.p.* (herb. E. A. Hodgson; fragments in herb. K. W. Allison and in herb. R. M. Schuster).

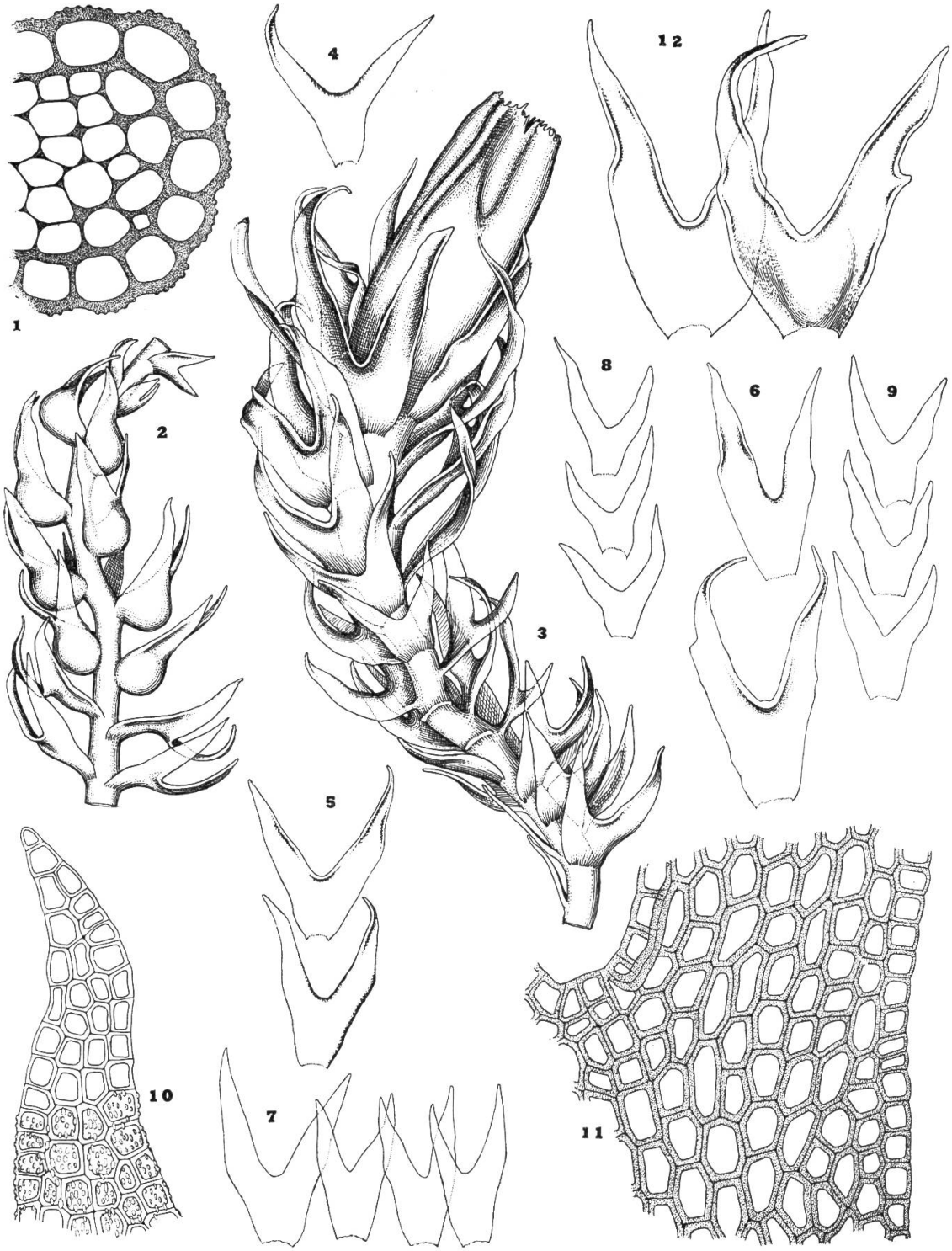
DISTRIBUTION. Known only from the type, and a specimen from New Zealand, Lord Auckland's Island — *J. D. Hooker* (S-PA).

* Characters marked with an asterisk are all considered to be generic in nature.

FIG. 1. *Isophyllaria murrayana*

1. Stem cross-section (×310) – 2. Shoot-sector, male plant (×30). – 3. Perianth-bearing shoot in lateral profile (×28). – 4-5. Medium-sized leaves (×30). – 6. Two large leaves (×30). – 7. Four leaves (×30). – 8-9. Underleaves (×30). – 10. Leaf lobe apex, cuticular papillae indicated in lower cells (ca. ×270). – 11. Base of leaf lobe and adjoining sinus (ca. ×270). – 12. Female bracts (×30).

All from *J. D. Hooker*, S-PA.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The last specimen consists of a dozen sterile and ♂ plants, and of a single plant with a mature perianth, unfortunately in poor condition, except for the gynoecial region (which is perfectly preserved). The plant is almost surely aquatic: it occurred admixed with *Pachyglossa tenacifolia* (Hook. f. et Tayl.) Herz. et Grolle, a species which I have seen growing in immense quantities on Stewart Island, New Zealand, always submerged or hardly emergent.

HOOKER's specimen is the same alluded to by HODGSON and ALLISON (1962 : 145) as follows: " In the Riksmuseum, Sweden, is one small stem labelled ' *Jung.* int. *Jung. tenacifolia*, Lord Auckland's Group ', without doubt collected by HOOKER, which Dr. ARNELL has identified as *B. quadripartitum (Temnoma quadripartitum)*." In checking additional material of the type of *Pachyglossa* I was able to find about a dozen additional stems of *Isophyllaria*.

I have had this plant in schedule, under another generic and species name, for the last three years, having clearly perceived that the HODGSON and ALLISON (1962) allocation of it to *Temnoma quadripartitum* was incorrect. The ambiguous, and in large part incorrect, diagnosis in HODGSON (1965) was inadequate to allow me to place her plant, but Mr. ALLISON kindly sent a fragment of the type, from Stewart Island. The preceding diagnosis is based exclusively on the HOOKER collection, and the Stewart Island material is identical. The HODGSON diagnosis states the cells in the type are " parvae, 10-20 μ ". This is quite incorrect; the diagnosis of the leaves as " incuba " is equally incorrect. The suggestion that it belongs in the *Herbertaceae* seems impossible to follow, since the ♂ plant has flat bracteoles lacking antheridia. My placement of the plant in the *Blepharostomataceae* near *Herzogiaria* remains, in my opinion, the only tenable one.

The genus is a relatively advanced one, with obvious affinities to the *Lophochaete-Archeochaete-Temnoma* complex; with this it agrees in the equally thick-walled, roughened, elongated cells, in the isophylly, the bracts and bracteole identical and the trigonous, long, terminal perianth only feebly narrowed to the mouth. Indeed, the perianth-bearing plant looks much like that of *Temnoma quadrifidum* or *Lophochaete quadrilaciniata*—with one major difference: the leaves, underleaves and bracts are consistently bifurcate, rather than quadrifid or bisbifid. In the consistently bifid leaves, underleaves, bracts and bracteole the genus stands sharply isolated in the *Blepharostomataceae*, and I am convinced the single species richly deserves segregation into a genus of its own.

I have seen only about 10 branches; these were all intercalary (eight definitely postical-intercalary, of which five were flagelliform and geotropic; two branches were possibly lateral-intercalary, but this could not be definitely determined owing to the state of preservation of the shoot-sectors). The branches are in several cases microphyllous from the start and are geotropic; in some cases ♂ shoots become microphyllous and flagelliform. In the, at least predominantly, intercalary branching, as well as in the ability to develop flagella or stolons, *Isophyllaria* shows a clear approach to the genus *Herzogiaria*. As is noted under this genus, it also consists of fuscous, opaque, aquatic plants—and also develops bifid leaves and underleaves on weak shoots. In spite of the obvious differences between the two genera, I suspect they are distinctly allied.

The sterile plant of *Isophyllaria* is confusingly similar to *Herberta*, approaching this genus in: (1) isophylly; (2) fuscous brown color; (3) narrow-based, cuneiform or narrowly obtrapezoidal-cuneiform and deeply bifid leaves and underleaves; (4) isodiametric, rather small marginal cells, with the intramarginal cells gradually more elongated, forming an ill-defined vitta which "runs out" into both lobes; (5) lack of rhizoids on leafy stems; (6) canaliculate leaf lobes and entire margins. However, no close affinity to *Herberta* can be postulated because of the following non-herbertoid characters: (1) somewhat succubous insertion of the lower leaves, with the leaves antically inclined, rather than postically decurved; (2) very thick-walled and completely non-collenchymatous leaf cells; (3) larger-celled layer of cortical cells, the cortical cells averaging 1.5-1.8× the diameter of the thin-walled but quite collenchymatous internal cells; (4) longly trigonous, non-herbertoid perianth.

HERZOGIARIA

Herzogiaria Fulf., Nova Hedwigia 1: 398, fig. 1-27, 1960.

Lepicolea auct. p.p.

TYPUS. *Herzogiaria teres* (Steph.) Fulf. = *Lepicolea teres* Steph.

A full discussion and description of this genus is given under its only known species.

Herzogiaria teres (Steph.) Fulf., Nova Hedwigia 1 : 398. 1960.

Lepicolea teres Steph., Kungl. Sv. Vet.-Akad. Handl., Bihang 26/3, num. 17: 26. 1901.

Lepicolea algoides Steph., Kungl. Sv. Vet.-Akad. Handl. ser. 4, 46/9 : 73, fig. 28 d-e. 1911.

Plants aquatic *, robust * and rigid *, blackish-brown *, 5-7 cm tall and (mature stems with leaves) 2.8-3.2 mm wide, radially symmetrical *, with irregular, sporadic branching; branches all axillary *, intercalary, from both * leaf and underleaf axils; some branches leafy and ascending, others descending *, microphyllous *, flagelliform *, with remote, distant leaves and underleaves. *Rhizoids* absent on leafy stems, frequent from underleaf bases of the flagelliform branches. *Stem* rigid *, subterete, 400-500 μ in diam. usually, with cortical cells rectangulate *, strongly elongated *, thick-walled * (with dark middle lamella), ca. (18)20-25(27)×(65)75-150 μ [1]; medullary cells gradually larger inward, to 30-36 μ in diam., remaining rather thick-walled (and with deeper middle lamella); cortical cells striolate * (like cells of leaf disks). *Leaves* and *underleaves* identical *, transversely * inserted (rarely faintly incubously or succubously inclined), on mature stems obliquely to rather widely spreading *, horny * and chartaceous *, very rigid *, opaque *, polystratose *, in dorsal aspect vertical, symmetrically * cuneate-obtrapezoidal, to ca. 2.2-2.4 mm long and 2.5-3.3 mm wide (at apices of the divergent segments), gradually broadened from a narrow *, cuneiform-obtrapezoidal * disk, bisbifid * for 0.7-0.85 * their length (median sinus

* Characters marked with an asterisk are considered to be primarily generic in significance.

[1] FULFORD (l. c.) states: "Walls thin... and with a wide band of brownish-yellow translucent secondary thickening."

descending to within 0.2, rarely 0.15 of base), occasionally trifid *, with one sinus deeper than the other, on weak axes and branches rarely bifid and then similar in form to those of *Isophyllaria;* disk and segments polystratose * (the linear-subulate *, rigid * segments 4-5 cells thick below and 6-7 up to 8-10 cells wide, very gradually tapering to a sharp, rigid, uniseriate apex formed by 2-4 superimposed cells). *Cells* with deep brown * middle lamellae (primary walls) and thick * strata of yellowish-brown * secondary thickenings, evenly thick-walled; cells of disk ca. (15)19-25(26)× (65)70-115(125) μ, averaging 3-5× as long as wide (surface aspect); cells of lobes elongated except on margins, the non-marginal cells (12-13)14-16(18-20)×48-62 μ (3-5× as long as wide), the marginal cells quadrate to short-oblong, ca. 18-20 μ wide and 20-26(32) μ long; cuticle striolate *; a few cells at the base of the V-shaped lateral sinuses, in the basal curve, subisodiametric, forming a knot-like swollen area or projection. No * *asexual reproduction.* Plants dioecious *; *androecia* eventually intercalary, on main axes or normal branches; bracts and bracteoles in from 2-4 to 6 or more series. *Bracts* variable, 4-, 3- or 2-fid, the 4-fid ones usually with 2 antheridia, the 2-fid with a single antheridium; bracts similar in size to leaves, but disk rather larger, somewhat but not strongly pouched at base and with lateral disk margins uncurved. *Bracteoles* flat *, usually remaining 4-fid even if bracts are 2-3-fid, lacking * antheridia. *Antheridia* notably short-stalked * (stalk ca. 60-70 μ long and 30-36 μ in diam.), the stalk 2-seriate below *, 2- or more seriate above; body short-ovoid, 160-175 μ in diam. and 175-180 μ long, the jacket layer of numerous * small *, quadrate to polyhedral irregularly * arranged cells, 12-15 μ in diam. *Gynoecia*, terminal * on leading axes, apparently lacking * innovations. *Bracts* and *bracteoles* grading imperceptibly into leaves; innermost bracts leaf-like but with broader, narrow-triangular (rather than linear-acuminate) segments, the margins crenulate to (locally) finely ciliate-crenulate or short-ciliate. *Archegonia* 7-10. *Perianth* (juvenile only) with mouth at least unistratose, unlobed, entire or subentire.

TYPE. Ushuaia, Tierra del Fuego, Argentina, anno 1896 — *Dusén* (G).

DISTRIBUTION. Southernmost South America. In addition to the type material, known from southern Chile: Isla Pacheco, ca. 52°10′ S. lat., 74°50′ W. long. — *Skottsberg*, type of *L. algoides.*

The species is diagnosed and discussed in some detail by FULFORD (1960). The horny and fuscous plant appears to be restricted to flowing, rocky streams.

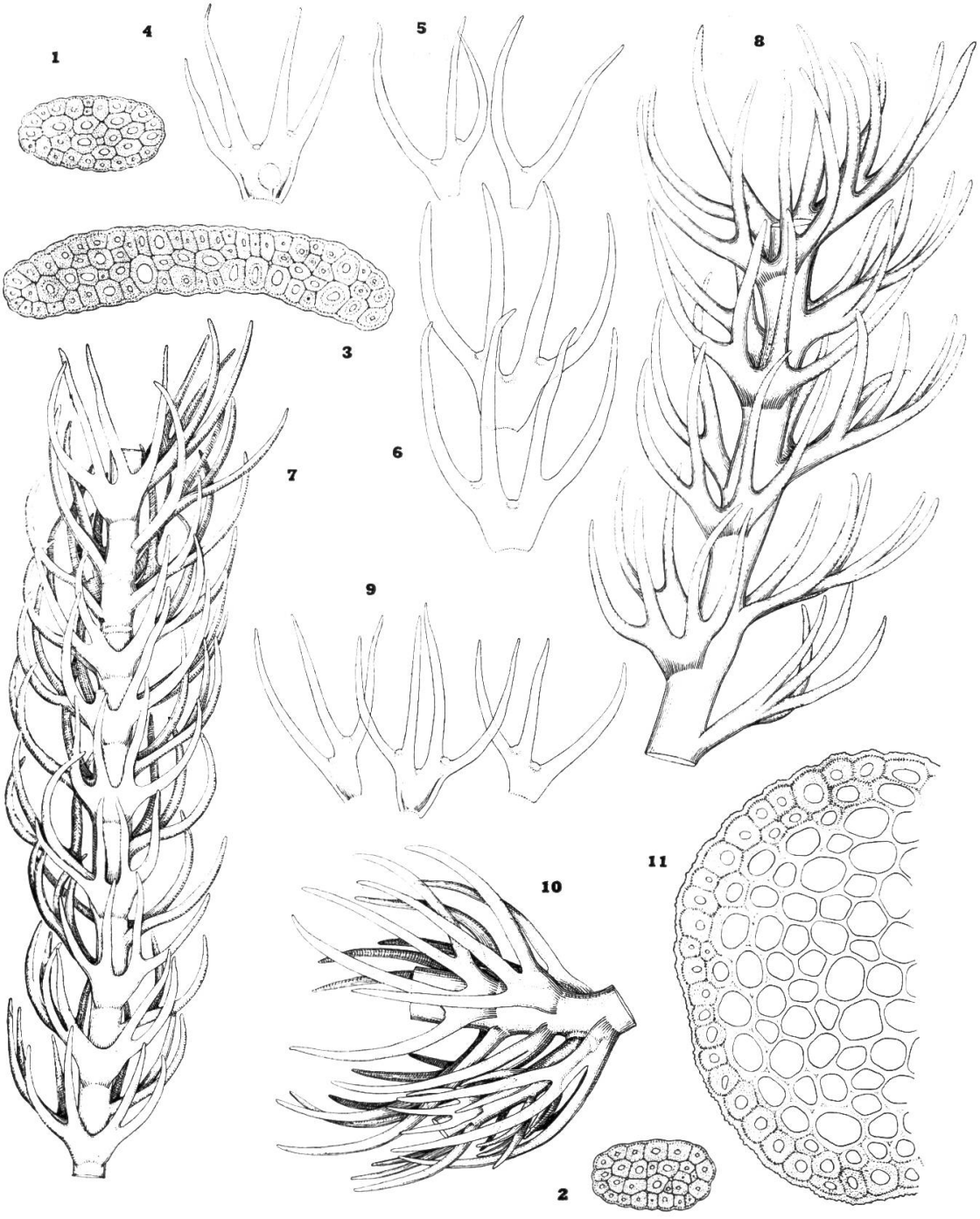
Herzogiaria is a monotypic genus showing immediate and unmistakable affinities to *Lophochaete*, *Archeochaete* and particularly *Isophyllaria.* It differs from all of these

* Characters marked with an asterisk are considered to be primarily generic in significance.

FIG. 2. *Herzogiaria teres*

1-2. Sections through leaf lobes (×960). – 3. Cross-section of leaf lamina (×960). – 4. Male bracteole with antheridium (×14). – 5. Two smaller than normal underleaves (×14). – 6. Two normal leaves (×14). – 7. Shoot-sector, ventral aspect (×11). – 8. Dorsolateral aspect of shoot-sector (×15.5). – 9. Two trifid male bracts and juxtaposed between the bracteole (×14). – 10. Lateral view of shoot-sector with ventral-intercalary branch (×14). – 11. Stem cross-section (×160).

All from type.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genera in the pluristratose lamina of leaves and underleaves and in the branching, which is apparently uniformly intercalary, issuing indiscriminately from axils of leaves or underleaves. The genus agrees closely with *Lophochaete* in the bisbifid, essentially transverse leaves, sporadically showing suppression of one or two lobes; in the biseriate antheridial stalk; in the near identity of the gynoecial bracts and bracteoles to the vegetative leaves (although the innermost bracts and bracteoles in *Herzogiaria* bear crenulate to denticulate margins). As in *Lophochaete*, there is a perianth whose mouth lacks cilia (it is described as entire; in *Lophochaete* it is lobed to crenulate to denticulate), and subfloral innovations are apparently absent. There is a further—and significant—agreement with *Lophochaete* in that the bases (curves) of the leaf sinuses produce a bulging, knot-like protuberance which seems to occur only in these two genera [1]. Both genera also agree in the androecia, which are strikingly similar in producing 1-2-androus bracts and lacking bracteolar antheridia.

The androecia of this species are often difficult to locate. There may be only 2-3 pairs of bracts (FULFORD, 1961: 399, states " in 6 or more series "); the bracts are often 2-3-fid, becoming asymmetric, while the flat bracteoles, which remain leaf-like, are bisbifid. The bracts are firm and almost horny like the leaves, but have a somewhat higher disk, which is moderately concave. Usually 1-2 antheridia occur; I have never seen more. The antheridia are characteristic: when mature they are ovoid-spherical, ca. 160-175 μ in diameter and 175-180 μ long, with the wall layer of characteristically small, irregularly oriented, quadrate to polygonal jacket cells, averaging only 12-15 μ in diameter. The stalk is very short, ca. 60-70(2) μ long and 30-36 μ in diameter; it consists of two rows of cells basally, and perhaps of 3-4 distally (although this could not be surely ascertained). The lack of bracteolar antheridia is significant in placing the genus in the *Blepharostomataceae*.

Branching is rather freely developed; all branches I have seen are clearly intercalary and axillary, from all three rows of segments; some branches become ascending and leafy, others—sometimes produced high up on the plant—become descending, remain microphyllous and remote-leaved, and form firm, wiry flagella; these flagella may in turn branch and form additional flagella. Branching of the flagella also seems to be always of the intercalary type. Rhizoids from underleaf bases of the flagella are common; I have not seen them elsewhere.

On occasional weaker plants there may be a rather high incidence of bifid leaves and occasionally bifid underleaves; such shoot-sectors show an unmistakable similarity to those of *Isophyllaria*. The two genera, however, are very distinct in that *Herzogiaria* has polystratose leaves, *Isophyllaria* has them unistratose.

The original impression of *Herzogiaria* is of a very distinct plant, owing to the rigid and horny, spreading, setaceous leaf lobes. However, even though the genus is well-founded, there is no basis for a family *Herzogiariaceae*—at least not on the basis of the criteria cited by FULFORD (1960) [2]. The polystratose leaves are an obvious

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[1] Similar areas recur in *Triandrophyllum (Herbertaceae)*.

[2] The striolate cuticle of stem and leaves as in e.g. *Temnoma* and *Isophyllaria* and the equally thick-walled cells are highly suggestive of the *Blepharostomataceae*. The form of the bifid leaves, on weaker axes, is exactly similar to the normal leaves and underleaves of *Isophyllaria*. As in *Isophyllaria*, the leaf lobes are "vittate"—in the sense that marginal cells are little or not elongated, intramarginal ones become quite narrowly oblong. And, as in *Isophyllaria*, the cells have

adaptive feature for aquatic existence, exactly as are those of the lophocoleoid genus *Pachyglossa* (a genus which all current workers agree in placing in the *Lophocoleaceae* — FULFORD, 1963, aside). I am more impressed with the purely intercalary branching as a generic criterion than I am with the polystratose leaves. The intercalary branching is probably also adaptive, in the sense that thus branching arises from the lower (older) sectors of plants, leading to only a limited extension in length of the aquatic shoot-system. Unlimited extension, such as is possible—and indeed almost unavoidable—with terminal branching, is thus eliminated.

ARCHEOPHYLLA

Archeophylla Schust., Jour. Hattori Bot. Lab. 26: 263. 1963; Trans. Brit. Bryol. Soc. 4: 802. 1965.

TYPUS. *Archeophylla schusteri* (Hodgs. et Allis.) Schust. = *Temnoma schusteri* Hodgs. et Allis.

Plants procumbent, erect or ascending, small, rather rigid, when exposed ± brownish, sparingly branched; branches mostly or almost exclusively postical and intercalary, infrequently lateral, of the Frullania-type. *Stem* slender, rigid, subterete, from (85)90-105 to 130-150 μ in diam., the cortical cells in only (10)11-15(16) rows, with ± thick external walls (the radial and internal walls often thinner except at angles), ± strongly enlarged but not forming a hyaloderm; cortical cells (18)20-27(30) μ in diam., not or moderately tangentially flattened, ca. (28)30-45(60) μ long, short-oblong in surface view); medullary cells 3-4(5) cell rows across, the medulla formed of only 8-16(18) cell rows, the cells with walls thickened, strongly collenchymatous, small, only (12)14-18(22) μ in diam. *Rhizoids* rather frequent, from the undivided base of underleaves, not from stem. *Shoots* ca. 650-900 μ to 1500-1600 μ wide, moderately to distinctly anisophyllous, the underleaves averaging 0.55-0.75 the length and 0.4-0.75 the area of the lateral leaves (sometimes with one fewer segment than lateral leaves). Lateral *leaves* remote, varying from barely succubous to transverse in insertion, subtransversely oriented, rigid, distant to barely contiguous, obliquely spreading to suberect to—more often—spreading, palmately symmetrically 3-4-fid, never bisbifid, on weak stems some leaves symmetrically bifid, basically cuneate to obdeltoid in outline, inserted on 4-5 cortical cell rows, divided for (0.55)0.60-0.75(0.80) of their length, the sinuses equal, V-shaped with rounded bases; undivided disk 5-7 cells high on mature leaves, ± obdeltoid to obtrapezoidal in basic outline; lobes rigid, setaceous, long acuminate, ± divaricate, 2-3-4 cells broad at base, gradually tapering to a uniseriate apex 7-13 cells long, the margins unarmed (rarely with a short basal accessory tooth on trifid leaves); sinus bases without a swollen area of smaller cells. *Cells* smooth or papillose-striolate, the cuticle very thick; middle lamella distinct;

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strongly, equally developed secondary walls, with the primary walls ("middle lamellae") conspicuous because of their deeper color.

Indeed, it seems to me that *Herzogiaria* and *Isophyllaria* have had a common origin in a subaquatic ancestral Lophochaete-like type.

oil-bodies large (1)2-3(4) per cell, nearly filling lumen, greyish, granular, ovoid to subrotundate; cells collenchymatous: trigones large to immense; cells of undivided discus little elongated, 1.2-2× as long as wide, cells of lobe bases hardly elongated, 1.2-1.5× as long as wide; basal cells of uniseriate terminal filaments subisodiametric or oblong, but the narrow, slender apical cells becoming strongly elongated (3-6× as long as broad). *Underleaves* smaller than lateral leaves, usually 3-4-lobed, but sometimes bifid, similar in form to lateral leaves, usually erect to spreading; discus 2-5 cells high; lobes 2-seriate at base only or uniseriate throughout, 5-8 to 9-13 cells high (occasional lobes ± aborted), rigid and setaceous. *Rhizoids* frequent, from abaxial face of the basal disk. *Asexual reproduction* lacking or by fragmenting leaf lobes. Plants dioecious; ♂ and ♀ shoots sometimes admixed; *androecia* highly differentiated, abruptly so, shortly and ± compactly spicate, formed of only (1)2-4(5) pairs of strongly saccate, gibbous, imbricate bracts. *Bracts* (3)4(5)-lobed for 0.5-0.6 their length, the entire discus saccate and ventricose, the free margins sometimes weakly involute, entire or with a small spinous tooth on one or both margins; lobes erect or suberect, not divaricate, often loosely to closely appressed to bract in front. *Bracteoles* small, like underleaves, flat, without antheridia. *Androecia* either intercalary on leading axes, which after producing a series of remote vegetative leaves may again produce an androecium, or sometimes on ± abbreviated lateral (terminal, Frullania-type) branches. *Antheridia* with stalk biseriate, ca. 23-25 μ in diam., rather short; body with cells numerous, ± irregularly oriented. *Gynoecia* terminal on leading stems, without a subfloral innovation if fertilization occurs (but often with 1-2 innovations if fertilization fails). Subfloral (subinvolucral) *bracts* usually larger than bracts themselves, 3-4(5)-fid, generally armed on margins of disk with stiff, short to long, alternate cilia or teeth, which may be arcuate or curved; subfloral leaves grading gradually into bracts above; bracts variable, oblong-ovate to cuneate to narrowly obtrapezoidal-obovate, erect and sheathing basal 0.3-0.5 of perianth, basically 3-4-fid to within 0.45-0.7 of the base; lobes slender, erect and gradually setaceous, not divergent or obscurely so, 2-3 to 4-6 cells wide at base, gradually attenuated, ± tortuous, entire-margined, but usually with 1-4 spinous teeth or cilia, which are almost never opposed (if at all present); lateral margins of disk entire or sometimes armed with several spinose teeth or cilia. *Bracteole* similar, somewhat smaller, usually 2-3(4)-fid only. *Perianth* obovoid-clavate, not stipitate, unistratose, terete below, to ca. 575-665 μ wide and 1550-2100 μ long, strongly triplicate in the terminal 0.25-0.3(0.5), the plicae rounded, contracted to the lobulate-ciliate, often decolorate mouth, which is basically closed; cilia crowded, in part arising from abbreviated, denticulate-ciliate lobes, slender, uniseriate (1-3)4-5(6-7) cells long, to 130-250 μ long, formed of thick-walled, elongated cells each ca. 18-20 μ wide and 26-50 μ long, the terminal cells to (7)9-13 × 40-80 μ. Capsule ovoid, brown; wall delicate and relatively thin (ca. 26-29 μ thick when 3-stratose, 28-32 μ thick when 4-stratose); inner layers very thin, largely of elongated, narrow, oblong to oblong-sigmoid, locally irregular cells bearing weak radial (nodular) thickenings, lacking distinct semi-annular bands (except sometimes innermost stratum), averaging ca. 5-6 to 6-7 μ thick, 13-15 μ wide and 50-80 μ long; epidermal cells larger, higher, delicate, often quadrate to short-oblong, averaging ca. 12-16 μ high, 16-22(25) μ wide and 25-40 μ long, the marginal 1-2 rows with nodular thickenings *(A. pungens)*,

or almost all longitudinal and occasional transverse walls with 1-2 distinct, pale yellowish to brownish nodular thickenings (which may be feebly tangentially extended). *Spores* rather finely to coarsely papillose, the papillae well separated, ca. 12-15 μ in diam., brown, ca. 1.6-2× the elaters in diam. *Elaters* short, strongly contorted, with abruptly and strongly attenuated apices, ca. 7-8(9) μ in median diam. and 60-95 μ long, bearing a single, very broad (7-10 μ), rather laxly helical spiral, the pointed and attenuated apices equally thick-walled.

Archeophylla is an isolated genus, combining certain primitive features found in the *Herbertaceae* (variable leaf-lobe number; branching largely or almost exclusively postical and intercalary—unlike in *Temnoma*, terminal branching is a rare and exceptional feature; the development of distinct, often coarse, nodose trigones; lack of cilia of the leaf margins; the frequent " high " insertion of the rhizoids on the underleaf disk) with a series of criteria typical of the *Blepharostomataceae* (reduced androecial bracteoles lacking antheridia; perianths shallowly lobulate at mouth, trigonous above; leaves with insertion not at all incubous), which are joined with several specialized traits (the peculiar, broadly unispiral elaters; the somewhat reduced size of the underleaves). Affinities, in *Blepharostomataceae*, appear to exist principally to *Temnoma*, less so to *Lophochaete* and *Archeochaete*.

Archeophylla differs from *Temnoma* in a series of criteria, among them the following: (1) leaves varying from (2)3-4-fid; (2) cells with conspicuous trigones and sometimes reduced, often merely pit-like connections between the cells; (3) largely or almost constantly postical-intercalary branching; (4) stem with short-oblong cortical cells which are larger in diameter than the medullary cells; (5) leaves with discus formed of short-oblong to hardly elongated cells; (6) perianth, although triplicate and ciliate at mouth, with the mouth rather tightly contracted; (7) perichaetial bracts with lobes never ciliate or dentate with paired, opposed teeth, the teeth alternate in a unique manner, or absent; (8) androecia short, highly differentiated, the bracts extraordinarily saccate and inflated; (9) rhizoids tending to form a compact group, arising well above the underleaf base. In general, the small size, plus the total lack of cilia or teeth of both leaf lobes and leaf disk will serve to separate all species of *Archeophylla* from *Temnoma*. Added to this, the frequent but almost entirely postical-intercalary branching give the genus a facies and characteristics of its own.

Accompanying the above gametophytic criteria are several derived from the sporophyte: (1) the short and contorted elaters are unique in bearing each a single, very broad, conspicuous spiral; (2) the capsule wall is only 3-4-stratose and relatively delicate owing to the almost total lack of tangential bands [1].

Although the plants appear superficially similar to certain species of *Temnoma*, similarities are mostly of a general nature that characterize also such genera as *Vetaforma* and *Lophochaete*. I know of no other bona fide member of the *Blepha-*

[1] The observations on capsule-wall anatomy must be supplemented with study of more adequate material, only a single (unopened) post-mature capsule of *A. schusteri* being available for study. On the few cross-sections I was able to prepare, the tristratose valve sectors were 26-29 μ thick, with epidermal cells 14-16 μ high, the two inner strata each 6.5-7 μ high. On the quadristratose sectors the wall was 28-32 μ high, with epidermal cells 12-15 μ high, the interior layers from 5-6 μ high (rarely and locally only 4.5 μ high). The thinness of the interior strata was notable.

rostomataceae with cells with trigones such as are possessed by the present plants linked with the peculiar, broadly 1-spiral elaters of *Archeophylla*. I leave the genus in the *Blepharostomataceae* because of the weak tendencies towards development of succubous leaves, the Temnoma-like aspect and the distinct anisophylly, the perianth form and the form of the androecium (bracteoles smaller than bracts, lacking antheridia in their axils).

The genus exhibits remote affinities to *Lophochaete*, as is evident from the unlobed margins of the leaves, the (optimally) quadrifid leaves produced, the transverse leaves, the brownish color and the contracted perianth mouth. However, the perianth is 3-plicate and ciliate at the mouth, as in *Temnoma*, and, as in *Temnoma*, the leaf sinuses are equal. Also, the cells with their coarse trigones are notably distinct. Equally distinctive are the simplified stem anatomy and the infrequent occurrence of terminal branches of any type.

Archeophylla serves, in some ways, as a model from which *Blepharostoma* may be derived. The number of cell rows of which the axis is formed may be strikingly similar, even though the enlarged cortical cells of *Archeophylla* represent a deviation. On apparently normal stems of *Archeophylla* the leaves are almost all 2-3-4-lobed, and the underleaves, with few exceptions, may be 2-3(4)-lobed even on mature stems, thus approaching *Blepharostoma*. Furthermore, on underleaves some lobes are uniseriate to the base, even though leaf lobes are always biseriate basally, or even 3-4-seriate (however, the uniseriate, long distal portions of the lobes strongly recall the leaf lobes of *Blepharostoma*). Furthermore, the quadrifid leaf form of the 4-lobed leaves, with the median sinus not deeper, is as in *Blepharostoma*. Indeed, it is possible to derive the gametophyte of *Blepharostoma* from that of *Archeophylla* by a process of leaf reduction, with elimination of the basal lamina of leaf and underleaf.

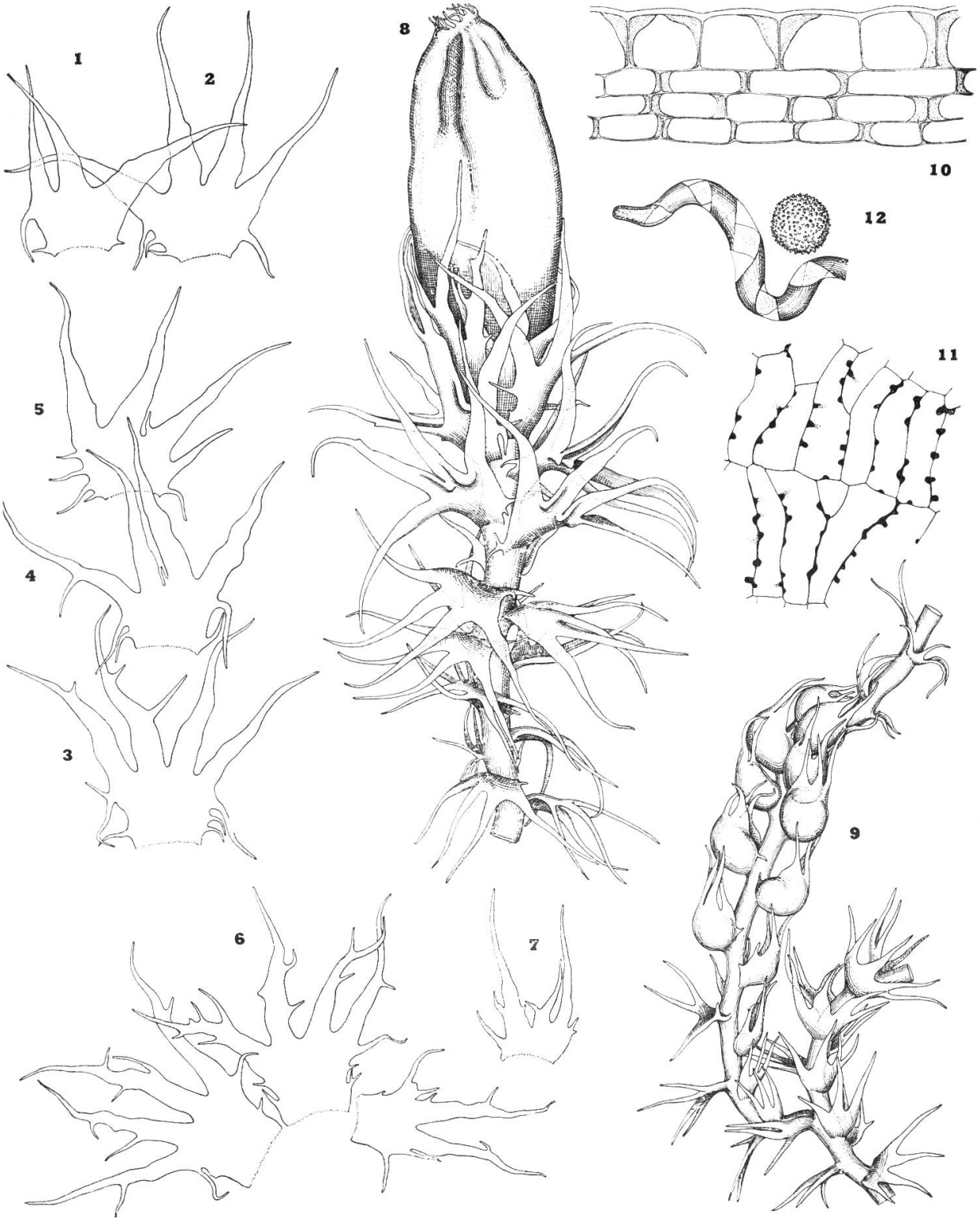
Key to species

1. ♀ Bracts with lobes 1-2-seriate to near base, often edentate; disk of bracts usually with a small basal tooth on each side, otherwise edentate; leaves with disk 2-4 cells high, wider than long, the lobes uniseriate for 8-11 cells, arising from a base 2(3) cells broad (rarely 2-seriate for basal 2 cells); cuticle coarsely verrucose-striolate; dwarf species
A. pungens (Herz.) Schust.

1*. ♀ Bracts with lobes at least 2-4 cells wide towards base, bearing sharp, non-opposed teeth; bract disk ± ciliate or spinose-dentate; leaves with disk over 4 cells high and with lobes not uniseriate to base (or to within 1-2 cells of base) 2

FIG. 3. *Archeophylla schusteri*

1-2. Transitions from ordinary to subfloral leaves (×26). – 3-5. Subfloral leaves (×26). – 6. Bracts and, at right, bracteole (×26). – 7. Small, atypical, inner accessory bract (×26). – 8. Perianth-bearing plant (ca. ×30). – 9. Male plant, sector of chief stem with postical-intercalary androecial branch (ca. ×30). – Capsule wall in cross-section (×570). – 11. Innermost cells, showing weak nodular thickenings, only locally extended as tangential spurs (ca. ×320). – 12. Elater and spore (×533).
All from *RMS 49860*.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2. Cuticle smooth; trigones extremely coarse, nodose, separated by narrow, thin walls; leaves 0.65-0.8 divided into (2)3-4 lobes, the lobe apices uniseriate for 9-13 cells; underleaves quite small, their disk 2-3(4) cells high only, but lobes 9-13 cells long; ♀ bracts ± patent, little concave, their lobes 4-6 cells wide at base, sparingly spinose-ciliate *A. schusteri* (Hodgs. et Allis.) Schust.

2*. Cuticle closely, conspicuously papillose-striolate; trigones ill-defined, occasionally large, never bulging, separated by ± thickened walls; leaves 0.55-0.65 divided into (3)4 lobes, the lobe apices uniseriate for 6-8(9) cells; underleaves large, disk 4-5 cells high, lobes 5-8 cells long; ♀ bracts in 2-4 series closely imbricate, forming a compact, spiny head (prior to perianth maturation), the mutually involute and closely appressed-imbricate bracts strongly concave, erect, their lobes 2-4 cells wide at base, copiously spinose-ciliate or spinose-dentate . . . . . *A. paradoxa* Schust.

Key to sterile plants

1. Leaf lobes (2)3-4 cells broad for basal one-half (7-9 cell tiers usually); cuticle smooth; trigones coarsely nodose, the walls thin, pit-like between. New Zealand . . . . . *A. schusteri* (Hodgs. et Allis.) Schust.

1*. Leaf lobes uniseriate except at most for basal 1-3 cell tiers, which may be 2 cells broad; cuticle closely, strongly papillose-striolate; cells with trigones ill-defined and often weakly developed. South America 2

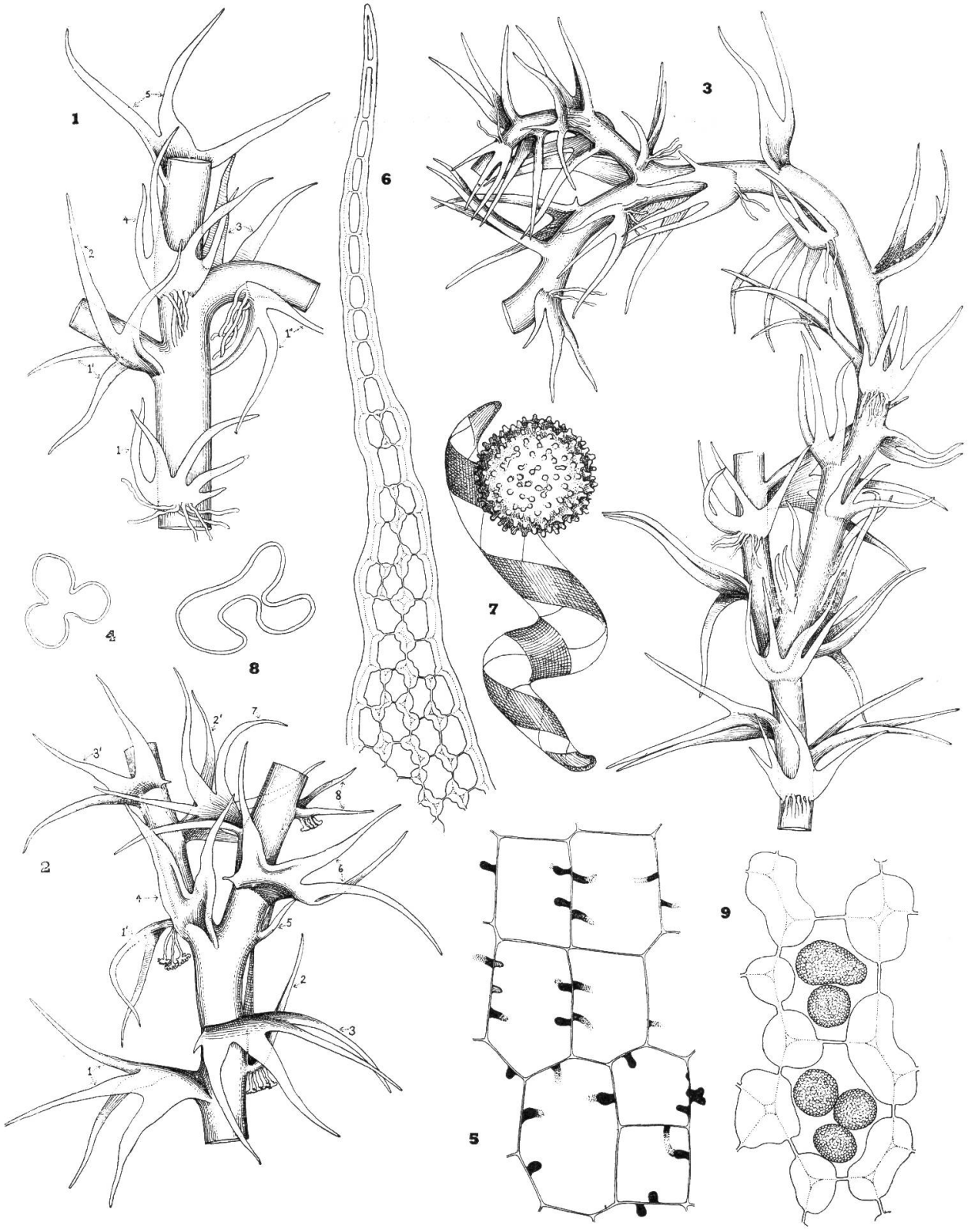
2. Disk of mature leaves and underleaves broadly obtrapezoidal, wider than high, only 2-4(5) cells high; leaf lobes uniseriate to base, where 2(3) cells broad, rarely the base of isolated lobes 2 cells wide above the insertion (for one cell tier only !); leaf lobes longly setaceous, of 8-11 cells in a single row . . . . . *A. pungens* (Herz.) Schust.

2*. Disk of mature leaves and underleaves narrowly obtrapezoidal, higher than wide, to 5-7(8) cells high; leaf lobes 2(3)-seriate for basal 2-3 cell tiers, leaf lobes less setaceous, the uniseriate tips only 6-8 cells usually *A. paradoxa* Schust.

FIG. 4. *Archeophylla schusteri*

1. Shoot-sector, postical aspect, with Frullania- and Microlepidozia-type branches (1 and 4, underleaves; 2, 3, and 5, lateral leaves: 2, bifid stem leaf associated with Microlepidozia-type branch, 3, bifid stem leaf associated with Frullania-type branch; 1′, first and bifid branch leaf; 1″ first and trifid branch underleaf) (×35). – 2. Shoot-sector, antical aspect, with Frullania-type branch (1, 3, 4, 6 and 7, lateral leaves of main stem; 2, 5, and 8, underleaves of main stem, in part with branched rhizoids at bases; 4, bifid dorsal leaf-half associated with branch; 1′, first branch underleaf; 2′-3′, first branch lateral leaves) (×35). – 3. Shoot-sector, postical aspect, with a postical-intercalary, axillary branch which (above) gives rise to a Frullania-type terminal branch (×44). – 4. Perianth cross-section, 1/6 from apex (×37.5). – 5. Epidermal cells of capsule, surface view (×485). – 6. Lobe of leaf (×142). – 7. Spore and elater (×1070). – 8. Perianth cross-section, upper 1/5 (×37.5). – 9. Two cells with oil-bodies (×604).

1-7. *RMS 49860*. – 8. *RMS 51196*. – 6. *RMS 51010*.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Archeophylla schusteri (Hodgs. et Allis.) Schust., Jour. Hattori Bot. Lab. 26:263. 1963.

Temnoma schusteri Hodgs. et Allis., Trans. Roy. Soc. N.Z., Bot. 1:147. 1962.

Plants rigid, small, light green to light brown, ca. 10-15(25) mm high, with leaves to 1500-1600 μ wide at maturity, sparingly and irregularly branched; branches almost all postical and intercalary, rarely sporadic branches lateral, terminal. *Stems* brownish, rigid, slender, to 130-150 μ in diam., erect or suberect, terete, symmetrical, formed of 10-12 to 15(16) rows of enlarged cortical cells—mostly 20-25 μ in diam. and (28)30-45 μ long—which are not tangentially compressed, surrounding a small-celled medulla (cells 13-15 μ in diam.), formed of 8-12 cell rows, the cells all collenchymatous (but exterior faces of cortical cells strongly thick-walled). *Leaves* subisophyllous, the lateral clearly larger, transversely oriented (± transversely inserted) and stiffly, obliquely or widely spreading or squarrose to (sometimes) suberect, nearly flat to weakly concave, palmately (2)3-4-lobed for 0.65-0.8 their length, obtrapezoidal to obtriangulate in shape, ca. 600-750-800 μ long and 775-925 (1000-1050) μ broad at divergent segment apices; sinuses V-shaped with rounded bases, equal or nearly so (in quadrilobed leaves the median sinus is not perceptibly deeper); lobes stiffly spreading, 2-3-4 cells broad at base, but with setaceous, uniseriate apices 9-13 cells long; lobes smooth-margined, edentate and eciliate; undivided base to 285-300 μ broad and 170-185 μ high, (5)6-7(8) cells high usually, obdeltoid to obdeltoid-reniform, narrowed at base. *Cells* with a somewhat yellow-brown, distinct middle lamella and coarse, yellowish to almost colorless, nodose trigones which are so extended that the thin walls between cells are reduced to pits (or nearly so); cuticle smooth, the free cell walls very thick; cells of basal disk ca. 23-27(29) × (25)30-38(52) μ, mostly somewhat oblong to oblong-polygonal; cells of bases of lobes ca. 21-24 × 26-32 μ to 25-27 × 30 μ, subquadrate to short-oblong; cells of bases of uniseriate filaments often subquadrate to quadrate, ca. 28-33 μ; cells of apices of lobes gradually attenuated and narrowed, becoming 8-13 × 36-45 μ to 10-11 × 50-58 μ in lobe tips (which are often decolorate); oil-bodies (1)2-3(4) per cell, granulate, very large, nearly filling cell lumen, ovoid to subrotundate, 8.5-9.5 × 9.5-14 μ to 10-12 × 12-16.5 μ, rarely to 11 × 20 μ. *Underleaves* ca. 480-550 μ long and 400-450(500) μ broad, usually (2)3-4-fid, occasionally all quadrifid, one or both lateral segments usually shorter; segments uniseriate throughout or biseriate at base only, 9-13 cells high usually; disk 3-5 cells high. *Rhizoids* common, arising from underleaf disk. ♂ *Bracts* relatively small, the entire basal portion strongly inflated (more strongly so than in *A. pungens*), the lobes erect or suberect. *Gynoecia* with 1-2 cycles of subfloral bracts with suberect basal portions, but the long stiff lobes widely spreading or even squarrose; subfloral bracts are usually larger than the bracts, 3-4(5)-fid, the long, tortuous lobes armed with 1-several stiff, normally non-opposed rigid teeth or cilia. *Bracts* variable, deeply 3-4-fid, the low disk narrow, obtrapezoidal, never strongly concave; lobes long, tortuous, armed as are those of subfloral bracts and bracteoles. *Bracteoles* similar, often smaller, often only 2-3(4)-fid. *Perianth* to 575-665 μ in diam. and 1550-2100 μ long, the contracted mouth ciliate, the cilia crowded. *Capsule* ovoid, the wall relatively thin, not fleshy, 26-29 μ thick (where 3-stratose) to 28-32 μ thick (where 4-stratose); epidermal cells much higher than inner cells, often quadrate

to short-oblong, ca. 12-16 μ high, 16-22(25) μ wide and 25-40 μ long, almost all longitudinal and occasional transverse walls with 1-2 distinct, pale yellowish to brownish nodular thickenings (which may be feebly tangentially extended). *Spores* rather coarsely papillose, the papillae well spaced, 12-15 μ in diam. *Elaters* short, strongly tortuous, ca. 7-8 μ in diam. and 60-95 μ long, the single broad spiral 8-10 μ wide.

TYPE. On trees in subalpine forest, Table Hill, Stewart Island, New Zealand, 5.2.1947 — *W. Martin 9355* (herb. E. A. Hodgson).

The few fragments of the type occurred admixed with *Acromastigum mooreanum.*

DISTRIBUTION. Stewart Island: along Pegasus Creek, 100-150 ft., 1-1.5 miles from the mouth and 1.8-2.5 miles from the mouth — *RMS 49860, 49871*; Tin Range, above the old tram line, ca. 1300-1500 ft., ca. 4-5 miles NW of the Pegasus River mouth — *RMS 51010.* North Island of New Zealand: Along Mangawhero River, 0.5-0.7 miles below Mangawhero Falls, on the Ohakune Mt. Road. Tongariro National Park, on the slopes of Mt. Ruapehu, at ca. 3500-3700 ft. — *RMS 51169*, with perianths, androecia; *RMS 50943.*

A rare and sporadically distributed plant, whose association with *Eotrichocolea polyacantha* is rather constant. I have not found the species on the South Island of New Zealand, but the lowlands of Secretary Island, Doubtful Sound, have the requisite ecological conditions; a prolonged search will surely locate it there.

ECOLOGY. Usually difficult to locate and never in pure patches: isolated stems creep amidst other *Bryophyta*, often so closely adnate to the golden-brown stems of *Acromastigum* that they can hardly be freely removed without breaking. The plants tolerate limited direct sunlight, and only when the substrate is constantly moist, without ever being flooded.

On Mt. Ruapehu on peaty, in part *Sphagnum*-covered, ground along a small rill near its juncture with the Mangawhero River, in open scrub (partly Manuka); here associated with *Herzogianthus vaginatus* (see Schuster 1961 a), *Blepharidophyllum xiphophyllum*, *Acrobolbus lophocoleoides*, *Eotrichocolea polyacantha*, *Leptoscyphus* spec., *Trichocolea australis*, *Lepidolaena magellanica*, etc.

Although the fragmentary type supposedly occurred " on trees ", I was unable to find the species as an epiphyte. My Stewart Island collections all occurred either on ground, in the areas where " moss mounds " (such as those figured in Martin 1950: tab. 60) occurred, usually under old stands of Manuka (*Leptospermum scoparium*), on gentle to steep slopes, or—a single time—amidst other bryophytes over spongy peat on rocks at the summit of one of the craggs in the Tin Range. The species was confined to more open, more freely insolated sites, and seems lacking from mature mixed hardwood-Podocarp forests; it almost always occurs as a rare and sporadic component of the " moss mound " vegetation. These so-called mounds consist, usually, largely of *Hepaticae* (*Clasmatocolea* spec., but even more often *Acromastigum mooreanum*, *A. anisostomum* and *Bazzania* spec., *Tetracymbaliella decipiens*, etc., accompanied by a wide range of species, some quite rare, such as *Trichotemnoma corrugatum*, *Eotrichocolea polyacantha*, *Acrobolbus lophocoleoides*, *Anastrophyllum schismoides*, *Adelanthus occlusus* and *Leptoscyphus* spec.).

DIFFERENTIATION. A distinctive plant, without close relatives. The variable leaf and underleaf-lobe number recalls *Vetaforma*, from which the present plant differs in (1) stem anatomy; (2) the transverse to weakly succubous leaf insertion; (3) the non-bisbifid trilobed to quadrilobed leaves, whose median sinus does not descend more deeply than the lateral sinuses; (4) the strongly collenchymatous cells, with conspicuous, knot-like trigones and darker colored, distinct middle lamellae; (5) largely intercalary branching; (6) the suberect to laterally patent, rather than postically deflexed leaves; (7) the distinct pigmentation. In some of these criteria *Archeophylla schusteri* recalls *Temnoma*, notably in (2), (3), (6) and (7). However, *Archeophylla schusteri* differs, in the first place, from *Temnoma* (as well as from *Vetaforma* and *Lophochaete*) in the development of large cortical cells surrounding a smaller-celled medulla. The variable number of leaf and underleaf lobes also serves to separate the genus from *Temnoma*, as do several other of the criteria cited above, notably (1), (4), (5). These same criteria also effectively separate the species from any species of *Lophochaete*. The extraordinary leaf cells, of course, readily separate the species from other members of the *Blepharostomataceae*.

A. schusteri is only remotely allied to its two congeners, *A. paradoxa* and *A. pungens*. It differs from both in (1) the smooth cuticle; (2) the unique, immense trigones of the leaf cells; (3) the form of the gynoecial bracts.

The bracts are immensely variable—much as in *A. pungens*. Indeed, the most complex and highly elaborated bracts of *A. pungens* approach the simpler bracts of *A. schusteri* in degree of complexity. The variability of the bracts has been documented in SCHUSTER (1965) and is portrayed by the associated figures.

Branching appears to be equally variable. Although, as in *A. paradoxa* and *A. pungens*, branching is very preponderantly postical-intercalary, isolated lateral branches of both the Frullania- and Microlepidozia-type sporadically occur in *A. schusteri*. I have not seen Microlepidozia-type branches in other species of *Archeophylla*.

Archeophylla pungens (Herz.) Schust., comb. nova.

Blepharostoma pungens Herz., Rev. Bryol. et Lichén. 29:189, fig. 2a-c. 1960.
Temnoma pungens (Herz.) Fulf., Mem. N. Y. Bot. Gard. 11:59. 1963. (p.p., as to type only!).

Plants dwarf, only 650-1000 μ wide and 12-15(20) mm long, slender, whitish-green to pale brown, growing over other *Hepaticae*. *Stem* slender, 90-100 μ in diam., pale greenish to brownish, with ca. 11-12(16) rows of large, thick-walled, short-oblong cortical cells and ca. 12-14 rows of collenchymatous medullary cells, subsimple to sparingly branched below; branches normally postical-intercalary (excep-

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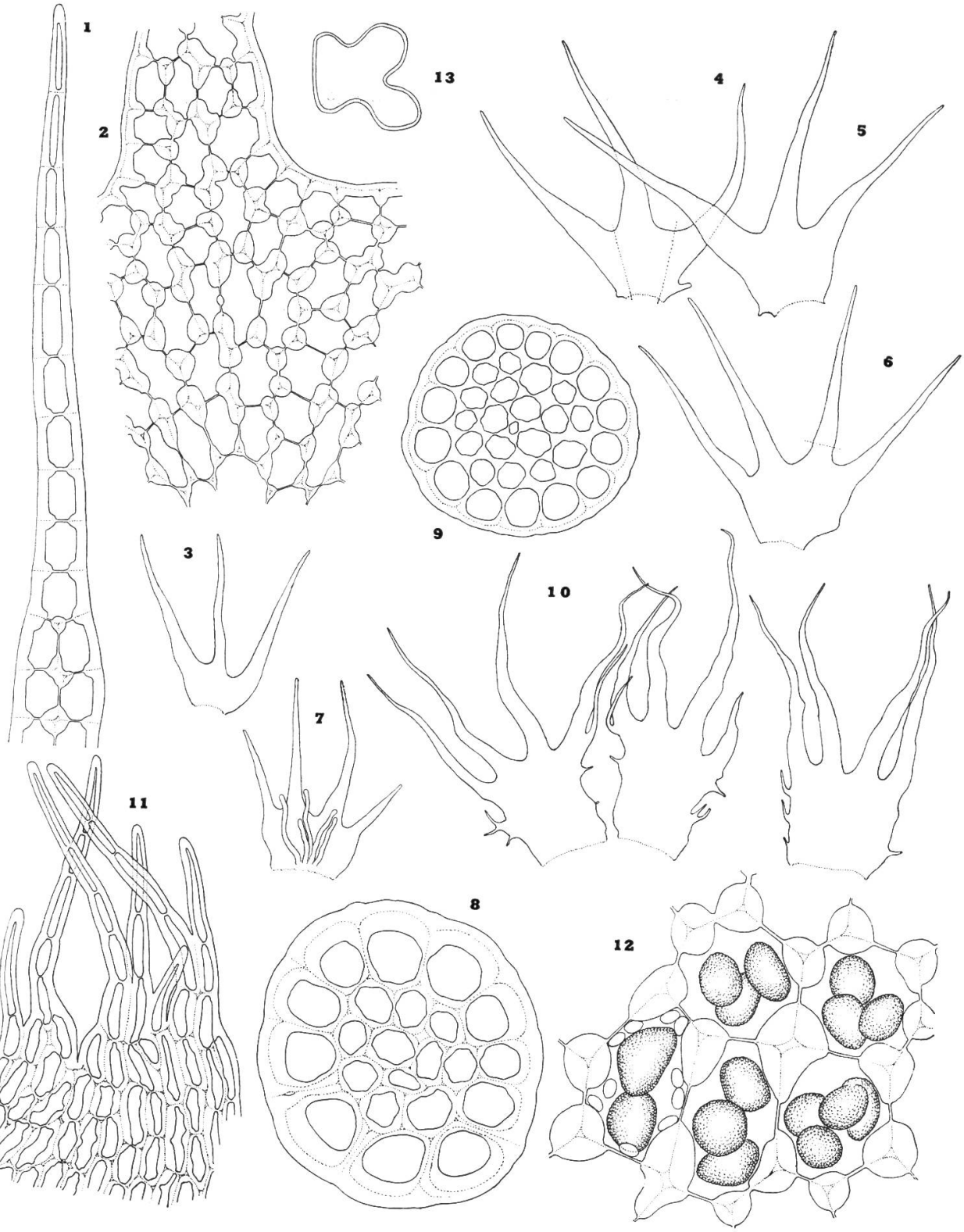
FIG. 5. *Archeophylla schusteri*

1. Lobe of leaf 6 (×225). – 2. Middle of disk of leaf 4 (×225). – 3. Small leaf (×48). – 4-6. Larger leaves (×48). – 7. Underleaf (×48). – 8. Stem cross-section (×380). – 9. Larger stem, cross-section (×220). – 10. Bracts and bracteole (×24.8). – 11. Perianth mouth (×177). – 12. Cells of disk, showing oil-bodies and (left cell) chloroplasts (×615). – 13. Perianth, cross-section, 1/4 from apex (×30).

1-8. Type. – 9, 11-13. *RMS 49860*. – 10. *RMS 51169*.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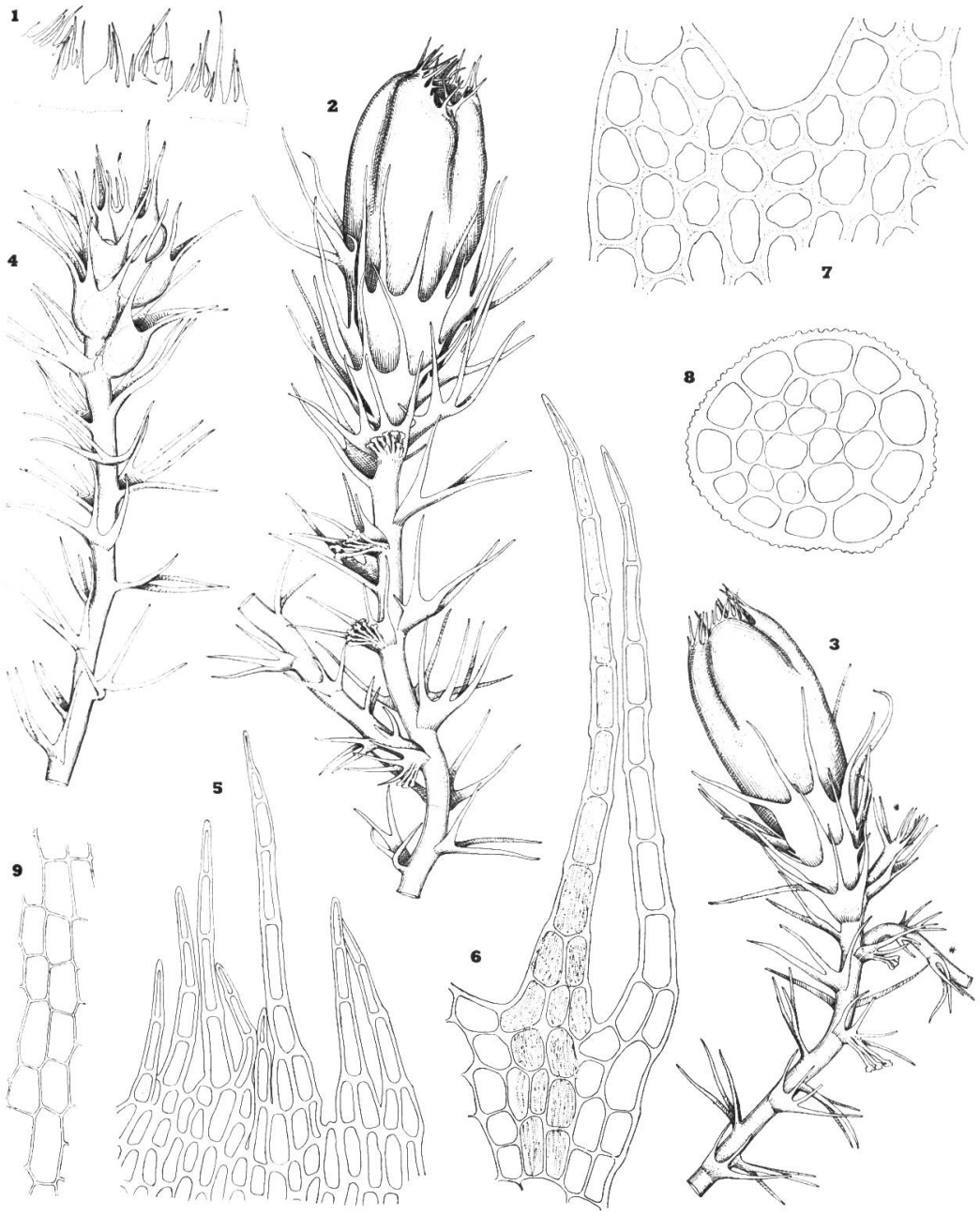
tionally Frullania-type). *Stem* to 2 cm long, only ca. 6 cells in diam.; cortical cells hardly differentiated from medullary. *Rhizoids* rare. Moderately anisophyllous; *leaves* transversely inserted and oriented, remote to (rarely) contiguous, stiffly spreading to erect-spreading, occasionally subsquarrose, cuneate-subquadrate, ca. 350-380 μ long, divided for 0.6-0.7 up to 0.8 their length into (3)4 entire-margined, slender, setaceous lobes which are uniseriate and ca. 8 cells long, arising from a base formed by 2-3 cells lying side-by-side; disk wider than long, obtrapezoidal, only 2-4(5) cells high and 8-12 cells broad, entire or (near androecia or gynoecia) occasionally with a spinous lateral tooth; lobes stiff, rigid, to 350 μ long, erect to weakly divergent. *Underleaves* similar but somewhat smaller, remote. *Cells* firm, in lobes averaging 18-20×40-50(56) μ, except near apices of lobes, with equally thickened walls, conspicuously, rather coarsely striolate-rugulose to striolate-papillose, the terminal cells of the lobes smooth or nearly so; laminar cells ca. 16-25×28-36(40) μ, thick-walled and with angles ± prominently thickened; cuticle striolate. Plant dioecious; *androecia* initially terminal, of few (usually 2-4) pairs of monandrous bracts. *Bracts* larger than leaves, similarly 4-lobed, the lobes uniseriate and 6-8 cells long, arising from a triangular base usually 2-4 cells wide; disk higher, usually 5-6 cells high, strongly concave; antical margin bearing 1-2 small, curved teeth. *Antheridia* single, the short stalk biseriate. *Gynoecial* plants somewhat more robust, *bracts* to 1050-1350 μ wide (leaves near gynoecia with disk often 4-5 cells high and 12 cells wide at base); bracts and subfloral leaves grading into each other, maximally variable with vigor; on weak plants bracts and bracteole with a quadrate or subquadrate disk, often with a basal tooth on each side and/or a spinous cilium-like tooth on one or both sides of apex of disk; bracts quadrifid for 0.55-0.65 the length, the lobes setaceous, like leaf lobes but longer; subfloral leaves often larger, more leaf-like (disk obtrapezoidal, with usually a widely patent, rigid cilium on each side), 0.65-0.75 quadrifid, the lobes setaceous, as on leaves; vigorous plants with bracts, bracteoles and subfloral leaves more complex: bracts and bracteole as large or larger than subfloral leaves, 4-fid for 0.5-0.6, the disk higher than wide and ± oblong, armed on each side with 1-2 spinous teeth or cilia (chiefly near outer lobe bases), the lobes broader (to 4 cells wide at base), armed with 1-3 stiff, rigid cilia (of which 2 are occasionally opposed); subfloral bracts and bracteole similar, 0.55-0.65 quadrifid, with a similarly high, oblong disk, the lobes similarly armed. *Perianth* cylindrical-ellipsoidal, 430-500×1000-1350 μ, 3-plicate in distal 0.4-0.65, contracted (often greatly so) to the lobulate-ciliate mouth; cilia of mouth crowded, rigid, straight, (2)3-6 cells long, arising from a base 2 cells broad, to 225 μ long, formed of rigid cells (12-15×34-56 μ; terminal cells only 6-8×30-40 μ usually). *Seta* ca. 7 cells in diam., with 16-18 epidermal cell rows. *Capsule* short-ovoid, the wall 3-stratose;

FIG. 6. *Archeophylla pungens*

1. Perianth mouth (×47). – 2. Perianth-bearing shoot with ventral-intercalary branch (×32). – 3. Same, with two ventral-intercalary branches at asterisks (×32). – 4. Androecial shoot (×35). – 5. Perianth mouth (×158). – 6. Half of a mature leaf, cuticular papillae drawn in on some cells (×158). – 7. Subfloral leaf, discal cells, with maximal development of collenchyma (×205). – 8. Stem cross-section (×275). – 9. Dorsal cortical stem cells (×158). All from *RMS 66010*.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epidermal cells subequal to the inner two cell layers in thickness, with coarse nodular thickenings only of the 1-2 cell rows adjoining valve margins, other cells hyaline, pellucid, free of thickenings; interior cell stratum with conspicuous, numerous, I-shaped nodular thickenings only; innermost layer with cells irregular in shape, principally with I-shaped (nodular) thickenings, whose ends are dilated as spurs on the free tangential wall; occasional to frequent cells with some or all tangential spurs extended across, resulting in local semi-annular bands. *Spores* relatively finely granular-papillate, 12-13 μ in diam. *Elaters* short, very contorted, ca. 7-9 μ in diam. and 72-100 μ long, with a single, broad spiral, ca. 7-7.5 μ broad.

TYPE. Alerce (*Fitzroya*) Forest, Chaihuin-Colun, South Chile — *G. H. Schwabe 26 p.p.*

DISTRIBUTION. Known from the sparing type, which was growing over *Plagiochila* species (*P. elata*, *P. rubescens*, etc.) and the following specimens: Chile: Cabo Tres Montes, Prov. de Chiloe, Puerto Barroso — *Roivainen 1673* (S-PA); Argentina: Los Cantaros, N of Puerto Blest, W end of Lago Nahuel Huapi, 20.3.1961 — *RMS 66010*, with capsules and androecia copious!

VARIATION. An evaluation of this species is impossible with only type material at hand. Since androecia and mature perianths are present in my collection and in the optimally developed ROIVAINEN material, maturity of the material must be assumed. Thus, a reduced species of *Archeophylla* is at hand which forms a veritable model from which *Blepharostoma* can be derived by further simplification and reduction of the lamina [1]. As HERZOG points out, the species is very characteristic, with its remote stem leaves and underleaves, which are stiffly patent with their long and thin, setaceous lobes. The leaves become denser near the androecia and gynoecia and somewhat larger; the increase in size results from the elaboration of a higher discus. Such subperigonial and subperichaetial leaves grade imperceptibly into the ♂ and ♀ bracts. According to HERZOG (1961), ♂ bracts attain their definitive size only after maturation of antheridia, and are then distinct from vegetative leaves because of their "vergrössertem und ausgehöhltem Blattgrund". At the base of the androecia initially slender innovations may arise, which may again become androecial. Unfortunately, HERZOG fails to discuss the branching patterns of the species. In my material all of the hundred-odd branches studied were postical-intercalary, a single furcately oriented branch below an androecium, which was

[1] The strikingly similar, bluntly triplicate perianth, contracted to the ciliate mouth, is suggestive, as are the form of the leaf cells, cuticle and facies of the weakest plants. All of these, as well as stem anatomy, suggest *Blepharostoma*.

FIG. 7. *Archeophylla pungens*

1. Three subfloral leaves (×25). – 2. Seta cross-section (ca. ×285). – 3. Lobe and section of disk of leaf 4 (×140). – 4-6. Leaves (×35). – 7. Innermost bracts and, at left, bracteole (×25). – 8. Elater (×285). – 9. Underleaf, showing the " high " insertion of rhizoids (×96). – 10. Shoot-sector with ventral-intercalary branch above, Frullania-type branch below (×35). – 11. Large leaf (×96). – 12. Shoot-sector with intercalary androecium (×35). – 13. Large leaves (×35).

1-8. *RMS 66010*. – 9-13. Type.


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terminal and of the Frullania-type, excepted. Study of HERZOG's type revealed a further 20-odd branches, two of which only were lateral and terminal.

Within the genus, the species is unique in having leaves with lobes that are uniseriate virtually to the base, much as in *Blepharostoma* [1], and in the low disk, commonly only (2)3-4 cells high. Among other characters, the biseriate antheridial stalk and retention of a disk separate the species from *Blepharostoma* s. str.

In well-developed plants from Cabo Tres Montes I found numerous ventral-intercalary branches (and a single terminal, lateral branch). In the almost exclusively postical-intercalary branching, *A. pungens* occupies an isolated position and differs at once from any species of *Temnoma*.

DIFFERENTIATION. This species may prove troublesome to recognize when sterile since, because of the dwarf size, it may be confused with the very similar *A. paradoxa*. It agrees with this in the low and entire disk of the leaves and in the largely uniseriate, strongly striolate, edentate leaf lobes. Differences from *A. paradoxa* are as follows: (1) the uniseriate leaf lobes are 8-11(12) cells long; (2) the disk is lower and narrower, never over 4 cells high; (3) perichaetial bracts, as in *Archeophylla schusteri*, tend to be smaller and narrower than subinvolucral leaves; they may have entire lobes, although at least the outer lobe on one or both sides may have a basal cilium; the disk is often entire, a basal tooth excepted.

A. pungens differs from *A. schusteri* in the coarsely verrucose-striolate cuticle; the setaceous leaf lobes, uniseriate almost to the base; the less deeply lobed and simpler subinvolucral leaves and gynoecial bracts; the almost exclusively postical-intercalary branches; the much less coarsely collenchymatous leaf cells. In the coarsely striolate cuticle and the less conspicuous development of trigones, and their lesser definition, *A. pungens* suggests *A. paradoxa*, also of Chile. However, gynoecia of these two species are drastically different—the ovoid, spinose-ciliate, compact gynoecium of *A. paradoxa* finding no parallel in the more highly reduced one of *A. pungens* [2]. Also, the leaves and underleaves of *A. paradoxa* have 2-3-4-

[1] The uniseriate lobes suggest *Temnoma quadripartitum* var. *pseudopungens*; that taxon, however, has a much higher disk and has the bases of the uniseriate lobes commonly armed with a stiff tooth on each side.

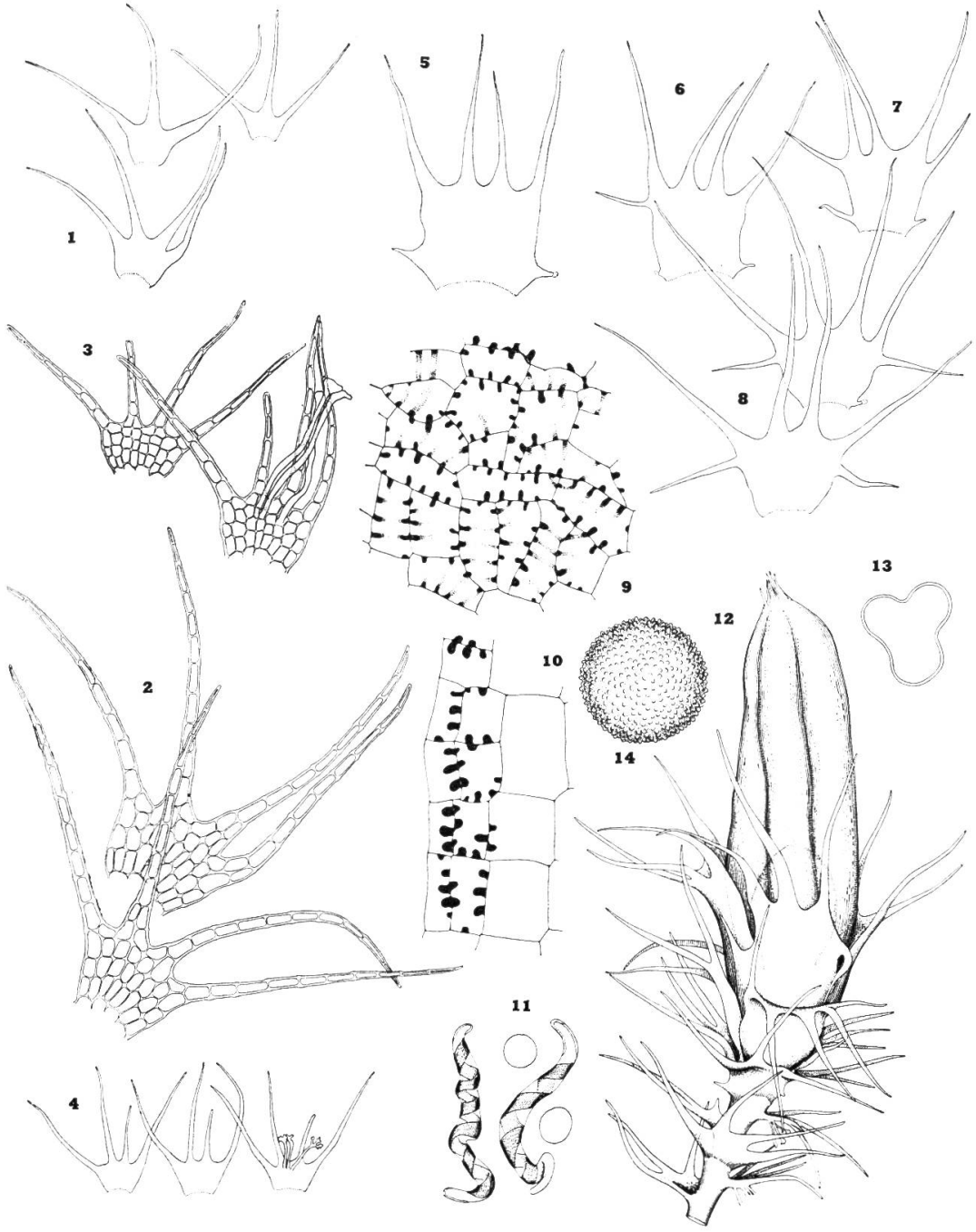
[2] In both collections of *A. pungens* with gynoecia the young gynoecia — without developed perianths — have strongly spreading bracts, mutually sheathing only on the disk, the attenuated lobes, at least, being spreading to even subsquarrose. Furthermore, bracts and subfloral leaves are not closely mutually imbricate. Thus the gynoecium of *A. pungens* is much more comparable to that of *A. schusteri* than to that of *A. paradoxa*.

Bracts and subfloral leaves in *A. pungens* seem to be extremely variable. The plants of ROIVAINEN (Cabo Tres Montes) have simpler gynoecia; subfloral bracts are 0.6-0.75 quadrifid,

FIG. 8. *Archeophylla pungens*

1. Three mature leaves (×45). – 2. Two mature leaves (×100). – 3. Two underleaves (×100). – 4. Three underleaves; note branched rhizoid apices, and origin of rhizoids high on disc (×45). – 5-6. Bracts of simple configuration (×45). – 7. Bracteole from same gynoecium (×45). – 8. Two subinvolucral leaves (×45). – 9. Innermost cells of capsule wall (×300). – 10. Epidermal cells of capsule wall, the valve margin at left (×300). – 11. Spores and elaters (×275). – 12. Perianth-bearing shoot; note tightly contracted mouth (×36.5). – 13. Apical 1/3 of perianth, in cross-section (×36.5). – 14. Spore (×1040).

1-8. *Roivainen 1673*. – 9-13. *RMS 66010*.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seriate lobes for much if not most of their length. The almost exclusively postical-intercalary branching of *A. pungens* is without an exact parallel in *A. paradoxa*.

The account of this species in FULFORD (1963) is defective in several ways: (1) she states rhizoids have not been seen; in the type, and both other collections studied, rhizoids are diagnostically abundant—as in the other two species of the genus; (2) her description is based on the male plant of *A. pungens* (insofar as this is derived from HERZOG's account), but the female plant of *A. paradoxa*! That description is thus composed of interwoven strands derived from two fully distinct taxa.

It is ironic that FULFORD places this species in *Temnoma*—a genus she describes as with exclusively lateral, terminal, Frullania-type branches—in spite of the fact that branching is almost wholly postical-intercalary.

The capsule of *A. pungens* is relatively short-ellipsoidal; its wall is, on the two examined capsules, uniformly 3-stratose. Epidermal cells, as in *Temnoma*, are hyaline and lack thickenings except adjoining the sutures. In this respect the species forms a transition to *Temnoma*. However the elaters are broadly unispiral as in *A. schusteri*, the type of the genus, and the perianth shows the identical very strong contraction to a tightly closed mouth. (Since even in *Temnoma quadrifidum* epidermal cells away from the valve margins may bear, here and there, nodular thickenings, criteria derivable from the epidermal cells are relatively ambiguous; evidently both genera show some variation in this respect.)

Archeophylla paradoxa Schust., Trans. Brit. Bryol. Soc. 4:810. 1965.

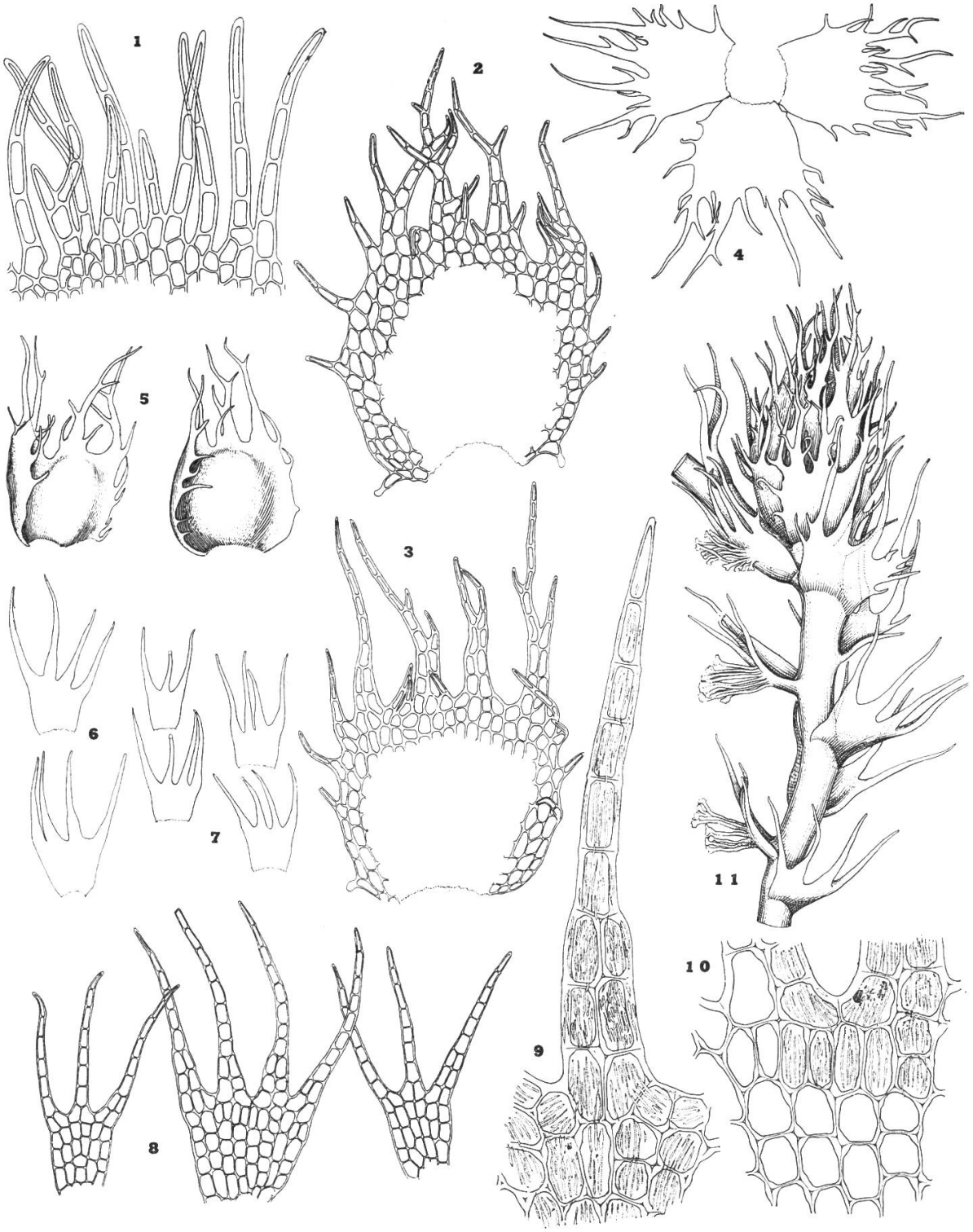
Plants light brown to yellow-brown, with leaves 600-920 μ wide and usually 8-20 mm long, procumbent to ascending in growth, sporadically and irregularly branched; branches of two types: postical-intercalary and (more rarely) lateral, terminal, of the Frullania-type (with bifid supporting stem leaf dorsal in position). *Stem* ca. 95-105 μ in diam., flexuous, terete, brown, slender, rather wiry; cortical cells in ca. 12 rows only, larger than medullary but not forming a hyaloderm, opaque and feebly thick-walled, striolate, 24-27(30) μ wide, 16-24 μ high and (30)36-45(60) μ

each side of the disk having a single spreading, long cilium; the bracts proper are smaller or no larger at least, are 0.55-0.65 quadrifid, without teeth of the lobes, but with the disk bases usually armed with solitary teeth and occasionally with a cilium of the disk apex below the lateral lobe bases (fig. 8/6). In the more vigorous plants, (*RMS 66010*, Los Cantaros) the subfloral bracts and bracts proper are more complex. Subfloral bracts are 4-5-lobed for 0.6-0.7, with often 1-3(3-4) slender cilia per lobe, of which rarely 2 are opposed. The bracts proper are much like the subfloral bracts, somewhat larger, sometimes only 0.5-0.55 quadrifid and no more copiously armed—again with, occasionally, a pair of cilia on a lobe, which may be opposed—reminiscent of the condition in *Temnoma*, even though the vast majority of cilia are single and non-opposite.

FIG. 9. *Archeophylla paradoxa*

1. Perianth mouth cells (×210). – 2-3. Female bracts of innermost series (×75). – 4. Subfloral cycle of bracts (×35). – 5. Two outer, subfloral bracts (×35). – 6. Two leaves (×35). – 7. Four underleaves (×35). – 8. Three leaves, the middle one of optimal size (×70). – 9. Leaf lobe, showing cells and cuticular papillae (×220). – 10. Cells of sinus and of two lobe bases (×220). – 11. Lateral aspect of female plant with unfertilized gynoecium and ventral-intercalary innovation (×41).

All from type.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long, in outline from subquadrate to short-oblong to oblong; medullary cells in ca. 12-15 rows only, (12)13-18 μ in diam., collenchymatous. *Rhizoids* sparse to frequent, arising rather above underleaf bases. Stems nearly isophyllous; lateral *leaves* remote, stiff, transverse to succubous-transverse (to 10-15° succubously oblique), nearly vertically oriented, suberect to obliquely spreading, never squarrose, obdeltoid to obtrapezoidal in outline, usually palmately 4-lobed (on weaker shoots, or near origin of mature shoots, often largely 3-lobed), 300-520 μ wide and 470-565(600) μ long; sinuses descending 0.55-0.65 the leaf length, the narrowly obtrapezoidal disk 5-6 cells high, entire-margined, setaceous and stiff, 2(3) cells wide at base, 2-seriate for basal 1-3 cell tiers, the apices uniseriate for 7-10 cells; sinuses V-shaped but with bases narrowly rounded, lacking knot-like groups of cells. *Underleaves* large, 3-4-lobed for 0.55-0.75(0.7) their length, narrowly obtrapezoidal, 250-300 μ wide and 300-365 μ long, rarely larger; sinuses and lobes as on leaves, but lobes narrower and slenderer, often unequal (1 or 2 slightly abbreviated). *Cells* firm, rigid, closely and conspicuously papillose-striolate; terminal cells of lobes ca. 8-10×43-48 μ (4 : 1 — 6 : 1); cells within uniseriate sectors of lobes ca. 20-24×(25)30-38 μ; median cells of disk (15)18-22(24)×24-36(38) μ; basal cells (18)20-25×30-45 μ. No *asexual reproduction* but possible reproduction by regeneration from the rather frequently caducous tips of leaf lobes. Plants dioecious; ♂ plants unknown; *gynoecia* on leading leafy shoot-apices, with subfloral innovations (if no sporophyte forms); unfertilized gynoecia forming a compact, ± ovoid spinose head, somewhat approaching that of *Chaetocolea*. *Bracts* in 2-4 progressively larger, closely imbricate series, except the innermost, which are usually smaller; subfloral (largest) bracts closely sheathing inner bracts and virtually hiding them, 4-5-lobed, broader than long to obtrapezoidal-quadrate (to ca. 750×750 μ), the lobes with alternate, spinose teeth and stiff cilia; innermost bracts oval to ovate, narrow-based, 425-550(620) μ wide and 700-800(850) μ long, 4-lobed for 0.45-0.55 their length, strongly concave, almost conchiform; lobes seemingly irregularly ramified because of the alternate cilia and spinose teeth, acuminate distally, 3-4 cells wide at base, erect (never divergent), the non-opposed spinose cilia of (1)2-4 elongated, rigid cells; disk margins with 2-4(5-6) spinose, often incurved, 2-4-celled teeth; disk quadrate-orbicular, concave. *Perianth* (juvenile) with crowded, slender cilia at mouth; cilia 4-7 cells long, often asymmetrically furcate (with a short, 1-2-celled "branch"); terminal cells linear, to 7-9×40-50(64) μ, rigid.

TYPE. South America: Otway Harbor, Gulf of Peñas, "Patagonia", Jan. 1876 — *Moseley, Challenger Expedition* (K).

Known only from the type material, which had lain, misidentified, in the Kew Herbarium for nearly a century. The type plants grew amidst a filmy fern in large quantity—evidently on a rock face. This is the same plant erroneously assigned to *Temnoma pungens* by FULFORD (1963).

DIFFERENTIATION. A distinctive species, similar to *A. schusteri* in the remote, essentially transverse, vertical leaves with narrowly lanceolate-acuminate, rigid, smooth lobes; in axial anatomy; in color; in branching patterns; in the tendency for some leaves even on reasonably mature shoots to be trifid, while weak shoots

show gross variation in leaf-lobe number; in the feebly elongated cells of the leaf disk, which have a very sharply demarcated middle lamella and distinct trigones; and in the tendency for 1-2 underleaf lobes to be partly aborted.

A. paradoxa, however, is amply distinct from *A. schusteri*, principally in (1) the much less conspicuous development of collenchyma; collenchyma production may indeed be virtually lacking in the ♀ bracts; (2) the closely and obviously roughened cuticle; (3) the much lesser level of anisophylly; (4) the lesser polymorphism in leaf-lobe number—mature shoots having the vast majority of leaves and underleaves quadrifid; (5) the somewhat less setaceous leaf lobes, uniseriate for a shorter distance; (6) the narrower leaf lobe bases; (7) the very different gynoecium.

Unfortunately, gynoecia with mature perianths are unknown in *A. paradoxa*. However, the capitate, ovoid, compact gynoecia seen (they were present in abundance) are unique. They remind one more of the gynoecia of *Chaetocolea* than of *A. schusteri*. The innermost bracts, as in *A. schusteri*, tend to be reduced in size, as contrasted to the bracts of the next outermost series, and are uniquely concave, with the strongly armed lobes narrow, erect and almost subramified in a staghorn-like fashion (the monopodially produced spinose cilia " pushing " the lobe somewhat to one side).

In most of the criteria cited above that separate *A. paradoxa* from *A. schusteri*, the first species is clearly more primitive, e.g. in criteria (1), (2), (3), (4), (5). In these five criteria, *A. paradoxa* agrees with *Temnoma* and serves to establish some connection with that genus.

LOPHOCHAETE

Lophochaete Schust., Rev. Bryol. et Lichén. 26 : 126. 1957; Schuster, The Bryologist 61 : 25,50. 1958; Schuster, The Bryologist 62 : 237. 1959; Scott, Nova Hedwigia 2 : 160. 1960; Schuster, Jour. Hattori Bot. Lab. 23 : 197, fig. I, 1-11. 1961; Schuster, Nova Hedwigia 5 : 42. 1963; Schuster, Jour. Hattori Bot. Lab. 26 : 209, 261. 1963.
Pseudolepicolea Fulf. et Tayl., Nova Hedwigia 1 : 412. 1960.

TYPUS. *Lophochaete fryei* (Perss.) Schust.

Plants moderate in size, usually yellowish to golden brown to fuscous; *stems* erect or suberect, irregularly, sparingly branched; branching lateral, axillary, from the axil of a normal leaf or underleaf, or terminal and of Frullania-type (rarely of the Microlepidozia- or Acromastigum-type; rarely with basiscopic, Radula-type lateral branching). *Stem* essentially isophyllous (ventral merophytes 6 or more cells wide), erect or ascending in growth, the cortical cells in 20-24 rows, barely or not larger than the medullary, slightly to strongly equally thick-walled, usually not highly differentiated; cortical cells rectangulate, 5-8× as long as wide; medullary cells in numerous rows (the medulla to 8-10 cells high), the cells slightly to very much thick-walled. *Leaves* symmetric, nearly transversely inserted, obtrapezoidal, the dorsal portion rarely succubously oblique, typically bisbifid to within 4-6(9) cells of base into 4 lobes, rarely with accessory lobes (then 5-8-lobed), the lobes

(3)4-8 cells broad at base, their margins entire. *Cells* with cuticle smooth or feebly roughened, the walls varying from thin to equally thick-walled. *Underleaves* similar to leaves, usually 4-lobed like them, with margins similarly entire. *Rhizoids* few, restricted to bases of underleaves (a few sometimes at bases of leaves). *Gemmae* absent. Plants dioecious or monoecious; *androecia* spicate; ♂ *bracts* like leaves, usually (3)4-lobed, often less deeply so than leaves (0.5-0.8 their length), the lobes sometimes broader, saccate at base; *bracteoles* like normal underleaves, lacking antheridia; *antheridia* 1 or 2 per bract; stalk biseriate; antheridial jacket layer of numerous cell rows, relatively irregularly oriented, not in sharply defined tiers; paraphyses absent. *Gynoecial* branches in the form of long, leafy shoots; *bracts* nearly identical to leaves, not or little larger, rarely with accessory lobes and/or non-opposed teeth; *bracteole* free from bracts, like normal underleaves, not or little larger, rarely with accessory lobes and/or non-opposed teeth. *Perianth* long, longly exserted at maturity, cylindrical below, but distal half or more strongly plicate, the plicae (3)4-5(6), with occasional weak supplementary folds; mouth strongly contracted, crenulate on the margins of the numerous lobes; with fertilization the perianth becoming markedly stipitate. *Sporophyte* boring only moderately into axis, its foot not descending below level of insertion of the bracts. *Seta* with 14-16 rows of epidermal cells, including 2 rings of cells within (the outer with 10-12 cell rows, the inner with 4 cell rows), thus 6 cells in diam.; with weak formation of a stem calyptra, the sterile archegonia elevated. *Capsule* broadly ellipsoidal, its wall 2-stratose; epidermal cells ca. 25-30 μ high; inner cell layer 15-20 μ high (immature capsules; thickenings not yet developed); capsule wall yellow-brown and very translucent (as contrasted to the purplish-brown and opaque capsule of *Temnoma*), bistratose, the epidermal cells 25-27 μ thick usually, the inner layer much smaller and 11-13 μ thick (total thickness usually 36-40 μ); epidermal cells with free wall exceedingly thin and delicate, not thickened; both transverse and longitudinal radial walls each with (1)2(3) vigorous yellow-brown nodular thickenings (in cross-section of valve appearing band-like), which extend only slightly on to the tangential walls as weak spurs; epidermal cells in surface view subquadrate to short-oblong, ca. 25-28 × 20-22 μ to 22-25 × 32-35 μ on an average; inner cell layer of rather regularly oblong cells in tiers (in the middle and bases of the valves), averaging (11)14-16(19) μ wide and 50-60 μ long, with strong, yellow-brown semi-annular to annular bands, the bands almost always complete on the free (inner) tangential faces. *Spores* light brown and translucent, finely and minutely granular-papillate, ca. 14-17.5 μ in diam., nearly twice the diam. of the elaters (which are 8-10 μ in diam. and bear 2 brownish spirals ca. 3 μ wide).

Following are the basic diagnostic features: erect to suberect growth; subsimple to sparingly branched stems, with irregular branches; transverse insertion of leaves, with the leaves symmetrically bisbifid and their margins not ciliate, the lobes 3-4 or more cells broad at base; gynoecia never regularly with innovations; perianth large, emergent, without perigynium at base, smooth externally, 4-5(6)-plicate at the contracted, ± closed mouth; sporophyte with capsule wall 2-stratose, the epidermal layer bearing thickenings; spores twice the diameter of elaters; antheridial stalk biseriate.

In the original diagnosis, validation of *Lophochaete* is by latin diagnosis of the sole included species, *Lepicolea fryei* Perss. (The Bryologist 49 : 47. 1946) [1]. The genus has been more recently discussed in SCHUSTER (1959 : 237), where a second species, *Blepharostoma quadrilaciniatum*, is referred to *Lophochaete*. Subsequently, a detailed, illustrated morphological study was published (Schuster 1961).

FULFORD and TAYLOR (1960) published the name *Pseudolepicolea*, with *B. quadrilaciniatum* as generic type ; this species was placed (Schuster 1959, 1961) into *Lophochaete*. If, as I assume, this last species is congeneric with *Lophochaete fryei*, *Pseudolepicolea* is a synonym of *Lophochaete*. FULFORD and TAYLOR state they saw no fertile material. Although they describe the ♂ plant, they copy SCHIFFNER's (1911) figure of a ♂ bract and their figure of an antheridium (fig. 30) is meaningless since it fails to show any detail as regards (1) stalk and (2) orientation of cells in the jacket.

The antheridial stalk of *Lophochaete* differs from that of *Blepharostoma* in being 2-seriate (Schuster 1957); I further emphasized (Schuster 1961) that the jacket layer was of " numerous cell rows, relatively irregularly oriented, not in... tiers ". *Blepharostoma* s. str. has antheridia with uniseriate stalks, and with the jacket layer of the antheridium, at least when young, formed of tiers of elongated cells. Any evaluation of the status of *Pseudolepicolea* must involve antheridial anatomy. Similarly, in *Lophochaete fryei*, the ♂ bracts bear only one antheridium (Schuster 1961).

The attempt by FULFORD and TAYLOR (l. c.) to place *Lophochaete* (*Pseudolepicolea*) in a separate family, the *Pseudolepicoleaceae*, proposed entirely on gametophytic criteria, is untenable. In a recent study (Schuster 1961) I concluded that *Lophochaete* and *Blepharostoma* belong to a single family in spite of differences between them in (1) perianth cross-section; (2) leaf form; (3) antheridial stalk; (4) asexual reproduction or its absence; (5) capsule-wall anatomy—criteria not studied by FULFORD and TAYLOR. My study of the capsule wall showed that both genera have a bistratose capsule wall, although considerable differences in anatomy occur. Furthermore, branching patterns and isophylly of the two groups were much the same. [2] The similarities between *Lophochaete* and *Blepharostoma* were further pointed out (Schuster 1961), thus there is little point in repeating them here.

Although originally a segregate from *Lepicolea* s. l. and *Blepharostoma* s. l., *Lophochaete* has affinities primarily with the two genera *Herzogiaria* and *Isophyllaria*. The three genera share almost perfect isophylly, a fuscous color, equally thick-walled leaf cells and other characters. *Lophochaete* differs from both of these genera in the almost constantly terminal, Frullania-type lateral branching; it further differs from *Herzogiaria* in the unistratose leaves and lack of swollen nodose areas at the bases of the leaf sinuses. The bisbifid leaves, of course, easily separate *Lophochaete* from *Isophyllaria*.

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[1] International Code of Botanical Nomenclature 1961, Article **32** and Article **39**; validation by " reference to a previously and effectively published description of the genus as a subgenus, section, or other subdivision of a genus ".

[2] The occasional presence of Microlepidozia-type terminal branches and postical-intercalary branches in *Lophochaete quadrilaciniata* can be exactly matched in *Blepharostoma trichophyllum*. The statement by HOLLENSEN (1964) that only Frullania-type branches occur in *B. trichophyllum* is in error.

In my opinion, *Lophochaete* is diagnosed by the almost constantly terminal, Frullania-type branching. No other branching has been found in *L. fryei*, the type of the genus, and in the two allied taxa *L. trollii* and *L. andoi*; in the neotype of *L. quadrilaciniata* I have studied scores of branches and, with two doubtful exceptions, found only Frullania-type branches. In the doubtfully distinct *L. quadrilaciniata* var. *georgica* I have seen one Microlepidozia-type branch and two postical-intercalary branches. I suspect that, Frullania-type branching aside, all other branching modes in *Lophochaete* represent sporadic atavistic reversions to less-fixed ancestral branching modes. This seems to be also true of the frequent basiscopic lateral branches, of the Radula-type, which occur in *L. quadrilaciniata* var. *pleomorpha*.

FULFORD (1963) regards *Pseudolepicolea* as distinct from *Lophochaete*. I think a generic distinction cannot be maintained, and place the former as a subgenus of the latter (Schuster 1963). ANDO (1963) has also recently treated the two groups as one genus, adopting the name *Pseudolepicolea*. In my opinion, *Lophochaete* represents a valid earlier name. The distinctions between the two groups, which are slight, emerge from the subjoined key to species.

Key to species and varieties

1. Leaf insertion strictly transverse; leaf cells often ± tiered; branching exclusively terminal, Frullania-type; cortical cells of stem not or almost imperceptibly smaller than medullary cells; no dentition of ♀ bracts. Northern Hemisphere . . . . . Subgen. *Lophochaete* 2

1*. Leaf insertion usually feebly incubous; cells in leaf lobes never tiered; branching variable: partly terminal (Frullania-, Microlepidozia- and Acromastigum-types, all sporadically present!), partially intercalary; occasionally also with basiscopic, lateral terminal branches; stem with cortical cells distinctly smaller than the medullary; dioecious; perianth 5-plicate. Southern Hemisphere
Subgen. *Pseudolepicolea* (Fulf. et Tayl.) Schust.
L. quadrilaciniata (Sulliv.) Schust. 4

2. Autoecious; interior cells of lobes 16-24 × 30-40 μ; cells in lobes much less elongated (mostly 1.5-2.5 : 1); marginal cells not with dilated and produced septa, lobes not crenulate, lanceolate, never setaceous; always with leaves and underleaves bisbifid, never trifid (supporting stem leaf of branch bifid); cuticle smooth; perianth mouth shallowly lobulate, the lobes denticulate at most; perianth 4-plicate above. Arctic North America, E Siberia
L. fryei (Perss.) Schust.

2*. Dioecious; interior cells of lobes 10-15 × 45-64 μ; cells in leaf lobes strongly elongated (mostly 3-6 : 1); marginal cells of lobes with transverse septa dilated outwardly, the lobes conspicuously crenulate; lobes often nearly setaceous; cuticle finely but conspicuously granulate-papillate; perianth mouth deeply 12-lobed, the lobes acute to acuminate; perianth 6-plicate above 3

3. Leaves and underleaves consistently bisbifid, even on weak, slender shoots; plants silky, the leaf lobes (of all but most vigorous plants) slenderly setaceous, only 2-4 cells broad at base; leaf lobe apices commonly uniseriate for a length of (2)3-4 cells; supporting stem leaf, at base of branch, always 2-fid; underleaves differing from leaves: usually with widely spreading lobes Japan, China . . . . . *L. andoi* Schust.

3*. Leaves and underleaves variable, (2)3-4-lobed intermixed on same stem, even on mature shoots; plants more rigid, not silky, the lobes sometimes slender but never silky-setaceous, usually 4-6 or more cells broad at base; leaf-lobe apices uniseriate for 1-2 cells at tip; supporting stem leaf 1-2-lobed; underleaves and leaves almost perfectly identical. Sikkim-Himalaya *L. trollii* (Herz.) Schust.

4. Leaves, underleaves and bracts polymorphous: sporadic to most appendages of mature axes with 1-4 accessory lobes, thus 5-8-fid; ♀ bracts and bracteoles ± resolved into accessory lobes, armed with scattered sharp teeth; with Radula-type lateral basiscopic branches (plus Frullania-type lateral branches) *L. quadrilaciniata* var. *pleomorpha* Schust.

4*. Leaves, underleaves and bracts regularly bisbifid, devoid of accessory lobing; ♀ bracts, subfloral leaves and bracteoles bisbifid, lacking accessory lobes, lacking dentition; no Radula-type basiscopic lateral branching developed 5

5. Leaf lobes narrow, slenderly lanceolate, 5-9× as long as wide, 4-5(6-7) cells wide at base; apical cells of lobes elongate, ca. 2-3× as long as wide *L. quadrilaciniata* var. *quadrilaciniata*

5*. Leaf lobes shorter, narrowly triangular-lanceolate, 3.5-5× as long as wide, 6-8 cells broad at base; apical cells hardly elongated, little longer than broad *L. quadrilaciniata* var. *georgica* (Steph.) Schust.

Lophochaete subgen. **Pseudolepicolea** (Fulf. et Tayl.) Schust., Nova Hedwigia 5 : 42. 1963.

Pseudolepicolea Fulf. et Tayl., Nova Hedwigia 1 : 412. 1960.

TYPUS. *L. quadrilaciniata* (Sulliv.) Schust.

The subgenus contains only the type species (I regard *L. georgica* as, at best, a weakly differentiated variety of *L. quadrilaciniata*).

Branching plastic: typically and sometimes almost solely of the Frullania-type, less often (sporadically at best) of the Microlepidozia- and exceptionally of the Acromastigum-type; sporadic to rare intercalary branching from older shoot-sectors, usually ventral, rarely lateral; some phenotypes with basiscopic, terminal, lateral Radula-type branches. *Stem* with cortical cells differentiated as a 1-stratose layer of smaller, often thicker-walled cells vis-à-vis the medullary cells. *Leaves* and *underleaves* bisbifid, with lobes formed of little elongated cells, not in tiers, the distal ends not angularly produced along margins (lobes thus quite smooth); leaves and underleaves sometimes with 1-4 accessory lobes, 5-8-lobed. Plants dioecious;

perianth 5-plicate. ♀ *Bracts* and *bracteoles* bisbifid or with accessory lobing, the margins entire or sporadically sharp-dentate.

L. quadrilaciniata is one of the most extraordinarily polymorphous species I have studied, as regards criteria often considered as of familial or generic importance. FULFORD and TAYLOR (1960 : 411-412) base their family *Pseudolepicoleaceae* and genus *Pseudolepicolea* on the presence of " branches of the terminal and axillary intercalary types" with the terminal branches of "the Frullania- and the Microlepidozia-types ". SCHIFFNER (1912 : 279-280) correctly described lateral terminal branching of the usual (Frullania-) type, as well as of the less common Microlepidozia-type, and incorrectly considered the 2- or 3-fid supporting leaf as belonging to the branch, as the primary branch leaf—chiefly because he was unwilling to admit " eine solche Anarchie in den Verzweigungsvorgängen ein und derselben Pflanze ". The " anarchy " in branching modes becomes even more striking when copious (personally collected) material is studied. Thus, in my material *(RMS 58343)*, assigned to a var. of *L. quadrilaciniata*, I could find only two types of branches: Frullania-type terminal branches and basiscopic, lateral, Radula-type terminal lateral branches ! The latter—sometimes found two or three from a single plant—arise smoothly from the parent axis, and, as in *Radula*, tend to be connate at their bases with the associated stem leaf.

Radula-type branching is exceedingly rare in families (and suborders) aside from the *Porellinae*, in which it appears confined to the *Radulaceae* and the gynoecia of *Lejeuneaceae*. However, I have found it to occur sporadically in several primitive species of *Scapania* (*S. obcordata* and allies), in several species of *Schistochila* and now in the present taxon.

Within *L. quadrilaciniata* one also finds excessive variation in lobing of the leaves, underleaves and bracts. Thus in *RMS 58343* it is " normal " to find mature, robust shoots with one to several accessory lobes of many or most leaves and underleaves, and of the ♀ bracts and bracteoles. The latter, furthermore, may develop scattered sharp accessory teeth as well. Such variability in leaf lobe and bract lobe number is quite lacking in the subgen. *Lophochaete*, except that sometimes one lobe per leaf and/or underleaf may be suppressed.

Lophochaete quadrilaciniata (Sulliv.) Schust., Jour. Hattori Bot. Lab. 23 : 199. 1961.
Sendtnera quadrilaciniata Sulliv. in Hooker, Jour. Bot. 2 : 317. 1850.
Leperoma (?) *quadrilaciniata* (Sulliv.) Massal., Nuovo Giorn. Bot. Ital. 17 : 253. 1885.
Lepicolea quadrilaciniata (Sulliv.) Steph., Sv. Vet.-Akad. Handl. 26/3 : 56. 1900.
Lepicolea georgica Steph., Sv. Vet.-Akad. Handl. 46/9 : 73. 1911.
Blepharostoma quadrilaciniatum (Sulliv.) Schiffn., Hedwigia 51 : 282. 1912.
Pseudolepicolea quadrilaciniata (Sulliv.) Fulf. et Tayl., Nova Hedwigia 1 : 413. 1960.
Pseudolepicolea georgica (Steph.) Fulf. et Tayl., l. c. : 416. 1960.

Plants usually in pure, extensive cushions, often in small montane brooks, over rocks, where subject to inundation, or permanently semi-submerged, fuscous,

usually 3-6(7-8) cm tall and 2-2.5(3) mm wide with leaves, erect in growth, with sparing, irregular branching; branches predominantly terminal-lateral, of the Frullania-type (rarely and sporadically of the Microlepidozia-type; exceptionally postical-terminal, of the Acromastigum-type); old and non-thrifty shoot-sectors sporadically with postical-, less often lateral-intercalary branches; occasionally with Radula-type basiscopic branches. *Stem* ellipsoidal in cross-section, soft-textured, ca. 250-285(360) μ in diam., with 1 stratum of reasonably distinctly defined, smaller, feebly or hardly thick-walled, often slightly tangentially flattened cortical cells, ca. (16)18-24 to 24-28 μ wide and 90-150 μ long; medulla ca. 6-7 to 11-12 cells high, of variably large, leptodermous cells ca. (22)25-36 μ in diam. *Leaves* almost perfectly transverse to ± incubous, subcontiguous to moderately imbricate, usually lax, often quite flaccid, broadly cuneate to obdeltoid, to ca. 1150-1275 μ long and 1025-1850 μ wide distally (lobe tips), bisbifid (exceptional leaves trifid or with one to several accessory lobes), median sinus descending ca. 0.65-0.75 the leaf length, the lateral sinuses to 0.55-0.6 the leaf length; disk ca. 4-5 to 8-12 cells high, entire-margined; lobes variable, ranging from 4-5 cells broad (var. *quadrilaciniata*) to 5-8(9-12) cells wide (var. *georgica*, *pleomorpha*), narrowly lanceolate, acuminate, the outer diverging typically at a wide angle (var. *quadrilaciniata*) to less divergent (var. *georgica*), terminating at the apex in a row of (2)3, rarely more, slightly to moderately elongated cells: basal cell of row ca. 25-28 μ wide and 34-40 μ long, median cell ca. 20-22 μ wide and 24-28 μ long, terminal cells ca. 15-16 (20)×23-36 μ, 1.4-2.25× as long as wide; cells at sinus bases sometimes forming a small, swollen group, at other times not differentiated. *Cells* leptodermous, striolate to almost smooth, in middle of disk ca. 20-27×36-72 μ to 18-24×45-70 μ, at lobe bases ca. 22-26×30-40 μ. *Underleaves* almost identical in form and size to leaves. No *asexual reproduction.* Plants dioecious; *androecia* becoming intercalary on leading stems; bracts and bracteoles in 3-8(10) series; *bracts* similar to smaller leaves, bisbifid, much less deeply lobed than leaves, the entire expanded disk concave, with typically 2 antheridia; *bracteoles* flat, like underleaves but often somewhat smaller. *Gynoecia*, if fertilized, without innovation. *Bracts* and *bracteoles* erect-sheathing, little differentiated from leaves, progressively somewhat larger, sometimes with accessory lobing, denser, with somewhat spreading lobes; lobe and disk margins subentire or entire ranging to armed with several sharp, non-opposed accessory teeth. *Perianth* ovoid-cylindrical, bluntly 5-plicate above, the contracted mouth ciliate.

TYPE. Tierra del Fuego — *Wilkes Expedition* (lost). Neotype: Chile, Rio Aysen Valley, on rocks, Jan. 1897 — *Dusén* (FH, G, K, NY, W).

The original specimen of *S. quadrilaciniata* Sulliv. was a specimen collected in Tierra del Fuego by the members of the Wilkes Expedition. The type appears to be lost; neither FULFORD and TAYLOR (1960) nor I could locate it at the Farlow Herbarium or at the U.S. National Herbarium—the two logical places where it might conceivably be housed; I have also looked for it, unsuccessfully, at Geneva, Vienna and in London (Kew and British Museum). In view of this, a neotype must be proposed, and I suggest the collection of Dusén be so considered. (This collection cannot serve as a "lectotype", as FULFORD and TAYLOR—1961: 414—suggested.)

DISTRIBUTION. Southernmost South America. Specific loci are cited under the varieties recognized.

DIFFERENTIATION. Differing immediately from other species assigned to *Lophochaete* in the smooth margins of the lobes of both leaves and bracts; the stem anatomy; the occasional, if rare, presence of Microlepidozia-type and ventral-intercalary branches; and the marked tendency in certain collections (including plants of the neotype) to have incubously oriented and feebly incubously inserted leaves.

VARIATION. I regard *L. quadrilaciniata* as a polymorphous species, showing, much as does *Temnoma quadripartitum*, considerable differences in vigor, associated with which the leaf lobes may be more or less attenuated. Extremes are regarded by FULFORD and TAYLOR (1960) as constituting two distinct species. My reasons for considering these two as conspecific are detailed under var. *quadrilaciniata*. The very aberrant plants from Cerro Garibaldi are assigned to a third variety, var. *pleomorpha*. These extremes are separated by the preceding key.

L. quadrilaciniata (Sulliv.) Schust. var. **quadrilaciniata**.

Plants with leaves and underleaves bearing narrower and typically longer lobes, usually (3)4-5(6) cells wide, very slenderly acuminate, the outer lobes often squarrose and strongly divaricate; leaf and underleaf lobes often characteristically twisted, often nearly flaccid; plants with leaf lobe number fixed: the leaves (and underleaves) of mature stems always bisbifid. Branching almost always of the Frullania-type, less often of the Microlepidozia-type; rarely with intercalary branching; apparently never with basiscopic branching of any type.

DISTRIBUTION. Chile: neotype collection. Argentina: Rio Grande, Tierra del Fuego, 25.1.1896 — *P. Dusén* (W), as " Azorella-Moose "; Valle Carbajal, Tierra del Fuego — *RMS 48732a*; Rio Harubre Valley, N of Ushuaia, Tierra del Fuego — *RMS 50429*; Fuegia, no other data — *Dusén 216* (G) [1]; no other data — *Dusén 244* (G) ♂, typical.

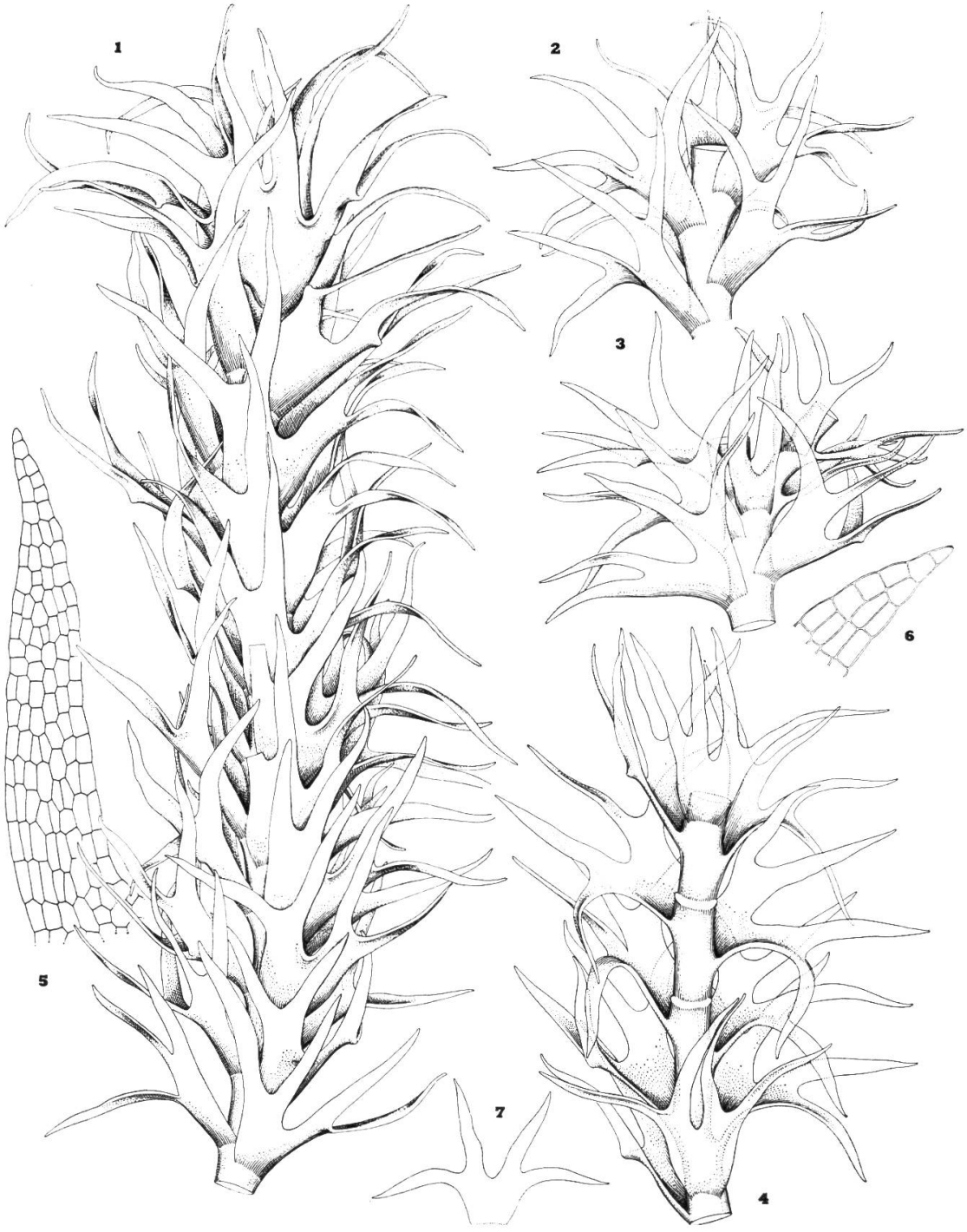
ECOLOGY. This abundant taxon occurs under a diversity of conditions, often where inundated, or where subject to periodic inundation, in montane rills. On moist soil between rocks, at stream edges *(RMS 48732a)*, it is associated with *Austrolophozia fuegiana*, *Triandrophyllum subtrifidum*, *Clasmatocolea* spec., *Balantiopsis* spec., etc.

[1] This is also cited as *L. quadrilaciniata* by FULFORD and TAYLOR; however, it has the leaf lobes much broader on mature leaves, varying on one leaf from 8+10+10+9, on another from 7+8+7+7. Also, the cells of the leaf tips are not elongated and are almost isodiametric; the leaf lobes are not strongly divergent. The plant keys to " *L. georgica* " in FULFORD and TAYLOR !

FIG. 10. *Lophochaete quadrilaciniata* var. *quadrilaciniata*

1. Shoot with gynoecium at apex (×16.3). – 2. Shoot-sector in antical aspect; note the feebly incubous insertion and orientation of the leaves (×21). – 3. Same, with a Frullania-type branch and bifid associated stem " half leaf " (×21). – 4. Shoot-sector, ventral aspect, with optimal development of incubous leaf orientation; two underleaves cut off (×21). – 5. Leaf lobe of leaf 7; note 8-cell width at base and feebly elongated terminal cells (×91). – 6. Leaf lobe apex (×145). – 7. Leaf (×16).

All from neotype.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DIFFERENTIATION. Taxonomically, this taxon appears to be a puzzlingly variable entity whose treatment is oversimplified in FULFORD and TAYLOR (1960); they attempt to separate it from " *L. georgica* " on the basis of the following characters: (1) leaf segments longer, " slenderly lanceolate, mostly 4 cells broad at the base "; (2) segments " widely divergent "; (3) tip cells of segments " about twice as long as wide ". In *RMS 48732a* (fig. 13 : 8-10) the segments are slenderly lanceolate and 4-5 cells broad at the base, but terminal cells are only 1.0-1.8× as long as wide. Also, the leaf lobes are much less widely divergent than FULFORD and TAYLOR (loc. cit.) imply, and approach those of " *L. georgica* " in orientation. Exactly the same constellation of characters occurs in mature (perianth-bearing) plants of *RMS 50429* (Rio Harubre Valley).

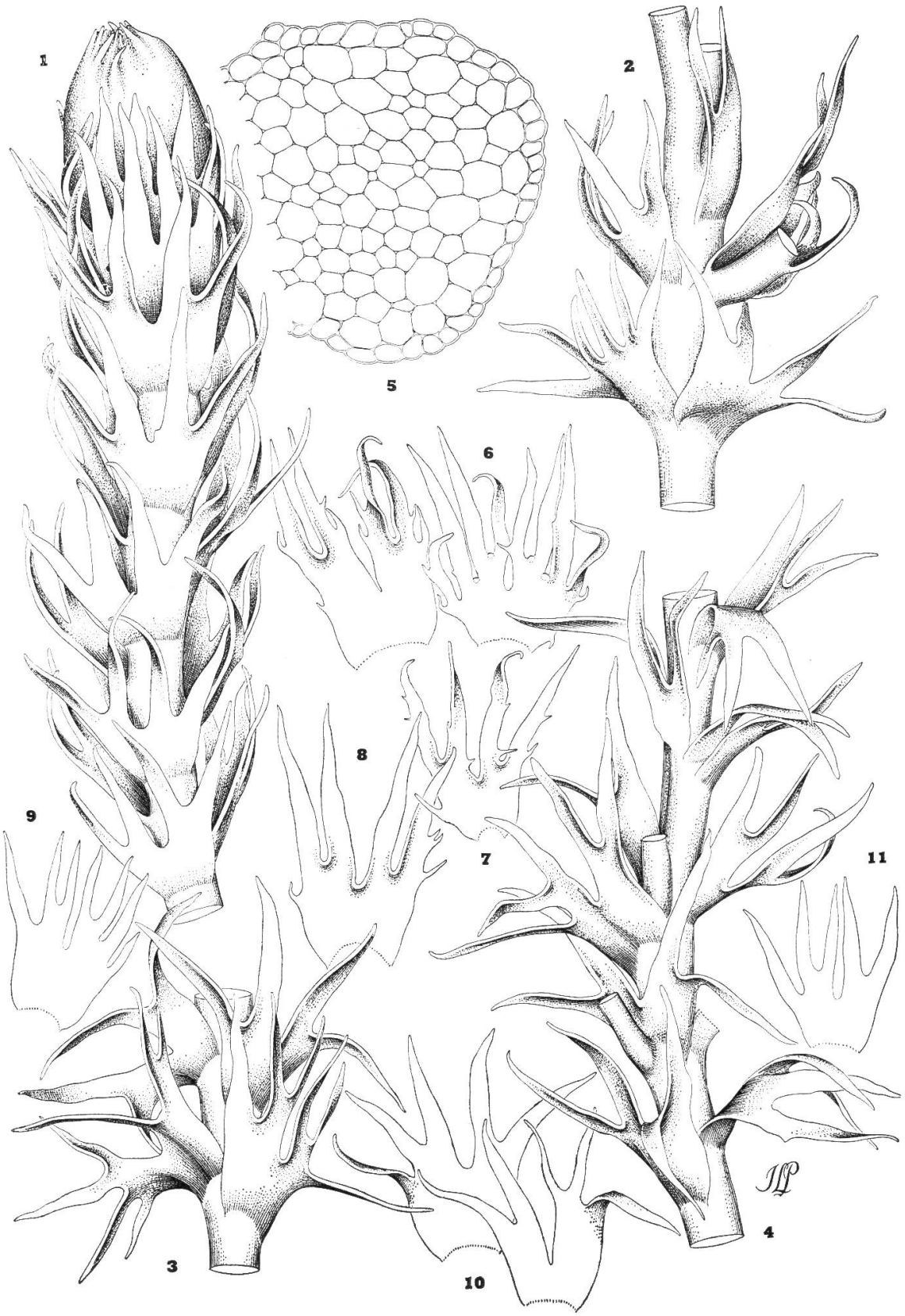
I have had occasion to study the neotype of *L. quadrilaciniata*. It is obvious that the description of FULFORD and TAYLOR is based solely on the weaker, sterile plants. On robust, sterile plants the leaf lobes almost constantly end in three superimposed cells. The basal cell of the uniseriate lobe apices varies as follows (width × length): 28×36, 27×35, 25×34, 25×36, 26×40 μ; median cells range: 22×24, 20×28, 20×26, 21×25 μ; terminal lobe cells vary 15-16×23-36 μ, and average 1.4-2.25× as long as wide. The leaves also have the segments much wider than the key in FULFORD and TAYLOR (1960 : 412, " segments... mostly 4 cells broad at the base ") would imply: the first four leaves I checked gave the following widths (in cells): 6+7+7+9; 6+7+5+6; 6+7+6+6; 9+8+7+7. The attempt at a separation of two " species " in FULFORD and TAYLOR thus founders when the very neotype of *L. quadrilaciniata* is studied.

The plants I collected at Valle Carbajal are also clearly divergent in : (1) intercalary branches and Microlepidozia-type branches are seemingly absent, all of the branches I have studied being of the Frullania-type; (2) the cortical cells of the stem, although a little smaller than the medullary cells (ca. 24-30 μ in width, somewhat tangentially flattened in most cases), are not so notably reduced in size as FULFORD and TAYLOR show in their figure 36, and as they describe on p. 412 [1]; (3) the sinuses of the leaves quite lack the thin-walled, swollen cells which they emphasize as a generic character and illustrate in their figure 35a-c.

Branching in the neotype of *L. quadrilaciniata* (based on study of material at G and W) is almost exclusively of the Frullania-type. I have seen only two Microlepidozia-type branches, one branch of the lateral-intercalary type, and have found

[1] My examination of the neotype fails to confirm figure 36 in FULFORD and TAYLOR (l. c.); they show cortical cells from about 0.3-0.5 the diameter of the medullary cells in the next two rows. On the type the tangential diameter of the cortical cells is usually from 0.5-0.9 that of the medullary cells.

FIG. 11. *Lophochaete quadrilaciniata* var. *quadrilaciniata* (1) and var. *pleomorpha* (2-11) 1. Perianth-bearing shoot (×33). – 2. Shoot-sector, antical aspect, with abnormal branching and, below, a sexfid leaf (×31). – 3. Shoot-sector, dorsal view, with 4-7-lobed leaves (×25). – 4. Shoot-sector, dorsal view, with terminal, Radula-type branch below and a ?Microlepidozia-type branch above; distal parts of shoot with teratological leaf and segment formation; second leaf from bottom, right, cut off near base (×25). – 5. Stem cross-section (×147). – 6-7. Gynoecial bracts and bracteole (×20). – 8. Subfloral bract (×20). – 9. Leaf with supernumerary lobing (×19.5). – 10. Two leaves (×20). – 11. Underleaf (×19.5). 1. *RMS 50429*. – 2-11. Type of var. *pleomorpha*.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one questionably of the Acromastigum-type. Thus in this species normal branching, involving at least 95% of the branches, is of the Frullania-type. Branching, when terminal, is furthermore often difficult to interpret, owing to the fact that the plants are quite radial and nearly free of rhizoids. Hence it is easily possible, by turning a plant, to confuse Frullania-type with Microlepidozia-type branching. The bifid supporting stem leaf associated with terminal branches is often armed on one side or the other with an accessory lobe or tooth.

L. quadrilaciniata var. **georgica** (Steph.) Schust., comb. et stat. nov. *Lepicolea georgica* Steph., Sv. Vet.-Akad. Handl. 46/9 : 73. 1911.
Pseudolepicolea georgica (Steph.) Fulf. et Tayl., Nova Hedwigia 1 : 416. 1960.

Plants with leaves and underleaves consistently bisbifid, without accessory lobes, bearing broader, typically more abbreviated lobes; leaf lobes commonly 5-8(9-10) cells broad at base, less gradually acuminate, the outer lobes only relatively more weakly divergent; leaf and underleaf lobes not or sporadically twisted, less flaccid. Branching of the Frullania-, less often Microlepidozia-type, and lateral- and postical-intercalary; apparently never with basiscopic branching of any type.

TYPE. South Georgia: Cumberland Bay — *Skottsberg 156* (G, S-PA).

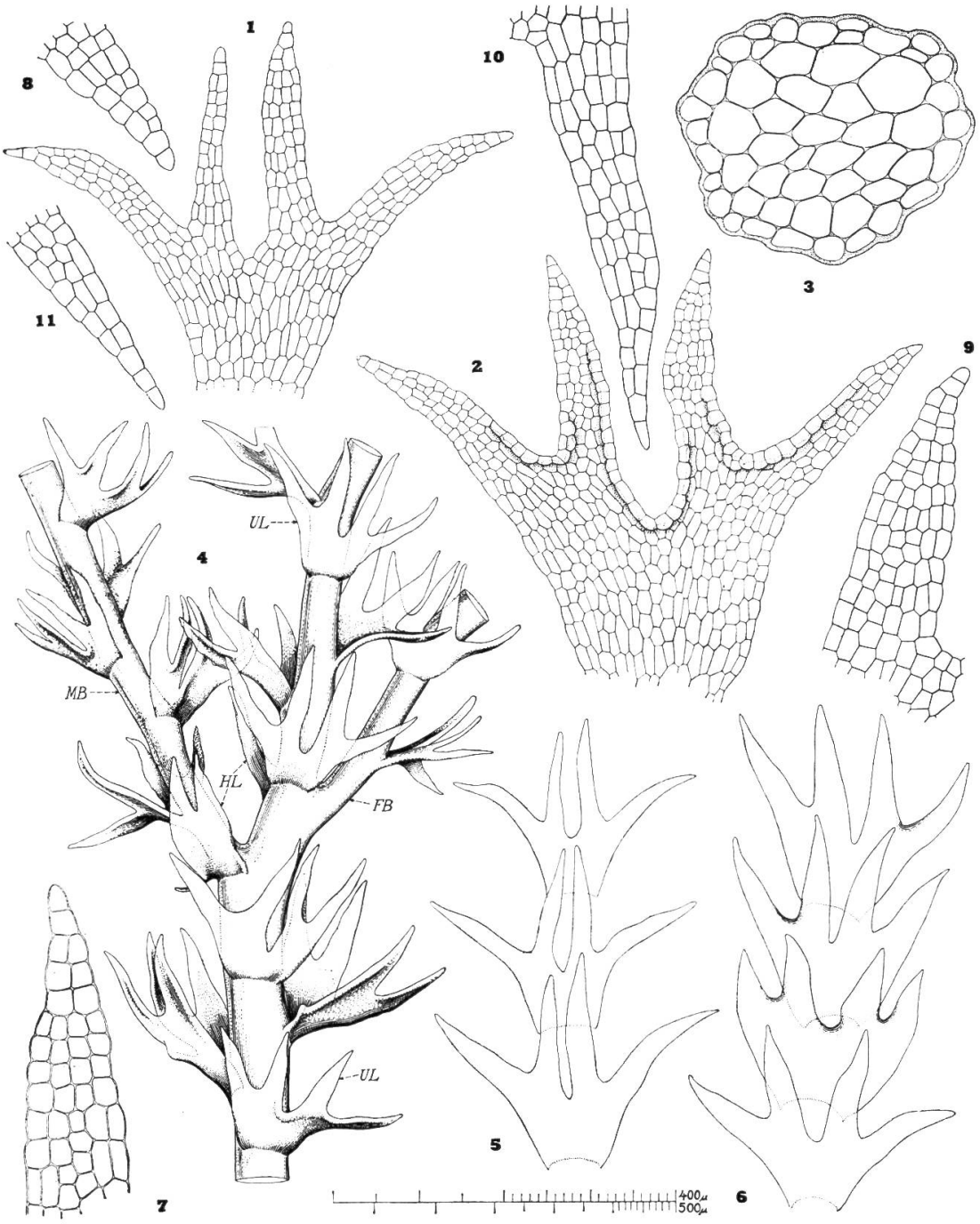
Var. *georgica* is a weakly defined segregate, which, with further study, may prove to be merely an environmental modification of typical *L. quadrilaciniata*. In any event, as the discussion under var. *quadrilaciniata* demonstrates, the recognition of this plant as a distinct species (Fulford and Taylor 1960) seems untenable. The width of the leaf lobes appears to reflect two factors: general vigor (e.g. the most vigorous sterile plants of the neotype of var. *quadrilaciniata* have lobes fully as broad as is considered typical of "*L. georgica*" by FULFORD and TAYLOR) and growth habits (the more aquatic forms, perhaps, having less elongated leaf lobes). Several collections cited under var. *quadrilaciniata* above show an approach to var. *georgica*, without, however, quite matching it.

L. quadrilaciniata var. **pleomorpha** Schust., var. nova.

Folia contigua, ± incuba, bis bifida vel 5-8-fida; amphigastria transversa, bis bifida vel 5-8-fida; bracteae femineae 4-5-6-fidae, lobis lanceolatis, paucidentatis.

Plants, fuscous, aquatic and subaquatic, forming immense, pure, blackish carpets at the edges of small alpine and subalpine rills. Stems with sparse branching, all (or very predominantly) of the Frullania-, Microlepidozia- and Radula-type; branches of the latter type basiscopic, lateral, arising connate to the abaxial base of an otherwise normal, bisbifid leaf. Leaves often with strongly spreading to squarrose lobes, somewhat incubously inserted and oriented, ranging to almost transverse, on mature shoots some bisbifid, but many with accessory lobing so that 5-8-lobed leaves ensue;

FIG. 12. *Lophochaete quadrilaciniata* var. *georgica* (1-9) and var. *quadrilaciniata* (10-11)
1. Underleaf (×75). – 2. Lateral leaf (×75). – 3. Stem cross-section (×170). – 4. Shoot-sector, ventral aspect (*MB* Microlepidozia-type branch; *FB*, Frullania-type branch; *HL* "half leaves"; *UL*, underleaves) (×30). – 5. Underleaves (×34). – 6. Lateral leaves (×34). – 7-10. Leaf lobes, each 6-7 cells wide at base (×98). – 11. Apex of a leaf lobe 8 cells wide at base (×98).
1-9. Type of var. *georgica*. – 10-11. Neotype of *L. quadrilaciniata*.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leaf lobes mostly 8-12 cells broad at base. Underleaves transverse and similar to lateral leaves in size and in variability in lobing. Leaf lobe width and abbreviated terminal cells of lobes as in var. *georgica*. Disk to 8-12 cells high. ♀ Bracts (and to a lesser extent subfloral leaves) also with accessory lobing, bisbifid to 5-6-lobed, and with lobes and disk bases with scattered, sharp teeth.

TYPE. Argentina: Tierra del Fuego, Cerro Garibaldi, S of Lago Escondido, ca. 700-800 m, in and at the margins of alpine and subalpine rills, along a west-facing slope, chiefly at the upper edge of the *Nothofagus* forest — *RMS 58343*.

The extraordinary plants referred here depart so drastically from the description of this species by SCHIFFNER (1912) and FULFORD and TAYLOR (1960) that it seems best to segregate them varietally. The, at least, sporadic development of Radula-type branches is unique, in this phenotype, in the *Herbertinae*. Similarly unique is the quite unparalleled polymorphism in number of lobes of the leaves, underleaves, bracts and bracteoles. The sharp dentition of the bracts and bracteoles is already " hinted at " in typical *L. quadrilaciniata*, but is carried to an extreme in the present phenotype. The leaves, which are soft and flaccid, as in var. *quadrilaciniata*, have the identical tendency to bear squarrose or reflexed outer lobes. The degree of development of supplementary leaf lobing varies widely; it is expressed almost entirely on mature, robust shoots. On branches, leaves and underleaves are apparently consistently bisbifid.

Although the aspect of the plant approaches that of var. *quadrilaciniata*, owing to the tendency for the strongly spreading lobes to be squarrose or even reflexed, lobes are most often 8-12 cells wide at the base, and the terminal cells of the lobes are mostly almost isodiametric, much as in var. *georgica*. These plants, then, are added evidence for treating *L. quadrilaciniata* in a broad sense.

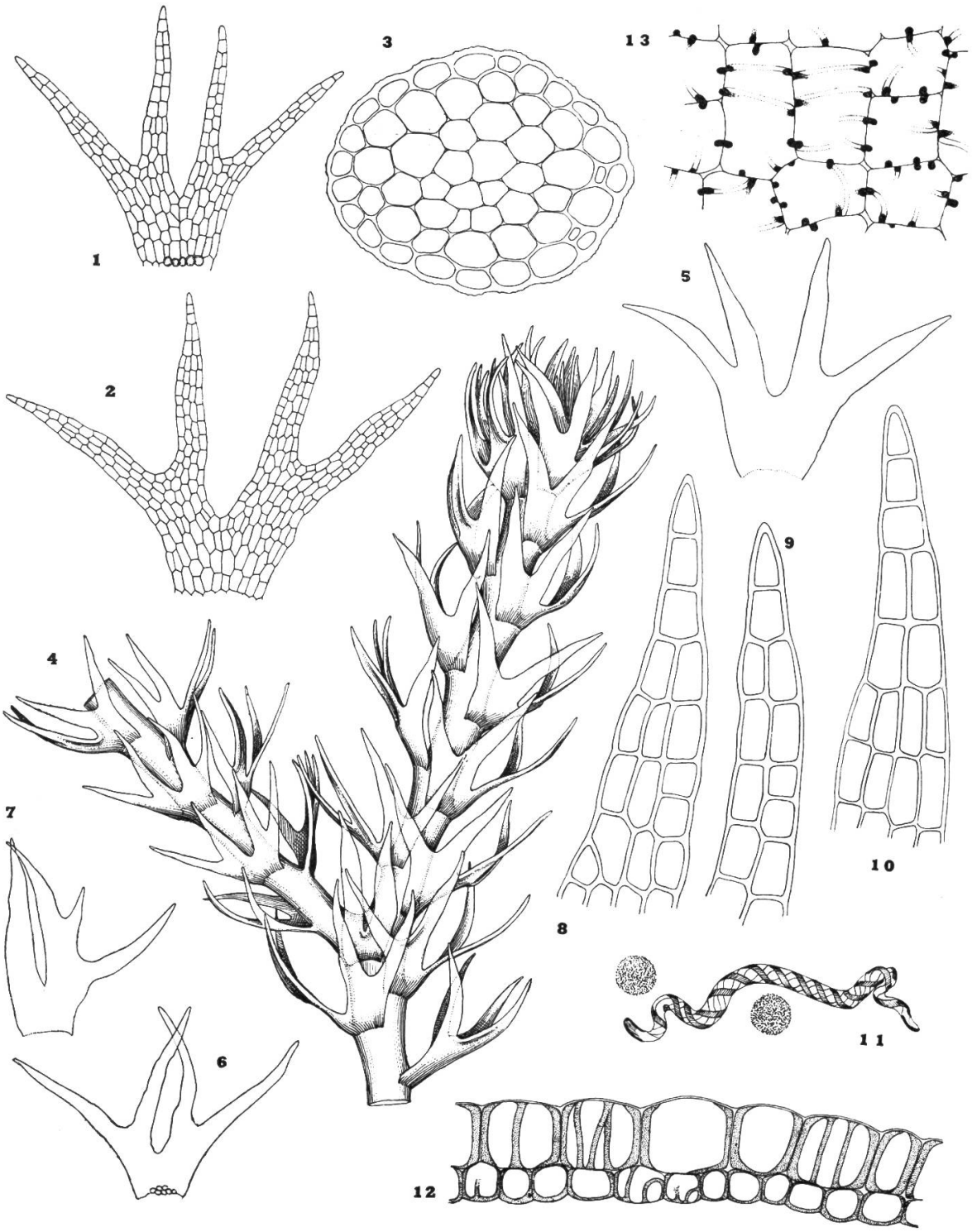
Lophochaete subgen. **Lophochaete**.

Branching entirely terminal-lateral, of the Frullania-type. *Stem* with cortical cells not or hardly smaller than medullary cells, feebly differentiated. *Leaves* bisbifid (sporadically in part trifid), with the linear-lanceolate to lanceolate-setaceous lobes formed of thick-walled, elongated cells; lobes with cells often tiered and the marginal cells in lobes tending to be angularly produced distally so that the lobes appear both crenulate and articulate (at least in and near gynoecia). *Perianth* either 4- or 6-plicate distally. ♀ *Bracts* and *bracteole* merely bisbifid, without sharp dentition.

I have repeatedly searched, without success, for evidence of branching other than terminal, Frullania-type branching, in all three taxa referred here. Subgen. *Lophochaete*, thus, is more advanced phylogenetically than subgen. *Pseudolepicolea*.

FIG. 13. *Lophochaete quadrilaciniata* var. *quadrilaciniata* (1-10) and *L. fryei* (11-13)

1. Underleaf (×48). – 2. Leaf (×48). – 3. Stem cross-section (×160). – 4. Shoot, dorsal view, with Frullania-type branch and a supporting bifid stem leaf (×21). – 5. Leaf (×36). – 6. Underleaf (×36). – 7. Supporting stem leaf, showing accessory lobing and tooth (×36). – 8-10. Apices of leaf lobes, showing variation (×210). – 11. Two spores and elater (×313). – 12. Capsule valve cross-section (×300). – 13. Epidermal cells of capsule wall (ca. ×250).
1-10. *RMS 48732a*. – 11-13. *Steere 18941* (from NW of Mt. Chamberlain, Alaska).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Except for this, and for the rather quantitative differences in axial anatomy, there are only slight differences between the two groups. Hence they could with propriety also be treated as merely constituting distinct sections. In any event, I cannot follow FULFORD (1963), who considers the two groups as distinct genera.

Subgen. *Lophochaete*, unlike subgen. *Pseudolepicolea*, always has the leaves distinctly transversely inserted, never at all incubous. The ♀ bracts and bracteole are almost identical to vegetative leaves, insofar as they never develop sharp marginal dentition.

Lophochaete fryei (Perss.) Schust., Rev. Bryol. Lichén. 26 : 126. 1957.
Lepicolea fryei Perss., The Bryologist 49 : 47. 1946.

Plants brownish, moderately robust, erect to ascending, sparsely branched (the branches often androecial basally); shoots 600-800 (1000) μ wide and 1-3(6.5) cm long. *Stems* rigid, 240 μ in diam., 10-12 cells in diam.; cortex 1-layered, of somewhat brownish and thick-walled cells, 4-6× as long as wide; epidermal cells barely larger than to subequal to the hyaline medullary cells; branches normally terminal and of the Frullania-type. *Rhizoids* rather frequent, in groups of 2-4 or more from the basal cells of the underleaves, rarely also from postical leaf bases. *Leaves* spreading from stem at base, but lobes suberect, broadly obdeltoid in outline, regularly bisbifid for 0.65-0.85 their length, 550-600(850) μ long and as wide or wider, measured near the apex; leaf lobes divergent, occasionally slightly falcate, erect or even slightly incurved towards stem, triangular-subulate to narrowly triangular, 4-6 (rarely 7) cells broad at base, entire-margined and not crenulate, the apex acuminate, ending in a uniseriate row of 2-4 (rarely 5) cells; sinuses unequal, median sinus deeper than 2 lateral sinuses, acute but often very narrowly rounded or obtuse at the very base, usually with a few isodiametric cells at the base of the sinus. *Cells* of leaf lobes thick-walled, near the leaf base becoming more leptodermous; trigones very small to obsolete, the walls nearly equal, the cells rounded at the corners; cells of the uniseriate apex 18-20×30-40 μ, of basal portion of the lobes 16-18(19-20) μ wide and 28-35(44) μ long, of undivided basal portion of the leaf (which is 5-8 cells high) 18-22×22-30(35) μ; cuticle smooth. *Underleaves* similar to leaves, usually slightly smaller, never with falcate lobes, usually 550-650 μ long; lobes usually only 3-4 cells broad at base. *Asexual reproduction* lacking. Plants autoecious, usually fertile; *androecia* usually at base of a lateral branch (often arising slightly below ♀ inflor-

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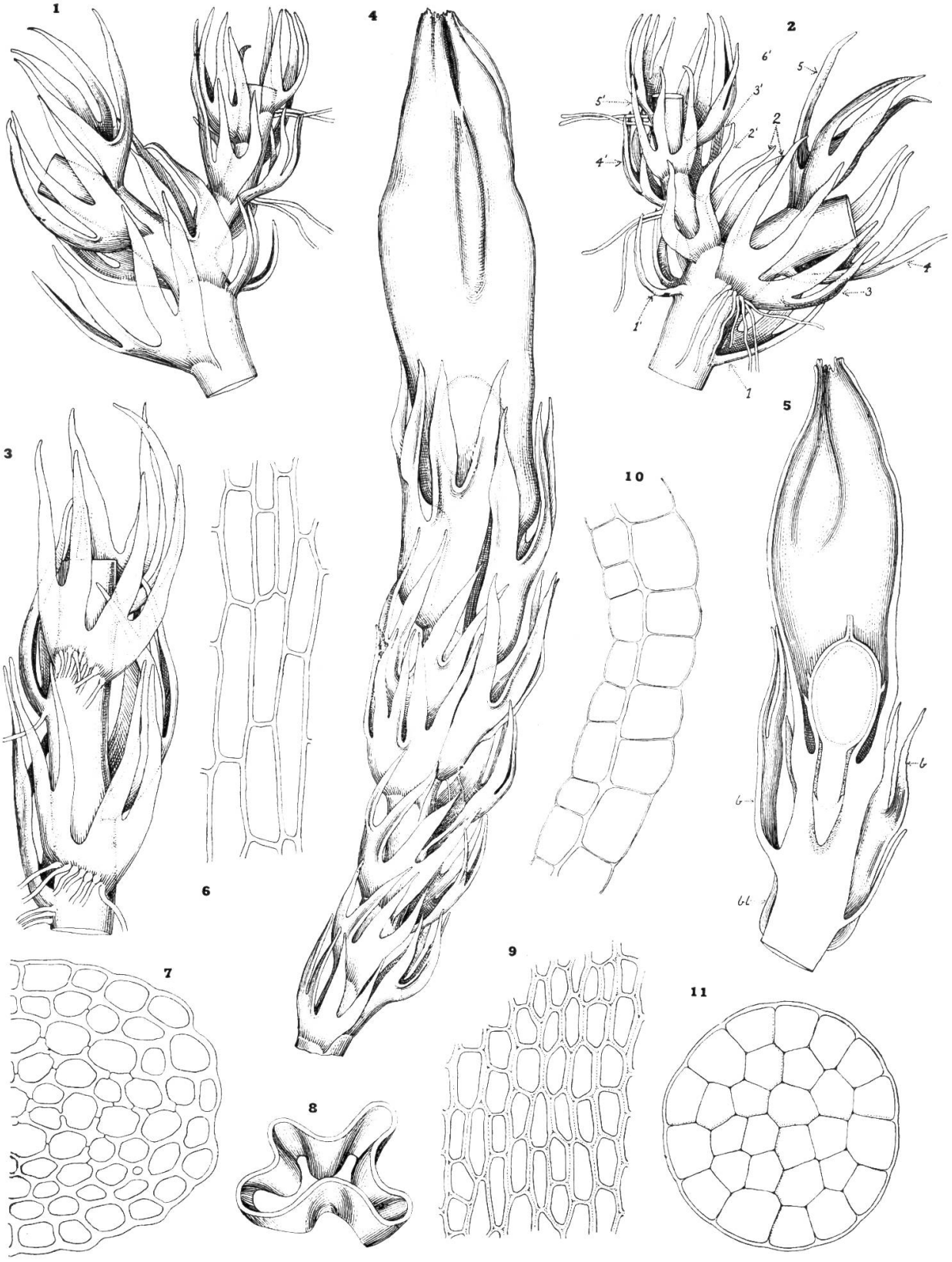
FIG. 14. *Lophochaete fryei*

1. Shoot-sector in antical aspect. – 2. The same in postical aspect (1, 2, 4 and 5, lateral stem leaves: 2, "half leaf" associated with Frullania-type branch; 3, stem underleaf with rhizoids at base; 1′ and 4′, branch underleaves with rhizoids at base; 2′, 3′, 5′ and 6′, branch lateral leaves) (×38). – 3. Shoot-sector, ventral aspect (×43). – 4. Shoot in antical aspect (×24). – 5. Shoot-apex with immature sporophyte, in longisection (*bl*, bracteole; *b*, bracts); note strong elongation of shoot-tip and shoot-calyptra formation (×24). – 6. Cortical cells of stem (×166). – 7. Stem cross-section (×250). – 8. Cross-section of apical ¼ of perianth (×35). – 9. Median perianth cells (×141). – 10. Cross-section of capsule wall (immature; with maturity both strata develop pigmented thickenings) (×250). – 11. Cross-section of seta (×175).

All from *Steere 18941*.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escence); if lateral on a ♀ stem, usually not proliferating distally and bud-like, with only 3-5 pairs of closely imbricate bracts; if androecial branch arising from a sterile shoot, the bracts usually more numerous and androecium proliferating vegetatively at apex; *bracts* similar to leaves but often smaller (500-600 μ long), less deeply divided, often only 3-lobed, at other times 4-lobed; sinus descending 0.55-0.65 the length of bracts; undivided basal portion of bract somewhat saccate, bearing one antheridium; androecial *bracteoles* usually trifid for 0.6-0.7 their length, slightly smaller than bracts (usually 450-480 μ long). ♀ Inflorescence terminal on a leading, long, leafy branch; ♀ *bracts* almost identical to leaves, slightly larger and slightly less deeply divided (1000)1150-1250 μ long and (750)1000-1550 μ wide, depending on degree of divergence of lobes; sinus descending ca. 800 μ, i.e. for 0.6-0.7 the length of bract; *bracteole* similar to underleaves, usually 4-lobed, rarely 3-lobed, 1100-1200 μ long and 800-1000 μ wide; distal portions of lobes of bracts and bracteoles distinctly crenulate-serrulate due to projecting cells; bracts erect, closely applied to basal half of perianth, the lobes not spreading. *Perianth* cylindrical, long-exserted, to 800×2000 μ, the upper 0.4-0.7 deeply 4-plicate, the plicae rounded to obtuse, often with slight supplementary plicae (then becoming 5-7-plicate); mouth of perianth contracted, shallowly lobed, the broad, shallow lobes crenulate-dentate due to projecting cells (free for 0.2-0.8 their length usually); cells of mouth 15-16×40-75 μ, thick-walled and with rounded corners; cells below the mouth 14-17×30-45 μ, regularly rectangulate, somewhat evenly thick-walled, in the perianth middle becoming 20-25(27) μ wide and 40-48 μ long. *Capsule* wall yellow-brown and translucent, bistratose; epidermal cells 25-27 μ thick usually; inner cell layer much smaller and 11-13 μ thick (total thickness usually 36-40 μ); epidermal cells with free wall thin and delicate; both transverse and longitudinal radial walls each with (1)2(3) vigorous yellow-brown nodular thickenings (in cross-section of valve appearing band-like), which extend only slightly onto tangential walls as weak spurs; epidermal cells in surface view subquadrate to short-oblong, ca. 25-28×20-22 μ to 22-25×32-35 μ, on an average; inner cell layer of rather regularly oblong cells in tiers (in the middle and bases of the valves), averaging (11)14-16(19) μ wide and 50-60 μ long, with strong, yellow-brown, semi-annular to annular bands, the bands always complete on the free (inner) tangential faces. *Spores* light brown and translucent, finely and minutely granular-papillate, ca. 14-17.5 μ in diam., nearly twice diam. of the elaters (which are 8-10 μ in diam. and bear 2 brownish spirals ca. 3 μ wide).

TYPE. St. Lawrence Island, Alaska, anno 1933 — *Geist* (S-PA).

DISTRIBUTION. Apparently endemic to the Bering Sea region, to arctic Alaska, eastward to the W coast of Hudson Bay; extending westward to Siberia. Known

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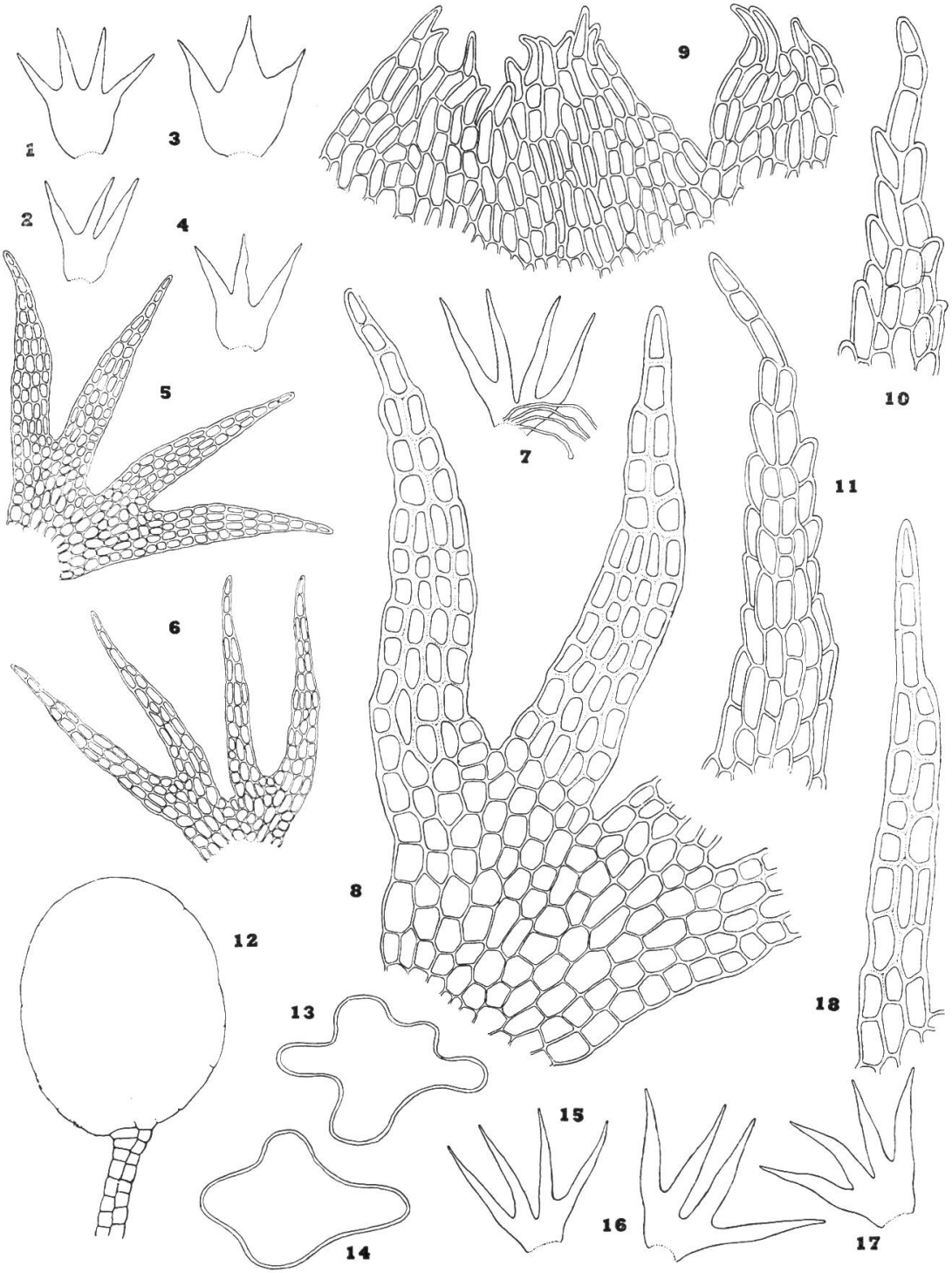
FIG. 15. *Lophochaete fryei*

1 and 3. Male bracts (×29). – 2 and 4. Male bracteoles (×29). – 5. Leaf (×60). – 6. Underleaf (×60). – 7. Underleaf with rhizoids at base (×29). – 8. Leaf, parts of two lobes omitted (×150). – 9. Perianth mouth (×120). – 10-11. Apices of lobes of female bract (×150). – 12. Antheridium (×150). – 13-14. Perianth cross-sections, $^1/_3$ from apex and through middle, respectively (×29). – 15. Underleaf (×29). – 16-17. Leaves (×29). – 18. Lobe of underleaf (×150).

All from *Steere 18193* (from Endicott Mts., Brooks Range, Alaska).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in Alaska from the headwaters of the Utokok River, in the west, to Schrader Lake, near Mt. Chamberlain, in the east, and from St. Lawrence Island; with a single locality known to date from east of that area: Northwest Territory, Chesterfield Inlet, W coast of Hudson Bay, anno 1936 — *Dutilly* (fide Steere 1953).

DIFFERENTIATION. *L. fryei* was described as a species of *Lepicolea*, on the basis of sterile plants. Without perianths, the generic assignment of the species is admittedly difficult. However, the abundant materials collected in Alaska by STEERE include several collections of *L. fryei*, some of which bear perianths. These plants clearly indicate that *Lepicolea fryei* belongs to *Lophochaete*, since the perianth is well developed, free, plicate above, as in the other *Blepharostomataceae*.

The species is remotely related to the antipodal *L. quadrilaciniata*, which has been critically studied by SCHIFFNER (1912). It differs from this in the following respects: (1) the lobes of the perianth mouth are merely crenulate-denticulate with teeth no more than one cell long; (2) involucral bracts are apparently never with accessory lobes or teeth, quite like the leaves and underleaves; (3) leaves and underleaves much more deeply divided; (4) autoecious inflorescence; (5) ♂ bracts more deeply 3-4-lobed, bearing only a single antheridium, rather than two; (6) tips of involucral bracts with the margins distinctly crenulate-denticulate to serrulate, due to projecting cells.

Closer affinities occur to the two other Northern Hemisphere species of *Lophochaete*, *L. andoi* of Japan and *L. trollii* of the Himalayas. However, both of these taxa have vegetative leaves strongly crenulate on the margins, smaller, narrower (but longer) cells, a finely roughened cuticle, and are dioecious. *L. andoi* also has a perianth divided at the mouth into twelve narrow, lanceolate-acuminate lobes (and, judging from the single badly weathered perianth of *L. trollii* seen, this species has a similarly deeply lobed perianth), while *L. fryei* has a perianth that is exceedingly shallowly and obscurely lobulate. The distinction of these taxa from *L. fryei* is dealt with in the key, and in the discussions following the taxonomic treatment of these two taxa.

L. fryei shows several peculiarities which are of significance, among them: (1) Branching is all terminal. The associated stem leaf of a terminal branch is bifid, with the postical half absent, replaced by the branch. Inserted at juncture of stem and branch, with its antical insertion virtually contiguous to the postical base of the supporting leaf, is a reduced 3-4-lobed leaf that represents the first branch appendage. This leaf, together with the closely juxtaposed bifid dorsal one, superficially forms a single structure from whose " axil " the branch appears to arise. Actually, this 3-4-lobed leaf-like structure belongs to the branch. The lateral position (with respect to the main stem) would superficially suggest it is the first branch leaf, but the presence

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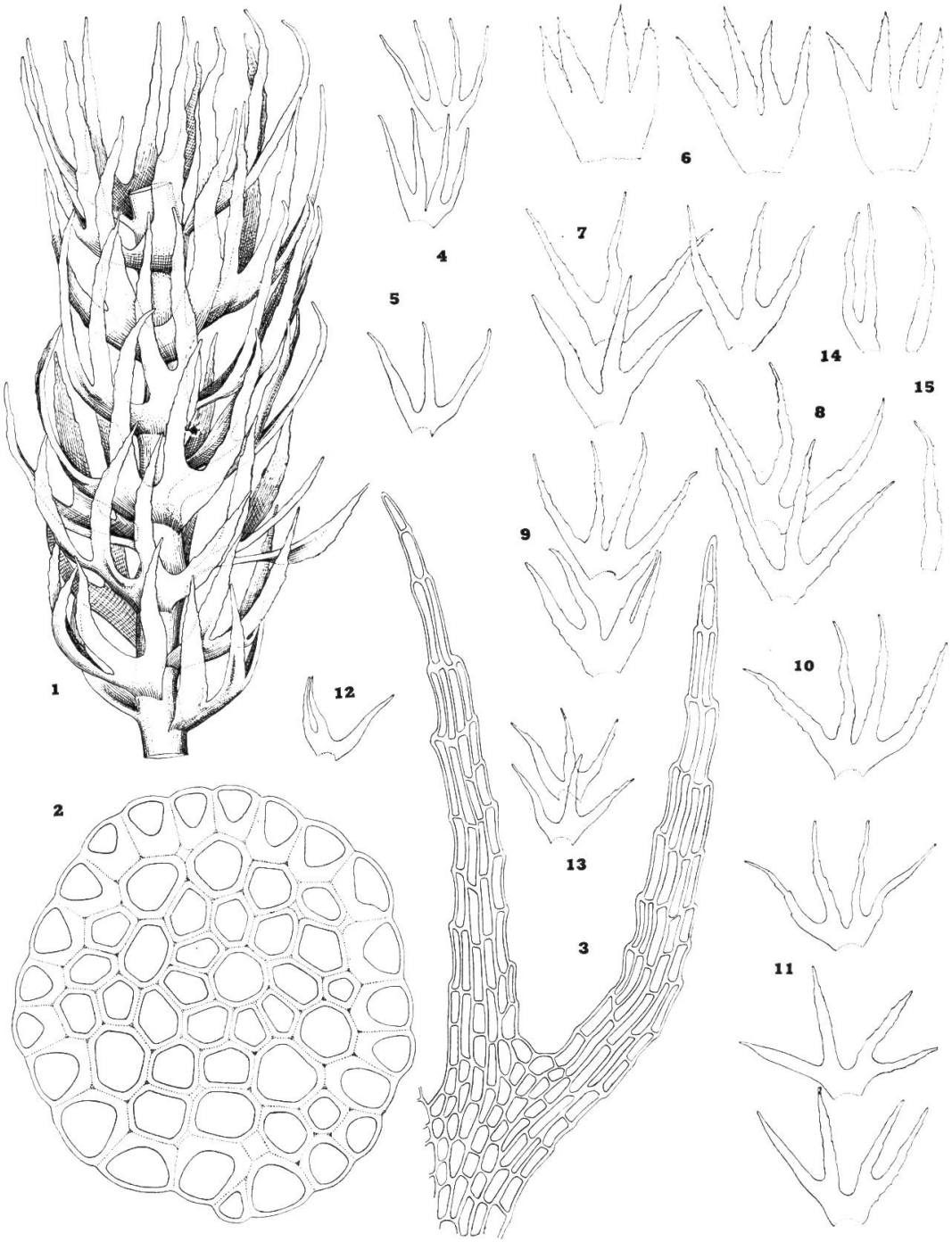
FIG. 16. *Lophochaete trollii*

1. Shoot-sector (×46). – 2. Stem cross-section (×460). – 3. Half of leaf 10 (×120). – 4-5. Small leaves (×27). – 6. Female bracts and bracteole (×30). – 7-8. Large, mature, trifid stem leaves (×27). – 9-10. Large quadrifid stem leaves (×27). – 11-12. Underleaves (×27). – 13. Small, trifid lateral leaves (×27). – 14-15. Bifid and monocrural " half leaves " adjoining Frullania-type branches (×27).

All from type.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of rhizoids at its base (and at the base of the leaves lying serially above it) definitely shows that the structure is the first underleaf of the branch. Branching, therefore, is exactly as in the genus *Frullania* (Evans 1912) and closely matches in detail that studied by the writer in *Anthelia*. (2) Leaves, although transversely oriented, are inserted very slightly succubously, with the antical portion of the line of insertion perceptibly oblique. (3) Rhizoids are largely restricted to the base of underleaves, but on robust shoots one or several rhizoids also occur at the postical leaf bases. This " undifferentiated type " of rhizoid distribution (Schuster 1958) is the most primitive type of rhizoid distribution pattern known in liverworts. It recurs again, for example, on sporelings and gemmalings of *Mylia anomala*, on mature plants of *Leptoscyphus cuneifolius* (a species with a persistently juvenile facies), and elsewhere. (4) With fertilization, the perianth becomes stipitate, the stem above the bracts becoming fleshy, somewhat swollen and elongating. (5) The sporophyte anatomy stands midway between that of *Temnoma* and *Blepharostoma*. The former genus, as has been brought out elsewhere (Schuster 1959), has a massive seta and a capsule wall with 3-5 strata, of which the outer is formed of large, pellucid cells devoid (except along the dehiscence lines) of thickenings, the inner strata of thinner cells bearing semi-annular bands. *Blepharostoma* has a bistratose wall, the two layers subequal in thickness (ca. 10 μ thick each) and both with thickenings. In *Lophochaete fryei* the wall is bistratose, as in *Blepharostoma*, but the outer layer is formed of large cells, 25-30 μ thick. The seta in *Temnoma* is massive, with ca. 19-20 epidermal cell rows and ca. four interior rings of numerous cells, the seta thus being 9-10 cells in diameter. In *Blepharostoma* eight rows of epidermal cells enclose only four rows of smaller interior cells. *Lophochaete fryei* has the seta intermediate in form: there are 14-16 epidermal cells that average a little larger in diameter than the two rings of interior cells (which, respectively, are formed of 10-12 rows and four rows of cells); the seta, therefore, is six cells in diameter. (6) Perianth cells in *Lophochaete fryei* are not sharply rectangulate, and not markedly elongate. By contrast, those of *Temnoma* are. In this respect, again, *Lophochaete* agrees more closely with *Blepharostoma*. (7) The perianth-bearing stems are rather freely branched, with usually 1-3 branches arising from near the perianth, of which one may (rarely) be situated directly below the bracts, thus being strictly a subfloral innovation. Such subfloral branches are evidently unknown in *Temnoma* and *Blepharostoma*, if perianths are matured.

Lophochaete trollii (Herz.) Schust., Jour. Hattori Bot. Lab. 23 : 199. 1961.
Blepharostoma trollii Herz., Ann. Bryol. 12 : 80, fig. 4g-i. 1939.
Pseudolepicolea trollii (Herz.) Grolle et Ando, Hikobia 3 : 177. 1963.

Plants brownish to blackish-green, densely pulvinate-caespitose, the stems to 10-12 mm high, rigid, brittle, very densely leafy, moderately freely, irregularly branched; branches all (or at least very predominantly) terminal, of the Frullania-type, often rather limited in length (and, because of the initially rather smaller leaves, above the branch origin, appearing somewhat clavate-cylindrical), 550-600 up to ca. 750-820 μ wide (with leaves) with the imbricate, hand-like, suberect but concave leaves strictly tristichous, isophyllous, thus perfectly terete in form. *Stems* deep brown, hardly flattened, ca. 85-110 μ in diam., 8-10(11) cells high, all cells (medullary

and cortical) subequally fuscous-pigmented; cortical cells rather numerous (ca. 21-24 rows), averaging equal in diam. to medullary cells (occasionally 1-2 μ greater in diam.), not tangentially flattened, their free tangential walls not or slightly thickened, but radial walls becoming strongly thickened internally, and interior tangential walls very strongly thickened; medullary cells all with walls conspicuously thickened; cell walls all pigmented, with darker, conspicuous middle lamellae. *Leaves* obliquely erect from a somewhat spreading base, the lobes often suberect, rather closely imbricate, on mature axes varying indiscriminately from trifid to bisbifid (but the majority bisbifid); leaves (when bisbifid) to 560-675 μ long, obdeltoid to narrowly obtrapezoidal-cuneiform and widened to (580)700-860 μ wide at tips of spreading lobes; when trifid, leaves to 630-650 μ long and 730-800 μ wide; sinuses descending (0.65)0.7-0.8 (lateral) or 0.8-0.9 (median), rounded at base, without swollen cells at base; lobes laciniiform, linear-subulate, at base (4)5-6 cells broad (width ca. 60-70 μ), the lobe margins repand-serrulate (owing to the dilated and produced transverse walls of the marginal cells), the upper portions of the lobes often appearing articulate (owing to the tiered arrangement of cells). *Cells* thick-walled and faintly, rather distantly, minutely asperulate-granulate; cells of lobes strongly elongated, the lobe tips usually terminated by 1-2 (on small leaves with narrow lobes rarely 2-4) uniseriate cells; cells in uniseriate tips of lobes ca. 45-50 μ long and 12-13 μ to 15-19 μ wide; cells in lobes strongly elongated, ca. (45)50-80(85) μ long and 10.5-12.5 μ wide (averaging up to 4-7× as long as wide), in large part lying in tiers, the lobes thus appearing articulated; disk only ca. 5 cells high (to median sinus) to 6-8 cells high (lateral sinuses); cells of disk irregular in size, mostly oblong and 11-14 μ wide and 30-45 μ long. *Underleaves* identical to leaves in form and size, the bisbifid ones with lobes not (or only sporadically) more widely patent than on leaves, to ca. 500-580 μ long and 720-850 μ wide; lobing and sinuses as on leaves; crenulations of margins as on leaves. *Rhizoids* usually absent or rare. No *asexual reproduction*. *Gynoecia* (two only seen) sometimes on rather short lateral branches. *Bracts* and *bracteole* identical, ca. 550-620 μ long and 415-480 μ broad, bisbifid, not or hardly larger than leaves, differing from leaves in that the lobes are shorter and often somewhat broader, linear-lanceolate to narrowly lanceolate, less gradually acuminate, somewhat more strongly crenulate-serrulate on the otherwise unlobed and edentate margins; disk higher than on leaves, eciliate, the median sinuses descending ca. 0.6-0.65, the lateral sinuses descending usually 0.5-0.6 the bract (and bracteole) length. Only decayed *perianth* known, whose lobes are seemingly broader, less lanceolate-acuminate than in *L. andoi* (but apices and margins mostly destroyed).

TYPE. Sikkim Himalaya: Tsomgo Lake, between Gangtok and Natu La, 3600-3900 m — *C. Troll*; the type fragment preserved in S-PA (ex herb. K. MÜLLER) has been studied.

DISTRIBUTION. Still known only from the type station.

DIFFERENTIATION. This species is allied most closely to *L. andoi* of Japan, agreeing in the acuminate, slender leaf lobes, the crenulate margins of the lobes and the narrow, elongated leaf cells which lie (in the upper portions of the lobes) in tiers, so that the lobes seem articulated in a characteristic fashion.

L. trollii differs from *L. andoi*, and from all other species of *Lophochaete*, in the very high incidence of trifid leaves and underleaves—as in the type material—although HERZOG (1939) does not allude to them. In many instances, leaves of one side of the stem may be all trifid for some distance, while on the opposite side of the stem they are quadrifid. This is not a size-related criterion—fully mature shoots frequently possess trifid leaves.

As in *L. andoi*, the cuticle bears minute, but well-defined, sharp, granule-like papillae; the statement in HERZOG that the cuticle is " laevissima " is incorrect.

Although HERZOG states the type is sterile, the fragmentary type (schizotype) at Stockholm bore gynoecia and an old, weathered perianth. The bracts are much shorter and less deeply quadrifid, with broader and shorter lobes, than in *L. andoi*; their margins are more distinctly crenulate-serrulate, as contrasted to the last species.

Axial anatomy: the stems of *L. trollii* are rather rigid and brittle (the brittleness is perhaps the result of the mode of preservation); they are deeply pigmented, the brownish pigmentation involving not only cortical cells, but, in virtually undiminished forms, the medullary cells as well. The stems are 8-10(-11) cells in diameter, with the cortical and medullary cells nearly equal in diameter, the cortical not or hardly tangentially flattened (rather regularly oblong and several times as long as wide). Most diagnostic is the fact that the free faces of the cortical cells are thin or hardly thickened, while the radial walls are, from outer to inner edges, progressively more strongly thick-walled. The inner tangential walls, bordering the medullary cells, and all of the walls of the medullary cells, are strongly thick-walled (although the cell walls forming the boundary between the cortical and the medullar stratum are notably more strongly thick-walled than those of any other region); the middle lamellae stand out conspicuously because of their deeper pigmentation. In the thickened medullary cells, and the relatively thin free tangential walls of the cortical cells, the axial anatomy of *L. trollii* is strikingly distinct from that of *L. andoi*. Indeed, when the axial anatomy of the three species of subgen. *Lophochaete* is compared, it is seen that there are notable differences among them. If further collections prove that no transitions occur, axial anatomy alone will warrant retaining them as distinct species.

Branching: I have seen only lateral, terminal, Frullania-type branches, except for possibly one postical branch (on an older, half-decayed stem sector, where the branching type was nearly impossible to determine). The terminal lateral branches have bifid dorsal " supporting " stem leaves on stem sectors with predominantly quadrifid leaves. However, on the frequent mature stems with a high incidence

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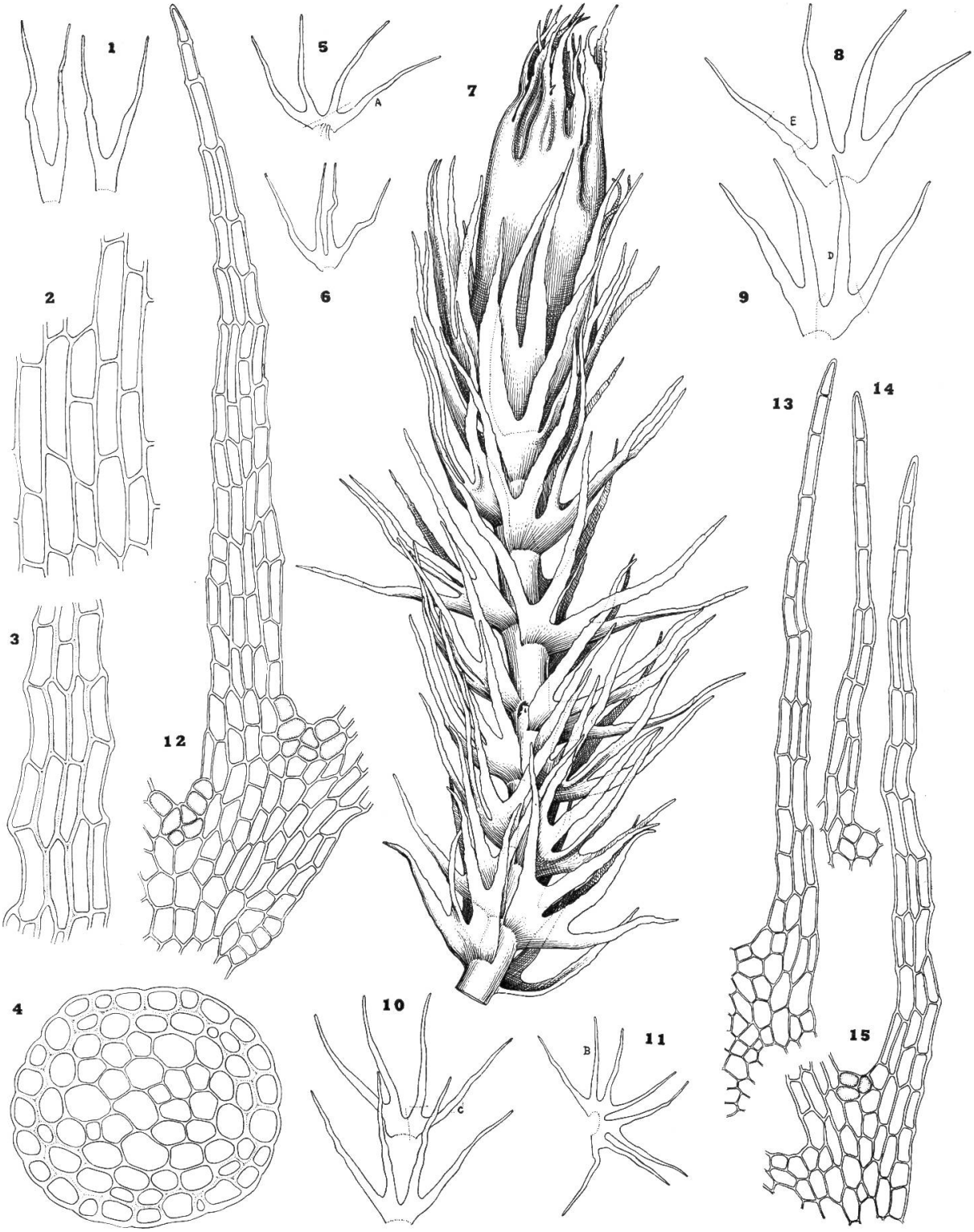
FIG. 17. *Lophochaete andoi*

1. Two stem leaves (" dorsal half ") associated with terminal branches (×25). – 2. Lateral cortical cells of stem (×185). – 3. Cells near base of leaf segment (*E* in leaf 8) (×185). – 4. Stem cross-section (×212). – 5. Branch underleaf (×25). – 6. Small branch leaf (×25). – 7. Perianth-bearing shoot (×32). – 8-9. Large leaves (×25). – 10. Two small leaves (×25). – 11. Branch leaf, and at lower right, branch underleaf, showing narrow basal union (×25). – 12. Lobe and basal disk of large leaf (*D* in 9) (×130). – 13. Lobe of branch underleaf (*A* in 5) (×130). – 14. Lobe of branch leaf (*B* in 11) (×130). – 15. Lobe and base of small leaf (*C* in 10) (×130).

All from type.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of trifid leaves, the supporting stem leaf always seems to be undivided, reduced to a simple, linear-lanceolate, subulate appendage. Such undivided supporting leaves have not been observed in any other species of the genus.

Lophochaete andoi Schust., Jour. Hattori Bot. Lab. 26 : 261. 1963.

Plants erect, caespitose, light brown, rather silky, varying greatly from main axes (which are Lophochaete-like) to the weaker branches (characteristically Blepharostoma-like), rather freely but irregularly branched. Mature shoots 1-2.5 cm high and 780-1350 (1700) μ wide, width varying with degree to which the leaves spread. *Stem* subterete, rather soft-textured, 145-175 μ in diam., cortical cells in ca. 24 rows, somewhat but not greatly thick-walled, subequal to medullary in diam. or little smaller, ca. (14)15-19(20) μ wide and (48)54-80(85) μ long, or somewhat tangentially flattened; medullary cells in ca. 7-9 tiers vertically, each ca. (18)20-22(24) μ in diam.; branches apparently uniformly of the Frullania-type (♀ plants), the associated stem leaf deeply bifid. *Leaves* and underleaves essentially identical in size, but leaves with lobes usually much less divergent. Leaves from (625)850-900 μ wide and 500-600 μ long to 1050-1325 μ wide and 900-975 μ long, cuneate to cuneate-obtrapezoidal in outline, transversely (to feebly incubously) oriented, insertion varying from transverse to feebly incubous, remote to subimbricate, obliquely to rather widely patent, the lobes of patent leaves often somewhat ascending; leaves regularly bisbifid, median sinus always deeper (descending 0.8-0.95 leaf length; disk here 4-5 cells high), the lateral sinuses shallower (sinus descending 0.75-0.87 leaf length; disk here to 8-9 cells high); lateral sinus bases often broader, rounded to truncate, usually with a small group of inflated, non-elongated, irregular cells; lobes moderately to strongly divergent, long and narrow, linear-lanceolate to filiform, often somewhat irregular and sinuous, crenulate owing to the projecting " shoulders " of the cells, where transverse cell walls protrude, on stem leaves 5-6 cells wide in basal sector, tapering to a uniseriate apex formed by (2)3-4 superimposed cells; lobes of branch leaves linear, sinuous, 2-3(4) cells wide basally, similarly tapering to a uniseriate apex as stem leaves. *Underleaves* like leaves, but generally with outer lobes much more divergent, from (small shoots) (900)950 μ wide and 550-625 μ long to (mature stems) (880)1250-1350 μ wide and 700-760 μ long; lobing and sinuses identical to those of leaves. *Rhizoids* usually absent or rare, colorless, only at underleaf bases. *Cells* firm, somewhat thick-walled, the cuticle with minute, round, rather sharp, scattered papillae; cells of tips of leaf and underleaf lobes (12)13-17×(40)45-65(72) μ, ca. 3-5× as long

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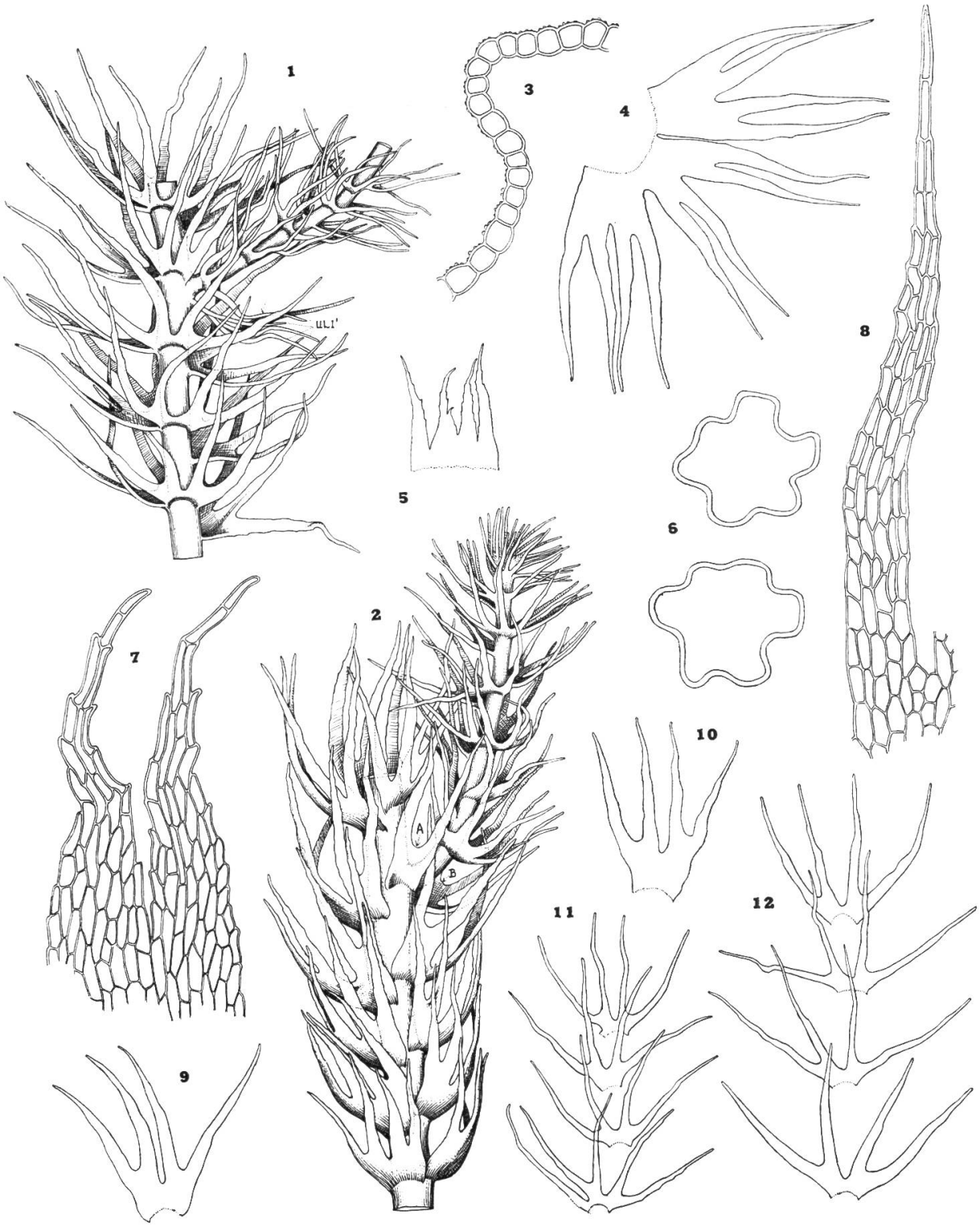
FIG. 18. *Lophochaete andoi*

1. Shoot, postical aspect, showing Frullania-type branch (*ULI'*, first branch appendage, an underleaf) (×28). – 2. Shoot, dorsal aspect, with branch with Blepharostoma-like aspect (*A*, bifurcate stem leaf, associated with branch; *B*, first branch underleaf, seemingly inserted on main stem just before juncture with branch) (×28). – 3. Part of perianth cross-section (×200). – 4. Bracts, and between them, bracteole (×25). – 5. One of the three main lobes of the perianth mouth (×25). – 6. Two cross-sections of perianth, taken from below the deepest sinuses (×35). – 7. Two lobes of perianth mouth (×110). – 8. Lobe of bract (×110). – 9-10. Large stem leaves (×25). – 11. Four small underleaves, the lowest with one leaf lobe adherent at left (×25). – 12. Four large underleaves (×25).
All from type.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as wide; cells in lobes elongated, ca. (11)12-15 × 50-64 μ, upper cells in tiers, lobes seemingly articulated; cells of undivided disk variable, irregular, from 12-15 × 30-35 to 20 × 40 μ. No *asexual reproduction*. Plants dioecious; ♂ plant unknown; *gynoecia* terminal on leading stem, without subfloral innovation (if perianth present). *Bracts* very similar to leaves, grading gradually into them, differing solely in the less spreading lobes and slightly greater length; bracts sheathing basal 0.5-0.6 of perianth, erect, narrowly oblong-obovate to oblong in outline, widest medially or distally, 530-600 μ wide and 1100-1200 μ long, regularly bisbifid (median sinus descending 0.75, lateral sinuses to 0.6-0.7), the lobes linear-lanceolate, 4-6 cells wide at base, acuminate, entire (except for crenulations similar to those of leaves), terminated by 2-4 elongated cells (ca. 15-17 × 75-90 μ). *Bracteole* much like bracts, identical in size (ca. 1075 μ long and 760-960 μ wide distally), slightly more deeply bisbifid than bracts. *Perianth* ca. 520-550 μ in diam. and 1750 μ long, unistratose throughout, rather delicate, slenderly ellipsoidal-cylindrical, tapering gradually to the moderately (but not strongly) contracted mouth, the distal one-third with 6 plicae (3 of which are often deeper); mouth deeply (350-500 μ) 12-lobed, 4 lobes derived from each floral leaf, the lobes lanceolate-acuminate, apices often tortuous or sinuous, 6-8 cells wide at base, the tips ending in 2-3 superimposed single cells (each cell (10)11-13 × 40-64 μ); lobe margins crenulate-denticulate because of the sharp, projecting upper " shoulders " of the marginal cells. *Bracts* not widely spaced, juxtaposed to bracteole; perianth little stipitate (as far as seen); a weak shoot-calyptra, the 4-6 sterile archegonia inserted partway up fertilized archegonium (calyptra).

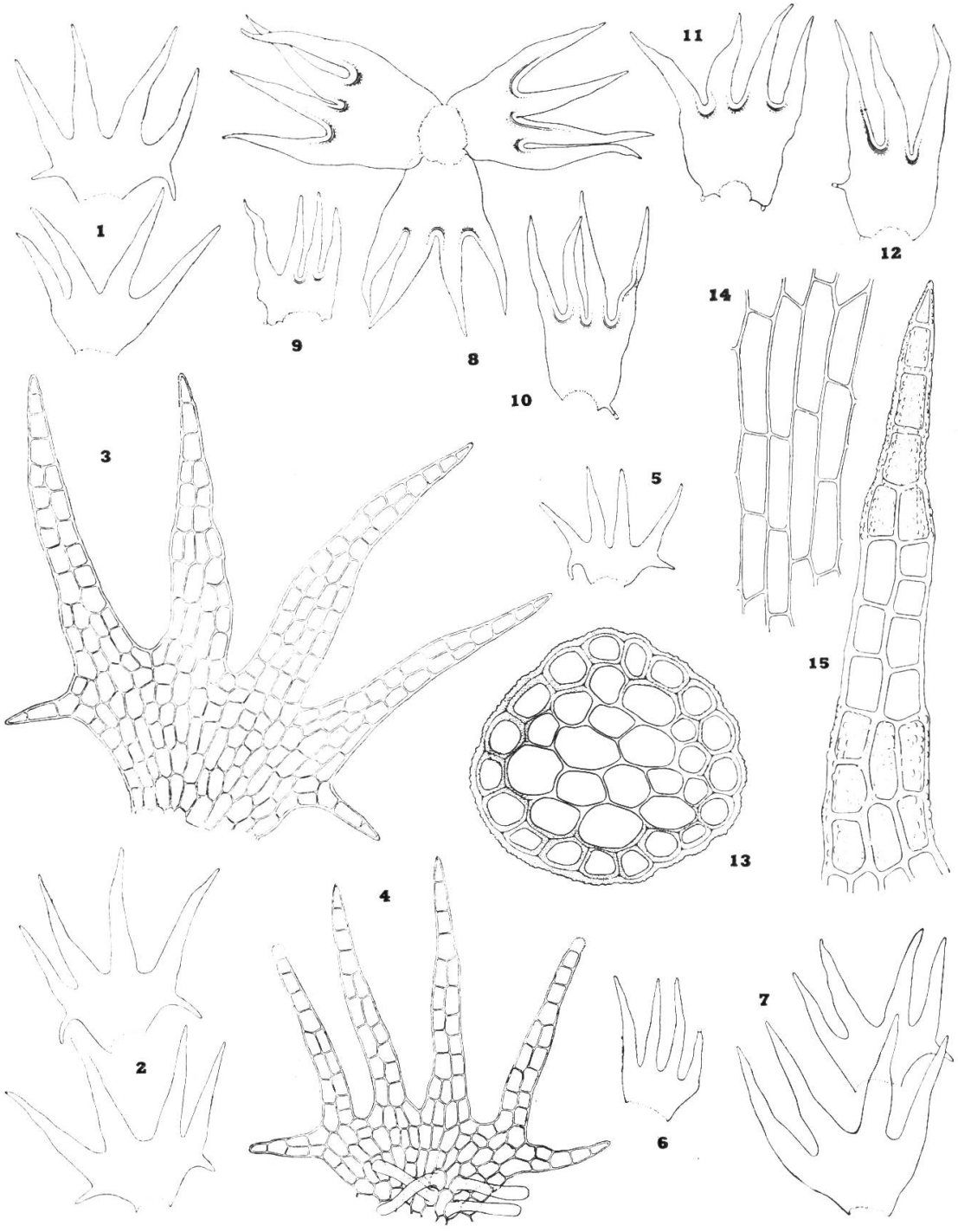
TYPE. Japan, Central Honshu Island, Kurobe Gorge, Toyama Prefecture — *S. Satomi* (holo- HIRO, sub num. 18370, as " *Lophochaete* cf. *trollii* ", det. H. ANDO; iso- S-PA).

DISTRIBUTION. Known only from the type and from a single collection from Szechwan Prov., China (Ando 1963). The Chinese plant, according to ANDO, is identical with the Japanese; his figures support this contention. ANDO, who did not have fertile material of *L. trollii* available for comparison, failed to appreciate the fact that there appear to be criteria, derived from both the sterile gametophyte and from the ♀ bracts, that separate the Himalayan *L. trollii* from the Japanese-Chinese *L. andoi*, and considered the two populations identical. Unless and until intermediate populations can be found, a species distinction must, I think, be maintained.

ECOLOGY. The type material occurred mixed with *Hypnum fujiamae*, *Blepharostoma trichophyllum*, *Cephalozia* spec., *Microlepidozia makinoana* and *Mnium punctatum*.

FIG. 19. *Archeochaete temnomoides*

1. Medium-sized leaves (×42). – 2. Large leaves (×42). – 3. Leaf (×106). – 4. Underleaf (×106). – 5-6. Underleaves; 6, atypical, with aborted lobe (×42). – 7. Two lateral leaves (×42). – 8. Innermost bracts and bracteole (×24). – 9. Subfloral bracteole (×24). – 10-12. Subfloral bracts (×24). – 13. Stem cross-section (×265). – 14. Cortical stem cells (×178). – 15. Leaf lobe, cuticular papillae drawn in above and below (×220).
All from type.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DIFFERENTIATION: A distinctive species, clearly allied only to *L. trollii*, with which it shares the strongly elongated cells and the acuminate apices of the leaf lobes, the rather distantly, but distinctly, delicately granulate-papillate cuticle and the crenulate-produced margins of the leaves and underleaves.

The differences between the two taxa seem adequate to warrant a full specific separation. Particularly distinctive for *L. andoi*, as contrasted with *L. trollii*, are: (1) the uniformly bisbifid leaves and underleaves—no exceptions being present, even on the weakest branches seen; (2) underleaves with lobes characteristically, widely divergent—the underleaf thus much broader and shorter than the leaf, although equal in basic size; (3) bracts much more deeply bisbifid, with disk less than 0.25 height of leaf, the lobes linear and almost setaceous; (4) leaf, underleaf and bract lobes faintly crenulate, rather than strongly so; (5) the Blepharostoma-like weaker branch leaves, with linear, filiform lobes only 2-3 cells broad basally: similar leaves are never produced by *L. trollii*.

The perianth mouth, with 12 slender, acuminate, prominent lobes, is another distinctive feature of *L. andoi*. In the single, weathered perianth of *L. trollii* which I have seen, the perianth lobes are shorter and not acuminate. There are also slight, and perhaps environmentally induced, differences in the leaf lobes and leaf cells. In *L. andoi* the lobes are much more attenuate—particularly on branch leaves, ending in usually 3-4 superimposed single cells; in *L. trollii* the lobes are short-acuminate and end most often in 2 single cells. In *L. andoi* marginal cells are rather weakly produced, the leaves thus slightly crenulate; in *L. trollii* the crenulations are considerably more pronounced. All in all, *L. andoi*, with its more acuminate and setaceous lobe apices, has a very different facies from *L. trollii*.

ARCHEOCHAETE

Archeochaete Schust., Jour. Hattori Bot. Lab. 26 : 262. 1963.

TYPUS. *Archeochaete kuehnemannii* Schust.

Plants creeping or erect to ascending, warm brown, hardly radial, sparingly and irregularly branched; sterile shoots ca. (900)1200-2100 μ wide (with leaves); branching sparing, usually of the Frullania-type (dorsal, supporting leaf bifid), rarely of the Microlepidozia-type and rarely postical and intercalary; usually with subfloral innovations that are terminal, basiscopic and infra-axillary, often from base of bracteole. *Stem* ± soft-textured; cortical cells short-oblong, in cross-section not or little tangentially flattened, their diameter subequal to that of medullary cells, thus without a defined cortex. *Rhizoids* rare, colorless to brownish, from bases of underleaves. Moderately to strongly anisophyllous: the underleaves ca. 0.35-0.6 the area of lateral leaves; lateral *leaves* from ca. 650 μ wide and 600-650 μ long to (700)900-1350 μ wide and 1000-1420 μ long, remote, transversely oriented, ranging from weakly succubous through transverse to very feebly incubous in insertion, widely patent to subsquarrose, cuneiform to narrowly obtrapezoidal in outline, length somewhat inferior to distinctly longer than their apical width, usually unequally to equally quadrifid, occasionally trifid, the median sinus occasionally slightly, but

never conspicuously deeper, the sinuses descending ca. 0.6-0.7 the leaf length; sinus bases typically rounded, without an area of swollen cells (or rarely with 1-2 inflated cells that are, typically, smaller than other cells); disk ca. (5)6-8 to 8-12 cells high, obtrapezoidal; disk entire-margined or bearing on one or both margins a single spinose tooth; lobes moderately divergent, narrowly to linearly lanceolate, 4-6(7) cells wide on sterile leaves, strongly spreading to squarrose, acuminate, entire-margined, the narrowed apices uniseriate for 2-4 to 4-6 cells. *Underleaves* of mature shoots 300-325 μ wide and 350-400 μ long to 425-670 μ wide and 675-900 μ long, partially 3- or all 4-fid for 0.65 their length, the median sinus usually not distinctly deeper; lobes erect to moderately divergent (outer lobes), linear-lanceolate, (2)3-4(5) cells broad at base, terminating in uniseriate filaments usually (3)4-5 cells long. *Cells* oblong to oblong-hexagonal in disk, thin- to barely thick-walled, with vestigial trigones, ca. 15-23 μ wide and 24-38 μ long; cells of tips of segments 16-25 × 20-60 μ to 25-34 × 42-55 μ; cuticle smooth or conspicuously verrucose-striolate; middle lamella moderately distinct. *Asexual reproduction* lacking. Plants dioecious; ♂ plants with *androecia* intercalary on leading stems or ± short to long lateral branches; androecia diffusely spicate, of 3-6 pairs of bracts; *bracts* oblong, ca. 450 μ wide and 820 μ long, less deeply quadrifid (to 0.5) than lateral leaves, the entire suberect base conspicuously inflated, the linear-lanceolate lobes erect to suberect; *bracteoles* small, underleaf-like, flat, without antheridia; bracts monandrous; no paraphyses; *antheridia* with the biseriate stalk 33 μ in diam. and ca. 75 μ long, formed of 9-14 cell tiers, the cells very short, much wider than high; antheridial body ca. 230 × 275 μ, of numerous small (ca. 22-30 × 25-35 μ), irregularly oriented cells. *Gynoecia* terminal on leading stems; with or without fertilization there may be an infra-axillary, terminal-basiscopic, postical, subfloral innovation (originating just below the bracteole or 1-2 leaf-cycles below the bracteole); with fertilization, the innovation remains small and juvenile. *Bracts* on mature gynoecia becoming ± remote from each other through the continued proliferation and elongation of axial tissue below the perianth, a coelocaule precursor forming, the sporophyte seemingly penetrating deeply into the axis apex. *Perianth* extraordinarily longly stipitate with maturity, terete below, inflated medially and/or distally, contracted in distal 0.4, the narrowed distal portion bluntly triplicate, the plicae inflated; near mouth often with weak accessory pleats and sulci; mouth strongly narrowed, lobulate and short-ciliate to ciliolate (teeth from 1-celled to 2-4-celled and uniseriate, the larger teeth often 2 cells wide at base; cells elongated, ca. 18-21 × 50 μ to 22 × 64 μ to 21-38 × 70-75 μ, somewhat thick-walled; terminal cells narrowly triangular, sharply pointed; uniseriate to near base). *Bracts* quadrifid, with triangular to lanceolate, edentate lobes, similar to leaves but sometimes with less acuminate (usually merely acute) apices; disk unarmed or with a basal tooth on one or rarely both sides; *bracteole* similar. Shoot-calyptra distinct. *Capsule* ovoid-ellipsoidal.

Archeochaete is a synthetic entity, effectively demonstrating the fallacy involved in attempting to segregate *Lophochaete* into a separate family (*Pseudolepicoleaceae* of FULFORD and TAYLOR 1960). This group was separated from the *Blepharostomataceae*, because, in contradistinction to *Blepharostoma*, the "leaves are strikingly bis-bifid" and the "perianth is 5-keeled or -plicate, while in *Blepharostoma* it is 3-keeled". *Archeochaete* shares with *Blepharostoma* the equally quadrifid leaves,

and the perianth with three inflated plicae. Yet, in other respects, the genus is closer to " *Pseudolepicolea* " (*Lophochaete*): the retention of a distinct disk; the leaf lobes 4-6 cells broad at base; the stem, formed of many rows of cells; the lack of gemmae; the quadrifid bracts that are, fundamentally, similar to the vegetative leaves; the form of the androecia and, above all, the basic facies, are those of *Lophochaete* (including *Pseudolepicolea*). Thus this genus forges another strong link between *Blepharostoma* and other genera of *Blepharostomataceae* which possess less reduced leaves.

The genus *Archeochaete* is in some respects intermediate between *Lophochaete* and *Temnoma*. As in the majority of species of *Temnoma*, there is no defined cortex; underleaves are somewhat reduced in size; leaves and underleaves possess sinuses of subequal depth; and, as in that genus, the perianth is trigonous. Also, as in certain species of *Temnoma*, we find predominantly Frullania-type lateral branching supplemented by occasional postical, intercalary branches. Yet the total lack of teeth or cilia of the ♀ bract margins and of the leaf lobes, the short-ciliate to denticulate-ciliate perianth mouth and the strongly contracted perianth apex all separate *Archeochaete* from *Temnoma*.

In *Archeochaete temnomoides* the distinctions between *Archeochaete* and *Temnoma* are slightly bridged, insofar as the leaves of this species almost constantly produce a single spinose tooth of one or both leaf margins; yet this species retains the entire-margined perichaetial bracts of *Archeochaete*, and has notably reduced underleaves.

In addition to the affinities to *Lophochaete* and *Temnoma*, *Archeochaete* is also allied to *Archeophylla*. The plants are similar in size and facies, the brown coloration and rather similar branching modes (in both genera occasional Microlepidozia-type branches have been seen). [1] More significantly, the leaves in neither *Archeophylla* nor *Archeochaete* are really bisbifid—the median sinus of quadrifid leaves normally not descending more deeply than the lateral sinuses; in both genera many underleaves and some lateral leaves are trifid rather than quadrifid. In *Archeochaete* there is no counterpart to the occasionally bifid leaves and underleaves of *Archeophylla*, and trifid lateral leaves occur only sporadically. Both *Archeophylla* and *Archeochaete* possess stipitate perianths that bear three inflated plicae distally; both genera have conspicuously inflated male bracts with reduced, almost setaceous lobes. Nevertheless, two well-differentiated genera are at hand; the lack of collenchyma in the cells of *Archeochaete* is a notable distinction. Also, the massive stems, of many more cell rows, with cortical cells never enlarged, further separate *Archeochaete* from *Archeophylla*.

Archeochaete is thus of exceptional interest, for it shows points of contact with *Blepharostoma* (form of perianth; similarity in depth of leaf sinuses), with *Temnoma* (number of plicae of perianth; similarity in depth of leaf sinuses), with *Lophochaete* (axial anatomy, to some extent; perianth form but not plica number; cell form; perianth mouth, form of leaf lobes and leaf insertion) and with *Archeophylla* (plication and contraction of perianth apex; branching; color; leaf form

[1] The basiscopic, terminal, usually weak and dormant innovations formed on gynoecial axes in *Archeochaete* represent a further point of distinction. They occur in no other *Blepharostomataceae* and, except for the advanced *Radulinae* and *Porellinae*, occur in *Jungermanniales* again only in a few *Scapaniaceae*.

and reduced size of underleaves; tendency towards reduction in leaf lobe number). *Archeochaete* and *Archeophylla* thus serve to further elaborate—and further interconnect—the various extremes known within the single family *Blepharostomataceae*.

The recently discovered *Archeochaete temnomoides*, in particular, forms a partial bridge between *Temnoma* (to which it is clearly allied in the non-bisbifid leaves, the roughened cuticle and, in particular, in the frequent presence of a sharp tooth of one or both margins of the disk of the leaves) and *Lophochaete* (to which the wholly edentate margins of the perichaetial bracts suggest an affinity).

Key to species

1. Cuticle smooth; leaves symmetrically quadrilobed; disk 8-12 cells high, not or very rarely with a small tooth; leaf lobes running out into acuminate tips formed of 4-6 cells (which are in part elongated and twice as long as wide); underleaves ca. 0.6 the area of lateral leaves, often 3-fid, with a disk to 8 cells high; cells of uniseriate leaf-lobe tips ± elongated, mostly 40-60 μ long. Tierra del Fuego . . . . . *A. kuehnemannii* Schust.

1*. Cuticle conspicuously roughened; leaves tending to be quite asymmetrically (3)4-lobed, the 2 ventral lobes smaller; disk only 5-8 cells high, often on one or both margins with a single sharp, spinose tooth; leaf lobes running out into sharp but not acuminate tips formed by 3-5 superimposed cells (which are all approximately isodiametric); underleaves only 0.35-0.45 the area of lateral leaves, deeply 4-fid, the disk only 3-5 cells high; cells of uniseriate leaf-lobe apices ± isodiametric, 20-30 μ long. Tristan da Cunha *A. temnomoides* Schust.

Archeochaete temnomoides Schust., spec. nova.

Plantae brunneae, repentes vel ascendentes; folia (3)4-lobata saepissime asymmetrica, lobis duobus ventralibus minoribus; discus 5-8 cellulas tantum altus, in uno marginum vel in ambis dente singulo parvo acuto praeditus; lobi foliorum acuti nec acuminati, apicibus e cellulis 3-4 superpositis formatis; amphigastria sat parva (c. 0.35-0.45 magnitudinis foliorum aequantia), profunde 4-lobata, disco 3-5 cellulas tantum alto; cellulae cuticulâ asperâ obtectae; bracteae bracteolaeque femineae 4-lobatae, lobis lanceolato-acuminatis, erectis, integris.

Plants medium-sized, creeping to ascending, rather vivid brown, 6-12(15) mm long and 900-1200 μ wide on mature shoots, often smaller, irregularly branched; branches infrequent, all seen terminal, of the Frullania-type; no subfloral innovations seen. *Stem* a little rigid, ± sinuous to flexuous, ca. 110-125 μ in diam., somewhat elliptical in section, only ca. 7 cells high, with cortical cells in ca. 15-18 rows; cortical cells in one layer, with wall brownish, feebly thick-walled (externally at least), the free walls striolate; cortical cells ca. (14)16-20(22) μ wide and 45-60 μ long, rectangulate; medullary cells about equal in diam., hyaline, leptodermous, ca. 16-21 μ in diam. *Rhizoids* sparing, but from many underleaf bases, light brownish. Quite anisophyllous: the underleaf area ca. 0.35-0.45 that of lateral leaves. Lateral *leaves* remote to scarcely contiguous, transversely inserted or to only 10-15° succubous, rather stiffly laterally widely patent, but the lobes somewhat incurved or only obliquely

spreading, the leaves thus somewhat concave, hand-like, rather asymmetric (ventral two lobes usually clearly smaller, narrower), ca. 460-575(775) μ wide and 520-565 (590-625) μ long, cuneate-obtrapezoidal, 0.6-0.7 divided into 4, less often 3 lobes; lobes entire-margined, linear-lanceolate, acuminate but not longly so, ending in 3-5 subisodiametric single cells in a row, the sinuses subequally deep (the lateral ones usually narrowly rounded at base; median often sharper), without swollen cells at base; disk obtrapezoidal, 5-8 cells high only, armed near middle of one or both (rarely none) lateral margins with a stiff, often recurved tooth usually formed of 3-4(5) cells superimposed, inserted in a base 2 cells broad; lobes little to moderately divergent, 4-6 cells broad at base. *Underleaves* rather variable, almost without exception 4-lobed for 0.7-0.8 their length, ca. (330)360-420 μ wide and 330-350(390) μ long, subquadrate to oblong, with 4 narrow, subfiliform lobes that are erect or feebly divergent, only 2(3) cells broad at base and uniseriate for much of their length; disk 3-4 to 4-5 cells high, often or usually with a sharp, laterally divergent tooth of one or both margins (similar to lateral discal teeth of leaves). *Cells* medium-sized, firm, equally but moderately thick-walled, those of the uniseriate leaf apices 16-25 μ wide and 20-30 μ long, subquadrate or short-oblong, the triangular terminal cell excepted; median cells irregular, averaging oblong, ca. (15)16-21(23)×24-38 μ; basal cells usually no larger, isolated cells excepted; cuticle, to tips of leaf lobes, sharply asperate-verruculose. No *asexual reproduction*. Plants dioecious; *gynoecia* terminal on apices of vigorous, main stems. Subinvolucral leaves progressively larger, grading into bracts, quadrilobed and obovate-cuneate, margins entire; *bracts* and *bracteole* identical, larger than leaves, obovate-cuneate, ca. 580-670 μ wide distally and 900-1050 μ long, strongly narrowed to base, 4-lobed for 0.55-0.65 their length, the lobes erect to feebly divergent, lanceolate to linear-lanceolate, ca. 7-9 cells wide at base, the apices not acuminate, ending in 2-4(5) superimposed, subisodiametric cells, as on leaf lobes; lobes and disk margins both edentate; sinuses V- to narrowly U-shaped or almost sublinear. *Perianth* (very juvenile only known) with contiguous to subremote, short, 1-3-celled teeth at mouth.

TYPE. Tristan da Cunha, Red Hill, on wet rock, ca. 600 m, 18.1.1938 — *Christophersen and Mejland 1222* (S-PA).

The type material occurs admixed with *Plagiochila fuscobrunnea*, *Lepidozia* spec., and a filmy fern. It was erroneously reported from Tristan da Cunha by ARNELL (1958) as *Blepharostoma quadripartitum*.

DIFFERENTIATION. This species is exceedingly distinct in all respects. When sterile, it looks like a somewhat smaller edition of *A. kuehnemannii*, particularly

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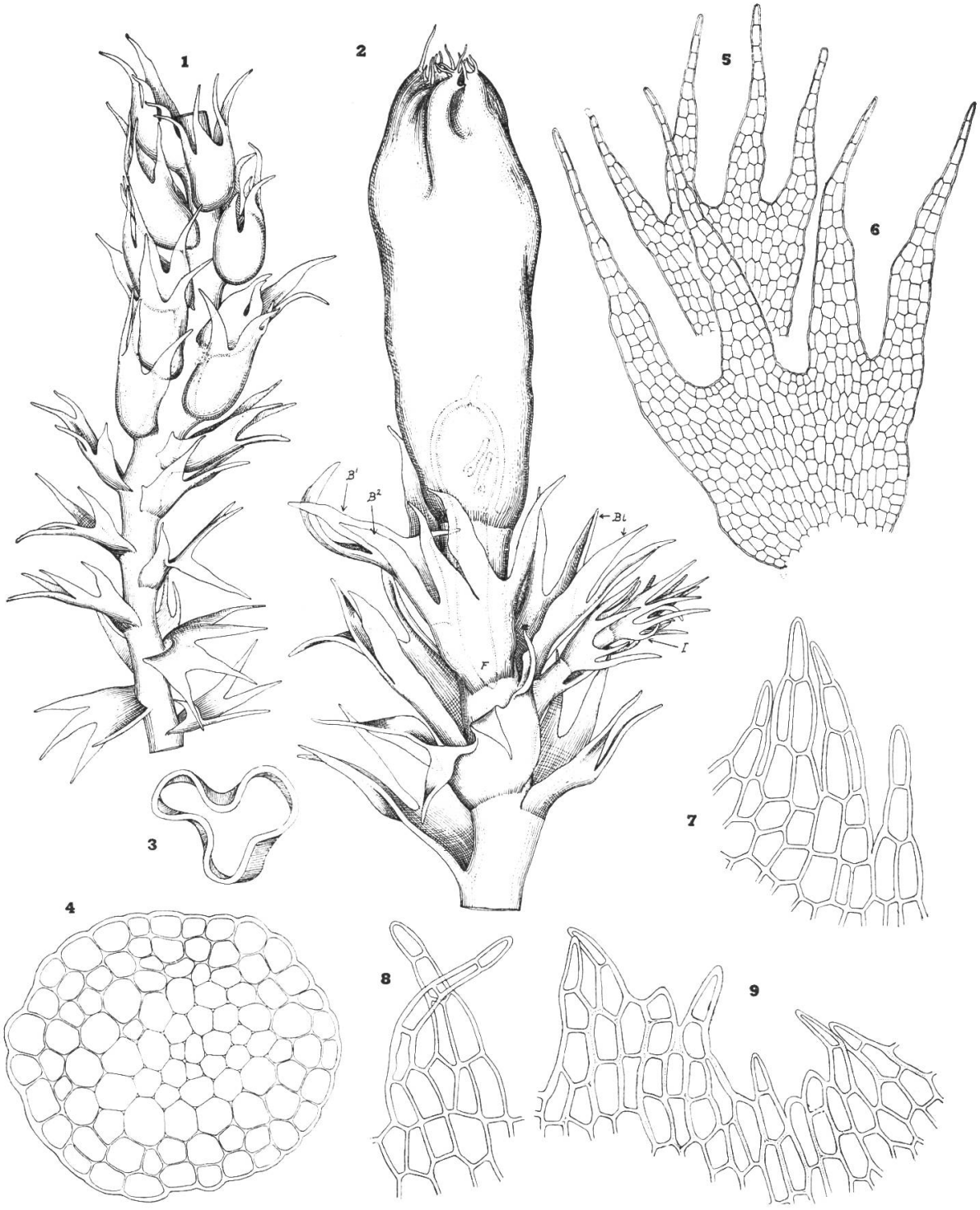
FIG. 20. *Archeochaete kuehnemannii*

1. Androecial shoot (×20). – 2. Lateral view of perianth-bearing shoot, with somewhat immature included sporophyte; note deep " penetration of foot " (*F*, " foot "; *I*, infra-axillary subfloral innovation; *Bl*, bracteole; B^1 and B^2, bracts) (×20). – 3. Cross-section, distal $^1/_8$ of perianth (×222). – 4. Stem cross-section (×155). – 5. Large underleaf, same stem sector as leaf 6 (×45). – 6. Large leaf (×45). – 7-9. Sectors of perianth mouth, showing variation in dentition (×120).

All from type.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because of the warm brown color, and the deeply quadripartite leaves with linear-lanceolate, entire-margined segments. The similarity is enhanced by the rather small underleaves, almost appressed to the stem—much smaller than in any species of *Temnoma* with which confusion can occur. Under the microscope, however, the rough cuticle and the very general occurrence of a sharp tooth of the middle of the disk margin (of vegetative leaves), usually both antically and postically, but at least on one of the margins, suggest *Temnoma*—in particular forms of *T. quadripartitum* and *T. palmatum*. The position of the lateral teeth of the disk separates the species from *T. quadripartitum*; unlike in that species, the teeth are high up on the disk margins, rather than basal. The much more deeply lobed leaves, with linear-lanceolate lobes, at once separate the species from *T. palmatum*. Confusion with other species of *Temnoma* is impossible. The gynoecium, of course, at once separates the species from any *Temnoma*: the quadripartite bracts are quite entire on the margins, both on the lobes and the disk.

Nevertheless, this species to some extent bridges the gap between *Temnoma* and *Archeochaete*. The single perianth (very immature), with the mouth fringed with stiff 2-3-celled teeth, also suggests *Archeochaete* rather than *Temnoma*.

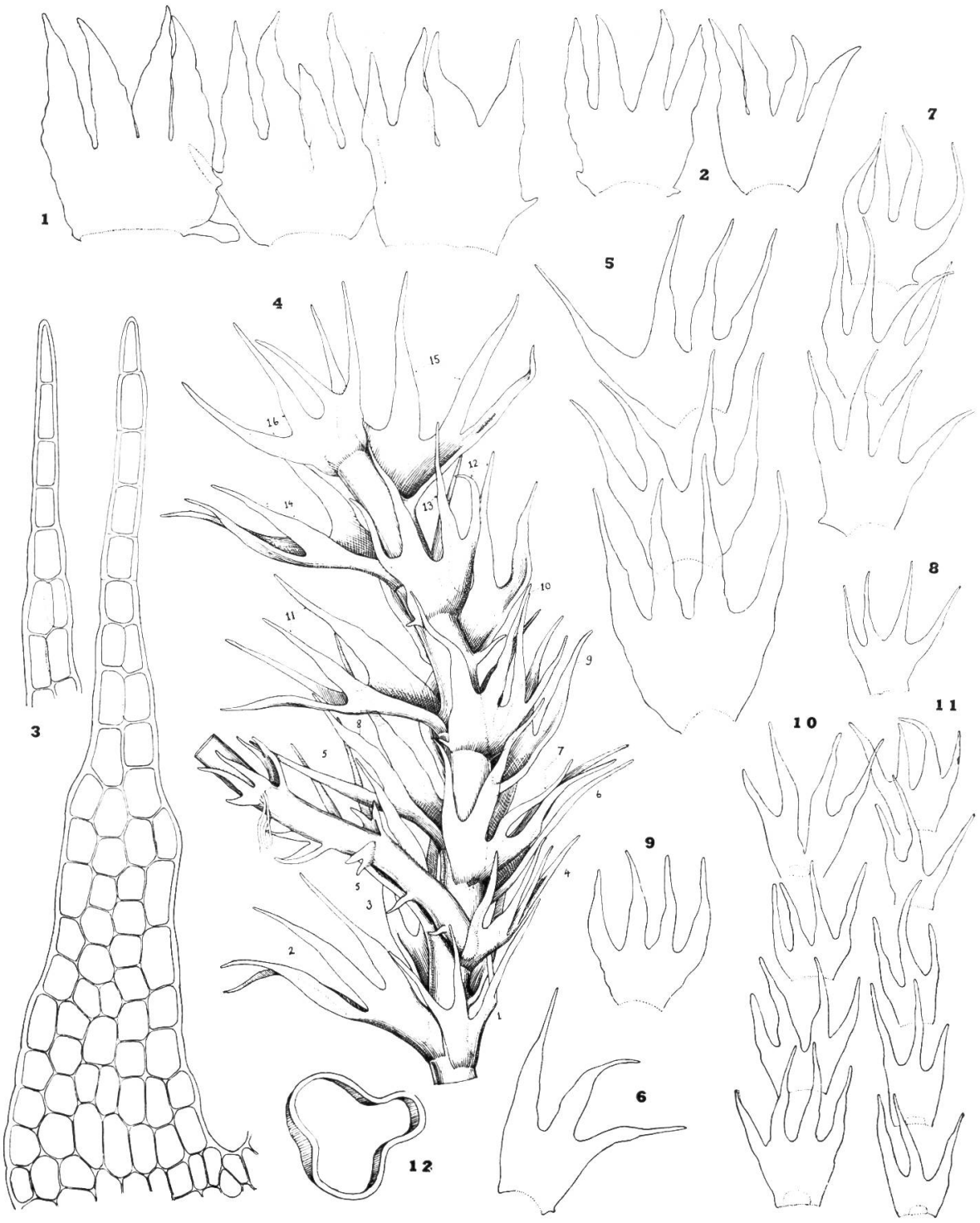
A. temnomoides is readily separated from *A. kuehnemannii* by a whole series of characters (most of which are cited in the preceding key). Suggestive are the differences in leaf surface (smooth in *A. kuehnemannii*; obviously papillose-verrucose in *A. temnomoides*) and leaf symmetry (symmetrically quadrifid in *A. kuehnemannii*; often asymmetrically so in *A. temnomoides*). Both species sporadically produce trifid lateral leaves and *A. kuehnemannii* often has trifid underleaves; in *A. temnomoides* the underleaves are almost constantly quadrifid. On some stems of *A. temnomoides* a rather high percentage of leaves are trifid, many more than I have observed in *A. kuehnemannii*, but there is, strikingly enough, no parallel tendency towards reduction in underleaf lobe number. The two species, thus, are distinct in this one feature: *A. kuehnemannii* tends to show a reduction of the underleaf lobe number associated with a retention of 4-lobed leaves; in *A. temnomoides* the opposite association exists.

Although in some ways (e.g., the presence of a tooth on one or both discal margins; the sharply papillose cuticle) *A. temnomoides* closely approaches taxa such as *Temnoma quadripartitum*, there are three marked vegetative differences: (1) the reduced underleaf size; (2) the tendency towards asymmetry of the leaves, with ventral—never dorsal—lobes reduced in size; (3) the marked ability to develop trifid leaves. In *Temnoma*, when, as is sometimes the case in subgen. *Temnoma* (e.g., *T. pulchellum*, *T. angustifolium*), the leaves become somewhat asymmetric, it is the dorsal lobes that become reduced in size.

FIG. 21. *Archeochaete kuehnemannii*

1. Bracts and bracteole, from a single cycle (×18.3). – 2. Two bracts, smaller gynoecium (×19.2). – 3. Apex of leaf lobe and whole leaf lobe (×125). – 4. Sterile shoot-sector, postical aspect, with postical-intercalary branch (×22.2). – 5. Three large sterile leaves (×22.2). – 6. Trifid stem leaf (×22.2). – 7. Three smaller leaves (×22.2). – 8. Small stem leaf (×22.2). – 9. Large underleaf, from shoot-sector from which leaves 5 were taken (×22.2). – 10-11. Medium-sized to small underleaves, the smaller mostly trifid (×22.2). – 12. Perianth cross-section, in distal $^1/_8$ (×22.2).

All from type.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Archeochaete kuehnemannii Schust., Jour. Hattori Bot. Lab. 26 : 262. 1963.

Plants light to vivid brown, 10-25 mm high and 1.5-2.25 mm wide (with leaves), irregularly branched; branches sparing, largely terminal and of the Frullania-type, a minority postical, axillary, intercalary; subfloral innovation, infra-axillary and postical, present or absent, sometimes developing even in presence of sporophyte-formation but then often remaining vestigial. *Stem* soft-textured, ca. 200-275 μ wide, somewhat elliptical to subterete in section; cortical cells hardly differentiated, in ca. 25-30 rows, short-oblong, ca. 22-28(30) μ wide, hardly to weakly tangentially flattened, subequal in diam. to medullary cells, which average (20)24-30(30-36) μ in diam. *Rhizoids* rare, colorless, from underleaf bases. Anisophyllous: underleaves 0.4-0.5 size of lateral leaves. Lateral *leaves* remote, transversely oriented (and almost transversely inserted; insertion ranging to feebly succubous; orientation ranging to feebly incubous), obliquely to widely spreading, with subsquarrose or squarrose lobes; leaves cuneiform to narrowly obtrapezoidal in outline, symmetrical, usually longer than wide at apices of the moderately divergent lobes, from ca. 700-1000 μ wide and 950-1050 μ long (smaller and ♂ axes) to 1000-1350 μ wide and 1150-1420 μ long (larger and ♀ axes), usually quadrifid, very exceptionally trifid for 0.6-0.7 their length; sinuses subequal, narrowly rounded at base, without a defined area of swollen cells at base (although there may be a few smaller cells); disk obtrapezoidal, 8-12 cells high, entire-margined; lobes long-acuminate, narrowly lanceolate, 4-6(7) cells wide at base (sterile leaves), the narrow apices uniseriate for a length of 4-6(7) cells (formed of narrow, elongated cells ranging from 45-60 × 18-20 μ distally to 42-55 × 25-34 μ towards base). *Underleaves* strongly variable, partially 3-, partially 4-lobed for 0.55-0.75 their length (median sinus not deeper to conspicuously deeper), from 480 × 675 μ to 670-770 × 875-900 μ, lobes (2)3-4 cells wide at base, attenuated distally and uniseriate for (3)4-5 cells usually. *Cells* oblong to oblong-hexagonal, leptodermous to slightly and equally thick-walled, without distinct trigones, in middle of disk ca. 25-35(38) μ wide and 40-60 μ long, near disk margins often more isodiametric; cuticle smooth; middle lamella moderately discrete. No *asexual reproduction.* Plants dioecious; ♂ plants somewhat more slender than ♀ plants, with *androecia* intercalary on leading stems or more or less abbreviated branches; androecia diffusely to somewhat compactly spicate, 800-900 μ wide (lobes excepted, with lobes to 1500 μ), of 3-6 pairs of contiguous to imbricate bracts; *bracts* more shallowly divided, the more extensive disk strongly ventricose, with antical margin incurved. *Gynoecia* terminal; *bracts* hardly sheathing perianth base, grading into subfloral leaves, little larger than leaves, little different from them in form : ca. 1080-1150 μ long and 925-1025 μ wide (small gynoecia) to 1440-1500 μ long and 1080-1150 μ wide, short-oblong, 4-lobed for 0.6-0.7 their length, the lobes erect or (outer pair) feebly spreading, narrowly triangular to lanceolate, acute but not acuminate, irregularly sinuous at times, edentate; sinuses narrowly V-shaped to incision-like; disk near or at base with a blunt to sharp tooth often present. *Perianth* longly stipitate with age, cylindrical-clavate to subclavate, ca. 3 mm long and (850)1000-1150 μ in diam., distal fourth contracted to the lobulate, short ciliate mouth, basically trigonous (but near tip occasionally with accessory plicae) in distal 0.2-0.25, terete below; cilia of mouth variable, from 1-celled to narrow teeth 2-4 cells long and 1-2 cells broad at base;

distal cells somewhat thick-walled, elongated, ca. 18-20×50 μ to 15-22×60-64 μ, occasionally 21×70 to 28×75 μ. Immature sporophyte with *seta* deeply penetrating into axis apex (axis elongating in apical portion), the bracts and bracteole becoming widely spaced. Immature *capsule* ovoid-elliptical in outline; calyptra with sterile archegonia inserted for a height up to half the distance from tip (thus with a shoot-calyptra developed).

TYPE. Argentina, Tierra del Fuego, *Sphagnum* bog 15-17 km W of Ushuaia, on road to Lapataia, at foot of S slope of Cerro Bandera — *RMS 58852.*

Growing amidst *Sphagnum*, *Blepharidophyllum*, *Cephalozia* spec., *Ptilidium ciliare* s.l., *Metahygrobiella dusenii*, *Leptoscyphus expansus*, and *Lophozia* cf. *patagonica*. Known only from the type.

DIFFERENTIATION. *A. kuehnemannii* is a distinctive taxon, admittedly with a facies which can lead to confusion with both *Lophochaete* and *Archeophylla*. The lack of well-developed collenchyma will at once separate the species from *Archeophylla*. The attenuate leaf apices, with the uniseriate tips longer than in any species of *Lophochaete*, are also distinctive. In *Lophochaete*, leaf tips are formed by, at most, 2-3 superimposed cells, which never average more than twice as long as wide. Of more significance, both leaves and underleaves of all species of *Lophochaete* are regularly bisbifid, whereas in *Archeochaete* the leaf sinuses are subequal.

Differences between *A. kuehnemannii* and *A. temnomoides* are given under the latter, and in the key. A more elaborate diagnosis and discussion of this species will be found in SCHUSTER (1965). The species is named in honor of Professor and Mrs. Oscar KÜHNEMANN of the University of Buenos Aires.

There are two extraordinary features isolating *A. kuehnemannii*. Firstly, the gynoecia subsequent to fertilization normally become provided with a long, fleshy stalk—the distance between the perianth and the first bract may approach the perianth length. With immature sporophytes, at least, the " penetration " of the sporophyte into this extension of the axis may be less extreme than in *Temnoma*, much of the stem remaining solid between the perianth base and the bracts. Obviously the extreme elongation of the axis apex is due to cell proliferation of the persistently meristematic shoot-tip, subsequent to fertilization. Immature gynoecia show no such elongation, and show the bracts and bracteole juxtaposed in a ring. With fertilization, the shoot-apex undergoes tremendous elongation and proliferation involving: (1) the tissues between bracts and perianth base; (2) tissues at the perianth base (resulting in elongation of the perianth itself); (3) tissues at the base of the calyptra, resulting in formation of a shoot-calyptra; (4) tissues which are already relatively well matured at the time of fertilization—the axial tissues on which are inserted the bracts and bracteole. As a consequence of marked elongation of cells in the latter zone, the bracts and bracteole become very widely spaced subsequent to fertilization.

It is my opinion that there is a " generalized " effect produced by the growth-stimulating substance secreted, presumably by the embryo, which results in the marked and widespread effects recounted above. This I regard as a primitive feature, which can be interpreted as suggesting that *Archeochaete*, as well as *Temnoma*, are primitive, unspecialized genera. By contrast, the effects of the growth-stimulating

substances in the higher *Jungermanniales* is, normally, much more localized and much more specific—suggestive of a physiologically more advanced and sophisticated system.

The second noteworthy feature is the frequent presence of abbreviated, possibly dormant, basiscopic, terminal " innovations " of gynoecial shoots. These, situated below (i.e. at the abaxial base) of a bracteole or underleaf, are similar in origin to the basiscopic branches of *Radula*. These branches are clearly terminal in origin—they possess no trace of a basal collar or any other interruption—and, like the branches of *Radula*, have no effect on the form or size of the associated leaf. It is noteworthy that where such basiscopic terminal branches occur in other *Jungermanniales* (*Radula*; at least in two species of *Scapania* s.l.) these branches are purely lateral in origin, never postical. In the many hundreds of gynoecia of *Temnoma* and other *Blepharostomataceae* which I have studied I have not again seen such branches. Although these branches are often situated directly below a bracteole, and hence are true innovations, they not infrequently arise 2-3 leaf-cycles below the bracts. They always appear to remain minute if a perianth matures and sporophyte develops; if fertilization fails, they may elongate.

After many hours of search I have located a single Microlepidozia-type branch in *A. kuehnemannii*, and also 2-3 ventral-intercalary branches (which seem in every case to issue from underleaf axils adjacent to or within androecia). Except for these isolated cases, the other vegetative branches are all of the Frullania-type, with a bifid " half-leaf ". In its branching, therefore, *Archeochaete kuehnemannii* is exactly like *Blepharostoma*.