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Botany

NEW SERIES, NO. 37

**Austral Hepaticae. 22. The Genus *Balantiopsis*
in New Zealand, with Observations on
Extraterritorial Taxa and a Phylogeny of
Balantiopsis and the Family
Balantiopsaceae (Jungermanniales)**

John J. Engel
G. L. Smith Merrill

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MURRA, J. 1946. The historic tribes of Ecuador, pp. 785-821. In Steward, J. H., ed., *Handbook of South American Indians*. Vol. 2, *The Andean Civilizations*. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.
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**John J. Engel
G. L. Smith Merrill**

*Department of Botany
Field Museum of Natural History
Roosevelt Road at Lake Shore Drive
Chicago, Illinois 60605-2496
U.S.A.*

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Abstract

Seven species of *Balantiopsis* are recognized in New Zealand, including *B. diplophylla* (Hook. f. & Tayl.) Mitt., *B. lingulata* Schust., *B. rosea* Berggr., *B. convexiuscula* Berggr., and *B. tumida* Berggr. The following new taxa are proposed: Ruizanthoideae Schust., *subfam. nov.*; Neesioscyphaceae Engel & Merr., *trib. nov.*; and *Balantiopsis verrucosa* Engel & Merr., the last a new species from New Zealand. The following new combinations are proposed: Balantiopsaceae subtribe Isotachidinae (Hatch.) Engel & Merr., *Hypoisotachis* (Schust.) Engel & Merr., *Balantiopsis* sect. *Pteridophylla* (Hatch.) Engel & Merr., *Balantiopsis montana* (Col.) Engel & Merr., *Balantiopsis splendens* (Steph.) Engel & Merr. (*Anisotachis splendens* (Steph.) Schust.), *Balantiopsis diplophylla* var. *hockenii* (Berggr.) Engel & Merr., and *Hypoisotachis multiceps* (Lindenb. & Gott.) Engel & Merr. (*Isotachis multiceps* (Lindenb. & Gott.) Gott.).

Results of a phylogenetic study of the genus *Balantiopsis* are presented, together with observations on intergeneric relationships in the family Balantiopsaceae. A discussion of character polarity and a reconstruction of ancestral character states are included. A realignment of the major taxa of Balantiopsaceae is proposed, based on morphological evidence that the perigynium of *Isotachis* and marsupium of *Balantiopsis* are homologous structures. An ancestral area analysis was undertaken to determine the geographical history of members of the family.

The analysis of 26 taxa and 25 characters, with *Triandrophyllum subtrifidum* as the outgroup, yielded four most parsimonious cladograms, each with a length of 114 steps, using the heuristic

search option of PAUP. Monophyly of *Balantiopsis* is supported by the possession of a pendant, geotropic marsupium. The position of subg. *Steereocolea* as the primitive element in the genus is supported; however, no support was found for maintaining *Anisotachis* as a distinct taxon, and the single species of the genus is transferred to *Balantiopsis*. Two subgenera of *Balantiopsis* are recognized (subg. *Steereocolea*, subg. *Balantiopsis*), as are two sections within subg. *Balantiopsis* (sect. *Balantiopsis*, sect. *Pteridophylla*) corresponding to units that were consistently resolved in the phylogenetic analysis.

Keys to the subfamilies, tribes, and subtribes of Balantiopsaceae and to the *Balantiopsis* species in New Zealand are included.

Introduction

The genus *Balantiopsis* contains 16 species and is basically south temperate in distribution, extending northward to Brazil (*B. brasiliensis* Steph.) and to Borneo, New Guinea, and the Philippines (*B. ciliaris* Hatt. and *B. philippinensis* H. Inoue, the latter endemic to the Philippines). Its distribution in south temperate regions is bicentric, with six species in southern South America and the remainder in temperate Australasia. The closely related genus *Anisotachis*, including the single species *A. splendens* (Steph.) Schust., occurs in southern South America. Four species of *Balantiopsis* occur in the Magellanian and Valdivian zones and (with one exception) the Falkland Islands: *B. asymmetrica* (Herz.) Engel, *B. bisbifida* (Steph.) Steph., *B. cancellata* (Nees) Steph., and *B. erinacea* (Hook. f. & Tayl.) Mitt. Two are

Valdivian + Juan Fernández: *B. purpurata* Mitt. and *B. crocea* Herz. For a discussion of the limits of these zones, see Engel (1978, 1990). For a map of the geographical range of *Balantiopsis* and the other genera of Balantiopsaceae, see Figure 1. Following Grolle (1983), we use the spellings Balantiopsaceae (rather than Balantiopsidaceae) for the family and Balantiopsoideae (rather than Balantiopsidoideae) for the subfamily. Herbarium citations follow the abbreviations in *Index Herbariorum* (Holmgren et al., Regnum Vegetabile 120, 1990)

The Genus *Balantiopsis* in New Zealand

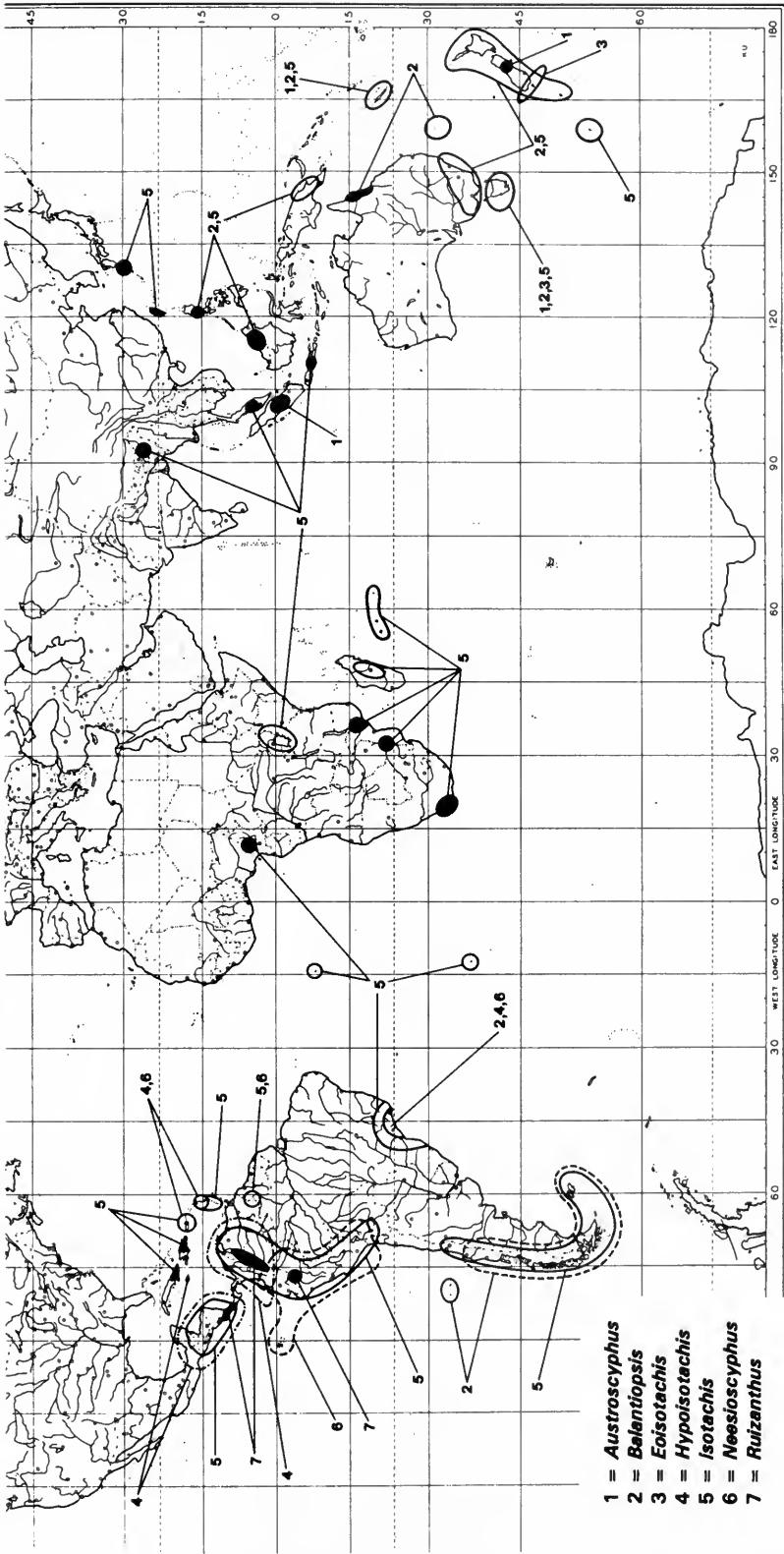
The genus *Balantiopsis* was established by Mitten (1867), based on *Jungermannia diplophylla* Hook. f. & Tayl., a New Zealand species. Later, Mitten (1885) described an additional species, *B. knightii*, from New Zealand. Colenso (1888) described *B. glandulifera*, as well as two *Chiloscyphus* species (*C. heterodontus* and *C. montanus*) that have since been proven to belong to *Balantiopsis*. Berggren (1898) added five additional New Zealand species to the genus: *B. aequiloba*, *B. convexiuscula*, *B. hockenii*, *B. rosea*, and *B. tumida*. Engel's (1968) revision of *Balantiopsis*, the first major contribution to the knowledge of the genus since Berggren's, recognized 11 species in the genus worldwide. Three species were recognized from New Zealand: *B. convexiuscula* (including *B. aequiloba*), *B. diplophylla* (Hook. f. & Tayl.) Mitt. (including *B. glandulifera*, *B. rosea*, *B. knightii*, and *B. hockenii*), and *B. tumida*. Schuster (1968) added an additional species, *B. lingulata*.

The results of our study of the New Zealand representatives of the genus are presented in this monograph. Our conclusions are based on the examination of specimens collected by Engel, Child, Hatcher, Hodgson, and others, plus all relevant type specimens. The result is a considerable refinement of species concepts and the acceptance of several additional taxa not previously recognized. This is followed by a phylogenetic analysis of members of the family Balantiopsaceae.

Balantiopsis Mitt. in Hook. f., Handb. New Zealand Fl. 751, 753. 1867. *Anisotachis* Schust., Nova Hedwigia 8: 282. 1964, *syn. nov.* *Steereocolea* Schust., Bull. Natl. Sci. Mus. Tokyo 11(1): 23. 1968.

Plants strongly anisophyllous, usually creeping or procumbent (unless growing submerged), less commonly ascending to stiffly erect, dull to quite nitid, translucent and rather delicate, with rose-red to deep red pigments or brownish pigmentation when developed. Branches ventral-intercalary and terminal, *Frullania*-type, sparing. Stems slender, in surface view with narrowly rectangular, firm-walled, cortical cells, in cross section the cortex in 1–2 rows of cells typically smaller and thicker-walled than those of the medulla; medullary cells \pm firm-walled. Rhizoids colorless or deep rose, smooth-walled, from stem near underleaf bases and (in *B. bisbifida*) from stem near base of ventral lobe of leaf. Leaves (in New Zealand taxa) distinctly complicate-bilobed, with a \pm sharp, well-developed carina (keel) that is curved and oriented at right angles to stem, the leaves (at least the ventral half) with an oblique, succubous insertion. Ventral lobe typically widely spreading to subsquarrose, at least slightly convex, short bifid, the segments hardly distinguishable in copiously ciliate plants, the lobe margins entire to conspicuously toothed or ciliate, the tips of the teeth, at least, formed of elongate cells, the ventral margin straight or recurved at ventral end and commalike to J-shaped or distinctly inverted U-shaped. Dorsal lobe erect or suberect, sometimes dorsally assurgent, variable in size, much smaller than to subequal to the ventral lobe, short bifid, the marginal armature usually similar to that of ventral lobe. Underleaves smaller than leaves, shallowly to deeply bifid, commonly with marginal armature like that of leaves. Cells thin-walled or, at most, moderately and evenly thick-walled, or the longitudinal walls sinuous-thickened, trigones lacking or minute, the cells short-rectangular or hexagonal, in median to basal parts of leaves elongate-rectangular, typically very narrow, often 3–5:1, characteristically in transverse, \pm regular tiers; margins of segments and distal sector of lobes at times with a border of tangentially elongate cells; cuticle finely to strongly striate-papillose or coarsely guttulate. Oil-bodies in all cells, hyaline or smoky gray to brownish, 2–13 per cell, granular to botryoidal.

Plants dioecious. Androecia on main shoot, or leading *Frullania*-type or ventral-intercalary branches, initially terminal in position but becoming intercalary; bracts \pm similar to leaves; antheridia (1)2–4 in axil of dorsal and ventral lobes, the stalk biseriate. Gynoecia on leading stems or branches, at time of fertilization with 1 or more rings of scalelike to densely ciliiform perigynial



Prepared by Henry M. Loppard
 © 1961 by The University of Chicago

FIG. 1. Total range of Balantiopsaceae Buch.

bractlets, no tubular perianth forming but instead a pendant, cylindrical, fleshy, conspicuously rhizoidous marsupium develops; mature gynoeceium with innermost subgynoeceial bracts with dorsal and ventral lobes nearly equal in size and form, the apex of each lobe distinctly divided. Calyptra distinct, carried down within the marsupium, the sterile archegonia lifted partway up the calyptra (i.e., a shoot calyptra).

Seta with 17–29 rows of epidermal cells surrounding an inner core of ca. 27–60 cells of \pm similar size. Capsule long-cylindrical, with spiral dehiscence, the wall uniformly of 3 layers, the outer layer of cells ca. equal to or thicker than both interior strata; outer layer (in surface view) with semiannular bands; innermost layer of cells with semiannular bands common, the bands sometimes forked and anastomosing to delimit fenestrae, or the cells with small nodular thickenings largely confined to the longitudinal radial walls, the thickenings at times extending onto both inner and outer tangential walls as faint spurs or semiannular bands.

Spores with exine brownish yellow, with a network of irregular, coalescing vermiform ridges that anastomose to form numerous irregular areolae; spore:elater diameter ratio 0.7–1.4:1. Elaters tortuous, bispiral, the spirals loosely wound.

The genus *Balantiopsis* is characterized by 1) complicate-bilobed leaves, the dorsal lobe smaller and folded over the ventral, the margins of the lobes often armed with teeth or cilia (Fig. 2:10); 2) elongate-rectangular leaf cells, thin-walled and delicate (Fig. 2:13,15) or with sinuous-thickened walls, lacking trigones, and oriented in transverse, \pm regular tiers (Fig. 9:6); 3) secondary pigments, often well-developed, reddish, purplish, or brownish; 4) the presence of a marsupium (Fig. 4:1,2), the sporophyte developing at its base; and 5) cylindrical capsules with spirally twisted valves (Fig. 2:17).

Most *Balantiopsis* species show considerable morphological variation. The development of teeth and/or cilia on the leaf margins is particularly variable, as are the relative size and shape of the dorsal leaf lobes. These often are highly variable from one population to the next, and sometimes even within the same population. Fortunately, other characters not emphasized in earlier treatments of the genus have proved helpful not only in delimiting species but also in distin-

guishing major subdivisions within the genus. These include form and insertion of the dorsal and ventral lobes, leaf cell size and number of oil-bodies per cell, cell-wall thickenings, form of the cuticle, and shape and papillosity of the marginal cells of the leaf.

The number of oil-bodies per cell has been found to be an important difference between species in the genus. *Balantiopsis rosea* and *B. verrucosa* have 2(3) oil-bodies per cell (typically one at each end of the cell); *B. convexiuscula* and *B. tumida* have 2–7 oil-bodies per cell; and *B. diplophylla*, *B. lingulata*, and *B. montana*, (5)6–11(13) per cell.

Cell size is also variable in the New Zealand species of the genus. For example, the leaf cells of *B. diplophylla* are up to 3 \times as large as those of *B. convexiuscula*. There are also differences in areolation between species. In *B. convexiuscula* the leaves are densely areolate (apparent even with a hand lens), the cells short-rectangular (2:1), and only 12–18 μm wide, with sinuous-thickened walls; the cells are arranged in precise, regular tiers so that the lobes have a characteristic ribbed appearance when dry. In *B. diplophylla* the cells of the distal third of the lobes are scattered, firm-walled, and short-rectangular to polygonal (ca. 2:1); only in the median sector and below do the cells become somewhat elongated and arranged in somewhat irregular tiers. The leaves of *B. montana* have a delicate, onion-skin-like texture related to the relatively large, thin-walled cells of the leaf, which are 23–34 μm wide and up to 110(122) μm long.

The shape and cuticular ornamentation of the marginal cells of the leaf lobes are also useful in species delimitation. In *Balantiopsis rosea* and *B. verrucosa* the marginal cells of both the ventral and dorsal lobes are tangentially elongated, forming a rather distinct border. The border cells have a finely striate-papillose cuticle, whereas the median lobe cells are coarsely papillose, with high, rounded (guttulate) papillae.

Color is also helpful in species differentiation and is usually retained in dried material: *B. rosea* and *B. diplophylla* are often rose-pink in color, whereas *B. convexiuscula* and *B. tumida*, when pigmented, are dull purplish; *B. montana* is typically pale translucent green to warm brown, with delicate, often highly nitid leaves.

Key to *Balantiopsis* in New Zealand

1. Leaf cells small (areolation dense), typically 12–16 μm wide, short-rectangular (2:1), at most 42 μm long, the cells in the distal sector with sinuous thickened walls; lobe margins minutely denticulate by projecting septa between the marginal cells, not bordered; dorsal lobe typically as broad as long, broadly orbicular to suboblate 2
2. Leaf margins (especially lobe apices) coarsely serrate, the teeth often terminating in elongate cilia; sinuses between apical segments V-shaped; dorsal leaf lobe somewhat smaller than the ventral; underleaves (often squarrose, spreading when plant suberect) smaller and deeply dissected (bifid to 0.5–0.6), with long, often curved, tapering cilia; plants prostrate to suberect, rather rigid, olive-green (or sometimes reddish-pigmented), terrestrial *B. convexiuscula* (p. 21)
2. Leaf margins (especially lobe apices) broadly dentate, with a short apiculus, lacking cilia; sinuses between apical segments shallow and lunate; dorsal and ventral leaf lobes subequal in size; underleaves rather large, broad, and shallowly bilobed (bifid to 0.4), often longitudinally plicate; plants typically erect, \pm soft-textured, brownish to often vinaceous, often submerged *B. tumida* (p. 24)
1. Leaf cells larger (areolation lax), at least 16 μm to as much as 35(40) μm wide (exc. where obviously secondarily divided), short-polygonal or elongate-rectangular, 65 μm or more long, with evenly thickened walls (not sinuous), often lax and thin-walled; lobe margins without projecting septa, sometimes with a differentiated border; dorsal lobe variable in shape; broadly to narrowly ovate to ligulate, typically much smaller than the ventral lobe, sometimes greatly reduced in size and deeply bifurcate 3
3. Leaf cells coarsely papillose (often grossly so, the papillae high and spherical to slightly elongated); marginal row of cells elongated and finely striate-papillose, forming a \pm distinct border; ventral lobe often canaliculate to conduplicately folded, the insertion strongly arched (U-shaped); dorsal lobe transversely inserted, the free margin not decurrent; oil-bodies 2(3) per cell, at opposite ends of cell 4
4. Leaves copiously armed with cilia, the ventral lobe with up to 20 cilia, the dorsal with up to 16; underleaves narrowly ovate, divided to 0.4, copiously ciliate; plants often clear wine-red *B. rosea* (p. 17)
4. Leaves with reduced armature, the ventral lobe 2–9 dentate-ciliate, the dorsal lobe with up to 5 lacinate-lobulate; underleaves broadly ovate to suborbicular, divided to 0.2 or less, sparingly armed; plants green to brownish or tinged with red *B. verrucosa* (p. 16)
3. Leaf cells finely striate-papillose (rarely almost smooth) throughout; marginal row of cells not elongated, not forming a distinct border; ventral lobe flat or at most moderately convex, longitudinally inserted, not or only moderately arched (at most J-shaped); dorsal lobe insertion oblique, the free margin decurrent; oil-bodies numerous (up to 13), scattered within cell 5
5. Leaf cells typically scattered in distal 0.3–0.5, not in evident transverse rows, the median cells polygonal to rather short-rectangular (ca. 2.5:1); ventral lobe rather broadly elliptic to broadly ovate *B. diplophylla* (p. 5)
5. Leaf cells in \pm evident transverse rows, the median cells elongate-rectangular (to 4:1); ventral lobe narrowly elliptic to lingulate 6
6. Dorsal lobe dorsally assurgent (at times distinctly so); ventral lobe plane or at most slightly convex, the insertion \pm straight or only slightly recurved (comma-like) at ventral end; ventral lobe margins with cilia mostly confined to the distal 0.3 of lobe *B. montana* (p. 12)
6. Dorsal lobe appressed, the keel sharply folded; ventral lobe convex, the insertion strongly recurved at ventral end (J-shaped); ventral lobe margins ciliate to the base *B. lingulata* (p. 14)

Subgenus *Balantiopsis*

Balantiopsis subg. *Schizophyllon* Hatt., J. Jap. Bot. 41: 129. 1966, *syn. nov.*

Section *Balantiopsis*

Balantiopsis diplophylla (Hook. f. & Tayl.) Mitt. Figures 3 and 4.

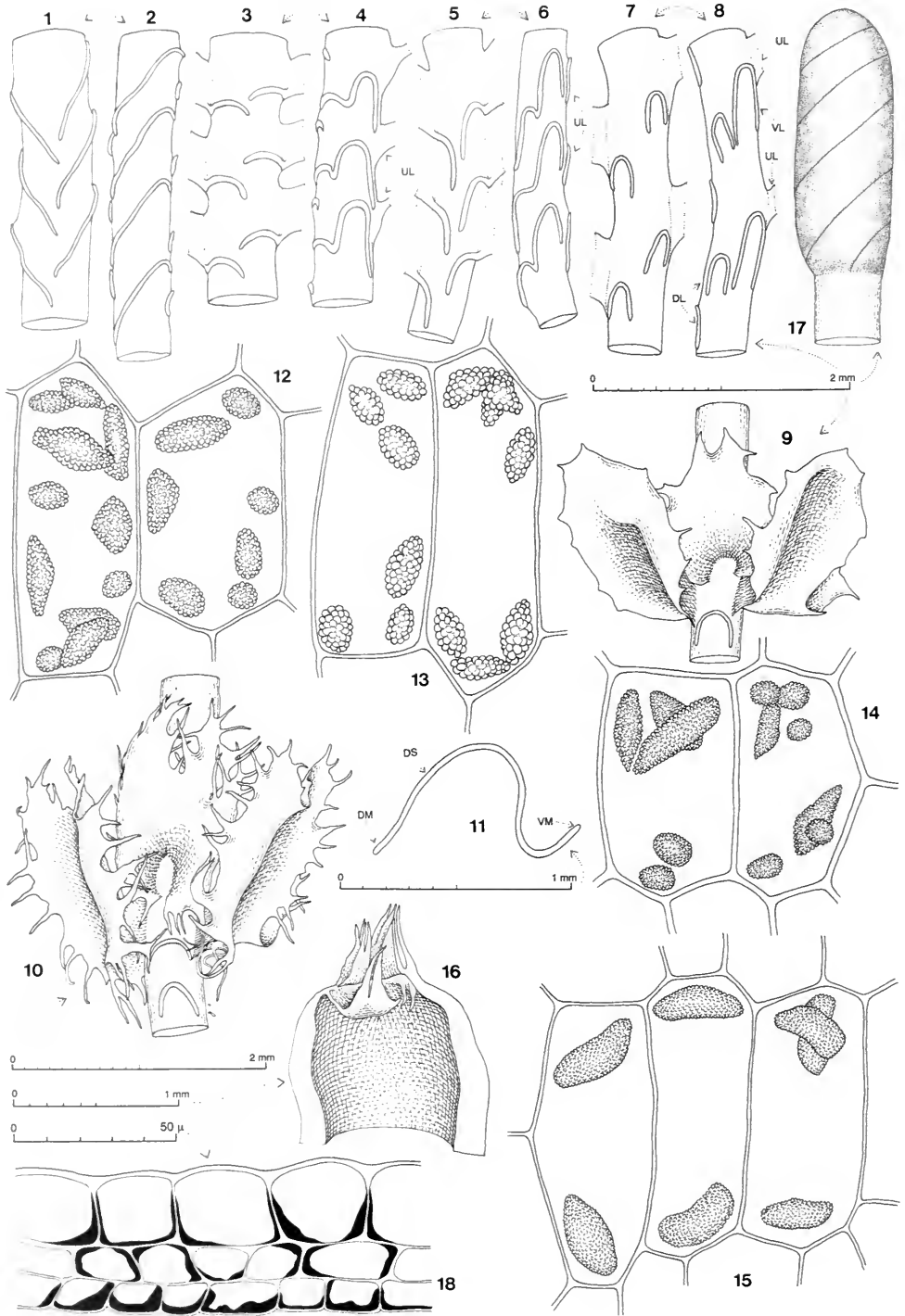


FIG. 2. *Balantiopsis* Mitt. General morphology. 1-8, Sectors of stem showing insertion lines, for each species the dorsal view at left and the lateral view at right (all at scale indicated for Fig. 8). 1, 2, *B. bisbifida*. 3, 4, *B. convexiuscula* (ul = underleaf). 5, 6, *B. verrucosa* (ul = underleaf). 7, 8, *B. erinacea* (ul = underleaf; vl = ventral lobe; dl = dorsal lobe). 9, Sector of main shoot of *B. verrucosa*, ventral view. 10, Sector of main shoot of *B. rosea*, ventral view (a pair of leaves between underleaf and uppermost scar removed for clarity). 11, Cross section of ventral lobe of leaf

Plants procumbent to loosely caespitose, whitish pale green to light green to warm brown, occasionally rose-tinted; shoots complanate, to 6 mm wide. Branching rather common, of *Frullania* and ventral-intercalary types, the frequency of each varying with growth habit of the plants. Leaves loosely to densely imbricate, rather sharply folded, the ventral lobe obliquely to widely spreading, to 3.4 mm long, the free margin of dorsal lobe \pm straight, the opposing dorsal lobes touching to moderately overlapping. Ventral lobe moderately convex (dorsally assurgent and concave in var. *hockenii*), the insertion moderately to distinctly J-shaped, the margin decurrent on the stem, the lobes broadly elliptic to broadly ovate, obscurely to distinctly bifid; segments acuminate, at times medium to broadly acute (then apiculate), (7)10–16 cells wide at base, terminating in a uniseriate row of 2–3 (var. *hockenii*) to 3–4 cells, the walls often thicker than those of the lamina cells; lamina margins gently and broadly curved, (1)2–8 dentate-ciliate to dentate-laciniate, occasionally entire (except for 2 apical teeth), the ventral margin 1–7 dentate-ciliate, each with a uniseriate row of 3–4 cells, the dorsal margin more sparingly armed; no border. Dorsal lobe variable, smaller than the ventral lobe, to ca. 3 \times the stem in width (often small and with a reduced lamina in var. *hockenii*), plane, the insertion transverse to somewhat oblique, then often abruptly curved and decurrent on the stem, the lobes narrowly to broadly ovate, shallowly to distinctly bifid, the segments often longer and more attenuate than in ventral lobe; margins 1–6-dentate-ciliate, occasionally entire, the dorsal (free) margin \pm straight, 0–3-dentate-ciliate. Underleaves large, about equal to or slightly larger than the dorsal lobes in size, weakly imbricate, appressed to moderately spreading, \pm plane, the insertion broadly U-shaped, narrowly to broadly ovate (exclusive of cilia), the underleaves bifid to 0.5 (the underleaves

small and more deeply bifid in var. *hockenii*); lobes linear to attenuate, \pm plane, with several cilia, the inner margins often entire; lamina margins ciliate to the base, at times with a lateral lobule approaching the lobes in size and shape, the ultimate lobe divisions and cilia terminating in a uniseriate row of 4–6 elongate cells, the margins decurrent on the stem. Ventral lobe cells in distal 0.35–0.5 of lobe typically scattered, short-rectangular to polygonal (ca. 2:1), and thin-walled but firm, the median cells in somewhat irregular transverse tiers, somewhat more elongate-rectangular and narrower, 27–38 μm wide \times 59–80(85) μm long; median cells of dorsal lobe similar to those of ventral lobe or slightly smaller; cuticle smooth to finely striate-papillose. Oil-bodies hyaline or gray, (5)6–11(13) per cell, coarsely granular to distinctly botryoidal (see under varieties).

Androecia terminal on main shoot or ventral-intercalary branches; bracts similar to leaves or, occasionally, more imbricate and more pigmented, with 1–2 abaxial bulges; antheridia 3–4 per bract, the stalk biseriate; paraphyllia present in bract axils, squamiform. Gynoecia on main shoot or ventral-intercalary or *Frullania*-type branches of varying lengths; bract margins undulate to crispate and sparingly dentate-laciniate. Marsupia green to deep rose in color, covered with rose-colored rhizoids.

Sporophyte not seen.

TAXONOMY—The most distinctive feature of this species is the field of scattered (irregularly arranged), \pm isodiametric cells of the distal third of the ventral lobe, evident under the dissecting microscope, as is the complete absence of a differentiated border (Fig. 3:4). All other New Zealand representatives of the genus have the cells arranged in regular, well-defined, transverse rows. The cuticle is finely striate-papillose and differs markedly from the often grossly papillose (gut-

←

of *B. rosea* (vm = ventral margin; ds = dorsal surface). 12, 13, Oil-bodies of median ventral lobe cells of *B. lingulata* ($\times 575$). 14, Oil-bodies of median ventral lobe cells of *B. convexiuscula* ($\times 1225$). 15, Oil-bodies of median ventral lobe cells of *B. rosea* ($\times 890$). 16, Longitudinal section through distal portion of young marsupium of *B. convexiuscula* showing perigynial bractlets at mouth. 17, Capsule of *B. bisbifida* showing spiral lines of dehiscence. 18, Capsule wall of *B. bisbifida*, cross section. (Figs. 1, 2 from Engel 11144, Chile, Prov. Valdivia, Volcán Quetrupillán; 3, 4, 16 from Engel 21686, New Zealand, South Is., Westland Prov., Westland Natl. Park, track to Lake Gault; 5, 6, 9 from type of *B. verrucosa*; 7, 8 from Engel 11978, Chile, Prov. Chiloé, Isla Chiloé, Cocaque area; 10, 11 from Child 5612, New Zealand, South Is., Southland Prov., Wilmot Pass Road to Deep Cove; 12 from Engel 20954, New Zealand, North Is., North Auckland Prov., Maungataniwha Range, Mangamuka Walkway; 13 from Engel 21139, New Zealand, North Is., North Auckland Prov., southern edge of Waipoua Forest; 14 from Engel 20986, New Zealand, North Is., North Auckland Prov., Omahuta Forest Kauri Sanctuary; 15 from Engel 21900, New Zealand, South Is., Otago Prov.: Mt. Aspiring Natl. Park, Blue Valley Track; 17, 18 from Engel 6389, Chile, Prov. Magallanes, Bahía San Nicolas.)

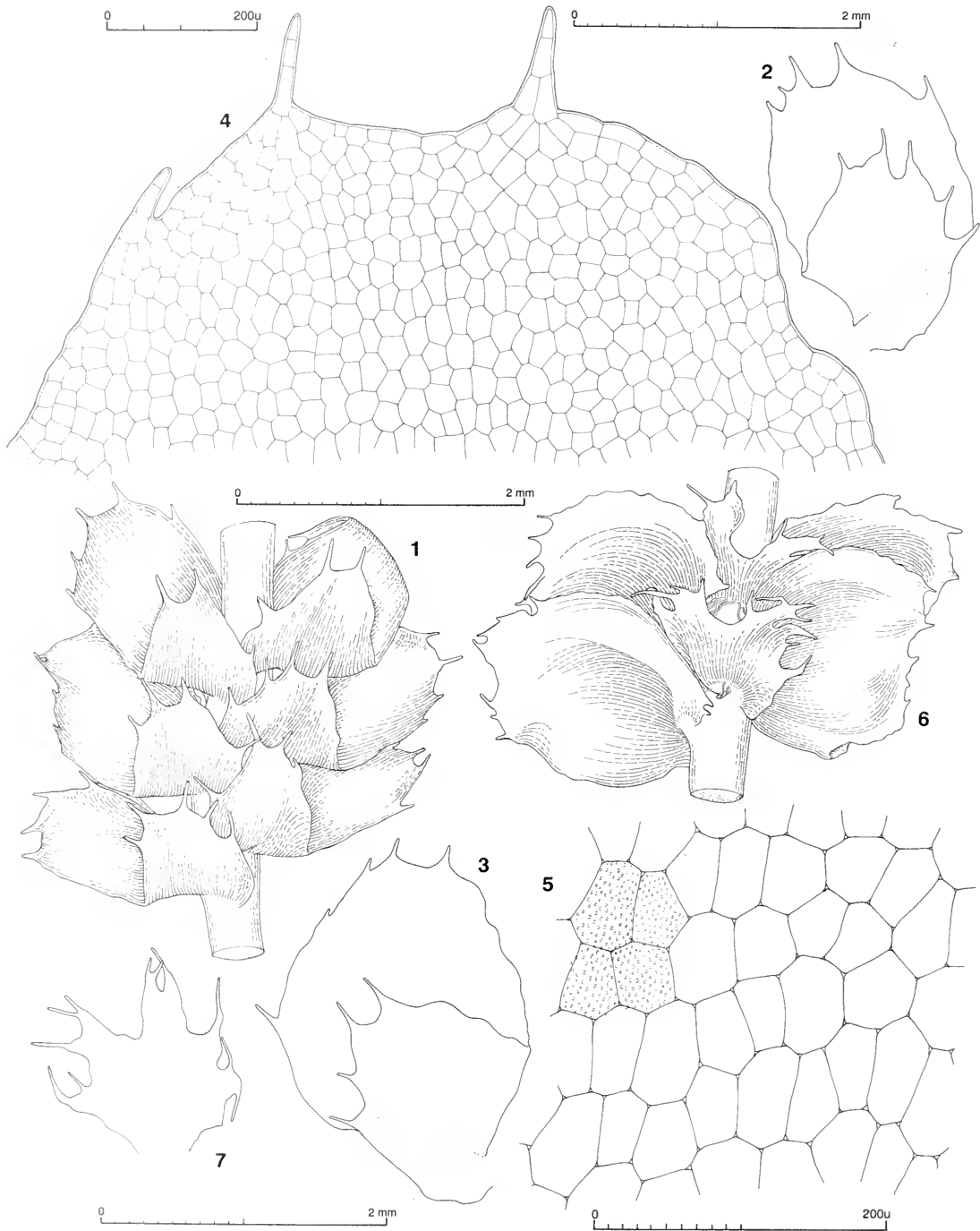


FIG. 3. *Balantiopsis diplophylla* (Hook. f. & Tayl.) Mitt. **1**, Sector of main shoot, dorsal view. **2, 3**, Leaves. **4**, Distal portion of ventral lobe of leaf. **5**, Median cells of ventral lobe. **6**, Sector of main shoot, ventral view. **7**, Underleaf. (All from type of *B. diplophylla* (FH).)

tulate) cuticle of *B. rosea* and *B. verrucosa*. The insertion of the ventral lobe is not or only moderately recurved (J-shaped, Fig. 3:6). The ventral lobes are broadly elliptic to broadly ovate.

Balantiopsis diplophylla was given a broad circumscription in Engel (1968) and would have included, in addition to the typical expression, the taxa we now recognize as *B. rosea*, *B. lingulata*, *B. montana*, and *B. diplophylla* var. *Hockenii*.

This species, *B. lingulata*, and *B. montana* together form a complex of closely related plants all sharing a similar leaf form, including a tendency for armature development, and leaf cells with many gray, opaque oil-bodies per cell. Care should be taken in differentiating these species, including the selection of optimally developed shoots within a population for study.

The aspect of this species at times approaches that of *B. convexiuscula*, with the ventral lobes similar in shape, armature, and orientation. The

leaf cells of *B. diplophylla*, however, are up to 3× as large as those of *B. convexiuscula*, which makes them easily distinguishable when the two species occur together. A distinctive growth form of *B. diplophylla* that occurs at higher elevations is often deeply rose-pigmented with strongly dorsally assurgent leaves, lending the plant a channelled appearance like that of a species of *Jungermannia*.

DISTRIBUTION—This species is reportedly distributed from Auckland Island in the south to New Zealand, Tasmania, Australia, New Caledonia, and the Philippines, but we have not reevaluated its variation in areas outside New Zealand. However, the typical expression of the species (as in the type, Fig. 3) is found predominantly on the subantarctic islands and the southern sector of South Island.

Two varieties may be recognized in New Zealand.

Key to Varieties of *B. diplophylla*

- 1. Ventral lobe broadly elliptic to broadly ovate, the sinus often conspicuous, often broadly rounded or angular, the apical segments terminating in a uniseriate row of 3–4 cells, the lobe margins up to 8-ciliate-dentate, the insertion typically J-shaped; dorsal lobe rather large, narrowly to broadly ovate, usually armed with at least a few divergent cilia; underleaves conspicuous, the sinus reflexed; oil-bodies smoky grayish brown var. *diplophylla*
- 1. Ventral lobe scarcely longer than wide, subelliptic, the sinus typically a mere narrow, rounded apical notch, the apical segments terminating in a uniseriate row of 2–3 cells, the lobe margins almost entire, the insertion nearly longitudinal, scarcely recurved; dorsal lobe often greatly reduced, often ligulate to vestigial and reduced to a bifurcate appendage; underleaves small and inconspicuous, the sinus plane, not reflexed; oil-bodies hyaline var. *hockenii*

Balantiopsis diplophylla* (Hook. f. & Tayl.) Mitt. var. *diplophylla

Jungermannia diplophylla Hook. f. & Tayl., Lond. J. Bot. 3: 377. 1844. *Gottschea diplophylla* (Hook. f. & Tayl.) Nees in G. L. & N., Syn. Hep. 624. 1846. *Gymnanthe diplophylla* (Hook. f. & Tayl.) Mitt. in Hook. f., Bot. Antarc. Voy. 2: 230. 1859. *Balantiopsis diplophylla* (Hook. f. & Tayl.) Mitt. in Thoms. & Murr., Rep. Sci. Res. Voy. Challenger Bot. 1(3): 87. 1885. Lectotype (*nov.*): Auckland Is., *Hooker* (FH!); isolectotype: (NY!). *Chiloscyphus heterodontus* Col., Trans. & Proc. New Zealand Inst. 21: 62. 1888 [1889], (“*heterodontata*”). Original material: New Zealand, North Is., sides of Mt. Tongariro, “County of East Taupo,” with type of *C. montanus*, 1887, *Hill*.

Plants often robust, procumbent to loosely caespitose. Leaves loosely to densely imbricate; ventral lobes obliquely spreading, broadly elliptic

to broadly ovate, often distinctly bifid, the apical segments acuminate to medium or broadly acute, the margins ciliate-dentate with up to 8 cilia; dorsal lobe rather large, narrowly to broadly ovate, usually armed with up to 7 divergent cilia. Oil-bodies scattered throughout cell, but with tendency for several to cluster at each end, pale smoky gray (chocolate-brown under lower magnification), (5)6–11 per cell, coarsely granular, the surface appearing papillose, 11.8–14.7 × 4.9–8.8 μm to 15.7–17.6 × 6.9–7.8 μm.

DISTRIBUTION AND ECOLOGY—The variety occurs in Auckland Island and New Zealand. The distribution of the species should be reevaluated according to the narrower circumscription documented here.

In New Zealand the variety is primarily a low-

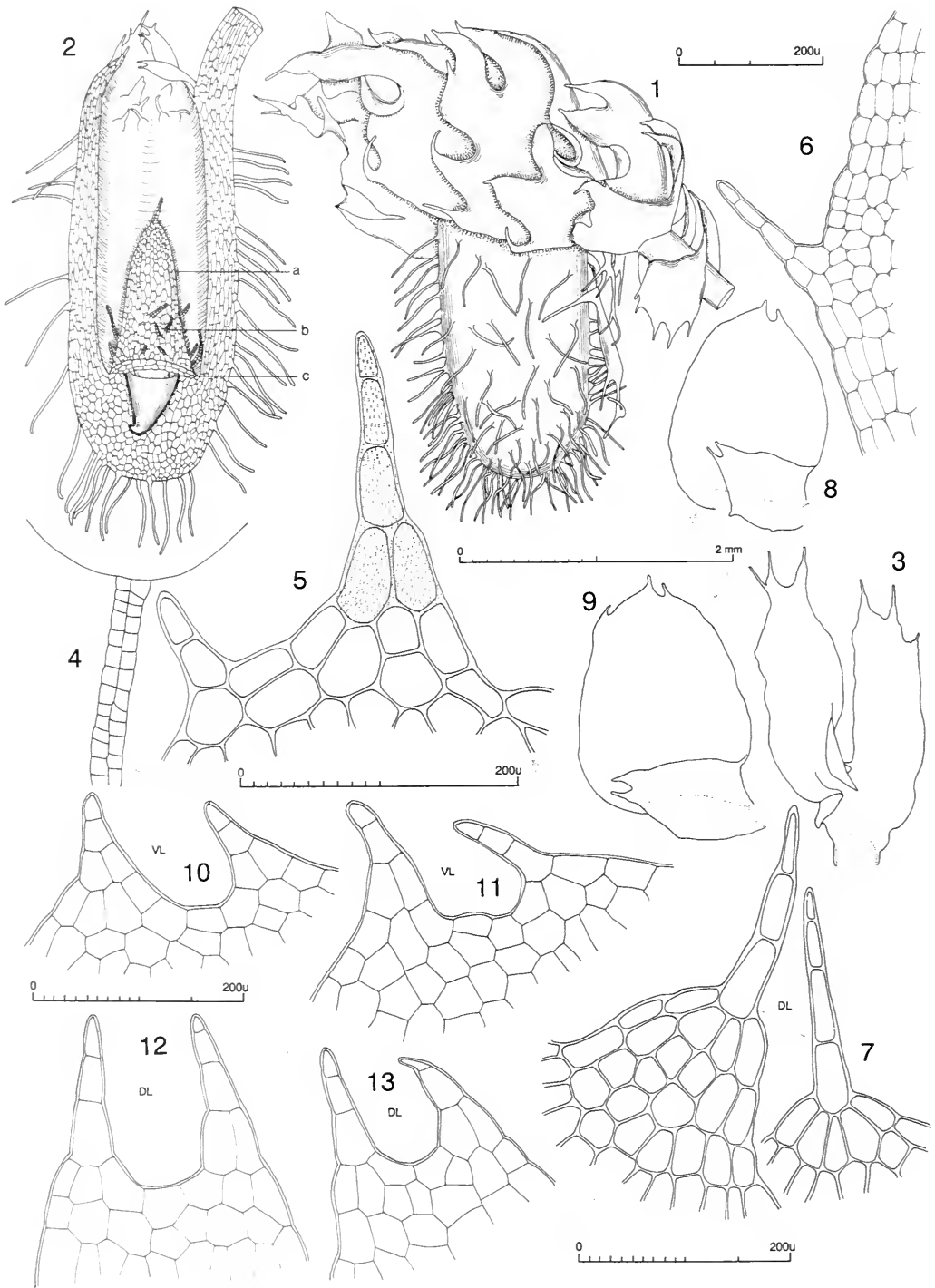


FIG. 4. *Balantiopsis diplophylla* (Hook. f. & Tayl.) Mitt. 1-7, var. *diplophylla*; 8-13, var. *hockenii*. 1, Female inflorescence ($\times 9$). 2, Median-longitudinal section of marsupium (a = shoot calyptra; b = unfertilized archegonium; c = seta) ($\times 10$). 3, Female bract ($\times 9$). 4, Antheridial stalk. 5, Segment of ventral lobe of leaf, cuticle shown in part. 6, Sector of ventral margin of ventral lobe. 7, Segments of dorsal lobe (dl) of leaf. 8, 9, Leaves. 10, 11, Distal portion of ventral lobes (vl). 12, 13, Distal portion of dorsal lobes (dl). (Fig. 1 from Kerr, New Zealand; 2 from

er- to middle-elevation forest plant of the southern half of South Island. It typically occurs on damp, shaded, clayey soil of steep slopes or banks (often those associated with watercourses) and boggy niches under shelter of, for example, manuka. It also occurs under *Gleichenia* and rushes in pakihis. The variety is occasionally present in the alpine zone, where it may be found under cover of tussocks.

SELECTED SPECIMENS SEEN—NEW ZEALAND, SOUTH IS., SOUTHLAND PROV.: Lake Hauroko, ca. 300 m, *Child H1566* (F); Fiordland Natl. Park, below Mt. Burns, E of Borland Saddle, S of South Branch of Borland Burn, 1225–1320 m, *Engel 18570* (F); *ibid.*, Burns Creek, Mt. Burns, ca. 915 m, *Child H5192* (F). OTAGO PROV.: Mt. Cargill, N of Dunedin, ca. 455 m, *Child H1329* (F); Swampy Hill, Dunedin, ca. 610 m, *Child H1929* (F); Hindon, ca. 300 m, *Child H2298*—c. mar. (F). WESTLAND PROV.: Westland Natl. Park, Gillespies Cook River Road, between Tornado Creek and Whelan Creek, *Engel 6590B* (F); *ibid.*, S margin of Lake Wahapo, *Engel 6736* (F); 1 km N of White Horse Creek, ca. 150–300 m, *Child H5414*, *H5385* (F); 10 km S of Greymouth, ca. 150 m, *Child H4946* (F); Rapahoe Range (or Twelve Apostles Range), N of Greymouth, ca. 150 m, *Child H5399* (F); Paparoa Range, Croesus Track, ridge between Granite Creek and Fagan Creek watersheds, 420 m, *Engel 19329* (F). NELSON PROV.: Paparoa Natl. Park, Inland Pack Track, SW of terminus of Bullock Creek Road, NE of the Punakaiki, ca. 35 m, *Engel 21659* (F); Dolomite Point Scenic Reserve, 30 m, *Fife 4862* (F); Big Totara River, ca. 60 m, *Child H5445* (F); 10 km S of Westport, ca. 30 m, *Child H4936* (F). NORTH IS., WELLINGTON PROV.: Mt. Ruapehu, Blythe Track off Ohakune Mt. Road, ca. 1220 m, *Braggins 92/79* as *B. rosea* (F). TARANAKI PROV.: Pukeiti Bush, near New Plymouth, *Hatcher 273* (F). NORTH AUCKLAND PROV.: NE Waitakere Range, Swanson University Reserve, Tram Valley Road, 95 m, *Engel 20451* (F); Rangitoto Is., immediately E of Auckland, 50–160 m, *Engel 20793* (F); McElroys Bush Reserve, western side of Mahurangi Harbour on Cowan Bay Road, 95 m, *Engel 20379* (F); Pohuehue Scenic Reserve, N of Auckland on State Highway 1, ca. 25 m, *Engel 21144*—c. mar. (F); Waipoua Forest, Lookout Track between Lookout Road and Waipoua River Road, above forest headquarters, ca. 240 m, *Engel 21071* (F); Mangamuka Walkway, Maungataniwha Range, ESE of Kaitaia, saddle on State Highway 1, 390 m, *Engel 20963* (F); Radar Bush, WSW of Cape Reinga, S of Mt. Te Pahi, ca. 100 m, *Engel 20853*.

Balantiopsis diplophylla var. *hockenii* (Berggr.)

Engel & Merr., comb. & stat. nov. Figure 4: 8–13.

Balantiopsis hockenii Berggr., On New Zealand Hep. 1: 46. f. 31. 1898, (“*Hockeni*”). Lectotype (*vide* Engel, 1968): New Zealand, South Is., Dunedin, *Berggren 3175* (LD!); isolectotypes: (FH!, GB!, UPS!).

Balantiopsis knightii Mitt. in Thoms. & Murr., Rep. Sci. Res. Voy. Challenger Bot. 1(3): 87. 1885. Original material: New Zealand, without specific location, *Knight* (NY!).

Plants typically prostrate. Leaves often dorsally assurgent, the ventral lobe subelliptic, typically hardly longer than wide, typically with a narrow, rounded apical notch, the margins few-toothed to almost entire; dorsal lobe often greatly reduced, narrowly ovate to ligulate, sharply bidentate at the apex, the margins entire, the dorsal lobe often vestigial and reduced to a bifurcate appendage; underleaves small, deeply bifid, sparingly ciliate, often concealed by dense rhizoids arising from the stem at their base. Oil-bodies scattered throughout cell, hyaline, (5)7–11(13) per cell, mostly ovoid to elliptic, some spherical, coarsely granular (the surface appearing coarsely papillose) to distinctly, botryoidal, $11.8\text{--}12.7 \times 4.9\text{--}5.9 \mu\text{m}$ to $11.8\text{--}15.7 \times 6.9\text{--}10.8 \mu\text{m}$, a few $14.7 \times 5.9\text{--}6.9 \mu\text{m}$.

TAXONOMY—This rather common expression is distinctive, even though it grades imperceptibly into more typical forms of the species. The ventral lobes are broadly rounded at the apex and characteristically \pm dorsally assurgent and then reflexed, lending the plant its distinctive aspect. The dorsal lobes are typically reduced in size (Fig. 4: 12, 13) and in extreme cases may be reduced to a minute, forked appendage at the base of the ventral lobe. A range of variation in development of the dorsal lobe often can be seen within plants of a single population or even on the same shoot.

Despite the above characterization of var. *hockenii* as a somewhat suboptimal expression of the species, it frequently bears marsupia.

NOMENCLATURE—The varietal epithet “*hockenii*” (based on *B. hockenii* Berggr.) is adopted here, since it has been commonly applied in New Zealand to this plant (cf. discussion in Hodgson, 1958), in preference to one based on *B. knightii* Mitt., which is older as a species.

DISTRIBUTION AND ECOLOGY—Occurring in New

Hatcher 303, New Zealand, North Is., North Auckland Prov., Waipoua Kauri Forest; 3 from *Weymouth*, Tasmania; 4 from *Engel 19329*, New Zealand, South Is., Westland Prov., Paparoa Range, Croesus Track; 5–7 from type of *B. diplophylla* (FH); 8–13 from type of *B. hockenii*.)

Zealand, with a range and ecology similar to those of the typical variety.

SELECTED SPECIMENS SEEN—NEW ZEALAND, SOUTH IS. SOUTHLAND PROV.: Fiordland Natl. Park, Borland Road, 14 km by road WNW from Borland Lodge, near South Branch of Borland Burn, W of Monowai, 855–870 m, *Engel 18688* (F). OTAGO PROV.: Mt. Maungatua, W of Mosgiel, ca. 500 m, *Engel 17784* (F); Morrisons Creek, N of Dunedin, ca. 300 m, *Child H1474* (F); W slope of Flagstaff, NW of Dunedin, 490–520 m, *Engel 17622* (F); S side of Mt. Cargill, just below summit, N of Dunedin, ca. 670 m, *Engel 17572* (F); Trotters Gorge Scenic Reserve, 1 km N of hut, ca. 120 m, *Child s.n. 136* (F); Fiordland, N of McKerrow River, Martin's Bay, *Hatcher 759* (F). WESTLAND PROV.: Turiwhate Falls on Route 73, *Engel 6542* (F); Westland Natl. Park, S margin of Lake Wahapo, *Engel 6741* (F); Arthur's Pass Natl. Park, Lower Otira Bridge, *Engel 6822* (F). CANTERBURY PROV.: Mt. Cook Natl. Park, E facing slope of Mt. Wakefield, just below Wakefield Falls, 870 m, *Engel 18156* (F). NELSON PROV.: Paparoa Range, N side of Tiropahi or Four Mile River between sea and Route 6, S of Charleston, 130–170 m, *Engel 19252* (F); Nelson Lakes Natl. Park, NE margin of Lake Rotoroa, W of St. Arnaud, 520 m, *Engel 21521* (F); Stony Creek, E of Westport, ca. 150 m, *Child H3543* (F). MARLBOROUGH PROV.: Pine Valley, Wairau River, ca. 150 m, *Child H4364A* (F). NORTH IS., HAWKE'S BAY PROV.: "Kiwi," Wairoa, *Hodgson* as *B. hockenii* (F). NORTH AUCKLAND PROV.: Waitakere, *Child 2261* (F); Waipoua Kauri Forest, *Hatcher 438* (F); McElroys Bush Reserve, western side of Mahurangi Harbour on Cowan Bay Road, 95 m, *Engel 20377*—c. mar. (F); SE of Goat Is. and between Goat Is. and Cape Rodney, N of Leigh, 30 m, *Engel 20255* (F); junction of Okahu Stream and unnamed stream, Kiwanis Reserve, ca. 5 km S of Kaitaia, N edge of Herekino Forest area, ca. 60–80 m, *Engel 20903* (F); Radar Bush, WSW of Cape Reinga, S of Mt. Te Pahi, ca. 100 m, *Engel 20844* (F).

Balantiopsis montana (Col.) Engel & Merr., comb. nov. Figure 5.

Chiloscyphus montanus Col., Trans. & Proc. New Zealand Inst. 21: 62. 1888 [1889] ("montana"), non *C. montanus* Steph., J. Proc. Roy. Soc. N. S. W. 48: 103. 1914. Lectotype (*nov.*): New Zealand, North Is., sides of Mt. Tongariro, "County of East Taupo," 1887, *Hill* (Colenso a. 1310) (WELT!).

Balantiopsis glandulifera Col., Trans. & Proc. New Zealand Inst. 21: 64. 1888 [1889], *syn. nov.* Original material: New Zealand, North Is., Mt. Tongariro, "County of East Taupo," *Hill* (Colenso a. 1428) (BM!, WELT!—c. mar.).

Plants loosely prostrate to ascending, typically pale translucent green, at times yellowish green to warm brown, sometimes tinged with red, often highly nitid; shoots markedly complanate, to 6 mm wide. Branching sparing, of *Frullania* type; ventral-intercalary branches sporadic. Leaves

soft-textured, loosely imbricate, not sharply folded, the ventral lobes widely spreading, to 3.2 mm long, the dorsal lobes dorsally assurgent, at times distinctly so, the opposing dorsal lobes slightly overlapping (excluding cilia) or not. Ventral lobe plane to feebly convex, longitudinally inserted and not or typically slightly recurved at ventral end, not decurrent or weakly so, \pm narrowly elliptic to lingulate, the apex rather blunt to truncate, the lobes very shallowly bifid; segments at times barely differentiated from marginal armature, acuminate, entire or sparsely ciliate, 4–7 cells wide at base, terminating in a uniseriate row of 3–5 elongate cells (to 3.5:1) with \pm thickened walls, the septa thickened in the corners and weakly projecting, the sinus hardly differentiated; lamina margins \pm straight, 5–13-ciliate, the armature often crowded in distal sector, the ventral margin with 3–8 cilia, weakly contracted at the base, the dorsal margin typically with fewer cilia; cilia slender, similar to those of apical segments; no border. Dorsal lobe much smaller than the ventral lobe, typically longer than wide and to 1.5 \times the width of stem (excluding armature), plane, the insertion \pm oblique, weakly and somewhat abruptly decurrent on the stem, the lobes narrowly ovate, very shallowly bifid or at times imperceptibly so, the segments as in ventral lobe; lobe margins curved, armed with up to 10 widely divergent cilia. Underleaves about equal to the dorsal leaf lobes in size, \pm distant, appressed, plane, the insertion broadly inverted U-shaped, the underleaves narrowly ovate, bifid to 0.6; lobes attenuate, the margins with several cilia, the sinus V-shaped to narrowly rounded, not reflexed; lamina margins ciliate to the base, with a lobuliform process on each side approaching the lobes in size and shape, the margins decurrent on the stem; cilia with a uniseriate row of 4–5(6) elongate cells. Ventral lobe cells in evident transverse rows, short-rectangular in the apical portion to elongate-rectangular in median and basal portions (ca. 4:1 in median sector), evenly thin-walled, the median cells 23–34 μm wide \times 74–110(122) μm long; median cells of dorsal lobe similar to those of ventral lobe; cuticle finely striate-papillose. Oil-bodies smoky gray, 8–11(12) per cell, coarsely granular.

Androecia terminal on leading ventral-intercalary branches; bracts similar to leaves but somewhat smaller (especially the dorsal lobe), with 1–2 abaxial bulges; antheridia 3 per bract, the stalk biseriate; paraphyllia present in bract axils, squamiform.

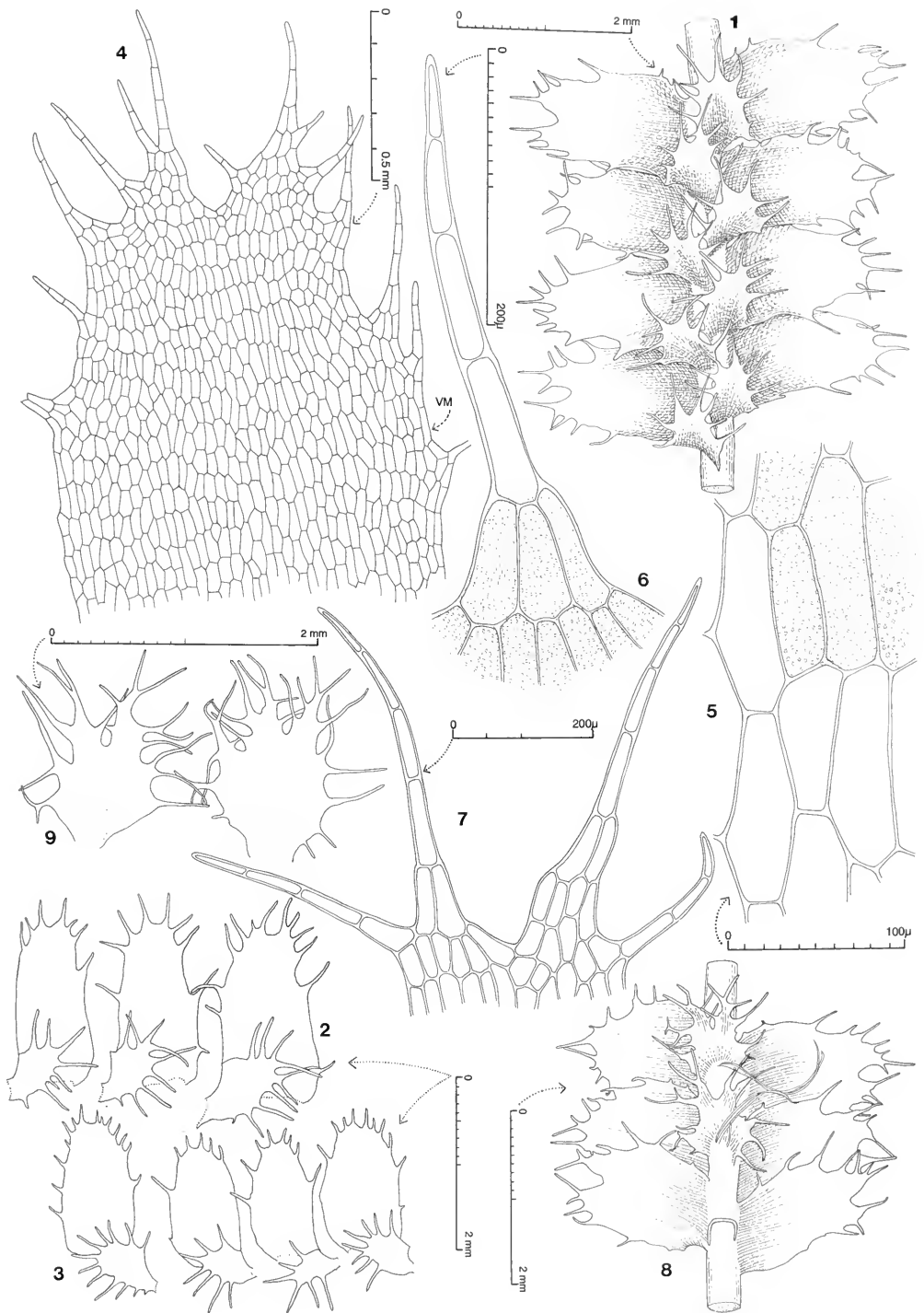


FIG. 5. *Balantiopsis montana* (Col.) Engel & Merr. 1, Sector of main shoot, dorsal view. 2, 3, Three leaves (top and 4 below. 4, Distal ca. 0.75 of ventral lobe of leaf (vm = ventral margin). 5, Median cells of ventral lobe (cuticular papillae shown in part). 6, Segment of ventral lobe of leaf. 7, Distal portion of dorsal lobe of leaf. 8, Sector of main shoot, ventral view. 9, Underleaves. (Figs. 1, 2, 4-9 from Engel 18525, New Zealand, South Is., Westland/Canterbury Prov. Boundary, Arthur's Pass Natl. Park, Arthur's Pass area, Upper Twin Creek Valley; 3 from Engel 21905, New Zealand, South Is., Otago Prov., Mt. Aspiring Natl. Park, Blue Valley Track.)

TAXONOMY—*Balantiopsis montana* is most similar to *B. lingulata* but is notable for the widely divergent, even more distinctly lingulate (parallel-sided, with a broadly rounded apex) but more sparingly ciliate ventral leaf lobes and the rather small, dorsally assurgent, spinulose-ciliate dorsal lobes. The number of cilia on the ventral lobe margins varies from 5 to 10, whereas *B. lingulata* may have up to 26 cilia. The ventral lobe armature tends to be concentrated in the distal sector of the lobe, accentuating the lingulate appearance of the lobes, whereas in *B. lingulata* the lobe is typically ciliate to the base. The plants are typically pale translucent green to warm brown, with delicate, membranous-textured, often highly nitid leaves. Both species have ciliate lobes that lack a differentiated border, segments and cilia with a uniseriate row of 4–5 elongate cells, and lingulate ventral lobes (at times narrowly elliptic in *B. montana*).

Balantiopsis montana is a prostrate to ascending plant that may develop reddish pigments and has leaves that are not sharply folded, the dorsal lobe being dorsally assurgent (Fig. 5:1). The ventral lobes are of a different form than in *B. lingulata*, being essentially plane or at most slightly convex, with the insertion (at most) only slightly recurved at the ventral end (comma-like, Fig. 5:7), and the median cells of the ventral lobe longer.

NOMENCLATURE—The original material of *Chiloscyphus montana* is a mixture of two elements, which Colenso himself thought might represent two species. One element, which Colenso regarded as the “young state” of the species, is “whitish pellucid, [the] leaves with fewer and more distant teeth,” and is referable to *B. diplophylla* var. *hockenii*. The other element, consisting of “aged” plants, “longer, dark-brown, more flexuous and sub-rigid, with its leaves more distinct,” is the major element in the enclosed micropacket labeled *Chiloscyphus montana* in Colenso’s own hand. This latter element is selected as the lectotype of the species.

The type of *Balantiopsis glandulifera* bears marsupia as well as young gynoecea in the earliest stages of development and consists of \pm flaccid, plagiotropic shoots with abundant rhizoids. The underleaves are small. The shape of the ventral lobes is suggestive of *B. lingulata*, but the ventral lobe insertion is essentially straight at the ventral end, and the dorsal lobes are somewhat dorsally assurgent and quite narrow. The ventral lobe cells are evidently tiered and elongate-rectangular (2.5–

3.5:1). These features seem to ally this plant with *B. montana*.

Chiloscyphus montana and *B. glandulifera* appeared in the same publication as did *Chiloscyphus heterodonta*, the type of which we have not seen. The type material of all three species came from Mount Tongariro, collected by Hill; *C. montana* and *C. heterodonta* were “picked out both from a quantity of broken vegetable rejectamenta.”

DISTRIBUTION AND ECOLOGY—Endemic to New Zealand, occurring sporadically on both South and North Islands. It occurs at a variety of elevations, from lower- to upper-elevation forests to the subalpine zone, and may be found, for example, in deep, well-protected pockets of stream banks, slopes, vertical banks, etc. In forests the species also occurs under wet, deeply shaded overhangs and on heavily shaded, dripping, vertical cliff faces, where it may form large, pure sheets or masses that are loosely attached and may even festoon the substrate. The species evidently requires sheltered, well-shaded, hyperhumid niches (see comments under *B. rosea*).

SELECTED SPECIMENS SEEN—NEW ZEALAND, SOUTH IS., SOUTHLAND PROV.: Fiordland Natl. Park, Borland Road, 14 km by road WNW from Borland Lodge, near South Branch of Borland Burn, W of Monowai, 855–870 m, *Engel 18713* (F). OTAGO PROV.: Trotters Gorge Scenic Reserve, 1 km N of hut, ca. 60 m, *Child H4413* as *B. diplophylla* (F); tributary of Siberia Stream, opposite Siberia Hut, WNW of Makarora, ca. 760 m, *Child H2989* as *B. diplophylla* (F); Mt. Aspiring Natl. Park, Blue Valley Track, above Blue River just N of confluence with Makaroa River, 430–480 m, *Engel 21905*. WESTLAND PROV.: Near Fox Glacier, 1940, *Knight* as *B. rosea* (F); Camp Creek, W of Alexander Range, 320–825 m, *Reif C29E, C289D* (F); Paparoa Range, ridge N of Sewell Peak, 890 m, *Fife 5163* as *B. convexiuscula* (F). WESTLAND/CANTERBURY PROV. BOUNDARY: Arthur’s Pass Natl. Park, Arthur’s Pass area, Upper Twin Creek Valley, 930 m, *Engel 18525* (F). CANTERBURY PROV.: *Arthur’s Pass Natl. Park, Bealey River, off Bealey Valley Track, 830–850 m, Engel 18460* (F). NELSON PROV.: Upper reaches of Porarari River, ca. 2 km W of the “Lone Hand,” 135–185 m, *Fife 6508* (F); lower basin of the Porarari River, 30–45 m, *Fife 6673*—c. δ (F); Paparoa Range, N side of Tiropahi or Four Mile River, W side of Route 6, ca. 500 m N of bridge over river, S of Charleston, 145 m, *Engel 19274* (F). NORTH IS., SOUTH AUCKLAND PROV.: Mt. Te Aroha, ca. 3 km E of Te Aroha, 900–940 m, *Engel 22125*—c. mar.

Balantiopsis lingulata Schust. Figure 2:12, 13.

Balantiopsis lingulata Schust., Bull. Natl. Sci. Mus. Tokyo 11: 26. 1968. Holotype: New Zealand,

North Is., Waipoua Kauri Reserve, Waikohatu Stream, near NS road, *Schuster 67-1764* (F!).

Plants caespitose, ascending to stiffly erect, opaque, dull green, occasionally tinged with red; shoots to 4.8 mm wide. Branching variable, at times predominantly terminal, sometimes predominantly ventral-intercalary. Leaves soft-textured, loosely imbricate, rather sharply folded, the ventral lobes widely spreading, to 2.2 mm long, the opposing dorsal lobes slightly to moderately overlapping (excluding cilia) or not. Ventral lobe weakly convex (more strongly so toward base), the insertion distinctly J-shaped, the margin decurrent on the stem, the lobes distinctly lingulate, very shallowly to rather distinctly bifid; segments at times barely differentiated from marginal armature, acuminate to \pm ciliiform, entire or with a cilium on lateral margin, 5–6 cells wide at base, terminating in a uniseriate row of up to 4–5 rather elongate cells (to 2.5:1) with somewhat thickened walls, the septa slightly thickened in the corners, not projecting, the sinus at times hardly differentiated; lamina margins slightly curved, armature variable: 14–20(26) cilia in optimally developed plants, often fewer, the lobes typically ciliate to the base, the ventral margin often sharply deflexed toward base and with a sector of the dorsal surface of lobe visible in ventral view, the margin with up to 6–14 cilia, the dorsal margin typically with fewer cilia; marginal cilia slender, similar to those of apical segments but the cells of uniseriate row somewhat longer (2.3–4.4:1); no border. Dorsal lobe much smaller than ventral lobe, typically longer than wide and to 2 \times the width of stem (excluding armature), plane, the insertion transverse to \pm oblique, weakly decurrent on the stem, the lobes ovate to oblong-ovate, typically gradually narrowing toward the apex, shallowly bifid or at times imperceptibly so, the segments as in ventral lobe except for somewhat longer cells of uniseriate row; lobe margins curved, armed with up to 10–16 widely divergent cilia. Underleaves subequal to the dorsal leaf lobes or somewhat smaller, contiguous to weakly imbricate, appressed to feebly spreading, plane, the insertion broadly inverted U-shaped, the underleaves narrowly ovate, bifid to 0.5; lobes long attenuate, the margins with several cilia, the sinus V-shaped to narrowly rounded, not reflexed; lamina margins ciliate to the base, often also with a lobuliform process on each side, the margins decurrent on the stem; cilia often bifurcate, with a uniseriate row of 4–5(6) elongate, thin-walled cells. Ventral lobe cells in

evident transverse rows, subsodiametric and \pm hexagonal in the extreme apical portion to elongate-rectangular in median and basal portions (to ca. 3.8:1 in median sector), evenly thin-walled, the median cells 20–28 μm wide \times 52–70 μm long; median cells of dorsal lobe similar to those of ventral lobe; cuticle finely striolate-papillose. Oil-bodies scattered throughout cell, pale, opaque, smoky gray, (4)5–11(14) per cell, mostly ovoid to elliptic to fusiform, some spherical, finely to coarsely granular (the surface appearing papillose), most 11.8–14.7 \times 4.9–6.9 μm , some 9.8–10.8 \times 6.9 μm , spherical ones 5.9 μm in diameter.

Androecia not seen. Marsupia rose to magenta, covered with rhizoids.

TAXONOMY—The concept of *B. lingulata* adopted here considerably broadens the circumscription of the species, previously known only from the type collection. Ciliate forms of this species superficially resemble *B. rosea*; see comments under that species. When optimally developed, *B. lingulata* has up to 26 cilia on the ventral lobe margins, and this will usually distinguish it from related species, *B. montana* and *B. diplophylla*. The type collection of *B. lingulata* consists of gynocia-bearing shoots that are consequently more copiously ciliate than in many collections of this species, particularly when sterile. Leafy hepatics with armed leaves are frequently more strongly armed on $\text{\textcircled{f}}$ shoots or in the vicinity of gynocia.

Schuster (1968) distinguished this species from *B. rosea*, but these species are quite unrelated; *B. lingulata* can be readily distinguished by the striate-papillose leaf cuticle and the absence of a differentiated border. Moreover, *B. lingulata* (in common with *B. diplophylla* and *B. montana*) has 5–13 oil-bodies per cell (Fig. 2: 12, 13), whereas *B. rosea* has only 2 (rarely three oil-bodies at opposite ends of the cell (Fig. 2: 15).

Suboptimal, less ciliate populations are likely to be confused with *B. diplophylla*, but the tiered, elongate-rectangular ventral lobe cells and the narrower, more lingulate outline of the ventral lobe of *B. lingulata* will aid in distinguishing the two species.

DISTRIBUTION AND ECOLOGY—Known from a few sporadic, lower-elevation sites (sea level to 90 m) on South Island and the northern sector of North Island, where it is rather frequent at elevations mostly under ca. 500 m. The species occurs over rock in streambeds and, like so many other members of the genus, is also found on the banks of streams as well as more mesic niches

such as protected, bryophyte-covered banks and shaded boulder faces. A population strikingly similar to the type occurred loosely attached to the lip of a springy area at the juncture of a roadside bank and the forest edge in a deeply shaded niche under *Blechnum* (Engel 21834). The type is from a moist *Dicksonia*-kauri forest (in shade under *Cyathea*), on smooth boulders or rocks along the edge of a shallow, clear stream, associated with *Schistochila nitidissima*. In shaded niches, such as those of the Engel collection and the type, the species does not develop pigmentation.

SELECTED SPECIMENS SEEN—NEW ZEALAND, SOUTH IS., OTAGO PROV.: Fiordland, near McKerrow Hut, head of Lake McKerrow, *Hatcher 1468* (F). WESTLAND PROV.: Cascade Road, just NE of Martyr Saddle and immediately N of Jackson River, S of Jackson Bay, ca. 20 m, *Engel 21834* (F). NELSON PROV.: Track to German Terrace, 6 km SSE of Westport on Nine Mile Road, 90 m, *Engel 21549* (F). NORTH IS., NORTH AUCKLAND PROV.: Mangatangi Stream, Huana, Auckland, *Child H808* as *B. convexuscula* (F); NE Waitakere Range, Swanson University Reserve, Tram Valley Road, 95 m, *Engel 20444* (F); Waitakere Hills, *Hatcher 153* (F); Trounson Kauri Forest, ca. 120 m, *Child H2111* (F); Waipoua State Forest, ca. 300 m, *Child H2124* as *B. rosea* (F); *ibid.*, *Hatcher 334*—c. mar. (F); *ibid.*, *Allison s.n.* as *B. rosea* (F); southern edge of Waipoua Forest, along Marlborough Road, *Engel 21139* (F); SE corner of Waipoua Forest, just N of Tutamoe, 540 m, *Engel 21114* (F); Omahuta Forest Kauri Sanctuary, E of Mangamuka Bridge, 260 m, *Engel 21014* (F); Mt. Te Aroha, ca. 3 km E of Te Aroha, 900–940 m, *Engel 22137* (F).

Balantiopsis sect. *Pteridophylla* (Hatch.) Engel & Merr., comb. nov.

Isotachis sect. *Pteridophylla* Hatch., *Nova Hedwigia* 3: 8. 1961; p. 44 of separate. Type: *Isotachis splendens* Steph.

Balantiopsis sect. *Erinacea* Engel, *Fieldiana* (Bot.) 25: 156. 1990, *syn. nov.* Type: *Jungermannia erinacea* Hook. f. & Tayl.

For a discussion of the section and its distinguishing characteristics, see p. 53.

Balantiopsis verrucosa Engel & Merr., sp. nov.
Figures 2: 5, 6, 9; 6.

Plantae virides vel brunneae vel rubescentes; folia lobis dorsalibus transversim insertis, ca. 5 laciniato-lobulatis, ventralibus saepe canaliculatis vel conduplicatis, ca. 2–9 dentato-ciliatis, insertione valde arcuate (littera 'U' simili); laminae foliorum marginatae, cellulis marginalibus striato-papillatis; amphigastria vix divisa atque sparsim

armata; cuticula guttulata; corpora oleosa 2(3), in extremis oppositis cellularum.

Holotype: New Zealand, South Is., Southland Prov., Fiordland Natl. Park, just SW of Mt. Burns, S of South Branch of Borland Burn, W of Monowai, 1010–1170 m, *Engel 18678* (F); isotype: (CHR).

Plants resembling *B. tumida*, typically procumbent to rather stiffly erect, loosely caespitose, light green to brownish or tinged with red; shoots complanate to weakly convex dorsally, the underleaves forming a broad ventral keel, the shoots to 3.5 mm wide. Branching sparse, of *Frullania* type; ventral-intercalary branches sporadic. Leaves soft-textured, densely imbricate, not sharply folded, the ventral lobe obliquely spreading, to 2 mm long, the opposing dorsal lobes broadly overlapping and extending across the stem. Ventral lobe convex to \pm canaliculate, the insertion strongly inverted U-shaped, the ventral margin narrowly decurrent on the stem, the lobes narrowly to broadly ovate, very shallowly bilobed to bidentate, the segments broadly acute, often apiculate, entire, 11–23 cells wide at base (when bilobed), terminating in a short apiculus of a single cell or a uniseriate row of 2(3) at most slightly elongate cells; lamina margins broadly curved, 2–9-ciliate-dentate, the ventral margin 4–5-ciliate-dentate, the armature terminating in a uniseriate row of up to 3 elongate cells, the dorsal margin often few-toothed to almost entire; lamina between the cilia \pm distinctly bordered by elongate cells. Dorsal lobe at times subequal to the ventral lobe in size and to 4.5 \times the width of stem (excluding armature), plane, the insertion oblique, strongly curved, becoming longitudinal, the free margin \pm subcordate at base and rather broadly decurrent on the stem, the lobes broadly ovate to suborbicular, the segments as in ventral lobe; lobe margins broadly curved, sparingly laciniate-lobulate, sometimes with lateral teeth approaching the segments in size and shape, the border cells as in ventral lobe. Underleaves large, about equal to the dorsal leaf lobe in size, densely imbricate, appressed, plane to weakly longitudinally plicate, the insertion quite narrowly inverted U-shaped, the underleaves broadly ovate to orbicular, bifid to 0.2 (rarely more); lobes narrowly acute, the margins with 1–2 cilia; lamina margins on each side rather sparingly laciniate-lobulate and ciliate to the base, the margins long-decurrent on the stem; ultimate divisions of lobe and marginal ar-

mature sometimes reflexed and directed toward the underleaf base, terminating in short, curved cilia composed of a uniseriate row of 2–3(5) rather short-elongate cells; underleaves bordered as in leaves. Ventral lobe cells in somewhat irregular transverse rows, elongate-rectangular (to 3.7:1 in median sector), thin-walled or the longitudinal walls moderately thickened but thinning at the angles, the median cells 16–24 μm wide \times (30)40–60 μm long to 20–24 μm wide \times 58–84 μm long; median cells of dorsal lobe similar to those of ventral lobe; cuticle of all but the marginal row of cells coarsely (often grossly) papillose, the papillae large, high and rounded, the marginal row of cells finely striate-papillose, sometimes lighter in color, forming a distinct border. Oil-bodies at opposing ends of cell, pale brown, 2 (rarely 3) per cell, fusiform to crescentic, coarsely granular, 11–13.4 \times 5.3–5.8 μm .

Androecia intercalary on main shoots; bracts similar to leaves except more imbricate, slightly pigmented and with 1–2 abaxial bulges; antheridia 2 per bract, the stalk biseriate; paraphyllia lacking. Gynoecia not seen.

TAXONOMY—This species superficially resembles *B. tumida* in size and habit and in the broadly ovate to suborbicular dorsal lobes, the often longitudinally folded ventral lobes, and reduced leaf armature. It can be readily distinguished, however, by the larger, coarsely papillose cells, the presence of a border, and the oil-body condition, which mark it as a sparsely ciliate relative of *B. rosea*.

The specific epithet refers to the strikingly verrucose (guttulate) cuticle of the leaves (Fig. 6:5). When seen in profile (e.g., along a fold in the leaf), the papillae are high and rounded at the summit; in surface view they are rounded, contrasting with the finely striate-papillose cuticle of the marginal row of lobe cells (Fig. 6:6).

DISTRIBUTION AND ECOLOGY—So far known only from South Island, New Zealand, in upper-elevation forests as well as subalpine and alpine zones. For example, it occurs under tussock cover in subalpine areas of *Chionochloa*, *Hebe*, *Dra-cophyllum*, etc.

SELECTED SPECIMENS SEEN—NEW ZEALAND, SOUTH IS., SOUTHLAND PROV.: Fiordland Natl. Park, Burns Creek, below Mt. Burns, ca. 915 m, *Child* 5179 (F); *ibid.*, head of Gertrude Valley, track to Gertrude Saddle, NE of Homer Tunnel, 1940–1970 m, *Engel* 21980 (F). OTAGO PROV.: Mt. Cargill, N of Dunedin, 700 m, *Child* H2674 as *B. tumida* (F); Swampy Hill, Dunedin, 610 m, *Child* H2645 (F); Fiordland, near McKerrow Hut,

head of Lake McKerrow, *Hatcher* 1462 (F). WESTLAND PROV.: Paparoa Range, ridge immediately N of Sewell Peak, 890 m, *Engel* 19023 (F). WESTLAND/CANTERBURY PROV. BOUNDARY: Arthur's Pass, 915 m, *Child* 2099 as *B. tumida* (F). NELSON PROV.: Paparoa Range, N flank of Mt. Euclid, ca. 0.5 km SE of Morgan Tarn, 1000–1065 m, *Fife* 6449 as *B. aequiloba* (F). MARLBOROUGH PROV.: Mt. Richmond, Richmond Range, ca. 1370 m, *Child* H4304 (F).

Balantiopsis rosea Berggr. Figures 2:10, 11, 15; 7.

Balantiopsis rosea Berggr., On New Zealand Hep. 1: 43, f. 28. 1898. Lectotype (*nov.*): New Zealand, South Is., Westland Prov., Teremakau, Mar. 1874, *Berggren* 3191 (LD!).

Plants with a hairy, feltlike appearance, pro-cumbent, loosely caespitose, light green, but typically rose-tinted to clear wine-red; shoots complanate to weakly convex dorsally, the ventral lobes stiffly but moderately deflexed, the underleaves at times forming a ventral keel; shoots often robust, to 3 mm wide. Branching sparse, of *Frullania* type; ventral-intercalary branches not seen. Leaves soft-textured and delicate, densely imbricate, not sharply folded, the ventral lobes obliquely spreading, typically longitudinally folded and “nested” in the ventral lobe of the leaf immediately above, to 2.5 mm long, the free margin of dorsal lobe (excluding cilia) \pm aligned along stem midline, the opposing dorsal lobes touching to somewhat overlapping. Ventral lobe typically longitudinally folded and distinctly conduplicate, the ventral (free) margin narrowly and rather sharply reflexed-erect (the lobe thus plicate), the insertion strongly inverted U-shaped, the ventral margin narrowly long-decurrent on the stem, the lobes narrowly elliptical, bifid to 0.2; segments laterally armed with 2–3 cilia (often in pairs), 8–15 cells wide at base, the segments terminating in a uniseriate row of 2–3(4) elongate cells; lamina margins rather straight, copiously ciliate to the base; cilia up to 20, setaceous, each terminating in a uniseriate row of 3–4 elongate cells, the septa thickened in the corners and weakly projecting; lamina between the cilia \pm distinctly bordered by elongate cells. Dorsal lobe ca. 0.5 \times the ventral lobe in length and 2–2.5 \times the width of stem (exclusive of cilia), plane to weakly longitudinally plicate, the insertion oblique, strongly curved, becoming longitudinal, the lobe \pm subcordate at base and rather broadly decurrent on the stem, the lobes narrowly ovate to triangular, the segments as in ventral lobe; margins of

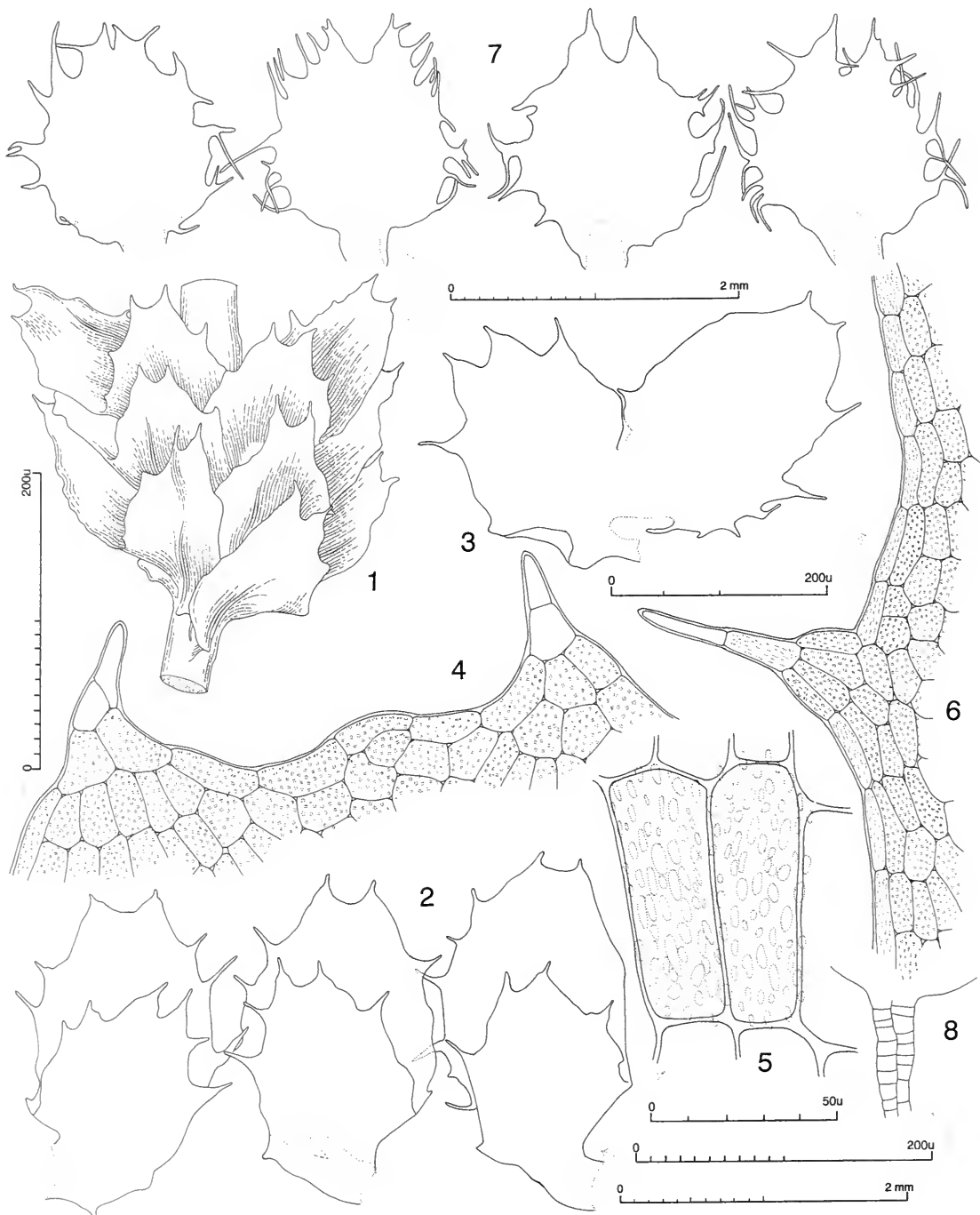


FIG. 6. *Balantiopsis verrucosa* Engel & Merr. 1, Sector of main shoot, dorsal view. 2, Leaves. 3, Leaf with lobes spread, dorsal lobe at left. 4, Distal portion of ventral lobe of leaf. 5, Median cells of ventral lobe showing cuticular papillae. 6, Sector of ventral margin of ventral lobe showing border. 7, Underleaves. 8, Antheridium. (Figs. 1-7 from holotype; 8 from *Child* 2674, New Zealand, South Is., Otago Prov., Mt. Cargill.)

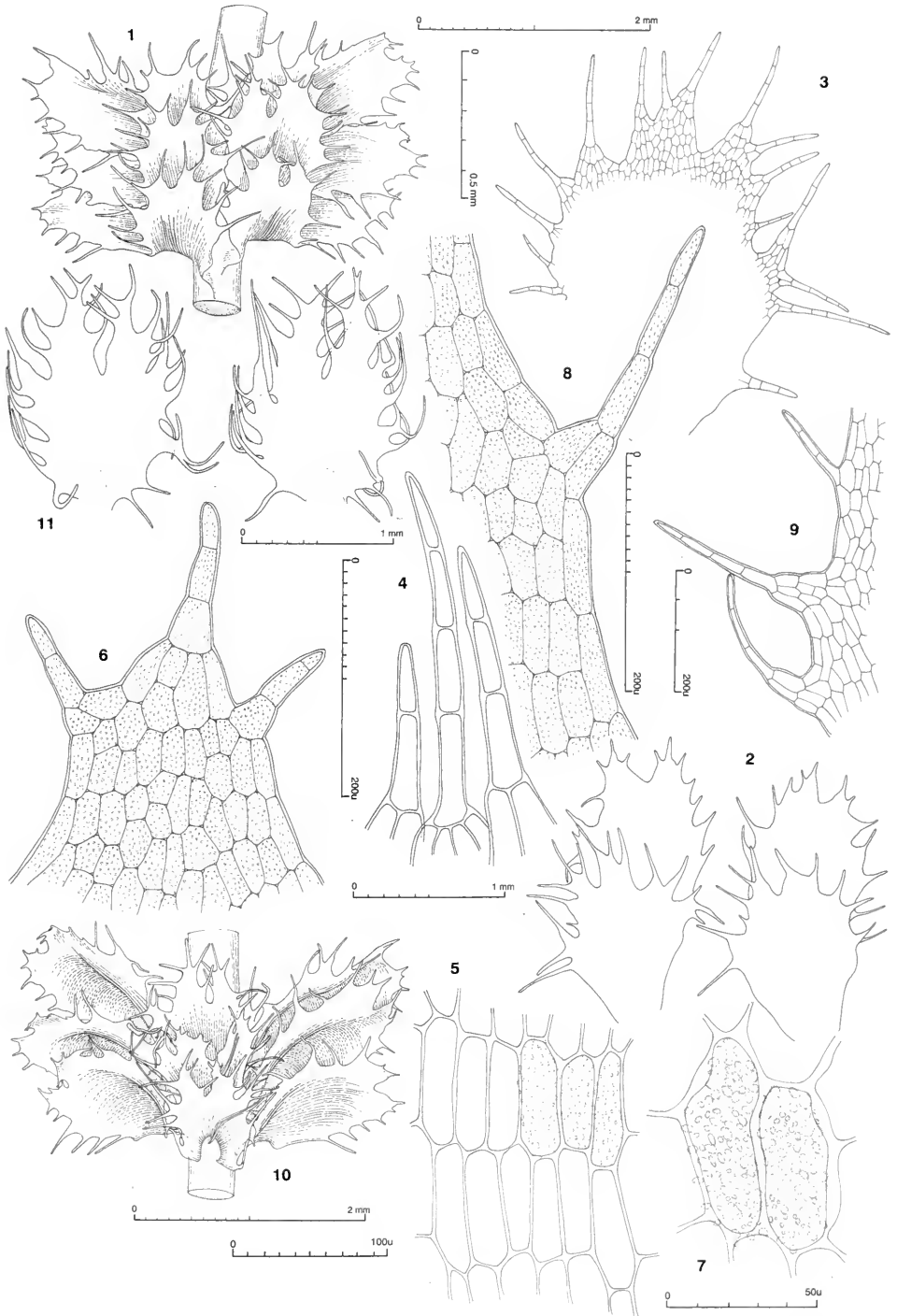


FIG. 7. *Balantiopsis rosea* Berggr. 1, Sector of main shoot, dorsal view. 2, Leaves. 3, Dorsal lobe. 4, Distal portion of dorsal lobes. 5, Median cells of ventral lobe showing (in part) cuticular papillae. 6, Distal portion of segment of ventral lobe of leaf. 7, Cells of ventral lobe segment base showing cuticular papillae. 8, Sector of ventral margin of ventral lobe showing border. 9, Sector of ventral margin of ventral lobe. 10, Sector of main shoot, ventral view (note details of ventral lobe insertion indicated for basalmost leaf pair). 11, Underleaves. (All from lectotype.)

lobe \pm curved, ciliate to base with up to 10 cilia, the cilia and border cells as in ventral lobe. Underleaves about 0.75 the leaves in length, densely imbricate, appressed to spreading, strongly concave-channeled at base (ventral view), plane to longitudinally plicate above, the insertion distinctly narrowly inverted U-shaped, the underleaves narrowly ovate, bifid to 0.4; lobes narrowly attenuate, at times ventrally sulcate, copiously armed with cilia that are often in pairs; lamina margins on each side sometimes with a lobuliform process approaching the main lobes in size, the margins otherwise copiously ciliate to the base, the margins dilated near base and long-decurrent on the stem; ultimate divisions of lobe and marginal armature terminating in subcapillary cilia composed of a uniseriate row of 4–5 elongate (5–10:1) cells; underleaves bordered as in leaves. Ventral lobe cells in somewhat irregular transverse rows, elongate-rectangular (to 4.4:1 in median sector), thin-walled or the longitudinal walls moderately thick-walled, but thinning at the angles, the median cells 18–29 μm wide \times 65–86 μm long; median cells of dorsal lobe similar to those of ventral lobe; cuticle of all but the marginal row of cells coarsely (often grossly) papillose, the papillae large, high, and somewhat elongate, the marginal row of cells finely striate-papillose, sometimes lighter in color, forming a distinct border. Oil-bodies at opposing ends of cell, smoky gray or pale yellowish brown, 2(3) per cell, irregular in shape: subscescentic to bottle-shaped to broad elliptic to fusiform, finely granular, the surface appearing finely papillose, 10.8–15.7 \times 4.9–5.9 μm , a few 8.8 \times 3.9 μm .

Androecia not seen. Marsupia long-cylindrical, with abundant rhizoids. Sporophyte not seen.

TAXONOMY—This handsome species is remarkable for the densely imbricate, profusely ciliate leaves and underleaves, which lend the plant a hairy, feltlike appearance. According to Berggren (1898, p. 43), “the ventral surface of the plant is quite like a felt from the close-set cilia.” The ventral leaf lobes are typically plicate and strongly conduplicate-folded (Fig. 2:10) and nested into the ventral lobe next above on each side (Fig. 7:10); the ventral lobe insertion is distinctly U-shaped (Fig. 2:10). As in the related *B. verrucosa*, the cuticle is coarsely papillose with high, rounded papillae (Fig. 7:7), and the lobes have a differentiated border of elongate, striate-papillose cells (Fig. 7:6).

Suboptimal expressions of *B. rosea* (e.g., Engel

21712) often have much less copiously ciliate lobe margins, with the ventral lobe insertion not or only weakly recurved, and lack the characteristic rose-red pigmentation. Plants of this facies superficially resemble *B. montana* but can be distinguished by the guttulate papillae, the differentiated border, and in fresh material, by the 2(3) oil-bodies per cell, one in each end of the cell.

Balantiopsis rosea is most apt to be confused with *B. lingulata*, but the latter differs from *B. rosea* in the striate-papillose cuticle, the absence of a border and the at best moderately convex ventral lobe, which is J-shaped at the ventral end; and in the greater number of oil-bodies per cell.

NOMENCLATURE—The lectotype has been chosen on the basis of the original description and illustration of the species (Berggren, 1898, pp. 43–44), despite the data on the labels of the Berggren specimens at LD, which are contradictory. A confusion of labels is the most likely explanation. The leaves and underleaves of *B. rosea* are described as abundantly ciliate, and the plants as rose-purple in color, growing together with *Isotachis lyallii*. However, the two specimens labeled as being from the type locality (Bealey River, Berggren 3190 and 3683, February 1874) lack any trace of secondary pigmentation, the leaves are only moderately ciliate, and no *Isotachis* is present. Both specimens are *B. lingulata*. A third specimen, labeled as from Teremakau (Berggren 3191, March 1874), contains the *Isotachis*, is rose-pigmented and copiously ciliate, and has been selected as the lectotype of the species. Unfortunately, none of the above specimens bear marsupia, which are described and illustrated by Berggren.

In his discussion of *B. rosea*, Berggren (1898, p. 44) made a puzzling observation: “A peculiarity which I did not notice in the other species . . . in so abundant a degree is the minute, rounded, hyaline granules in the cellulose.” At first, we took this to be a reference to oil-bodies, but since *B. rosea* typically has only 2 (rarely 3) oil-bodies per cell, this cannot be the case. Instead, we think that what Berggren saw were the abundant high, rounded papillae characteristic of this species (and *B. verrucosa*) and that are strikingly evident, even at moderate magnification.

DISTRIBUTION AND ECOLOGY—Endemic to New Zealand, where it occurs in middle- to upper-elevation forests as well as the subalpine zone. In forests the species may occur on well-shaded, moist cliff faces, where it forms large, pure masses that are loosely attached and may become pen-

dant from the substrate. It also is present in protected hollows on slopes or at the bases of banks, where it is loosely, barely attached to the substrate. Such niches are quite similar to those occupied by *B. montana*, and both species seem to require sheltered, hyperhumid, well-shaded sites; under such conditions neither species develops red pigmentation. Along the Mangawhero River, (Tongariro National Park), *B. rosea* occurs in hyperhumid sites along with *Herzogianthus* on steep, moist, peaty, mossy banks in a low *Nothofagus solandri* var. *cliffortioides* forest (Engel 21290). On wet roadside banks within forests *B. rosea* is frequently associated with *Isotachis lyallii*. In subalpine areas it occurs on the sides of rills, etc.

SELECTED SPECIMENS SEEN—NEW ZEALAND, SOUTH IS., SOUTHLAND PROV.: Fiordland, Wilmot Pass Road to Deep Cove, ca. 300 m, *Child H5612* (F). OTA-GO PROV.: Mt. Aspiring Natl. Park, Blue Valley Track, above Blue River just N of confluence with Makarua River, 430–480 m, *Engel 21900* (F). WESTLAND PROV.: Haast Pass Road, near Gates of Haast, ca. 300 m, *Allison s.n.* (Child H850) (F); Westland Natl. Park, track to Lake Gault, NE of Lake Matheson, NW of town of Fox Glacier, ca. 100–200 m, *Engel 21710* (F); *ibid.*, track to Alex Knob, off track to Louisa Peak, 1170 m, *Engel 18975* (F). CANTERBURY PROV.: Mt. Cook Natl. Park, SW facing cliffs off Wakefield Track, overlooking Hooker River, E of town of Mt. Cook, 720 m, *Engel 18189*. NORTH IS., WELLINGTON PROV.: Tongariro Natl. Park, west-facing steep bank of Mangawhero River, off Ohakune Mt. Road, ca. 1200 m, *Engel 21290* (F). SOUTH AUCKLAND PROV.: Omatika, Kaimai Range, 855 m, *Bartlett* (F).

Balantiopsis convexiuscula Berggr. Figures 2: 3, 4, 14, 16; 8.

Balantiopsis convexiuscula Berggr., On New Zealand Hep. 1: 44, f. 29. 1898. Lectotype (*vide* Engel, 1968): New Zealand, North Is., Auckland Prov., Coromandel, *Berggren 3188* (LD!); isolecotypes: (FH!, GB!, UPS!).

Balantiopsis aequiloba Berggr., On New Zealand Hep. 1: 46, f. 30 H-O. 1898. Lectotype (*vide* Engel, 1968): New Zealand, North Is., Auckland Prov., Coromandel, *Berggren 3184* (LD!); isolecotype: (UPS!).

Plants rigid, procumbent, light green to olive-green to yellowish brown, occasionally rose-tinted, dull when dry; shoots dorsally convex, \pm ventrally channeled, the ventral lobe apices strongly decurved; shoots complanate, to 3(4) mm wide. Branching sparse to common, pseudodichotomous, of *Frullania* type; ventral-intercalary branches common. Leaves appearing transversely

ribbed when dry, imbricate, rather sharply folded, the ventral lobe widely spreading, to 1.9 mm long, the free margin of dorsal lobe \pm straight, aligned along the stem midline, the opposing dorsal lobes touching to somewhat overlapping. Ventral lobe moderately to strongly convex, the insertion moderately to distinctly inverted U-shaped, the margin decurrent on the stem, the lobes narrowly elliptic, bifid to 0.2; segments acuminate, normally entire, rarely with a tooth, (8)10–15 cells wide at base, terminating in a uniseriate row of 3–4 cells, the septa thickened in the corners and feebly projecting; lamina margins rather straight to gently curved, sharply serrate to serrate-laciniate, the ventral margin with 2–5 (8) stout teeth, each with a uniseriate row of 3–4 cells, the dorsal margin \pm straight in proximal sector, then arched distally, sparingly armed with 1–4 slender teeth; no border; margins of ventral lobe and principal teeth minutely denticulate by projecting septa of marginal cells. Dorsal lobe somewhat smaller than the ventral lobe but more than half its length and typically broader, ca. 2 \times the stem in width, weakly convex, the insertion transverse, not decurrent on the stem, the lobes subquadrate to \pm orbicular, bifid to 0.25, the segments similar to those of ventral lobe; dorsal (free) margin broadly curved, 4–8(11)-toothed, at least some of the opposing teeth approaching size of the segments; margins of dorsal lobe and marginal teeth denticulate as in ventral lobe. Underleaves considerably smaller than the leaves, contiguous to imbricate, slightly to widely spreading, \pm plane to broadly recurved, the insertion broadly U-shaped, with the margins decurrent on the stem, the underleaves narrowly ovate to subrectangular in outline, appearing laciniate-divided *in situ* but basically bifid to 0.5–0.6; lobes parallel-sided to weakly attenuate, \pm plane, the ultimate lobe divisions and cilia curved, biseriate for much of their length, terminating in a uniseriate row of 4–6(7) elongate cells, the median sinus reflexed; lamina margins ciliate, sometimes on each side with a lobuliform process approaching the main lobes in size and shape. Ventral lobe cells in \pm regular transverse tiers, in distal sector small, short-rectangular (2:1) or almost isodiametric, the cell walls typically sinuous-thickened, gradually becoming longer toward base; median cells 12–15(17) μ m wide \times 26–40 μ m long; median cells of dorsal lobe more uniformly short-rectangular; cuticle smooth to minutely striolate-papillose. Oil-bodies tending to cluster at opposite ends of cell but sporadically to commonly with 1 or more in central portion of

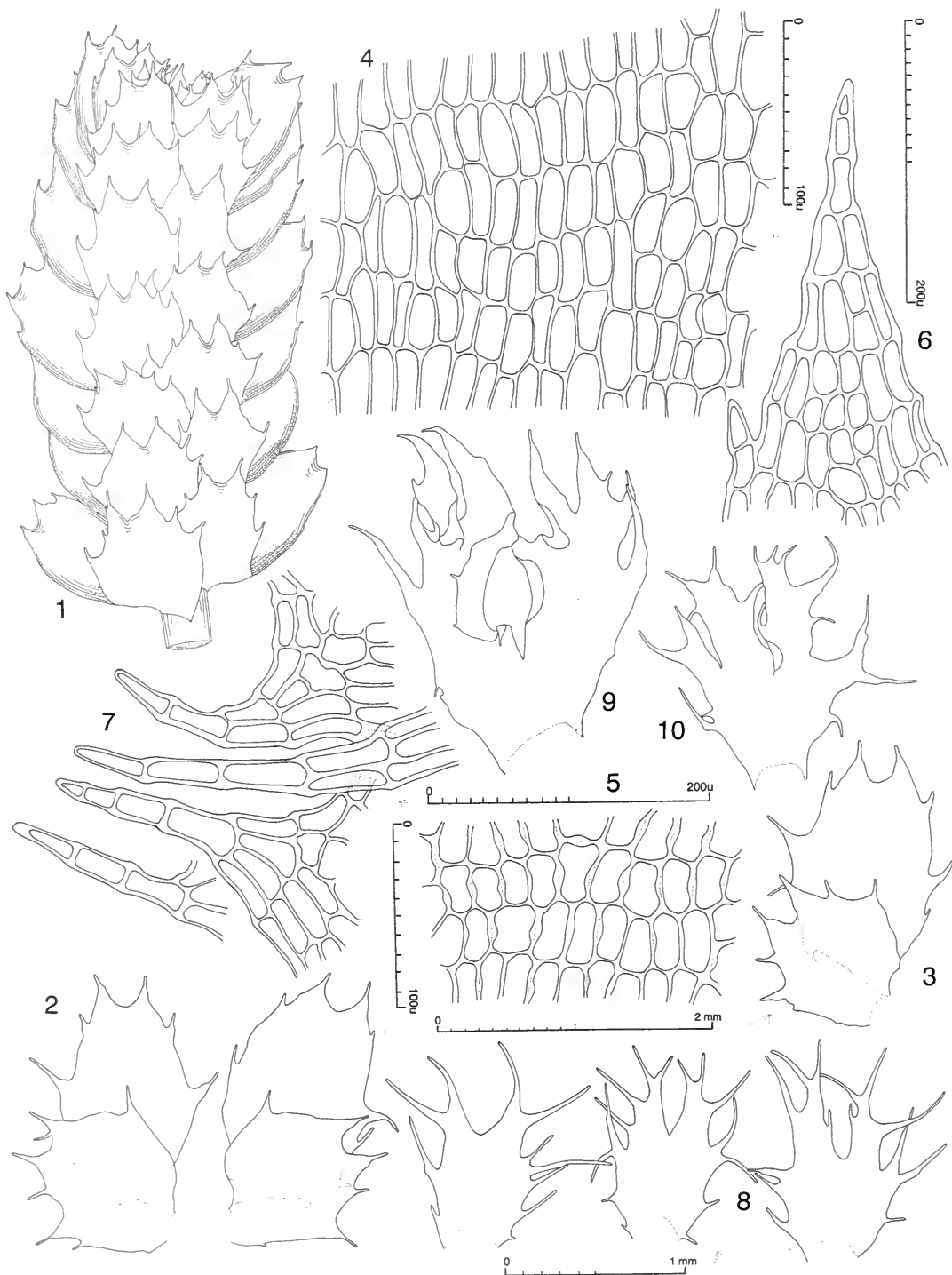


FIG. 8. *Balantiopsis convexiuscula* Berggr. 1, Portion of plant, dorsal view ($\times 11$). 2, 3, Leaves. 4, Median cells of ventral lobe. 5, Subapical cells of ventral lobe of leaf; note intermediate thickenings. 6, Segment of ventral lobe of leaf. 7, Armature of ventral margin of ventral lobe of leaf. 8, Underleaves. 9, ♀ Bract ($\times 10$). 10, ♀ Bracteole ($\times 10$). (Fig. 1 from material admixed with type of *B. diplophylla*; 2-4, 6-8 from lectotype of *B. convexiuscula*; 5 from *Hatcher 618*, New Zealand, South Is., Otago Prov., trail between Gunn's Hut and Hidden Falls; 9, 10 from *Hatcher 1007*, New Zealand, North Is., Pukeiti Bush near New Plymouth.)

cell, hyaline and glistening, (2)5–7 per cell, short-to often long-elliptical to fusiform, some spherical, finely to coarsely granular, $8.8\text{--}12.7 \times 3.9\text{--}5.9 \mu\text{m}$, those spherical or nearly so $4.9\text{--}5.9 \times 3.9 \mu\text{m}$.

Androecia not seen. Gynoecia on main shoot or on ventral-intercalary branches of varying lengths; bract margins very irregular, undulate to distinctly crispate, occasionally reflexed, dentate-laciniate. Marsupia green to rose, rhizoids colorless or magenta.

Capsule long-cylindrical, with spiral dehiscence, the wall $31\text{--}34 \mu\text{m}$ thick, of 3 layers, the outer layer of cells ca. equal to thickness of both interior strata; outer layer of cells short-rectangular, large, the longitudinal and transverse walls with thin, localized, sheetlike thickenings, without nodular or bandlike thickenings; innermost layer of cells with longitudinal radial walls with somewhat thick, continuous sheets of wall material, with semiannular bands narrow.

Spores not seen. Elaters $11.5\text{--}13.4 \mu\text{m}$ wide, tapered to tips, bispiral, the spirals $3.8 \mu\text{m}$ wide, loosely wound.

TAXONOMY—This species is a close ally of *B. tumida*, the two sharing a suite of features, including 1) dense areolation, the ventral lobe cells only $12\text{--}16 \mu\text{m}$ wide; 2) swollen and projecting septa, the lobe and segment margins consequently minutely denticulate (Fig. 8:7, 8); 3) sinuous wall thickenings in the cells of the distal sector of the leaf lobes (Fig. 8:5); and 4) broadly orbicular dorsal lobes, with at least one lateral tooth on each side of the margin similar in size and shape to the apical segments (Fig. 8:1–3). *Balantiopsis convexiuscula* is distinguishable from *B. tumida* by its coarsely serrate, often almost laciniate leaves, the teeth often terminating in an elongate cilium. The ventral lobes typically are convex and obliquely spreading, whereas in *B. tumida* they are often longitudinally folded and strongly ventrally secund. The dorsal lobes are narrower than in *B. tumida* and with free margins only narrowly overlapping versus broadly overlapping and extending beyond the opposite side of the stem in *B. tumida*.

Balantiopsis convexiuscula has a characteristic appearance: when dry, the plants are a dull, dark olive–green, the dorsal lobes appearing densely areolate and ribbed from arrangement of the cells in regular, undulate transverse rows. It frequently has been encountered in admixture with *B. diplophylla* but is immediately distinguishable by its

much smaller cells, dense and regular areolation, and color. Berggren (1898) describes the areolation of *B. aequiloba* (a synonym of *B. convexiuscula*) as the densest in the genus.

DISTRIBUTION AND ECOLOGY—Similar in distribution to *B. tumida*, ranging from New Zealand to Tasmania and southeast Australia, and compared to that species, occurring at lower elevations and for the most part tolerating more mesic sites. The species is rather common in lower- (sea level) to middle-elevation forests, occurring on moist, shaded (often clayey) soil, particularly of mossy banks, etc., or over rock of dripping or seepage areas of cliff faces. It frequents well-protected sites such as cavelike overhangs of cliffs, under cover of vegetation (*Blechnum*, etc.), and is found less often on stream banks, boggy ground, or rotted logs. At stream sites it occurs ascending from often clayey soil in the splash zone or near water level, where the plants are subject to inundation. The species also occurs on rock of intermittently dry creek beds. It occurs only sporadically in subalpine sites.

SELECTED SPECIMENS SEEN—AUCKLAND IS.: Disappointment Is., *Macmillan 83/159* (F). NEW ZEALAND, SOUTH IS., SOUTHLAND PROV.: Fiordland natl. Park, just SW of Mt. Burns, S of South Branch of Borland Burn, *Engel 17597*; *ibid.*, Stuart Mts., W shore of Lake Thomson N of stream draining from Lake Wade, 300 m, *Fife 7739* as *B. diplophylla* (F); W of Monowai, 1010–1170 m, *Engel 17597* (F). OTAGO PROV.: Saddle W of road to Mt. Cargill, N of Dunedin, 500 m, *Engel 17547* (F); Mt. Cargill, just below summit, N of Dunedin, ca. 670 m, *Engel 17568* (F); Flagstaff, NW of Dunedin, ca. 610 m, *Child H1663* (F); Fiordland, trail between Gunn's Hut and Hidden Falls, ca. 30 mi SE of Lake McKerrow, *Hatcher 618, 541* (F); *ibid.*, near McKerrow Hut, head of Lake McKerrow, *Hatcher 1461* (F). WESTLAND PROV.: Haast, 6 mi N of bridge, sea level, *Child H871* (F); near Fox Glacier, 1940, *Knight* (F); Westland Natl. Park, track to Lake Gault, NE of Lake Matheson, NW of town of Fox Glacier, ca. 100–200 m, *Engel 21686*—c. mar. (F); near Gillespies Beach, W of Fox Glacier, ca. 30 m, *Child H4862* (F); Westland Natl. Park, near Alex Knob track, *Engel 6702* (F); *ibid.*, Lake Wombat, *Engel 6695* (F); Mt. Hercules Scenic Reserve, near Hercules Creek on Route 6, *Engel 6563* (F); Arthur's Pass Natl. Park, N of Kellys Creek near Highway 73, above campground, N of Otira, 420–475 m, *Engel 18346* (F); Camp Creek, W of Alexander Range, 630–880 m, *Reif C206E, C278b* (F); Paparoa Range, Croesus Track, ridge between Granite Creek and Fagan Creek watersheds, 450 m, *Engel 19294* (F). CANTERBURY PROV.: Arthur's Pass Natl. Park, Bealey River, off Bealey Valley Track, 830–850 m, *Engel 18464* (F). NELSON PROV.: Madman's Creek, ca. 2 mi S of Route 6 bridge over Little Totara River, *Fife 4647* (F). NORTH IS., TARANAKI PROV.: Pukeiti Bush, near New Plymouth, *Hatcher 283* (F). SOUTH AUCKLAND PROV.:

Mt. Te Aroha, ca. 3 km E of Te Aroha, 900–940 m, *Engel 22115* (F). NORTH AUCKLAND PROV.: Huia, SW of Auckland, ca. 30 m, *Linzey* (Child 3031) as *B. diplophylla* (F); Omahuta Forest Kauri Sanctuary, E of Mangamuka Bridge, 260 m, *Engel 20986, 21030* (F).

Balantiopsis tumida Berggr. Figure 9.

Balantiopsis tumida Berggr., On New Zealand Hep. 1: 45, f. 30 A–G. 1898. Holotype: New Zealand, South Is., “ad flumen Teremakau in montibus prov. Canterbury,” *Berggren 3186* (LD!); isotypes: (FH!, GB!).

Plants ascending to suberect, caespitose, often submerged, pure green to brownish green, often rose-tinted to deep wine-red in exposed sectors of leaves; shoots moderately dorsally convex, to bilaterally compressed, with the ventral lobes ventrally secund; shoots often robust, to 4.5 mm wide. Branching sporadic, of *Frullania* type; ventral-intercalary branches occasional. Leaves soft-textured, closely imbricate, sharply folded, the ventral lobes obliquely spreading to rather stiffly ventrally secund, to 2.8 mm long, the opposing dorsal lobes broadly overlapping and extending a little beyond the opposite side of stem. Ventral lobe strongly convex, the insertion strongly inverted U-shaped, the free margin decurrent on the stem, the lobes typically longitudinally folded and distinctly conduplicate (at times merely canaliculate), elliptical, bifid to 0.2, the segments bluntly obtuse grading to medium to broad acute, often terminating in a short apiculus of 1–2 cells, entire, 18–28 cells wide at base; lamina margins \pm straight to gently curved, sparingly armed, the ventral margin narrowly reflexed-erect, with 1–5 rather slender ciliiform teeth ending in a uniseriate row of 3–5 cells, the dorsal margin with fewer teeth or none; no border; margins of ventral lobe and principal teeth indistinctly denticulate by projecting septa of marginal cells. Dorsal lobe almost equal to the ventral lobe in length but much broader, to 3.5 \times the width of stem, weakly convex to longitudinally 2–3 plicate, the insertion somewhat curved, not or slightly decurrent on the stem, the lobes subquadrate to \pm orbicular, broadly dentate, bifid to 0.2, the segments often stronger than those of ventral lobe, entire, the intervening sinus typically lunate; margins of the lamina broadly and \pm symmetrically curved to nearly hemispherical, few-toothed, with at least 1 lateral tooth on each side similar to the segments; margins of dorsal lobe and principal teeth denticulate as in ventral lobe. Underleaves large, equal to the dorsal leaf lobes in size but often inconspicuous,

hidden among the deflexed ventral leaf lobes, imbricate, appressed to spreading, the insertion broadly U-shaped, with margins decurrent on the stem, the underleaves broadly ovate to suborbicular in outline, often longitudinally plicate, bifid to 0.4; lobes attenuate, \pm plane, the ultimate lobe divisions and cilia terminating in a uniseriate row of 4–5 elongate cells; margins of the lamina rather sparingly ciliate, rarely with lateral processes approaching the lobes in size. Ventral lobe cells in \pm regular transverse tiers, isodiametric to short-rectangular (2:1), thin-walled but firm, indistinctly sinuous-thickened, gradually becoming longer toward base; median cells 12–16(18) μm wide \times 30–42 μm long; median cells of dorsal lobe somewhat smaller, more uniformly short-rectangular; cuticle smooth to minutely striolate-papillose. Oil-bodies confined to opposite ends of cell or at times scattered within cell, hyaline and often glistening, 2–5(7) per cell, ovoid to elliptical to fusiform to \pm linear, occasionally subcrescentic to spherical, granular, the spherules somewhat protruding beyond membrane, 5.9–10.8 \times 2.9–3.9 μm , \pm linear ones 9.8 \times 2.9 μm , spherical ones 2.9–3.9 μm .

Androecia terminal on main shoot or relatively long ventral-intercalary branches; bracts similar to leaves or, occasionally, slightly smaller, occasionally with a slight abaxial bulge; antheridia 1–2 per bract. Gynoecia not seen.

TAXONOMY—When well-developed, *B. tumida* is a striking plant, growing \pm erect in thick, often deep wine-red cushions on stream banks or submerged to emergent in flowing water. The apical segments of the dorsal and ventral lobes are broadly acute to bluntly obtuse, terminating in a short apiculus of 1–2 cells (Fig. 9: 1, 2, 5). The ventral leaf lobes are longitudinally folded to distinctly conduplicate and rather stiffly ventrally secund; the underleaves are large, often longitudinally plicate, and hidden among the deflexed ventral lobes.

Berggren (1898) describes *B. tumida* as fastigiate branched, but most of the robust, caespitose forms we have seen are only sparsely and sporadically branched. This species is a close relative of *B. convexiuscula* (for further discussion see under that species).

DISTRIBUTION AND ECOLOGY—Known from New Zealand (sporadic in South and North Islands), Tasmania, and southeast Australia. The species typically occurs in especially wet sites. In the forest zone it may be found on silty soil and

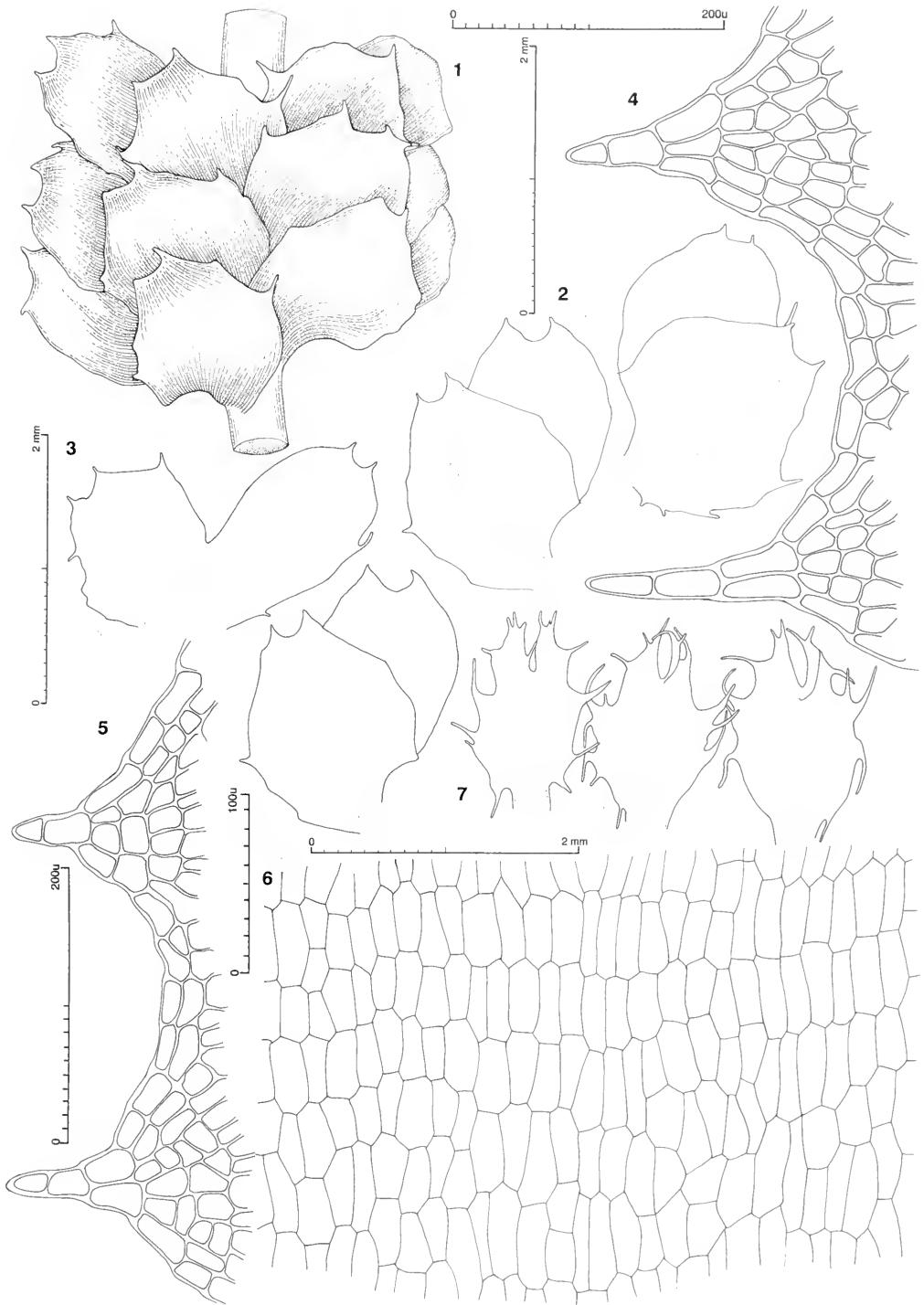


FIG. 9. *Balantiopsis tumida* Berggr. 1, Portion of plant, dorsal view. 2, Leaves (3). 3, Leaf with lobes spread, dorsal lobe at left. 4, Distal portion of dorsal lobe of leaf. 5, Distal portion of ventral lobe of leaf. 6, Median cells of ventral lobe. 7, Underleaves (3). (All from type.)

rocks associated with rivulet banks, creek beds, etc., where it may be subject to periodic inundation. At Waipoua Forest, for example, it occurs with *Schistochila nitidissima* on the tops of soft, conglomerate rocks and boulders in the bed of Waikohatu Stream, which flows through a kauri forest with *Weinmannia silvicola* (Engel 21039). Also at Waipoua Forest it occurs in mucky areas with scattered pools in a rich, damp forest dominated by *Weinmannia silvicola* (Engel 21116). In the subalpine zone the species typically occurs over silty soil of rills or over soil between rocks at rivulet margins, etc. In alpine areas it occurs over soil at cliff bases, particularly under grass cover.

SELECTED SPECIMENS SEEN—NEW ZEALAND, SOUTH IS., SOUTHLAND PROV.: Fiordland Natl. Park, Burns Creek headwaters, Mt. Burns, ca. 1370 m, *Child H5145* (F); *ibid.*, Stuart Mts., W shore of Lake Thomson N of stream draining from Lake Wade, 300 m, *Fife 7687* as *B. convexiuscula* (F); *ibid.*, head of Gertrude Valley, on track to Gertrude Saddle, NE of Homer Tunnel, 1940–1970 m, *Engel 21988* (F). OTAGO PROV.: Summit of Mt. Maungatua, W of Mosgiel, 825 m, *Engel 17722* (F); Mt. Cargill, N of Dunedin, ca. 455 m, *Child H665* as *B. convexiuscula* (F); Fiordland, trail between Gunn's Hut and Hidden Falls, ca. 30 mi SE of Lake McKerrow, *Hatcher 663* (F). WESTLAND PROV.: Near Clark's Bluff, Haast Road, ca. 90–150 m, *Child H4487, H4486* (F); Mt. Aspiring Natl. Park, Cross Creek, 1.1 km N of Haast Pass, 540 m, *Engel 21867* (F); Westland Natl. Park, track to Lake Gault, NE of Lake Matheson, NW of town of Fox Glacier, ca. 100–200 m, *Engel 21681* (F); 8 mi W of Turiwhate, Route 73, *Engel 6763* (F); Camp Creek, W of Alexander Range, 770 m, *Reif C249A* (F); Paparoa Range, ridge immediately N of Sewell Peak, 890 m, *Engel 19033* (F). WESTLAND/CANTERBURY PROV. BOUNDARY: Arthur's Pass Natl. Park, Temple Basin ski area, Arthur's Pass, *Engel 6503C* (F). NELSON PROV.: Paparoa Range, N flank of Mt. Euclid, below Morgan Tarn, 1065–1160 m, *Fife 6319* (F); Abel Tasman Natl. Park, Porters Rock Track, ca. 915 m, *Child H4657* (F). MARLBOROUGH PROV.: Waikakaho Valley, W of Tuamarina, ca. 300 m, *Child H3273* (F). NORTH IS., NORTH AUCKLAND PROV.: Waipoua Forest, Waikohatu Stream, on State Highway 2 just upstream from culvert, 290 m, *Engel 21039* (F); SE corner of Waipoua Forest, just N of Tutamoe, 540 m, *Engel 21116* (F).

Systematics

Since its beginnings in the 1950s, phylogenetic systematics, or cladistics, has become a widely used procedure for reconstructing phylogenies of groups of plants and animals and for constructing classifications. Botanical cladistics was inaugurat-

ed by the work of Koponen (1968), a bryologist, but until recently few bryologists have made use of this approach to understanding phylogenetic relationships. Initially, manual Hennigian methods were employed (e.g., Mishler & Churchill, 1984; Hyvönen, 1989), but more recently computer programs, such as PAUP and Hennig86, have been used. Most of these recent studies have been concerned with mosses (among them Mishler, 1985; Bruggeman-Nannenga & Roos, 1990; Zander, 1993; Zomlefer, 1993; Hedenäs, 1994; and Hyvönen & Enroth, 1994), and relatively few have dealt with hepatics (Thiers, 1993; Hyvönen & Piippo, 1994).

In the course of our study of the genus *Balantiopsis* in New Zealand, we developed certain hypotheses concerning the relationships between species and the primitive and advanced states (polarity) of characters, including some apparent instances of convergence and parallelism. A cladistic analysis was undertaken in order to test these hypotheses and to reconstruct the evolutionary history of the genus *Balantiopsis* in the context of the Balantiopsaceae as a whole.

The methods used in this analysis are not referenced extensively here. Manuals to computer programs for phylogenetic analysis such as PAUP (Swofford, 1991), MacClade (Maddison & Maddison, 1992), and Hennig86 (Farris, 1988) provide a good introduction to theoretical concepts and contain thorough discussions of cladistic methodology with extensive references. The basic works on the subject are Hennig (1966) and Wiley (1981); an excellent up-to-date introduction to cladistic theory and practice is Forey et al. (1992).

Choice of Taxa

For this portion of our study, in addition to the New Zealand species of *Balantiopsis*, we surveyed and reevaluated all species of the genus. (For detailed descriptions of the extraterritorial species of *Balantiopsis*, see Engel, 1968.) Representatives of all genera of Balantiopsaceae were included in the analysis as outgroups (Watrous & Wheeler, 1981; Maddison et al., 1984) in order to resolve relationships within the genus *Balantiopsis* as well as to assess relationships between the major subgroupings within the family (Table 1). With the exception of *Isotachis*, these genera are either monotypic (*Anisotachis*) or have relatively few species (*Ruizanthus* with two, *Eoisotachis* with two, *Austroscyphus* with four, *Neesioscyphus*

TABLE 1. Taxa included in systematic analysis.

<i>Anisotachis splendens</i> (Steph.) Schust.
<i>Austroscyphus phoenicorhizus</i> (Grolle) Schust.
<i>Balantiopsis asymmetrica</i> (Herz.) Engel
<i>B. bisbifida</i> (Steph.) Steph.
<i>B. brasiliensis</i> Steph.
<i>B. cancellata</i> (Nees) Steph.
<i>B. ciliaris</i> Hatt.
<i>B. convexiuscula</i> Berggr.
<i>B. crocea</i> Herz.
<i>B. diplophylla</i> (Hook. f. & Tayl.) Mitt.
<i>B. erinacea</i> (Hook. f. & Tayl.) Mitt.
<i>B. lingulata</i> Schust.
<i>B. montana</i> (Col.) Engel & Merr.
<i>B. philippinensis</i> H. Inoue
<i>B. purpurata</i> Mitt.
<i>B. rosea</i> Berggr.
<i>B. tumida</i> Berggr.
<i>B. verrucosa</i> Engel & Merr.
<i>Eoisotachis stephanii</i> (Salm.) Schust.
<i>Isotachis intortifolia</i> (Hook. f. & Tayl.) Gott.
<i>I. lyallii</i> (Hook. f. & Tayl.) Mitt.
<i>I. montana</i> Col.
<i>Neesioscyphus argillaceus</i> (Nees) Grolle
<i>N. carneus</i> (Nees) Grolle
<i>Ruizanthus venezuelanus</i> Schust.
<i>Triandrophyllum subtrifidum</i> (Hook. f. & Tayl.) Fulf. & Hatch.

with five). To represent *Isotachis*, we selected *I. intortifolia*, *I. lyallii*, and *I. montana*, all New Zealand species (see Phytogeography, p. 56) but representative of the range of variation in the genus (for a discussion of monophyly of *Isotachis*, see Intergeneric Relationships, p. 47). *Ruizanthus venezuelanus* was chosen to represent *Ruizanthus* since sporophyte data were available for this species (Schuster, 1985a). Similarly, of the four known species of *Austroscyphus*, *A. phoenicorhizus* was selected as the placeholder for this genus since the most complete data (e.g., on oil-bodies) were available for this species. *Neesioscyphus* is represented by *N. argillaceus* and *N. carneus* (Grolle, 1964), species for which both gametophytic and reproductive structures are known.

We also chose the primitive, generalized liverwort *Triandrophyllum subtrifidum* as an outgroup because it is clearly not a member of the Balantiopsaceae but is sufficiently similar in gross morphology to allow polarization of most of the characters used in the analysis. Data were available for the outgroup on all characters used in the analysis. To test the effect of additional outgroups on the analysis, we experimented with inclusion of two additional taxa, *Lepicolea attenuata* and *Diplophyllum taxifolium* (for a discussion of the ef-

fect of these taxa on the results of the analysis, see Results, p. 43). *Triandrophyllum* and *Lepicolea* occupy a near-basal position relative to other leafy hepatics in the classification system of Schuster (1966, 1979); *Diplophyllum* has complicated bilobed leaves similar to those of *Balantiopsis* but has a simple perianth with no accessory gynoecial structures and straight valvular capsule dehiscence. The 26 taxa included in the analysis are listed in Table 1.

With the exception of *R. venezuelanus* (Schuster, 1985a), data used in the analysis were verified by examination of herbarium specimens. Oil-bodies are ephemeral cell inclusions and are soon lost in drying; data for oil-bodies of many taxa were necessarily obtained from literature reports. All characters are treated as unordered to avoid making *a priori* assumptions concerning character polarity, which may or may not have a sound phylogenetic basis. Over reliance on generalizations concerning the relative primitiveness or advancedness of characters has been cited as an obstacle to progress in understanding the evolution of bryophytes (Mishler & Churchill, 1984, p. 421). Taxa with more than one state of a given character were treated as polymorphic with respect to that character and assigned both values; in the analysis, PAUP (p. 41) was instructed to treat these as instances of polymorphism rather than uncertainty as to character state. The data matrix showing the assignment of character states for each taxon is shown in Table 2.

Character Descriptions and Coding

GAMETOPHYTE

General

1. *Symmetry*. Anisophylly is typical of most leafy hepatics, but the Balantiopsaceae include both anisophyllous and subisophyllous forms. Pronounced anisophylly is commonly associated with a plagiotropic habit (e.g., *Isotachis minima*, with small, deeply bifid underleaves and abundant rhizoids; Fig. 11). Unfortunately, isophylly is a somewhat ambiguous term, since it may refer to leaves and underleaves that are similar in size (surface area) only. Strict isophylly, in which underleaves are undistinguishable from leaves, is rather uncommon in liverworts. The term subisophylly is applied here to taxa in which the un-

TABLE 2. Data matrix used in cladistic analysis of *Balantiopsis* and related genera.

Taxa	1	2	3	4	5	6	7	8	9	0	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	
<i>T. subtrifidum</i>	0	1	0	1	0	0,1	2	0	0	1	0	2	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>R. venezuelanus</i>	1	0	0	0	0	1	1	0	0	1	0	2	0	2	0	0	1	0	0	1	0	1	0	0	0	2	0
<i>N. argillaceus</i>	1	1	0	1	0	2	1	0	1	1	0	2	0	2	0	0	1	0	0	-	0	0	1	1	2	0	0
<i>N. carneus</i>	1	0	0	0	0	2	1	0	1	1	0	2	-	2	-	0	1	1	0	-	0	0	1	1	3	0	0
<i>A. phoenicorhizus</i>	1	1	1	1	0	-	1	0	0	1	0	2	0	1	1	0	1	1	2	2	0	2	-	-	-	0	0
<i>A. splendens</i>	1	0	1	1	1	1	1	1,2	0,2	2	2	2	0	2	1	1	1	2	2	-	-	-	-	-	-	-	-
<i>E. stephanii</i>	0	0	1	1	0	1	0,1	0	0	1	0	2	0	1	1	0	0	1	2	-	-	-	-	-	-	-	-
<i>I. intortifolia</i>	0	0	1	1	0	0,1	0,2	0	0	2	0	2	0	1	0	0	1	0	1	2	1	-	-	-	-	1	1
<i>I. montana</i>	1	1	1	1	0	0,1	0,2	0	0	1	0	2	0	1	0	0	0	0	0	2	1	0	-	-	-	1	1
<i>I. lyallii</i>	1	0	1	1	0	0,1	2	0	0	1	0	0	0	1	0	0	0	0	1	2	1	0	1	1	1	1	1
<i>B. bisbifida</i>	1	1	1	0	0	1	1	0	1	1	0	2	0	2	0	1	1	0	0	1	2	-	1	1	1	1	1
<i>B. asymmetrica</i>	1	0	1	1	0	2	1	0	1	1	0	2	0	1	0	1	1	0	0	1	2	0	1	1	1	1	1
<i>B. brasiliensis</i>	1	0	1	1	1	2	1	1,2	1	1	2	1,2	0	1	1	0	1	0	0	-	2	-	-	-	-	-	-
<i>B. philippinensis</i>	1	-	-	1	1	2	1	1	1	1	2	1	0	1	1	1	0	0	-	-	-	-	-	-	-	-	-
<i>B. crocea</i>	1	1	1	1	1	2	1	0,1	1	0,1	1	1	0	1	2	1	1	0	0	1	-	-	-	-	-	-	-
<i>B. ciliaris</i>	1	0	1	1	1	2	1	0	0	0	2	0,1	1	1	2	0	1	0	0	2	-	0	-	-	-	-	-
<i>B. purpurata</i>	1	0	1	1	1,2	3	1	0	0	0	2	2	0	2	0	0	1	0	0	1	2	0	1	1	1	1	1
<i>B. cancellata</i>	1	0	1	1	1	2	1	2	0	1	2	0	1	2	2	1	0	1	1	2	2	0	1	1	1	1	1
<i>B. erinacea</i>	1	1	1	1	2	1	1	2	2	1	2	0,1	0	1	2	0	0	1	0	2	-	0	-	-	-	-	-
<i>B. diplophylla</i>	1	1	1	1	1	2,3	1	0,1	0,1	1	2	1,2	0	2	0	0	1	0	0	2	0	-	-	-	-	1	1
<i>B. montana</i>	1	1	1	1	1	2	1	0	1	0	1	1	0	2	2	0	1	0	0	-	0	-	-	-	-	-	-
<i>B. lingulata</i>	1	1	1	1	1	2	1	1	1	1	2	0,1	0	2	2	0	1	0	0	2	0	-	-	-	-	-	-
<i>B. verrucosa</i>	1	1	1	1	1	1,2	1	2	1	1,2	2	0	1	2	1	1	1	1	2	-	0	-	-	-	-	-	-
<i>B. rosea</i>	1	0	1	1	1	2	1	2	1	2	2	0	0	1	2	1	1	1	1	2	2	0	-	-	-	1	1
<i>B. convexiuscula</i>	1	0,1	1	1	1	2	1	2	0	1	2	1	1	2	2	0	0	1	0	1	2	0	1	1	1	1	1
<i>B. tumida</i>	1	0,1	1	1	1	1	1	2	0	2	2	2	1	1	2	0	0	1	0	1	-	0	-	-	-	-	-

derleaves resemble leaves in both form and size (e.g., *Eoisotachis stephanii*, *Isotachis intortifolia*). For example, *Anisotachis splendens* is scored as anisophyllous because its deeply conduplicate bilobed leaves differ strongly from underleaves in form. In the similar size of the leaf lobes and underleaves (as well as in its turgid, julaceous habit), this species mimics *Eoisotachis*. This facies is characteristic of species that grow erect and submersed or emergent in small streams or pools, etc. All *Balantiopsis* species are considered anisophyllous.

Symmetry is treated as a binary character: subsophyllous (0), moderately to strongly anisophyllous (1). This character could be scored in 25 of 25 (100%) of the ingroup taxa.

2. *Pigmentation*. Strong pigmentation is characteristic of the family Balantiopsaceae. *Balantiopsis rosea* and *Isotachis lyallii* are both notable for the intense wine-red color that develops in exposed sites. *Anisotachis*, *Eoisotachis*, *Ruizanthus*, and *I. intortifolia* are also deeply red-pigmented. Other species are characteristically brownish in color and only sporadically reddish-tinged (e.g.,

Balantiopsis montana, *B. verrucosa*, *Isotachis montana*, *Austroscyphus phoenicorhizus*). The only taxon not scored with respect to pigmentation was *B. philippinensis*, known only from the type, in which this character is impossible to assess with certainty.

Pigmentation is treated as a binary character: red to wine-red (0), brownish or tinged with red (1). This character could be scored in 24 of 25 (96%) of the ingroup taxa.

3. *Branching type*. Types of branching modes and their relative frequency are considered highly significant in assessing phylogenetic relationships among hepatics. Although of demonstrated taxonomic utility, for purposes of phylogenetic analysis, we consider frequency of occurrence to be less informative than evidence of the ability to produce a given type of branching. Terminal branching is lacking in *Neesioscyphus* (Grolle, 1964), *Ruizanthus* (Schuster, 1985a), and the outgroup taxon, *T. subtrifidum*. All other taxa (including all *Balantiopsis* species) produce terminal, *Frullania*-type, as well as ventral-intercalary,

branches. The only species not scored was *Balantiopsis philippinensis*.

Branching type is treated as a binary character: only intercalary branching present (0), branching terminal and intercalary (1). This character could be scored in 24 of 25 (96%) of the ingroup taxa.

4. *Rhizoid origin*. In *Balantiopsis bisbifida* (Engel, 1968, p. 95, & fig. 65), *Neesioscyphus carneus* (Grolle, 1964), and *Ruizanthus venezuelanus* (Schuster, 1985a, p. 73, & fig. 6:6), rhizoids originate at the bases of the leaves as well as underleaves. In all other taxa included in the analysis, rhizoids occur only at the bases of underleaves.

Rhizoid origin is treated as a binary character: at bases of leaves and underleaves (0), only at bases of underleaves (1). This character could be scored in 25 of 25 (100%) of the ingroup taxa.

Leaves

5. *Depth of division between lobes*. The "typical" *Balantiopsis* leaf is strongly bilobed to at least 0.6; this character corresponds to the width of the "keel" in a conduplicate-bilobed leaf. In *B. ciliaris*, the keel is only 1–2 cells wide; in *B. purpurata*, the dorsal lobe sometimes appears displaced and inserted on the lamina of the ventral lobe. In *B. erinacea*, the dorsal lobe is detached and either immediately juxtaposed to the ventral or completely free. In *Eoisotachis*, *Isotachis*, *Ruizanthus*, and two *Balantiopsis* species (*B. asymmetrica* and *B. bisbifida*), the leaf is \pm regularly and shallowly bilobed or bisbifid to no more than 0.5. In *Neesioscyphus argillaceus* and *N. carneus* the apex is shallowly and unequally bilobed (Grolle, 1964, figs. 2:1, 2; 3:3). In *Austroscyphus phoenicorhizus* the leaf apex is unlobed to retuse (Fig. 10:3); however, in *Austroscyphus iwatsukii* (Kitag.) Schust. (not included in the analysis), the leaves are distinctly bilobed.

Division between lobes is treated as an unordered multistate character with three states: bilobed or bisbifid to 0.5 or less (0), deeply bilobed, to 0.6 or more (1), dorsal lobe displaced or detached (2). This character could be scored in 25 of 25 (100%) of the ingroup taxa.

6. *Relative lobe size*. The leaves of leafy hepatics are fundamentally bilobed from the earliest stages of development at the shoot apex (Evans, 1939, p. 61.) In nearly all of the taxa treated here, the leaf is bilobed or bisbifid in varying degrees,

with distinct dorsal and ventral lobes, which differ in relative size. In the outgroup taxon, *Triandrophyllum subtrifidum*, and in *Isotachis*, the dorsal-most lobe commonly exceeds the ventral in size; in *Balantiopsis*, as a rule, the dorsal is much smaller than the ventral lobe. The extreme condition is reached in *B. purpurata* (Engel, 1968, fig. 80) and in *B. diplophylla* var. *hockenii*; in the latter, the dorsal lobe may be a slender, deeply bifurcate appendage of the ventral lobe. In *Neesioscyphus* (*N. argillaceus* and *N. carneus*), the dorsal lobe is much smaller than the ventral (Grolle, 1964, figs. 2:1, 2; 3:3). In *Austroscyphus phoenicorhizus*, the leaves are unlobed to retuse; *A. iwatsukii*, however, has deeply bilobed leaves.

Relative lobe size is treated as an unordered multistate character with four states: dorsal lobe larger than ventral (0), subequal to ventral (1), ca. 0.25–0.5 the ventral (2), 0.2 the ventral or less (3). *Austroscyphus phoenicorhizus*, with unlobed leaves, was scored inapplicable. This character could be scored in 24 of 25 (96%) of the ingroup taxa.

7. *Leaf insertion*. Leaf insertion is essentially transverse in *Isotachis intortifolia* and *I. montana* (Fig. 12:1, 7) and weakly to distinctly incubous in *I. lyallii* (Fig. 14:1) as well as in the outgroup taxon, *T. subtrifidum*. In all the remaining taxa, the leaves are weakly to distinctly succubous in insertion. Assessment of the leaf insertion in many *Balantiopsis* species and in *Anisotachis* is complicated by the recurvature of the insertion of the dorsal and ventral lobes (Fig. 2:1–8), each of which is treated as a separate character (8 and 9).

Leaf insertion is treated as an unordered multistate character with three states: transverse (0), succubous (1), incubous (2). Taxa with variable insertion (e.g., with transverse to weakly succubous insertion, as in *Eoisotachis*) were treated as polymorphic with respect to this character and assigned both values. This character could be scored in 25 of 25 (100%) of the ingroup taxa.

8. *Ventral lobe insertion*. Seen in ventral aspect, the ventral lobe insertion in some *Balantiopsis* species is strongly arched and abruptly recurved toward the base of the shoot so that the line of insertion resembles an inverted U (*B. convexiuscula*, Fig. 2:4; *B. verrucosa*, Fig. 2:6). The ventral lobe insertion in *Anisotachis splendens* is also strongly U-shaped (Schuster, 1972, fig. 5:6). In other species of *Balantiopsis* the insertion is moderately recurved (J-shaped, e.g., *B. diplo-*

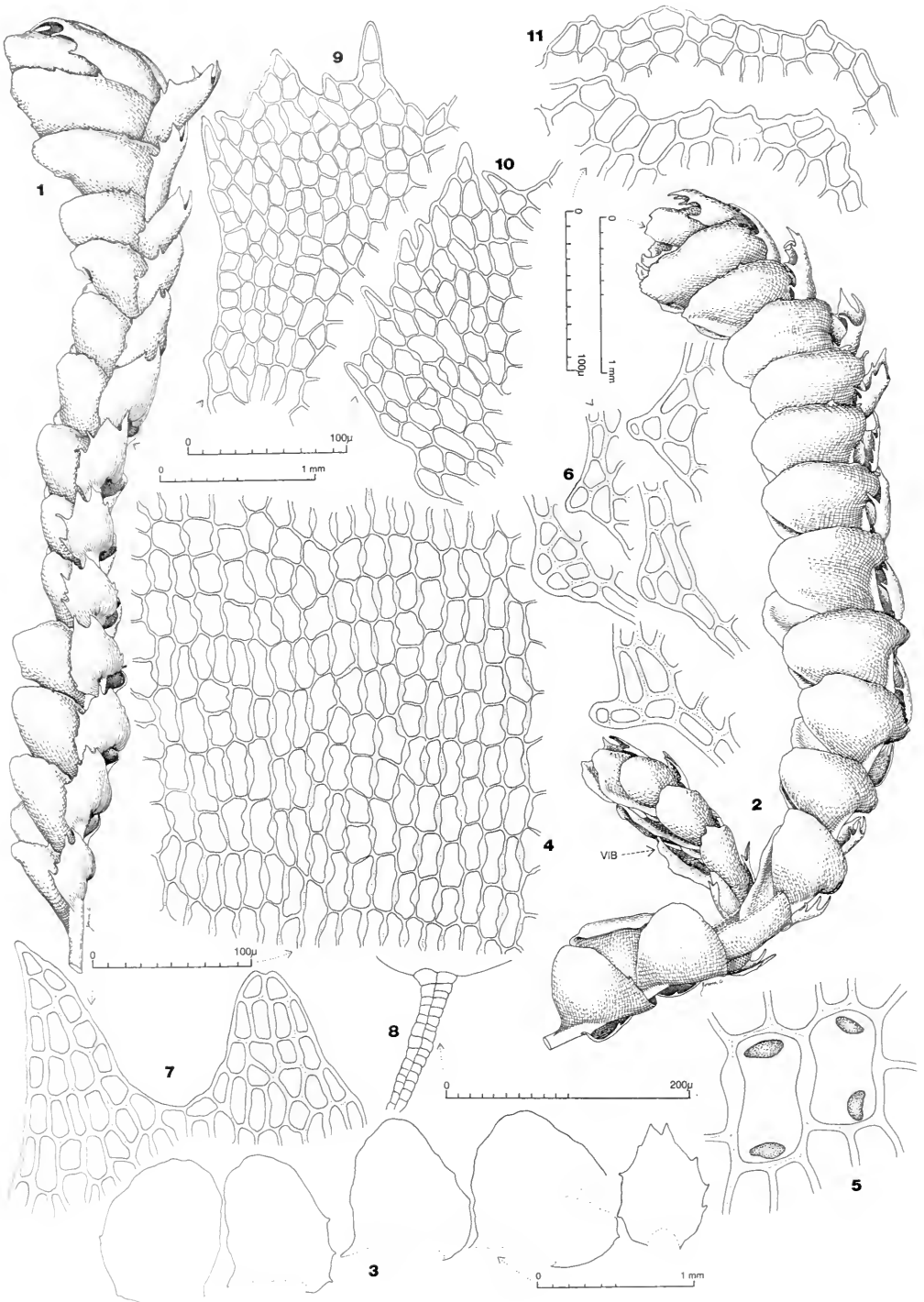


FIG. 10. *Austroscyphus phoenicorhizus* (Grolle) Schust. 1, Ventral-lateral view of main shoot. 2, Lateral view of main shoot with ventral-intercalary branch (vib). 3, Leaves and, to right, an underleaf. 4, Median leaf cells, showing tiering of cells and intermediate thickenings. 5, Oil-bodies ($\times 615$). 6, Teeth of ventral margin of leaf. 7, Distal sector of underleaf. 8, Antheridium. 9, 10, Portion of lobule of δ bract. 11, Apex of δ bract. (Figs. 1, 2 from Engel 15916, Tasmania, Great Western Tiers, vicinity of Devils Gullet Lookout; 3-7 from Engel 19903, Tasmania, Hartz Mts. Natl. Park, summit area of Hartz Peak; 8-11 from Ratkowsky 78/73, Tasmania, Mt. Wedge.)

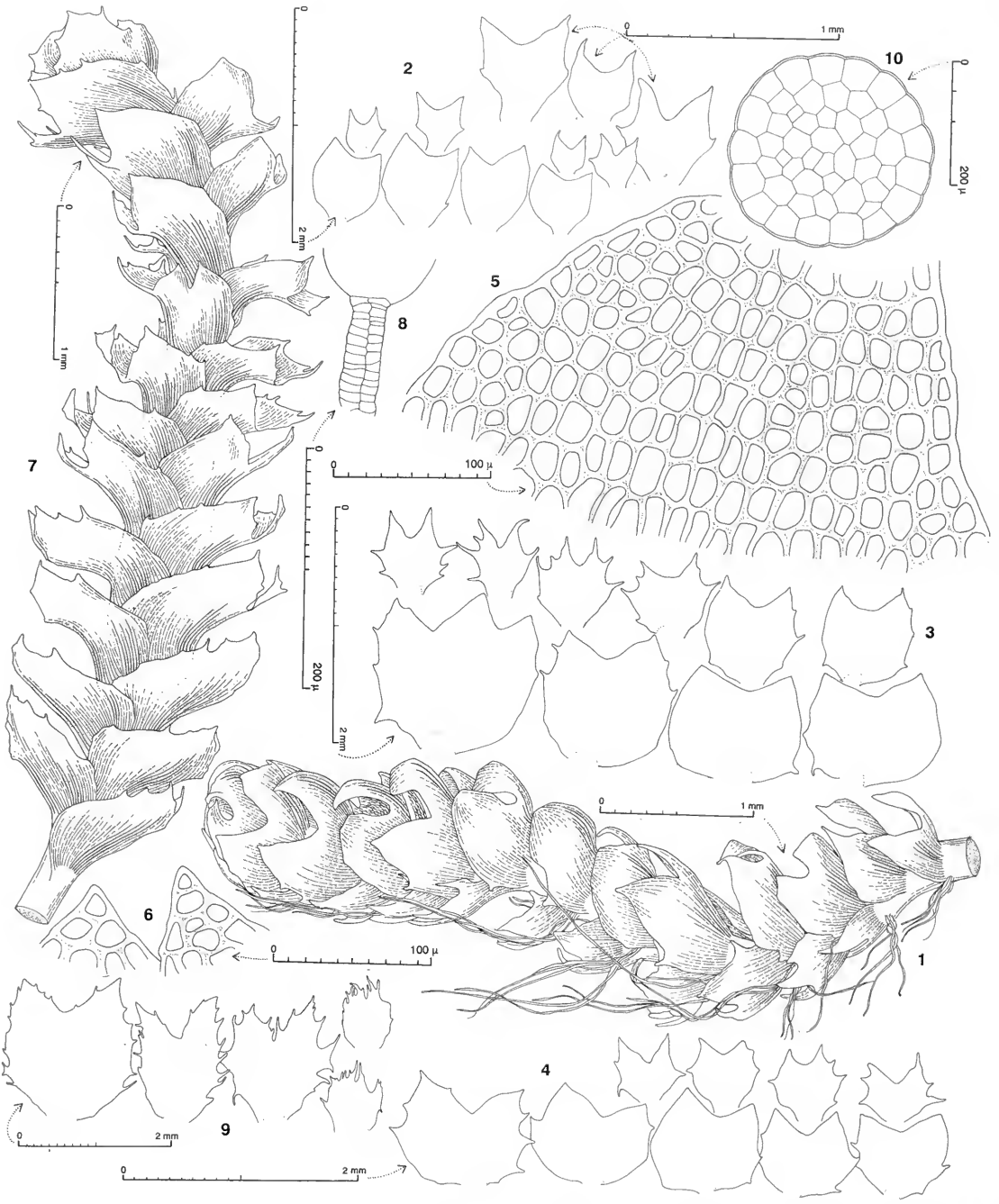


FIG. 11. *Isotachis minima* Pears. 1, Leading shoot, ventral-lateral view. 2-4, Leaves. 5, Portion of leaf lobe, showing cells in ill-defined tiers. 6, Leaf lobe apices. 7, Sector of main shoot showing poorly differentiated androecium, dorsal view. 8, Antheridial stalk. 9, Largest inner ♀ bracts and, in middle, bracteole; to right are two perigynial bractlets at same scale. 10, Seta, cross section. (Figs. 1, 4 from Sept. 1939, Hodgson, New Zealand, North Is., South Auckland Prov., Whakarewarewa Thermal Reserve; 2, 5, 6 from type of *I. minima*; 3 from Engel 17630, New Zealand, South Is., Otago Prov, W slope of Flagstaff, NW of Dunedin; 7-9 from Child 47, New Zealand, North Is., South Auckland Prov., Waiotapu, Rotorua; 10 from Child 1382, New Zealand, South Is., Otago Prov., Flagstaff.)

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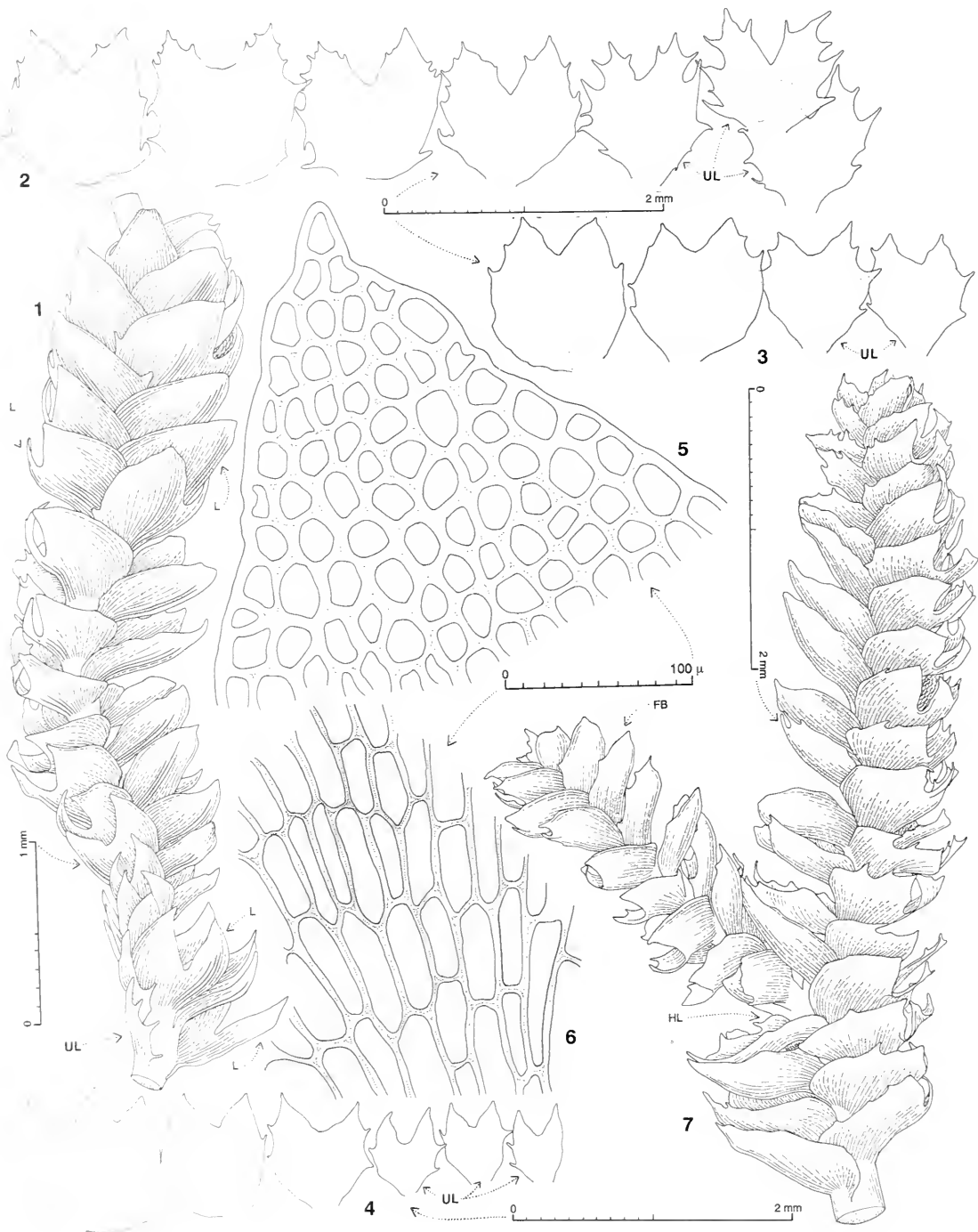


FIG. 12. *Isotachis montana* Col. 1, Sector of main shoot, the distal sector shown in dorsal aspect, the basal sector in lateral aspect (l = leaf; ul = underleaf). 2–4, Leaves and underleaves (ul). 5, Distal sector of leaf lobe (cuticle not shown). 6, Median-basal leaf cells. 7, Sector of main shoot with *Frullania*-type branch (FB; HL = half-leaf), dorsal view. (Figs. 1, 4–6, from type of *I. montana*; 2, from *Hatcher 1429*, New Zealand, South Is., Otago Prov., Fiordland, near McKerrow Hut, head of Lake McKerrow; 3, 7 from *Child 4859*, New Zealand, South Is., Westland Prov., near Gillespies Beach, W of Fox Glacier.)

phylla, Fig. 3:6), only weakly recurved (comma-like, e.g., *B. montana*, Fig. 5:8), or straight.

Ventral lobe insertion is treated as an unordered multistate character with three states: straight or comma-like (0), J-shaped (1), U-shaped (2). This character could be scored in 25 of 25 (100%) of the ingroup taxa.

9. *Dorsal lobe insertion*. In some *Balantiopsis* species the line of insertion of the dorsal half of the leaf is an almost uninterrupted extension of the insertion of the ventral half and is only slightly bent at the junction between the two. Seen in dorsal aspect, the base of the dorsal lobe is strongly oblique to longitudinal in orientation, with the free margin long-decurrent on the stem (e.g., *B. rosea*, Fig. 7:1; *B. verrucosa*, Fig. 2:5). In *B. bisbifida* and *B. asymmetrica* the line of leaf insertion is essentially straight (Fig. 2:1, 2; Hässel de Menéndez & Solari, 1975, fig. 35:11, 12).

In other *Balantiopsis* species the insertion of the dorsal lobe is transverse, at right angles to the axis of the stem, with the free margin scarcely decurrent (e.g., *B. convexiuscula*, Figs. 2:3; 8:1, 2). In these species, the insertion line appears sharply bent at the junction between the dorsal and ventral lobes (Fig. 2:4). In other *Balantiopsis* species and in *Anisotachis splendens*, the dorsal lobe insertion is strongly arched, and inverted U-shaped, like the ventral (e.g., *B. erinacea*, Fig. 2:7, 8).

Dorsal lobe insertion is treated as an unordered multistate character with three states: \pm transverse (0), oblique to longitudinal (1), U-shaped (2). This character could be scored in 25 of 25 (100%) of the ingroup taxa.

10. *Ventral lobelleaf planation*. In *B. rosea*, *B. tumida*, *B. verrucosa*, and *Anisotachis splendens*, the ventral lobe of the leaf is often sharply canaliculate or conduplicately folded to strongly plicate (Fig. 2:10, shown in section in Fig. 2:11). However, in most *Balantiopsis* species, the ventral lobe is merely convex, without any sharp folding or plication (e.g., *B. diplophylla*, Fig. 3:1, 6). In *B. montana* the ventral lobes are widely spreading, horizontally oriented, and essentially flat (Fig. 5:1). In *B. asymmetrica*, *B. bisbifida*, *Austroscyphus*, *Eoisotachis*, *Isotachis montana*, *I. lyallii*, and *Ruizanthus*, the leaf is moderately to strongly concave; in *Isotachis intortifolia* the entire leaf is often strongly plicate.

Ventral lobe/leaf planation is treated as an unordered multistate character with three states: essentially flat (0), convex or concave (1), canaliculate

to conduplicately folded or plicate (2). Taxa expressing varying degrees of plication or folding were treated as polymorphic with respect to this character and assigned both values. This character could be scored in 25 of 25 (100%) of the ingroup taxa.

11. *Dorsal lobe orientation*. The "typical" *Balantiopsis* leaf is deeply conduplicate-bilobed, with a \pm distinct keel (e.g., *B. rosea*, Fig. 7:1). In some species, however, the dorsal lobe is dorsally assurgent (*B. montana*, Fig. 5:1). In *B. asymmetrica* the dorsal lobe margin, seen in dorsal aspect, is moderately inflexed to narrowly incurved and erect (Engel, 1968, fig. 1; Hässel de Menéndez & Solari, 1975, fig. 35:1). In *B. bisbifida* the leaf is bisbifid, and the leaves are \pm symmetrical and merely concave, as are the leaves of *Ruizanthus*, *Neesioscyphus*, *Eoisotachis*, and *Isotachis* spp. The complicately bilobed leaves of other hepatic genera (e.g., *Scapania*, *Diplophyllum*) are regarded as nonhomologous and independently derived.

Dorsal lobe orientation is treated as an unordered multistate character with three states: leaves concave, not conduplicately folded (0), keeled but dorsal lobe assurgent (1), conduplicate-folded, the dorsal lobe appressed to the ventral (2). This character could be scored in 25 of 25 (100%) of the ingroup taxa.

12. *Leaf armature*. Development of teeth or cilia on the margins of the leaves is highly variable in *Balantiopsis*, although individual species typically have a characteristic range of variation. The extreme condition occurs in *B. ciliaris*, in which the ventral lobe has up to 32 cilia (to 95 on both lobes, Hattori, 1966). *Balantiopsis rosea* and *B. lingulata* have ventral lobe margins with up to 14 to as many as 20 cilia. Other species, such as *B. convexiuscula*, have the lobes moderately armed, the ventral lobe with 2–9, or at most 13, teeth or cilia. *Balantiopsis tumida* and *B. verrucosa* at times have almost unarmed margins (Fig. 9:2, 3).

Leaf armature is treated as an unordered multistate character with three states: margins copiously armed (0), moderately armed (1), almost unarmed (2). Taxa with variable armature (i.e., moderately armed in some populations to almost unarmed in others) were treated as polymorphic with respect to this character and assigned both values. This character could be scored in 25 of 25 (100%) of the ingroup taxa.

13. *Projecting septa*. In some *Balantiopsis* spe-

cies, the margins of the leaves, particularly in the distal sector, are minutely denticulate by projecting septa of marginal cells. This character is present in *B. convexiuscula* (Fig. 8:6, 7), *B. tumida*, *B. cancellata*, and *B. ciliaris* (Piippo, 1984, fig. 16c). *Neesioscyphus carneus* was not scored.

Projecting septa are treated as a binary character: lobe margins without projecting septa (0), with projecting septa (1). This character could be scored in 24 of 25 (96%) of the ingroup taxa.

Underleaves

14. *Underleaf lobing*. The underleaf apex varies from truncate-entire or more often retuse to short-bilobed in *Anisotachis splendens* (Hässel de Menéndez & Solari, 1975, fig. 37:1, 4) to deeply bifid and dissected to 0.5 or more (e.g., *B. convexiuscula*, Fig. 8:8). Other taxa (e.g., *B. verrucosa*, Figs. 2:9; 6:7) have underleaves only shallowly bifid, to 0.2–0.4 or less.

Underleaf lobing is treated as an unordered multistate character with three states: truncate-entire (0), shallowly bifid, 0.2–0.4 or less (1), deeply bifid to 0.5 or more (2). This character could be scored in 25 of 25 (100%) of the ingroup taxa.

Cells

15. *Leaf areolation*. Regular transverse tiering of leaf and underleaf cells is characteristic of *Balantiopsis* (Berggren, 1898, p. 44) and, indeed, is “almost a trademark of the entire suborder” (Schuster, 1985a, p. 72). This is often accentuated by the elongate-rectangular to linear shape of the cells. In many taxa with conspicuous tiering of cells (e.g., *B. rosea*, Fig. 7:5), the cells are grouped in conspicuous “panels” of 6–10 long, narrow cells that often appear secondarily divided. In *B. diplophylla* (Fig. 3:4), *B. asymmetrica*, *B. bisbifida*, and *B. purpurata* the leaf cells are \pm isodiametric and scattered, without any suggestion of tiering. The leaf cells of *Austroscyphus phoenicorhizus* are also tiered (Fig. 10:4). In *Ruizanthus* the underleaves display noticeable tiering, but the leaves do not (Schuster, 1985a, fig. 8:15). *Neesioscyphus carneus* was not scored.

Areolation is treated as an unordered multistate character with three states: cells typically scattered (0), cells indistinctly tiered (1), leaf cells in evident transverse rows (2). Taxa with tiering only sporadically expressed (i.e., present in some

leaves but not others, or only in certain sectors of leaves) were treated as polymorphic with respect to this character and assigned both values. This character could be scored in 24 of 25 (96%) of the ingroup taxa.

16. *Leaf border*. Many Balantiopsaceae have leaves with a \pm distinct border formed by differentiation of the marginal row of cells. In some species (e.g., *B. verrucosa*), bordering also takes the form of a striking difference in the cuticle: the finely striate-papillose marginal cells are in sharp contrast to the coarsely guttulate papillae of the cells immediately adjacent to the marginal row (Fig. 6:6). It should be noted that *Ruizanthus lopezii*, which was not included in the analysis, has a distinct border (Schuster, 1985a, fig. 8:11–13), but of a different type.

Leaf border is treated as a binary character: no border (0), marginal cells forming a \pm distinct border (1). Taxa with an indistinct border were assigned both values. This character could be scored in 25 of 25 (100%) of the ingroup taxa.

17. *Leaf cell size*. Some species of *Balantiopsis* have relatively small cells, lending the leaves a dense, subopaque appearance (e.g., *B. cancellata*, *B. convexiuscula*). Others have much larger cells, to 40–50 μm wide, and lax areolation, with a \pm translucent quality. Comparison of cell width ranges in different species indicated a discontinuity at ca. 18 μm , which was used as a basis for scoring this character.

Leaf cell width is treated as a binary character: 12–18 μm wide (0), 19–53 μm wide (1). Cell width measurements were taken from cells that were not secondarily divided. For consistency, measurements were made in the median sector of the leaf, and in the case of deeply bilobed leaves, from the median sector of the ventral lobe. This character could be scored in 25 of 25 (100%) of the ingroup taxa.

18. *Wall thickenings*. Cell walls in the taxa studied may be uniformly thin- or thick-walled or may exhibit characteristic thickenings. In many species, the median portion of the longitudinal walls is noticeably thickened, the walls thinning abruptly to the corners of the cells (e.g., *B. rosea*, Fig. 7:7). In species with short-rectangular cells, the walls of the longitudinally aligned rows of cells often appear sinuate, due to these unequal wall thickenings (e.g., *B. convexiuscula*, Fig. 8:5; *Austroscyphus phoenicorhizus*, Fig. 10:4). In *Neesioscyphus carneus*, intermediate thickenings are

present, as well as knotlike trigones (Grolle, 1964, fig. 2:3); in *Ruizanthus venezuelanus* (Schuster, 1985a), the median leaf cells are thin-walled but with moderate trigones. Conspicuous, bulging trigones are present in *Isotachis intortifolia*.

Wall thickening is treated as a binary character: uniformly thin- or thick-walled (0), intermediate thickenings (1). Taxa with only sporadic intermediate wall thickenings were assigned both values. Presence or absence of trigones was not considered in determining the type of wall thickening. This character could be scored in 25 of 25 (100%) of the ingroup taxa.

19. *Cuticle*. Cuticular patterns in the Balantiopsaceae vary from smooth to striate-papillose to coarsely verrucose. In leaves of *Balantiopsis cancellata*, *B. rosea*, and *B. verrucosa* (Fig. 6:5), as well as *Isotachis intortifolia*, the papillae are coarse, high, and spherical, with only a few large papillae per cell, a condition we term "guttulate": the papillae resemble spherical droplets of oil or resin (Stearn, 1966). In other species (e.g., *B. montana*, Fig. 5:4), the cuticle is finely and rather distantly striate-papillose with many papillae per cell. The leaves of *Anisotachis*, *Austroscyphus phoenicorhizus*, and *Eoisotachis* are essentially smooth, without any perceptible cuticle.

Leaf cuticle is treated as an unordered multi-state character with three states: striate-papillose (0), guttulate (1), smooth (2). This character could be scored in 25 of 25 (100%) of the ingroup taxa.

20. *Oil-bodies*. In the taxa included in the analysis, the number of oil-bodies ranges from 5–11 per cell (e.g., *B. montana*, Fig. 2:12, 13) to comparatively few (2–7 per cell in *B. convexiuscula*, Fig. 2:14) to 2 (rarely 3) large oil-bodies per cell, situated at opposite ends of the cell (e.g., *B. rosea*, Fig. 2:15). The state of 2 oil-bodies per cell is also found in the three *Isotachis* species included in the analysis, in *Anisotachis splendens* (Hässel de Menéndez & Solari, 1975), and in *Austroscyphus phoenicorhizus* (Fig. 10:5). *Ruizanthus venezuelanus* has 2–3(4) oil-bodies per cell (Schuster, 1985a). Oil-bodies of *Neesioscyphus carneus* and *N. argillaceus* are not known, but Gradstein et al. (1977) report 2–3(4) per cell in an undetermined *Neesioscyphus* species from Ecuador. The outgroup taxon, *T. subtrifidum*, is reported to have 4–10 oil-bodies per cell (Hässel de Menéndez & Solari, 1975) and 3–5(6) per cell (Stewart, 1978). Oil-body data were not available for *Eoisotachis*, *B. brasiliensis*, or *B. philippinensis*.

Oil-bodies are treated as an unordered multi-

state character with three states: numerous, 8–13 (0), few, 2–7 per cell (1), 2 (rarely 3) per cell (2). This character could be scored in 20 of 25 (80%) of the ingroup taxa.

Reproductive

21. *Accessory gynoecial structures*. Gametophyte–sporophyte interactions associated with the protection of the developing sporophyte are considered to be of major significance in the classification of hepatics. In the outgroup taxon, *Triandrophyllum*, the sporophyte is described as surrounded only by a simple perianth, i.e., a structure of appendicular (foliar) origin, not involving stem tissue (Hässel de Menéndez & Solari, 1976, p. 102). *Austroscyphus*, *Neesioscyphus*, and *Ruizanthus* display stages in the elaboration of a stem perigynium. *Neesioscyphus argillaceus* (Grolle, 1964, fig. 3:2) has a well-developed, exerted perianth and a feebly developed basal perigynium. *Austroscyphus phoenicorhizus*, *A. iwatsukii* (Kitagawa, 1984, fig. 1:6, 7). *Neesioscyphus carneus* (Grolle, 1964, fig. 1:2), and *Ruizanthus venezuelanus* (Schuster, 1985a, fig. 7:3) have an immersed perianth and short, hypanthium-like perigynium. Gynoecia of *Anisotachis* or *Eoisotachis* are unknown.

Schuster (1984, fig. 30, p. 869) traces the stages in evolution of a stem perigynium from a simple perianth condition (fig. 30:3), as the result of "a ring-like upgrowth of axial tissue below the receptacle," giving rise initially to what we refer to as a basal, hypanthium-like perigynium. The extreme development in this sequence is the elaboration of a tubular, fleshy, erect stem perigynium (fig. 30:5, *Isotachis*) with what are interpreted as remnants of the perianth and "perichaetial bracts" at its mouth.

A well-developed geotropic marsupium is present in all species of *Balantiopsis* for which gynoecia are known. Schuster (1984, fig. 30, p. 869) traces the evolution of the marsupium along four possible lines, two of which are relevant here. The first of these derives a marsupium (7) from a stage with a simple perianth (3); the other derives a marsupium (6) from a stem perigynium stage (5) "by initiation of prostrate growth." Of the other two possibilities, one derives a marsupium (7) directly from a hypothetical stage (1), "not known in any extant genus," in which no protective structures surround the archegonia, proceeding directly to a marsupium without an intermediate

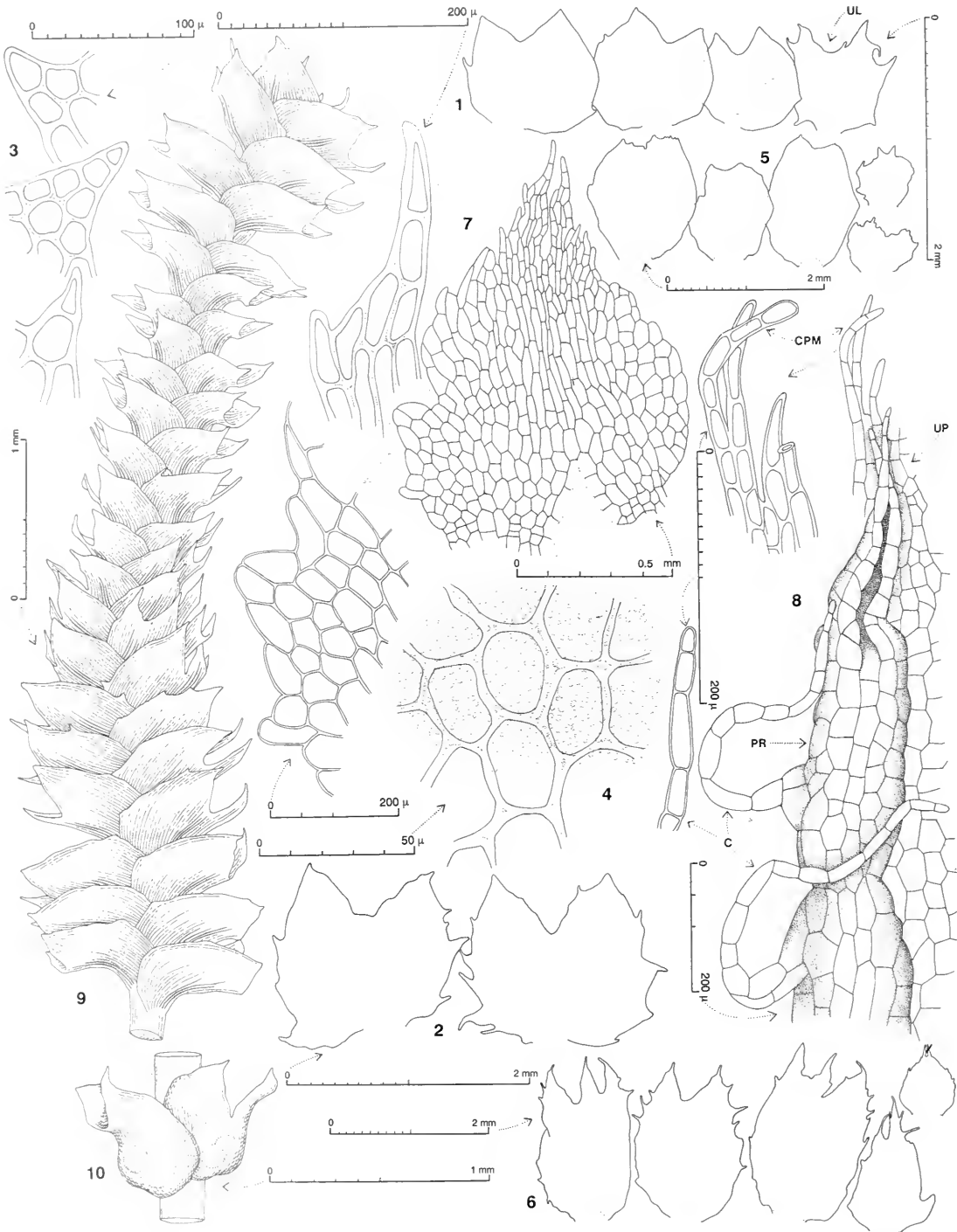


FIG. 13. *Isotachis montana* Col. 1, Leaves and underleaves distant from young gynoecium. 2, Enlarged subgynocelial leaves (basal to young gynoecium). 3, Teeth of leaf margin. 4, Upper-median leaf cells (just below sinus base; cuticle shown in part). 5, Largest inner ♀ bracts and, in middle, bracteole; two perigynial bractlets shown to right. 6, Largest inner ♀ bracts and, in middle, bracteole; two perigynial bractlets shown to right. 7, Bractlet, a portion of lobe enlarged at left, a portion of median-basal area shown at lower left. 8, Inner face of perigynium, distal sector (up = unistratose portion; cpm = cilium of perigynium mouth; pr = polysratose rib, on which thin-walled cilia (c))

perianth stage. This is a theoretical possibility, since no demonstrable perianth is present in *Balantiopsis* (except perhaps in *B. bisbifida*), but an unlikely one, since a well-developed perianth is present in related, and presumably more primitive, genera in the family (e.g., *Neosioscyphus*). The other option leads to a marsupium (8) accompanied by a "calyptral perigynium" and a perianth (e.g., *Arnellia*). No member of the Balantiopsaceae develops such a structure.

In *Isotachis*, a conical-cylindrical, fleshy, erect stem perigynium is present (Fig. 14:8), and in *Balantiopsis*, a conspicuous, geotropic marsupium develops (Fig. 4:1, 2). At maturity, both structures bear numerous, minute scalelike or ciliiform processes around the mouth and just within the mouth (Figs. 14:9, *I. lyallii*; 13:8, *I. montana*; 4:2, *B. diplophylla*; 2:16, *B. convexiuscula*). There is no evidence of a tubular perianth at any stage of development.

We have studied gynoecia of *B. bisbifida* and *B. diplophylla* from the earliest stages of development, when the marsupium is present only as a small bulbous distention of the apex. We also examined fully developed marsupia of these species as well as *B. asymmetrica*, *B. cancellata*, *B. convexiuscula*, and *B. lingulata*. In *B. convexiuscula*, for example, 3–4 cycles of perigynial bractlets (called "perichaetial bracts" by Schuster [1984, p. 868]) are present (Fig. 2:16), surrounding the mouth. The margins of these bractlets are typically ciliiform, and in *B. diplophylla* they are densely so, the cilia consisting of uniseriate rows of cells up to 13 cells in length.

Examination of developing perigynia of *Isotachis* spp. reveals that the early stages of development are virtually identical to the young marsupia of *Balantiopsis* spp. Several indistinct cycles of perigynial bractlets, 8–10 in number, are present surrounding the archegonia. As in *Balantiopsis*, these bractlets are free from one another, and there is no trace of a tubular perianth. The outermost perigynial bractlets are \pm regularly bifid (or sometimes bisbifid), with a broadly ovate disc, surmounted by 2(4) slender lobes (*I. montana*, Fig. 13:5, 6; *I. minima*, Fig. 11:9). The mar-

ginal and submarginal cells of the disc are thin-walled and irregularly short-rectangular; the cells of the lobes are more regular in shape, thick-walled, and elongate (Fig. 13:7). Toward the center, the bractlets become progressively smaller and narrowly ovate-lanceolate, terminating in 4 cilia consisting of a uniseriate row of 4–6 cells. An interesting feature observed in *I. montana* is the several projecting ribs on the inner perigynium wall (Fig. 13:8). When fully developed, the outer surface of the perigynium sometimes bears one or more bractlets inserted near the base, identical in shape and areolation to those found at the shoot apex in young gynoecia; the innermost bractlets remain at the apex, surrounding the mouth, or inserted just within it; mature marsupia of *Balantiopsis* spp. also occasionally have bractlets inserted on the outer wall.

The resemblance between the longitudinal sections of a stem perigynium of *Isotachis* (Fig. 14:8) and a marsupium of *Balantiopsis* (Fig. 4:2) is particularly striking. Remarkably similar are the thickness and general form of the stem calyptra, the thickness of perigynium and marsupium walls, and the fleshy, basal portion in which the sporophyte foot is embedded, the position of bractlets at or near the summit, etc.

Accessory gynoecial structures are treated as an unordered multistate character with three states: accessory structures none or with hypanthium-like basal perigynium (0), erect tubular stem perigynium (1), marsupium (2). This character could be scored in 15 of 25 (60%) of the ingroup taxa.

22. *Number of antheridia per bract.* Antheridia vary from 4–5 per bract in *Ruizanthus* (Schuster, 1985a, p. 71) to solitary in *Austroscyphus phoenicorhizus*. The remaining taxa included in the analysis had 2–3 antheridia per bract (Fig. 13:10).

Number of antheridia per bract is treated as an unordered multistate character with three states: 2–3 (0), 4–5 (1), antheridia solitary (2). This character could be scored in 18 of 25 (72%) of the ingroup taxa.

are inserted, the cilia crowded, only a few shown for clarity). 9, Sector of main shoot showing differentiation of androecium, dorsal view. 10, Opposing δ bracts, *in situ*, dorsal view. (Figs. 1, 2 from type of *I. elegans* (WELT); 3, 4 from type of *I. montana* (WELT); 5 from *Hatcher 1429*, New Zealand, South Is., Otago Prov., Fiordland, head of Lake McKerrow; 6, 7, 9, 10, from *Sorensen s.n.*, New Zealand, South Is., Southland Prov., Orepuke; 8 from *Hatcher 569*, New Zealand, South Is., Otago Prov., Fiordland, ca. 30 miles SE of Lake McKerrow.)

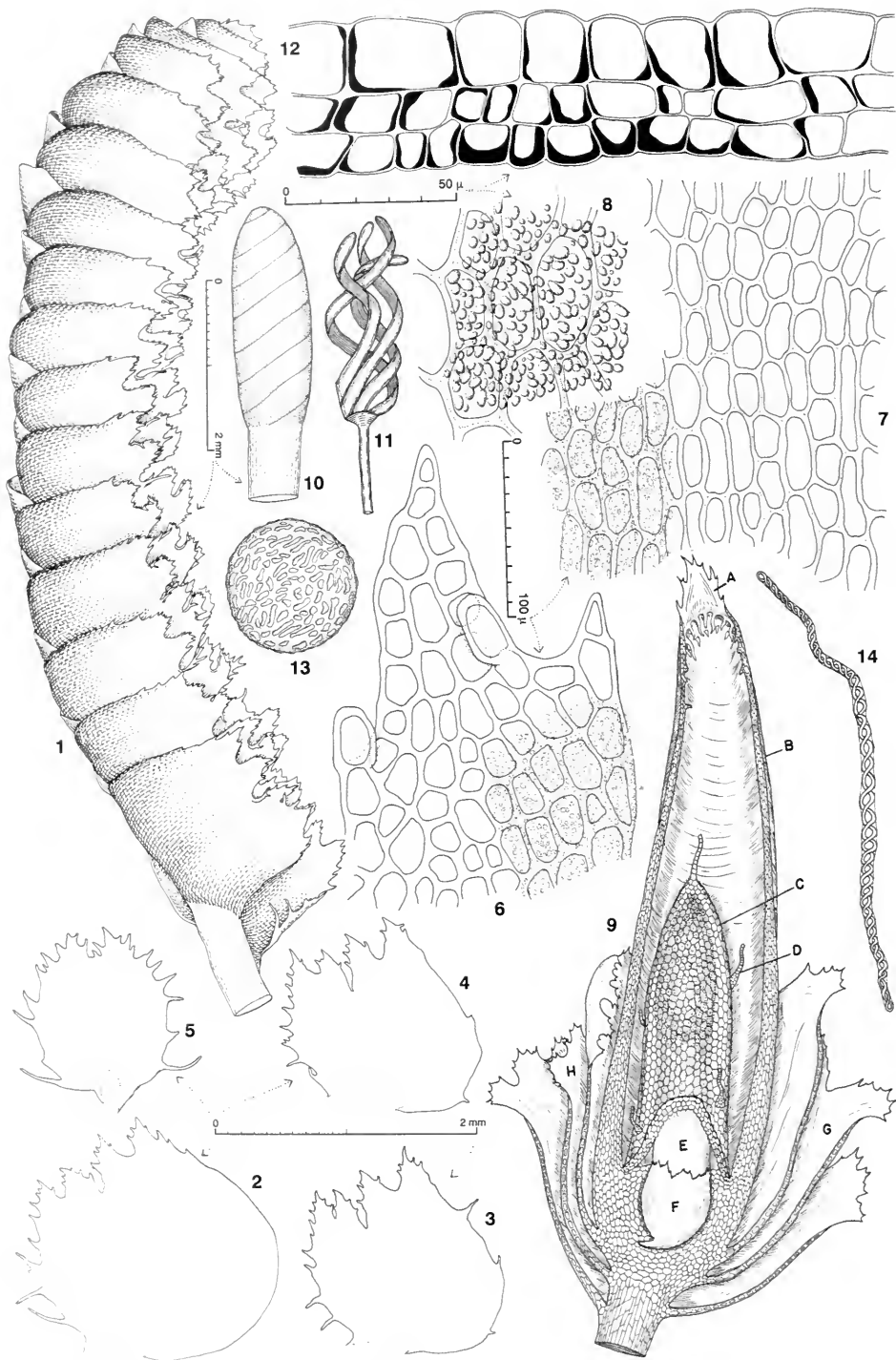


FIG. 14. *Isotachis lyallii* Mitt. 1, Portion of main shoot, lateral view. 2-4, Leaves. 5, Underleaf. 6, Leaf lobe, cuticular detail shown in part. 7, 8, Upper-median leaf cells (near lobe bases). 9, *Isotachis*-type perigynium and subtending bracts, median-longitudinal section (A = perianth; B = perigynium; C = calyptra; D = sterile archegonia; E = seta; F = foot) ($\times 40$). 10, Mature capsule showing spiral lines of dehiscence. 11, Capsule after dehiscence showing spiral valves ($\times 20$). 12, Capsule wall, cross section. 13, Spore ($\times 1895$). 14, Elater ($\times 340$). (Figs.

SPOROPHYTE

23. *Capsule shape*. In *Balantiopsis*, marsupia are not uncommon, but sporophytes are rarely seen. Sporophytes are known in five species: *B. asymmetrica*, *B. bisbifida*, *B. cancellata*, *B. convexiuscula*, and *B. purpurata*, four of which are described here for the first time (see below). Capsules are spherical in *Triandrophyllum* and *Ruizanthus* and \pm cylindrical in *Neesioscyphus*, *Isotachis*, and *Balantiopsis*. Only immature sporophyte are known in *Austroscyphus* (*A. iwatsukii*, Kitagawa, 1984). Sporophytes of *Anisotachis* and *Eoisotachis* are unknown.

Capsule shape is treated as a binary character: spherical (0), ovate-cylindrical to cylindrical (1). This character could be scored in 9 of 25 (36%) of the ingroup taxa.

24. *Capsule dehiscence*. A remarkable characteristic of the sporophytes of most members of the suborder Balantiopsineae (*sensu* Schuster, 1972) is the spiral dehiscence of the capsule wall (*Balantiopsis bisbifida*, Fig. 2:17; *Isotachis lyallii*, Fig. 14:10, 11; *N. bicuspidatus*, Grolle 1966, fig. 1). Capsules of *Rhizanthus* are unique in the family for the straight lines of dehiscence (Schuster, 1985a). Spiral capsule dehiscence also occurs in some Calypogeiaceae, in some Geocalycaceae (*Saccogynidium*), and in *Plagiochila* (e.g., *P. gigantea*, Schuster, 1966, p. 591), where it is regarded as an independent development.

Capsule dehiscence is treated as a binary character: valves straight (0), valves spiral (1). This character could be scored in 9 of 25 (36%) of the ingroup taxa.

25. *Capsule wall thickness*. In the taxa included in the analysis for which sporophytes are known, capsule wall thickness varies from 2–5 cell layers. In general, the outermost cell layer of the capsule wall is composed of larger cells that are about equal in width (in surface view) to 2–3 of the cells of the inner layer(s), but the relative thickness of the different layers (in cross section) is variable. In *T. subtrifidum* the capsule wall is 4–5 layers thick, with the cells of the outer layer roughly equal in thickness to two of the inner layers (Hassel de Menéndez & Solari, 1975, fig. 21:

10–12). In *N. carneus* (Grolle, 1964, fig. 1:9), the wall is 3–4-stratose (3-stratose above, 4-stratose below), and in *N. argillaceus* 2-stratose, with the outer wall only slightly thicker than the inner layer(s). In *Ruizanthus venezuelanus* (Schuster, 1985a, fig. 6:14), the outer of the 2 (to 3) wall layers is represented as only slightly thicker than the inner. The capsule is uniformly 3-stratose in *Balantiopsis* (Fig. 2:18) and *Isotachis* (Inoue, 1974, fig. 5:1), with the outermost layer equal to, or often exceeding, the combined thickness of the two inner layers. We elected to score wall thickness merely as number of strata, without respect to their relative thickness.

Another capsule wall characteristic worthy of mention is the absence or only weak development of secondary thickenings on the outer tangential walls in Balantiopsaceae, seen in *Ruizanthus* (Schuster, 1985a, fig. 6:13) and *Neesioscyphus* (Grolle, 1964, figs. 1:11; 3:13), as well as in *Balantiopsis* and *Isotachis*, where, for the most part, thickenings are confined to the inner tangential wall, with thickenings extending, buttress-like, onto the radial walls (cf. Fig. 2:18 and Inoue, 1974, fig. 5:1). All observed sporophytes of *Balantiopsis* are of this type. The extreme condition is seen in *Gyrothyra*, of the related Gyrothyraceae, where the capsule valves lack secondary thickenings (Schuster, 1972, p. 361).

Capsule wall thickness is treated as an unordered multistate character with four states: 4–5-stratose (0), uniformly 3-stratose (1), 2-stratose (or 2–3-stratose) (2), 3–4-stratose (3). This character could be scored in 9 of 25 (36%) of the ingroup taxa.

Other potential characters

26. *Perianth*. In the outgroup taxon, *T. subtrifidum*, the developing sporophyte is surrounded only by an involucre consisting of the ♀ bracts and bracteole, plus a simple perianth, presumably formed by connation of the innermost cycle of “leaves.” *Austroscyphus*, *Neesioscyphus*, and *Ruizanthus* have a tubular perianth, plus a short, hypanthium-like stem perigynium. In *Isotachis* and *Balantiopsis* no discernable perianth is pres-

←

1–2, 5, 6–8 from type of *Jungermannia lyallii*; 3–4 from type of *I. rosacea*; 9, 11, 14 from *Hatcher 1038*, New Zealand; 10, 12–13 from *Engel 17916*, New Zealand, South Is., Westland Prov., between the confluence of Jackson River and Arawata River and Lake Ellery; Figs. 9, 11, 14, after Hatcher 1960–61.)

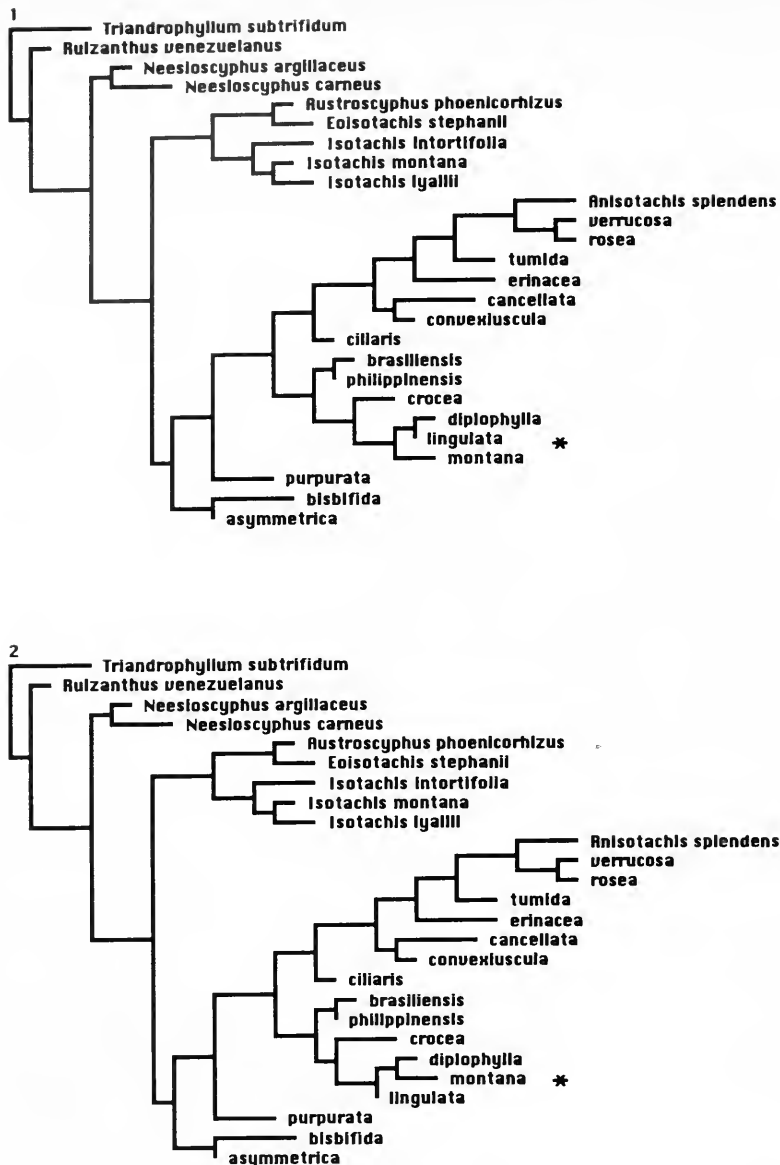


FIG. 15. Four most parsimonious cladograms. The length of the branch segments is proportional to the number of apomorphies supporting that branch. Branches of zero length have no supporting apomorphies. Cladograms 1–3 are identical except for the resolution of the *B. diplophylla* group (indicated by *). Note also the difference in placement of *B. ciliaris*: in 1–3 this species is resolved as a member of the clade representing sect. *Pteridophylla*; in 4, as a member of sect. *Balantiopsis*, which alters the topology of the two sections. (A consensus cladogram of these four trees is shown in Fig. 17.)

ent, and there is no hint of fusion of the minute bractlets, which surround the opening, into a tubular perianth (Figs. 2:16; 4:2).

Normal ♀ bracts and bracteole, in the usual sense, are also absent in *Isotachis* and *Balantiopsis*. In leafy hepatics generally, these are formed from the cycle of leaves immediately adjacent to

the perianth, but here there is no differentiated inner cycle of bracts and bracteole. Instead, the innermost cycle of larger subgynoecial leaves have assumed the appearance and the function of ♀ bracts and bracteole and for convenience are usually described as such.

This character is closely associated with acces-

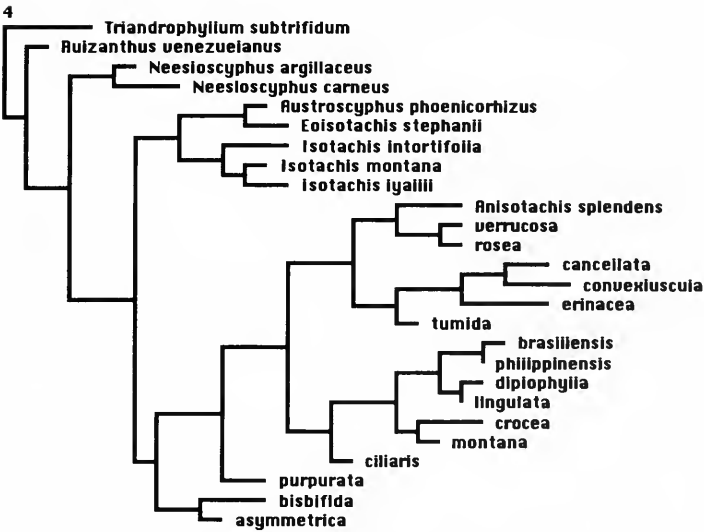
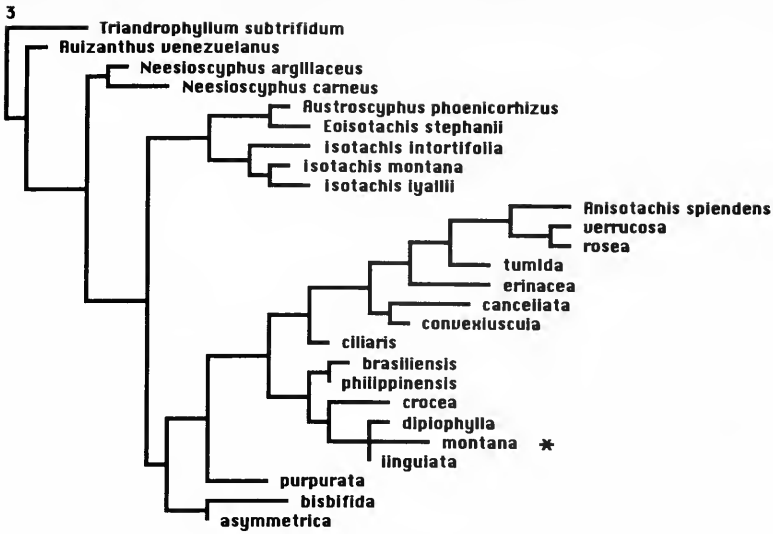


FIG. 15. Continued.

sory gynoecial structures (character 21), since the absence of a perianth appears to be a result of the elaboration of these structures which have taken over its function. We experimented with adding to the data set a perianth character (perianth present vs. perianth none), the results of which are discussed below (p. 47). In the end, we decided not to score the presence or absence of a perianth separately to avoid attaching too much weight to this character complex.

Results

We used MacClade 3.04 (Maddison & Maddison, 1992) for entering data and editing the data matrix, PAUP 3.1.1 (Swofford, 1991) for searching for most parsimonious trees, and MacClade for exploring the resulting cladograms, randomly resolving polytomies, etc. Both programs were run on a Macintosh Quadra 840AV.

The analysis of 26 taxa (Table 1) and 25 char-

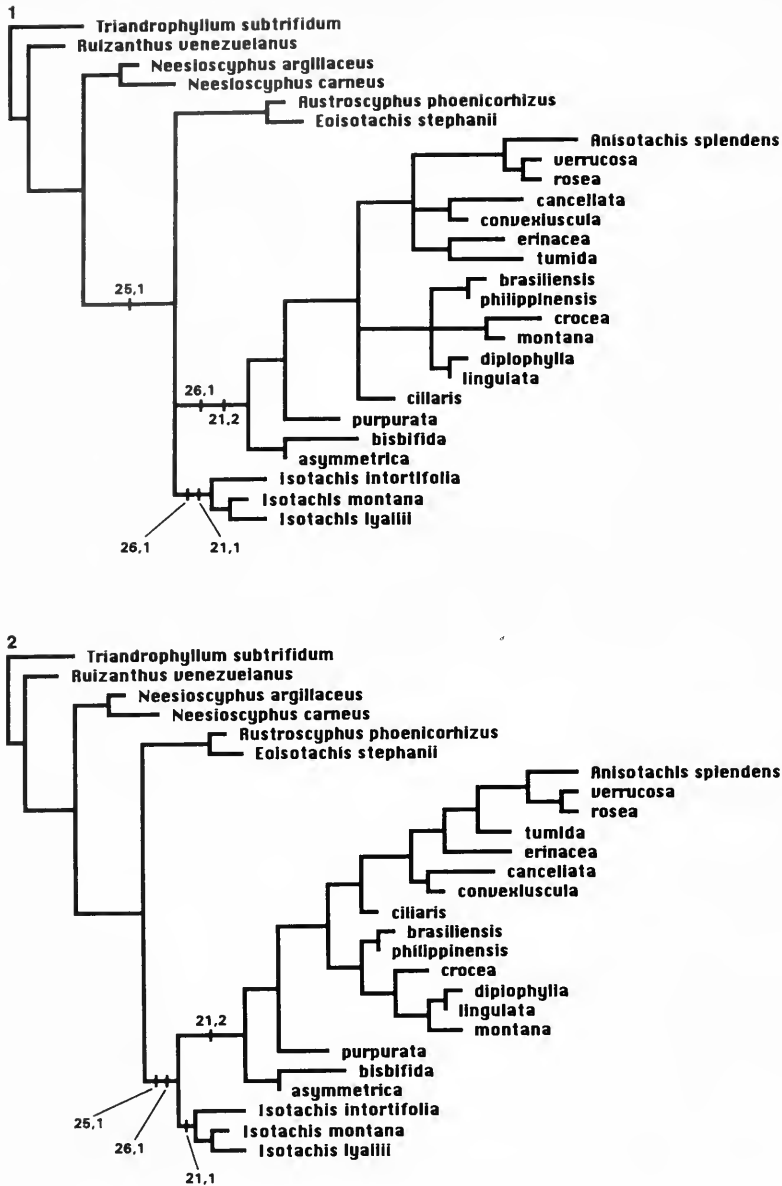


FIG. 16. Consensus cladograms of 13 trees resulting from the inclusion of character 26 (perianth present vs. absent): 1, Adams consensus; 2, majority consensus. For discussion see text.

acters, with *T. subtrifidum* designated as the outgroup, yielded four most parsimonious cladograms (Fig. 15), each with a length of 114 steps, with a consistency index of 0.560, a retention index of 0.660, and a rescaled consistency index of 0.370, using the heuristic search option of PAUP, with tree-bisection-reconnection (TBR) branch-swapping performed and steepest descent option in effect. Use of a random addition sequence with

100 replicates yielded no shorter trees. In the cladograms presented here, the ingroup is represented as monophyletic, with the outgroup as paraphyletic to the ingroup taxa. Cladograms 1–3 (Fig. 15) are identical except for the resolution of the species complex involving *B. diplophylla*, *B. lingulata*, and *B. montana*; cladogram 4 differs in the placement of *B. ciliaris*, with some differences in the topology of the clades corresponding to

antiopsaceae was not supported. Eleven most parsimonious cladograms resulted, each with a length of 136 steps. In the strict consensus of these 11 cladograms, *Ruizanthus* occupies a near-basal position, as a sister taxon to a clade containing the remaining genera of the family and *Diplophyllum*. With the exception of the placement of *Diplophyllum*, the sister group relationships shown in the cladogram (most importantly, those within *Balantiopsis*) are unaffected, and consequently we chose not to include this genus as an outgroup.

A thorough test of the monophyly of the family is beyond the scope of this monograph. However, monophyly of the family was assumed as an initial hypothesis of relationship and used as a basis for selection of genera to include in the analysis. Representatives of all genera considered to belong to the family Balantiopsaceae were included. The primary goal of the analysis was to resolve ingroup relationships within *Balantiopsis*. These genera, plus *Triandrophyllum*, constitute functional outgroups (Watrous & Wheeler, 1981) used for resolution of relationships within the functional ingroup, *Balantiopsis*. Addition of more distant outgroups (*Lepicolea*, *Diplophyllum*) would not be expected to affect relationships within *Balantiopsis* if these are already fully resolved.

Character State Reconstructions

In addition to determining the polarity of characters used in the analysis, we used PAUP to reconstruct the ancestral character states at internal nodes within the cladogram. Two options are provided in PAUP for this purpose (Swofford, 1991). The first, accelerated transformation (ACCTRAN), tends to favor a single origin for a given character state, followed by reversal(s). The second, delayed transformation (DELTRAN), favors independent origins of a character state (parallelism), thus requiring fewer reversals. Both result in the same number of steps on the tree, but the locations at which changes occur may differ. We experimented with both methods. The comments that follow are based on DELTRAN reconstructions. Where the reconstructions of a character differ appreciably or one seems preferable to the other, we present both. The optimal reconstructions of selected characters are shown in Figure 17, an Adams consensus of the four most parsimonious cladograms.

isophylly) is generally regarded as the primitive condition in leafy hepatics (cf. Schuster, 1972, p. 330). However, the primitive Balantiopsaceae (*Ruizanthus*, *Neesioscyphus*, *Austrosocyphus*) are strongly anisophyllous, and the julaceous, subisophyllous taxa (*Eoisotachis*, *Isotachis intortifolia*) are resolved in the consensus cladogram as derived. Subisophylly is indicated in the cladogram as a homoplasy (probably habitat-related) and within the context of this family is a derived state, not a retention of a primitive state.

2. *Pigmentation*, CI = 0.273. Red to wine-red pigmentation (0) is plesiomorphic in the ingroup taxa. Sporadic changes from red to "brownish or tinged with red" (1) mostly involve terminal taxa. Pigmentation is variable, and scoring of state (1) was somewhat subjective. Moreover, the absence of reddish pigmentation is no indication that the species is incapable of producing pigment under certain conditions, and the intensity of pigmentation, when present, is no doubt related to environmental factors.

3. *Branching*, CI = 1.000. The plesiomorphic state is presence of only intercalary branching (0). The absence of terminal branching distinguishes *Neesioscyphus* and *Ruizanthus* from the other members of the family. We think it is likely that terminal branching has been lost in *Neesioscyphus* and *Ruizanthus* and that the polarity 0 > 1 may be an artifact of the selection of *Triandrophyllum* (which lacks terminal branching) as an outgroup. Schuster (1972, p. 330) indicates "branching both terminal and intercalary" as generalized and "branches purely terminal or purely intercalary" as derived.

4. *Rhizoid origin*, CI = 0.333. The plesiomorphic state in the study taxa is rhizoids present only at the bases of the underleaves (1). Rhizoids originating from the bases of lateral leaves, as well as from underleaves, evolved independently in three terminal taxa—*Ruizanthus*, *Neesioscyphus carneus*, and *B. bisbifida*.

5. *Division between lobes*, CI = 1.000. The plesiomorphic state is shallowly bilobed or bisbifid (0), evolving to deeply bilobed (1) only once, as a synapomorphy of subg. *Balantiopsis*. Evolution to "dorsal lobe displaced or detached" (1 > 2) occurs twice, in *B. erinacea* and within *B. purpurata*, suggesting that these may be different states (displaced vs. detached) and thus autapomorphies of their respective species.

6. *Relative lobe size*, CI = 0.667. Dorsal lobe

subequal to the ventral (1) is the plesiomorphic state. Dorsal lobe larger than the ventral (0 or 0 & 1) is a condition occurring only in *Isotachis* and in the outgroup taxon, *T. subtrifidum*, associated with incubous leaf insertion. According to the DELTRAN reconstruction, reduction of the dorsal lobe (1 > 2), occurred independently three times—in *Neesioscyphus*, in subg. *Steereocolea* (*B. asymmetrica*), and in subg. *Balantiopsis*, where it supports sect. *Balantiopsis*. Extreme reduction in the dorsal lobe (1 > 3) occurs in *B. purpurata* and within *B. diplophylla* (var. *hockenii*). A reversal to dorsal lobe subequal to the ventral (2 > 1) occurs in sect. *Pteridophylla* in such species as *B. tumida* and *Anisotachis splendens*, while other species have relatively reduced dorsal lobes. The ACCTAN reconstruction has the change from 1 > 2 occurring early at the base of the clade uniting all the ingroup taxa save *Ruizanthus*, necessitating multiple reversals, a much less satisfactory reconstruction.

7. *Leaf insertion*, CI = 0.800. Succubous insertion (1) is plesiomorphic in Balantiopsaceae. Succubous insertion evolves to incubous (2) only once, in *Isotachis*. Transverse insertion (0) occurs only as a polymorphism within terminal taxa (*Eoisotachis*, *Isotachis*). Schuster (1972, p. 353) says of the suborder Balantiopsineae, "primitively subtransverse (incubous to transverse in *Isotachis*; weakly succubous in *Eoisotachis*), derivatively strongly succubous (*Gyrothya*, *Neesioscyphus*)." Our analysis shows that the strongly succubous (and strongly anisophyllous) taxa (e.g., *Ruizanthus*, *Neesioscyphus*) are primitive in the family.

8. *Ventral lobe insertion*, CI = 0.857. The plesiomorphic state is straight or comma-like (0), evolving to U-shaped (2) only once, supporting sect. *Pteridophylla* (in trees 1–3 with *B. ciliaris* preserving the ancestral state). The J-shaped insertion (1) is characteristic of sect. *Balantiopsis*, with most species being either J-shaped or polymorphic (0 & 1) with respect to this character. The most significant indication is that J-shaped and U-shaped are alternative states, not a continuum (i.e., the polarity of this character is 1 < 0 > 2, not 0 > 1 > 2).

9. *Dorsal lobe insertion*, CI = 0.571. The plesiomorphic state is \pm transverse (0). Dorsal lobe insertion oblique to longitudinal (1) is a homoplasy occurring several times in the cladogram. U-shaped dorsal lobe insertion (2) is also a ho-

moplasy but confined to sect. *Pteridophylla* (*Anisotachis*, *B. erinacea*). The polarity of this character is indicated as 1 < 0 > 2, not a continuum 1 > 0 > 2 as had been expected.

10. *Ventral lobelleaf planation*, CI = 0.560. The plesiomorphic state is convex or concave (1). In tree 4, evolution from convex to flat (1 > 0) supports subg. *Balantiopsis*. Flat to plicate, etc., (1 > 2) occurs three times: once in *I. intortifolia* and twice in sect. *Pteridophylla*. Canaliculate to conduplicately folded or plicate leaves/ventral lobes (2) appears at first glance to be a homoplasy. It could be argued that the plicate ventral lobes of sect. *Pteridophylla* should not be scored the same as the plicate leaves of *Isotachis intortifolia*. Plicate leaves may simply be another aspect of the same kind of habitat modification as subsisophyly in this species (see character 1).

11. *Dorsal lobe orientation*, CI = 1.000. Leaves concave, not conduplicate (0) is the plesiomorphic state, evolving to complicate leaves with appressed dorsal lobe (2) only once, supporting subg. *Balantiopsis*. Assurgent dorsal lobes (1) is a synapomorphy of the *B. crocea*–*B. montana* species pair.

12. *Leaf armature*, CI = 0.636. Leaves almost unarmed (2) is the plesiomorphic state of this character. It evolves from unarmed to moderately armed (2 > 1) near the base of subg. *Balantiopsis*, with *B. purpurata* retaining the primitive condition, and evolves independently to copiously armed (0) at several points within the cladogram in both sect. *Balantiopsis* and sect. *Pteridophylla*.

13. *Projecting septa*, CI = 0.333. Leaf margins denticulate by projecting septa of the marginal cells originated independently three times, in *B. ciliaris*, in *B. convexiuscula*–*B. cancellata*, and in *B. tumida*.

14. *Underleaf lobing*, CI = 0.250. Shallowly bifid underleaves (1) is the plesiomorphic state in Balantiopsaceae. This character serves as a good illustration of the differences between ACCTAN and DELTRAN character reconstructions. The DELTRAN reconstruction has deeply bifid underleaves (2) arising independently seven times; ACCTAN shows deeply bifid underleaves as the plesiomorphic state in the family, retained in *Ruizanthus* and *Neesioscyphus*, but evolving to shallowly bifid once and then reversing five times. This character is highly homoplasious and phylogenetically uninformative.

15. *Areolation*, CI = 0.500. Scattered arrangement of cells (0) is plesiomorphic in the family, evolving to distinctly tiered (2) near the base of subg. *Balantiopsis*, with *B. purpurata* retaining the primitive condition. Tiered arrangement of cells apparently also evolved independently in the common ancestor of the *Eoisotachis*–*Austroscyphus* clade. A reversal from distinctly tiered to scattered cells (2 > 0) occurs in *B. diplophylla*.

16. *Border*, CI = 0.250. Absence of a differentiated border is the plesiomorphic state in the family, although a border is present in *Ruizanthus lopezii*, which was not included in the data set. A border is shown evolving four times, at the base of the *B. verrucosa*–*B. rosea*–*Anisotachis splendens* clade, in *B. cancellata*, in *B. crocea*, and in subg. *Steereocolea*. However, within sect. *Pteridophylla* the border is of a special type, always occurring in association with guttulate papillae (19,1), and perhaps should not be considered the same character state as the border in other species (e.g., *B. asymmetrica*, *B. crocea*).

17. *Leaf cell size*, CI = 0.250. Larger cells (1), defined as more than 20 μm wide, is the plesiomorphic state. Larger cells evolve to small cells (0) at four points on the cladogram but in *Balantiopsis*, only in sect. *Pteridophylla*. In tree 4, it supports a “small-celled group,” consisting of *B. cancellata*, *B. convexiuscula*, *B. erinacea*, and *B. tumida*. Elsewhere, small cells evolve supporting the *I. montana*–*I. lyallii* clade and in *Eoisotachis*.

18. *Wall thickenings*, CI = 0.250. Evenly thickened walls (0) is the plesiomorphic state. Intermediate thickenings (1) evolved in four places on the cladogram but only once in *Balantiopsis*. In Figure 15:4, intermediate thickenings support sect. *Pteridophylla*; in Figure 15:1–3, with *B. ciliaris* included in sect. *Pteridophylla*, this species alone lacks intermediate thickenings. Elsewhere, intermediate thickenings support the *Austroscyphus*–*Eoisotachis* clade and are present in *N. carneus* and *I. lyallii*.

19. *Cuticle*, CI = 0.400. Finely striate-papillose cuticle (0) is the plesiomorphic state. Guttulate papillae (0 > 1) evolved three times, in *I. intortifolia*, the *B. verrucosa*–*B. rosea* clade, and *B. cancellata*. Within *Balantiopsis* guttulate papillae are confined to sect. *Pteridophylla*. Smooth cuticle (2) occurs in the *Austroscyphus*–*Eoisotachis* clade and again in *Anisotachis*.

20. *Oil-bodies*, CI = 0.333. The plesiomorphic

state in the family is relatively few (2–7) oil-bodies per cell (1). Evolution to 2(3) oil-bodies per cell (1 > 2) occurs twice, supporting the *Austroscyphus*–*Eoisotachis*–*Isotachis* clade, and once in subg. *Balantiopsis*. Numerous oil-bodies (0) is a condition occurring only in sect. *Balantiopsis*, in three species, *B. diplophylla*, *B. montana*, and *B. lingulata*. In Figure 15:1–3 these three taxa are resolved as a single clade.

21. *Accessory gynoecial structures*, CI = 1.000. The plesiomorphic condition is “accessory structures none or with hypanthium-like basal perigynium” (0). Evolution of an erect stem perigynium (1) occurs only once, in *Isotachis*. *Balantiopsis* is resolved as monophyletic, based on the presence of a marsupium (2), the synapomorphy of the genus. The cladogram supports an independent origin of an *Isotachis*-type perigynium and a marsupium. However, the early stages of development suggest a greater degree of homology between these structures than has been previously supposed; see also the notes on the effect of including a perianth character in the data set, below.

22. *Antheridia*, CI = 1.000. The plesiomorphic state is 2–3 antheridia per bract (0), evolving to 4–5 per bract (0 > 1) in *Ruizanthus*, and from 2–3 to solitary (0 > 2) in *Austroscyphus*. Solitary antheridia may be a characteristic of the latter genus, since *A. iwatsukii* also has this condition (Kitagawa, 1984).

23. *Capsule shape*, CI = 1.000. Spherical capsules (0) is the plesiomorphic state and is retained in *Rhizanthus*, whereas cylindrical capsules is an apomorphy of the clade containing all the other genera of Balantiopsaceae.

24. *Capsule dehiscence*, CI = 1.000. Straight capsule valves (0) is the plesiomorphic state, with spiral valves (1) supporting the clade uniting all of the ingroup taxa except *Rhizanthus*.

25. *Capsule wall thickness*, CI = 1.000. The outgroup condition, 4–5-stratose (0), does not occur in the ingroup. The plesiomorphic state in the Balantiopsaceae is “2-stratose (or 2–3-stratose)” (2), shown evolving to uniformly 3-stratose (1) at the base of an *Austroscyphus*–*Eoisotachis*–*Isotachis*–*Balantiopsis* clade in both Figures 17 and 16:1. This is deceptive, however, since capsule wall thickness is not reported for *Austroscyphus*, and sporophytes of *Eoisotachis* are unknown. In Figure 16:2, however, character state (1) is an apomorphy of an *Isotachis*–*Balantiopsis* clade, as

is perianth absent (26,1). Thus, relatively thin walls appear to be the plesiomorphic condition in this group of leafy liverworts, and the regularly 3-stratose condition is characteristic of all but the most primitive members of the family.

26. *Perianth*, CI = 0.500. When a perianth character is included, 13 most parsimonious trees are obtained. The Adams consensus of these trees (Fig. 16:1) is almost identical to that shown in Figure 17 (the result obtained when this character is not included), except for the presence of a polytomy involving the *Austroscyphus*–*Eoisotachis*, *Balantiopsis*, and *Isotachis* clades, respectively. Note that the majority consensus of these 13 trees (Fig. 16:2) is identical to Figure 15:1, except for the resolution of *Isotachis* as a sister taxon to *Balantiopsis*.

The optimal reconstructions of the accessory gynoecial structures (21) and perianth (26) characters are indicated on both cladograms. Perianth present (0) is the plesiomorphic condition, retained in *Ruizanthus*, *Neesioscyphus*, and *Austroscyphus*. The Adams consensus shows the loss of a perianth (1) occurring independently in *Balantiopsis* and *Isotachis*; in the majority consensus, loss of a perianth is an apomorphy of a *Balantiopsis*–*Isotachis* clade.

Discussion of Phylogenetic Relationships

Intergeneric Relationships

The genus *Balantiopsis* was the primary focus of this study, but the inclusion of representatives of other genera allows some observations concerning relationships of genera and the phylogeny of the Balantiopsaceae. Schuster (1972) established the suborder Balantiopsineae (“Balantiopsidinae”) with four “unifying characters”: 1) a tendency to form accessory structures for protection of the developing sporophyte (a marsupium or an erect stem perigynium); 2) retention of, in all cases, at least a vestige of a perianth; 3) bifid underleaves, with rhizoids for the most part localized near their base; and 4) spirally dehiscent capsules. More recently, with the discovery of *Ruizanthus* (Schuster, 1985a), the characters of the suborder have been modified to accommodate this primitive taxon, which has spherical capsules with straight valvular dehiscence.

Ruizanthus and *Neesioscyphus* are resolved as the earliest divergent lineages on the cladogram

(Fig. 17). They share the lack of terminal branching (character 3,1) and the development of rhizoids at the bases of the leaves as well as the underleaves (4,0, also present in *B. bisbifida*). The position of *Ruizanthus* in the cladogram is consistent with the view that this genus is the most primitive one in the family. In addition to spherical capsules and lack of spiral dehiscence, the subfamily Ruizanthoideae is supported by an autapomorphy, antheridia 4–5 per bract (22,1). *Neesioscyphus* is resolved as a separate clade, a sister taxon to the major clade that includes all of the other genera (except *Ruizanthus*); the latter is supported by a uniformly 3-stratose capsule wall (24,1).

Schuster (1985b) discusses the similarities of *Ruizanthus* and *Austroscyphus* (as *Acroscyphus*) and places the latter in the Ruizanthoideae based on the prediction that *Austroscyphus* would prove to have nonspiral capsule valves. Schuster (1990, p. 250) suggests that these two genera are “the remnants of the ancestral complex from which other Balantiopsidinae, all apomorphic in the spirally coiled capsule valves, evolved.” Immature sporophytes of *A. iwatsukii* are illustrated by Kitagawa (1984), but mature capsules have not yet been observed in this genus. On the basis of information in the data set and in the absence of data on mature sporophytes, the cladogram presented here does not support the inclusion of *Austroscyphus* in the Rhizanthoideae.

Austroscyphus, *Eoisotachis*, and *Isotachis* make up a clade, roughly corresponding to the subfamily Isotachidoideae, minus *Neesioscyphus*. Schuster (1972, 1979) and Grolle (1972, 1983) include *Eoisotachis*, *Isotachis*, and *Neesioscyphus* (the last including species now placed in *Austroscyphus*) in the Isotachidoideae, characterized by “an erect apparatus—perianth, perigynium, or combination thereof,” in contrast to Balantiopsidoideae, where “there has been the evolution of a bilateral rather than radial gynoecial system” (Schuster, 1972, p. 355). The implication is that a change from an erect, symmetrical perigynium to a geotropic, bilaterally symmetric marsupium is “a response to prostrate growth” (l.c., p. 355).

The relationships between the functional outgroups (i.e., the other genera of Balantiopsaceae included in the analysis) are not fully resolved, and the results of the analysis must be considered tentative as far as these genera are concerned. A good example of this is the position of *Austroscyphus* in the cladograms presented here. In habit and gynoecial features *Austroscyphus* is closest to

TABLE 3. Proposed classification of higher taxa of Balantiopsaceae.

Family Balantiopsaceae Buch
Subfamily Ruizanthoideae Engel & Merr.
<i>Ruizanthus</i>
Subfamily Balantiopsoideae
Tribe Neesioscypheae Engel & Merr.
<i>Neesioscypus</i> , <i>Austroscypus</i>
Tribe Balantiopseae
Subtribe Isotachidinae (Hatch.) Engel & Merr.
<i>Isotachis</i> , <i>Eoisotachis</i> , <i>Hypoisotachis</i>
Subtribe Balantiopsinae
<i>Balantiopsis</i> (<i>Anisotachis</i> , <i>Steereocolea</i>)

Neesioscypus, and yet the two are resolved in separate clades in Figures 15–17. Shared features of these two genera include 1) succubously inserted leaves; 2) anisophylly; 3) a tubular, exserted or immersed perianth; 4) a hypanthium-like stem perigynium; and 5) a distinct involucre of bracts and bracteole formed by the innermost cycle of leaves and underleaf (adjacent to the perianth). The data are incomplete, since sporophytes of *Austroscypus* are imperfectly known. In the classification below, *Austroscypus* has been placed with *Neesioscypus*. An *Austroscypus*–*Eoisotachis* clade is a consistent feature of all the cladograms generated in the course of this study, and yet these two genera are strikingly different in almost all respects: the latter is a julaceous, subsophyllous plant, similar to many *Isotachis* species (e.g., *I. intortifolia*). Gametangia and sporophytes of *Eoisotachis* are unknown, but we think it will eventually prove to have an erect stem perigynium of the *Isotachis*-type.

Monophyly of *Isotachis* is supported by the erect, fleshy stem perigynium (21,2), incubous leaf insertion (7,2), and dorsal leaf lobe larger than the ventral (6,0). Without inclusion of a perianth character (26), the resulting cladogram (Fig. 17) suggests that the marsupium of *Balantiopsis* and the *Isotachis*-type perigynium evolved independently from an ancestor with a *Neesioscypus*-like basal stem perigynium (21,0). However, as indicated previously, there is persuasive morphological evidence that these are homologous struc-

tures. In Figure 16:2, *Isotachis* is resolved as a sister group to *Balantiopsis*; this clade is supported by loss of perianth (26,1) and a uniformly 3-stratose capsule wall (25,1). A species of *Isotachis* that combines both primitive and advanced features is *I. multiceps*, the type of *Isotachis* subg. *Hypoisotachis* (see p. 55), which is anisophyllous, has microphyllous stolons and a 2(3)-stratose capsule wall as in *Neesioscypus* spp. and solitary antheridia (as in *Austroscypus*) with an erect stem perigynium of the *Isotachis*-type.

It is clear from this discussion that the concept of a subfamily Isotachidoideae should be abandoned in favor of a classification that reflects the close relationship between *Isotachis* and *Balantiopsis*. We propose a realignment of the genera of Balantiopsaceae, summarized in Table 3. The following new taxa and combinations are necessary.

Subfamily Ruizanthoideae Schust., subfam. nov.

Balantiopsaceae subfam. Ruizanthoideae Schust. in Clarke & Duckett, *Bryophyte Systematics* 75. 1979. *New Manual Bryol.* 2: 998. 1984. *nom. inval.*

Ramificatio solum ventro-intercalaris; folia 2–3 cuspidata vel 3–4 lobata; antheridia 4–5 per bracteam; capsulae sphaericae, parietibus 2(3) stratosi, valvis strictis non spiralibus.

Type: *Ruizanthus* Schust., *Phytologia* 39: 240. 1978.

Tribe Neesioscypheae Engel & Merr., trib. nov.

Ramificatio solum ventro-intercalaris; folia succuba, asymmetricè breviter 2-lobata; perigynium breve, hypanthium simile; perianthium praebens, exsurgens vel immersum; parietibus capsularum 2–4 stratosi.

Type: *Neesioscypus* Grolle, *Oesterr. Bot. Z.* 111: 19. 1964.

Subtribe Isotachidinae (Hatch.) Engel & Merr., comb. & stat. nov.

Family Isotachidaceae Hatch., *Nova Hedwigia* 2: 579. 1960 (“Isotachaceae”). Subfamily Isotachidoideae (Hatch.) Grolle, *J. Bryol.* 7: 210. 1972.

Type: *Isotachis* Mitt.

Key to Subfamilies, Tribes, and Subtribes of Balantiopsaceae

1. Capsule spherical, dehiscing by straight valves; antheridia 4–5 per bract Subfamily Ruizanthoideae Schust. [*Ruizanthus*]
1. Capsule cylindrical, dehiscing by spiral valves; antheridia 2–3 per bract, or solitary. Subfamily Balantiopsoideae 2

2. Sporophyte enclosed in a tubular, exerted or immersed perianth at the summit of a shallow, hypanthium-like stem perigynium; innermost cycle of leaves and underleaf (adjacent to the perianth) forming a distinct involucre of bracts and bracteole that are equal to or larger than vegetative leaves; capsule wall (*Neesioscyphus*) 2–4-stratose Tribe Neesioscypheae Engel & Merr. [*Neesioscyphus*, *Austrosocyphus*]
2. Sporophyte enclosed in a stem perigynium or marsupium, a tubular perianth not formed; innermost 3–4 cycles of leaves and underleaves present as small, scalelike bractlets that fringe the opening of the stem perigynium or marsupium, the involucre consisting of large subgynoecial leaves; capsule wall uniformly 3-stratose. Tribe Balantiopseae 3
3. Sporophyte protected by an erect, symmetrical, tubular stem perigynium; leaves not complicatebilobed; leaf cells not, or in indistinct tiers Subtribe Isotachidinae (Hatch.) Engel & Merr. [*Hypoisotachis*, *Isotachis*, *Eoisotachis*]
3. Sporophyte protected by a pendant, geotropic, asymmetrical marsupium; leaves complicatebilobed (rarely simple and bisbifid); leaf cells typically distinctly tiered Subtribe Balantiopsinae [*Balantiopsis* (incl. *Anisotachis*, *Steeereocolea*)]

Balantiopsis

Monophyly of *Balantiopsis* is supported by a pendant, asymmetrical, geotropic marsupium (21,2). We recognize two subgenera (subg. *Steeereocolea* and subg. *Balantiopsis*) within the genus, and within the subg. *Balantiopsis*, two sections (sect. *Balantiopsis* and sect. *Pteridophylla*), corresponding to units that were consistently resolved in the cladograms presented here. *Anisotachis splendens* is resolved as a terminal branch within *Balantiopsis* sect. *Pteridophylla*. The support for each of these infrageneric taxa is discussed below. The disposition of species is shown in Table 4.

Subgenus *Steeereocolea* (Schust.) Schust.

Steeereocolea Schust., Bull. Natl. Sci. Mus. Tokyo 11(1): 23. 1968. *Balantiopsis* subg. *Steeereocolea* (Schust.) Schust., J. Hattori Bot. Lab. 36: 357. 1972 [Jan. 1973].

Leaves shallowly bilobed to bisbifid (to 0.5 or less), not conduplicately folded; leaf insertion simple, oblique, the line of insertion \pm straight; dorsal lobe erect to spreading-reflexed toward the stem base; leaf cells scattered.

Steeereocolea was proposed as a monotypic genus by Schuster (1968), based on the presence of an “inflated, quite well-developed” perianth in the early stages of gynoecial development in the type species, *B. bisbifida*. We have not seen the specimen on which his description was based. Later, Schuster (1972, p. 357) reduced *Steeereocolea* to a subgenus of *Balantiopsis*, citing an Engel collection of *B. bisbifida* from the *Hero ex-*

pedition to southern Chile with pendant marsupia and a “vestigial perianth” (cf. Engel, 1978). Schuster suggests that perianth formation may be variable in this species.

At maturity, *B. bisbifida* has a well-developed marsupium, as does *B. asymmetrica*. In neither species can we confirm the presence of a tubular perianth at any stage of development. Notwithstanding, Schuster’s characterization of subg. *Steeereocolea* as “the starting point in evolution within the Balantiopsidoideae” (Schuster, 1972, p. 357) is supported by the position of these species in the cladogram. *Balantiopsis bisbifida* and *B. asymmetrica* are resolved as sister taxa, and these two species

TABLE 4. Conspectus of Genus *Balantiopsis* Mitt.

Subg. <i>Steeereocolea</i> (Schust.) Schust.
<i>B. bisbifida</i> (Steph.) Steph.
<i>B. asymmetrica</i> (Herz.) Engel
Subg. <i>Balantiopsis</i>
Sect. <i>Balantiopsis</i>
<i>B. purpurata</i> Mitt.
<i>B. diplophylla</i> (Hook. f. & Tayl.) Mitt.
var. <i>diplophylla</i>
var. <i>hockenii</i> (Berggr.) Engel & Merr.
<i>B. lingulata</i> Schust.
<i>B. philippinensis</i> H. Inoue
<i>B. brasiliensis</i> Steph.
<i>B. montana</i> (Col.) Engel & Merr.
<i>B. crocea</i> Herz.
<i>B. ciliaris</i> Hatt.
Sect. <i>Pteridophylla</i> (Hatch.) Engel & Merr.
<i>B. tumida</i> Berggr.
<i>B. convexiuscula</i> Berggr.
<i>B. cancellata</i> (Nees) Steph.
<i>B. erinacea</i> (Hook. f. & Tayl.) Mitt.
<i>B. splendens</i> (Steph.) Engel & Merr.
<i>B. verrucosa</i> Engel & Merr.
<i>B. rosea</i> Berggr.

were placed first in the genus by Engel (1968). Both species are included in subg. *Steereocolea* by Hässel de Menéndez & Solari (1975).

Balantiopsis asymmetrica and *B. bisbifida* are unique in the genus in having an essentially straight succubous leaf insertion and noncomplicately bilobed leaves with erect to spreading-re-

flexed dorsal lobes. The presence of rhizoids at the bases of leaves as well as underleaves (17,0) is a homoplasy found in *B. bisbifida*, *Ruizanthus*, and *N. carneus*.

The two species of the subgenus may be distinguished as follows.

Key to Species of *Balantiopsis* subg. *Steereocolea*

1. Dorsal lobe equal to or slightly larger than the ventral; median ventral lobe cells 24–36 μm wide; underleaves bilobed to 0.5 or more; rhizoids originating at bases of both leaves and underleaves *B. bisbifida*
1. Dorsal lobe at most 0.5 the ventral; median ventral lobe cells 31–53 μm wide; underleaves bilobed to 0.4 or less; rhizoids only at bases of underleaves *B. asymmetrica*

Balantiopsis bisbifida (Steph.) Steph.

Isotachis bisbifida Steph., Bih. Kongl. Svenska Vetenskapsakad. Handl. 26 (III, 17): 24. 1901. *Balantiopsis bisbifida* (Steph.) Steph., Spec. Hep. 4: 101. 1910. *Steereocolea bisbifida* (Steph.) Schust., Bull. Natl. Sci. Mus. Tokyo 11(1): 25. 1968. Original material: Chile, Prov. Magallanes, Isla Desolación, *Dusén* 228 (G!).

DESCRIPTION—Engel (1968, 1978); Schuster (1968, 1972); Hässel de Menéndez & Solari (1975).

ADDITIONAL DATA—Oil-bodies in all leaf cells, scattered throughout cell, occupying small fraction of cell volume, light brown, 4–8(11) per cell, ovoid to elliptic to fusiform to crescentic, some spherical, coarsely papillose, 12–16 \times 5–8 μm , a few 6–7 \times 6 μm .

Seta with 25 rows of epidermal cells surrounding an inner core of ca. 40 cells of about equal size to the outer layer, the epidermal and inner cells uniformly thin-walled. Capsule long-cylindrical, with spiral dehiscence, the wall 31–38 μm thick, of 3 layers, the outer layer of cells ca. equal to thickness of both interior strata; outer layer of cells short-rectangular, large, the inner tangential wall with irregular semiannular bands extending onto the radial longitudinal walls but gradually thinning and ending short of the outer tangential wall, the radial walls appearing slightly sinuous in surface view, the outer tangential wall devoid of thickenings; innermost layer of cells with semiannular bands pale, common, the bands not forked.

Spores 10.6–11.5 μm , the exine brownish yellow, with a network of very wide, irregular, coa-

lescing vermiform ridges that anastomose to form irregular but rather deeply set areolae; spore:elater diameter ratio 0.9–1.2:1. Elaters tortuous, (8.6)10.1–12 μm wide, bispiral, the spirals 2.9–4.3(4.8) μm wide, loosely wound.

DISTRIBUTION AND ECOLOGY—Engel (1978, 1990).

SPECIMEN SEEN—CHILE, PROV. VALDIVIA: SW slope of Volcán Quetrupillán, immediately SW of Laguna Los Patos, Forestal Trafún, 1450–1600 m, *Engel* 11144 (F).

Balantiopsis asymmetrica (Herz.) Engel

Balantiopsis latifolia var. *asymmetrica* Herz., Rev. Bryol. Lichénol. 23: 53. f. 11. 1954. *Balantiopsis asymmetrica* (Herz.) Engel, Nova Hedwigia 16: 93. 1968. Lectotype (*vide* Engel, 1968): Chile, Prov. Aisén, Puerto Magdalena, *Schwabe* 20a (JE!).

DESCRIPTION—Engel (1968); Hässel de Menéndez & Solari (1975).

ADDITIONAL DATA—Seta with 29 rows of epidermal cells surrounding an inner core of ca. 60 cells of similar size, the outer layer and peripheral cells of the inner core thicker-walled and with corner thickenings, the innermost cells delicate and thin-walled. Capsule long-cylindrical, with spiral dehiscence, the wall 42–48 μm thick, of 3 layers, the outer layer of cells ca. equal to thickness of both interior strata; outer layer of cells short-rectangular, large, the radial walls with sporadic, small, nodule-like thickenings mostly on longitudinal walls but sometimes on transverse walls, the longitudinal and transverse walls with thin, slightly sinuous, continuous sheets of pigmented material; innermost layer of cells with longitudinal

radial walls with thick, continuous sheets of wall material, with semiannular bands pale, common, rather wide, sometimes forked and anastomosing to delimit fenestrae.

Spores 12–13 μm , the exine pale yellowish brown, with a network of irregular, coalescing vermiform ridges that freely anastomose to form numerous, shallow areolae; spore:elater diameter ratio 1.2–1.4:1. Elaters tortuous, 9.1–10.1 μm wide, bispiral, the spirals 2.9–3.8 μm wide, loosely wound.

DISTRIBUTION AND ECOLOGY—Occurring in Valdivian and Magellanian zones of southern South America and in Juan Fernández. A plant of mossy forests (e.g., of *Nothofagus betuloides*, *N. pumilio*, *Drimys*, and *Berberis ilicifolia* at Puerto Churrucá, Isla Desolación, or of *N. dombeyi* and *Saxegothaea* in the Refugio Antillanca area) at sea level for most of its range, but to the north extending to ca. 730 m. It typically occurs on rock walls or on soil in protected hollows of cliff bases or moist cliff ledges, at times in densely shaded niches.

SELECTED SPECIMENS SEEN—CHILE, PROV. MAGALLANES: Isla Desolación, Puerto Churrucá, head of Brazo Lobo, *Engel 5838* (F, MSC); Fiordo Peel, N shore of Caleta Amalia, *Engel 5435* (F, MSC); S side of Isla Madre de Dios, head of fiord E of Mt. Roberto, *Engel 5141* (F, MSC). PROV. AISEN: At landing cove near glacier on N side of Fiordo Témpano, *Engel 4376C* (F, MSC). PROV. OSORNO: Near road to Refugio Antillanca, 12.1 km by road below Refugio, 550 m, *Engel 11516* (F); near road (10–11 km) to Refugio Antillanca, between Laguna El Encanto and Lago Toro, 730 m, *Engel 4082* (F, MSC). PROV. CAUTIN: Parque Nacional Villarrica, N slope of Volcán Villarrica, 6.1 km by road S of park entrance, 1150 m, *Engel 11192* (F).

Subgenus *Balantiopsis*

Leaves deeply bilobed (to 0.6 or more), sharply keeled and conduplicate-folded; leaf insertion complex, the line of insertion flexed or sharply bent; dorsal lobe much smaller than the ventral and appressed to the ventral (rarely assurgent); leaf cells in tiers (rarely scattered).

The subgenus is supported by two synapomorphies, deeply bilobed leaves (5,1) that are strongly conduplicate folded (11,2). In this subgenus the line of leaf insertion is fundamentally succubous (as in the more primitive subg. *Stereocolea*), but it becomes more complex by elaboration of the insertion of the dorsal and ventral halves of the leaf. The insertion of the ventral lobe progresses

from essentially straight at the ventral end to J-shaped (in sect. *Balantiopsis*) or from straight to strongly recurved and U-shaped (an apomorphy of sect. *Pteridophylla*). The insertion of the dorsal lobe may be oblique and decurrent on the stem, \pm transversely inserted, or strongly arched and U-shaped (9,2) in *Anisotachis* and *B. erinacea*. The line of leaf insertion is typically bent at the insertion of the keel between the ventral and dorsal lobes. The displacement or complete detachment of the dorsal lobe (5,2) is a homoplasy, occurring in *B. purpurata*, the basal species in sect. *Balantiopsis*, and in *B. erinacea*, arguably the most specialized species in sect. *Pteridophylla*. The presence of a differentiated leaf border is a homoplasy found also in subg. *Stereocolea* and in *Ruizanthus lopezii*; unique to several species of sect. *Pteridophylla*, however, is the cuticular differentiation on the cells of the leaf border.

Variation in leaf armature is taxonomically bothersome, in some cases varying considerably within species. Extreme development of leaf armature (12,0) is a homoplasy originating independently several times, in *B. lingulata* and *B. ciliaris* (sect. *Balantiopsis*) and in *B. rosea* (sect. *Pteridophylla*). Sparingly armed leaves (12,1) are apparently the plesiomorphic condition in the family (Ruizanthoideae, Neesioscyphaceae, subg. *Stereocolea*), and both sections of subg. *Balantiopsis* contain one or more species with almost unarmed leaves (e.g., *B. tumida*, *B. diplophylla*).

In our study of the New Zealand species of *Balantiopsis* (all members of subg. *Balantiopsis*), we initially recognized three groups of species, each containing two to three species. The first group centered on *B. diplophylla*, *B. lingulata*, and *B. montana*, with relatively large, scattered (irregularly arranged) leaf cells, relatively large numbers of oil-bodies per cell, a striate-papillose cuticle, and a straight to at most J-shaped insertion of the ventral leaf lobe. A second group, consisting of *B. rosea* and *B. verrucosa*, was characterized by guttulate papillae, a differentiated leaf border of striate-papillose cells, and two oil-bodies per cell, situated in opposite ends of the cells. A third group, consisting of *B. convexiuscula* and *B. tumida*, had small, short-quadrate leaf cells and lacked a differentiated border but had distinctly denticulate margins formed by the projecting septa of the marginal cells. Inclusion of the extraterritorial species of the genus, however, makes it clear that this was a geographically biased view of relationships. For example, *B. cancellata*, an American species, combines the small cells, dense

areolation, and projecting septa of *B. convexiuscula* and *B. tumida* with the coarsely guttulate papillae and differentiated border of *B. rosea* and *B. verrucosa*.

In the consensus cladogram presented here (Fig. 17), two major groupings are apparent within subg. *Balantiopsis*, one comprised of generalized species (sect. *Balantiopsis*) and the other of relatively specialized species (for which the oldest available name is sect. *Pteridophylla*). Uncertainty with respect to the placement of *B. ciliaris* is reflected in the consensus cladogram by making this species a member of an unresolved polytomy; *B. purpurata*, on the other hand, is resolved as the basal (earliest divergent) species in the subgenus (for a discussion of our placement of these species in sect. *Balantiopsis*, see below).

Section *Balantiopsis*

Ventral lobe flat or concave, the insertion \pm straight, comma-like, to J-shaped; dorsal lobe insertion oblique to longitudinal; leaf cells scattered to indistinctly tiered; leaf cells evenly thin-walled; cuticle striate-papillose (never guttulate).

The section is characterized by several features: 1) straight to at most J-shaped insertion of the ventral lobe; 2) generally larger leaf cell size; 3) evenly thin- or thick-walled leaf cells, lacking intermediate thickenings; and 4) relatively large numbers of oil-bodies per cell. The tendency toward extreme reduction of the dorsal lobe, seen in *B. diplophylla* var. *hockenii* and *B. purpurata*, is found only in sect. *Balantiopsis*.

Balantiopsis purpurata Mitt.

Balantiopsis purpurata Mitt. in Thomson & Murray, Rep. Scient. Results *Challenger*. Bot. 1(3): 86. 1885. Original material: Juan Fernández, *Saunders* (FH!, NY!).

DESCRIPTION—Engel (1968).

ADDITIONAL DATA—Seta with 17 rows of epidermal cells surrounding an inner core of ca. 27 cells of about the same size, the epidermal cells firm-walled, the inner cells thin-walled and delicate. Capsule long-cylindrical, with spiral dehiscence, the wall delicate, 22–28 μm thick, of 3 layers (in median and basal sectors, 2-stratose above), the outer layer of cells ca. equal to thickness of both interior strata; outer layer of cells short-rectangular, large, the radial walls exceed-

ingly thin-walled and delicate, with small nodular thickenings (as seen in surface view) but frequently extending as spurs onto the inner tangential wall; innermost layer of cells with small nodular thickenings largely confined to the longitudinal radial walls, the thickenings smaller and less prominent than those of outer layer, the thickenings at times extending onto both inner and outer tangential walls as faint spurs or semiannular bands.

Spores 8.6–9.6 μm , the exine pale brownish yellow with a network of irregular, coalescing vermiform ridges that freely anastomose to form numerous, shallow areolae; spore:elater diameter ratio 0.75–0.9:1. Elaters tortuous, 10.1–12 μm wide, bispiral, the spirals 3.8–4.3 μm wide, loosely wound.

This species occupies a basal position in subg. *Balantiopsis* and is resolved as the sister taxon to the clade containing all of the other species of the subgenus. This species seems more appropriately placed in sect. *Balantiopsis* than as a monotypic taxon, coordinate with the other species of the subgenus. It is also similar in many respects to subg. *Steereocolea* but has distinctly (and deeply) complicately bilobed leaves. The cells are scattered in arrangement as in subg. *Steereocolea* as well as in *B. diplophylla*, which appears to be its counterpart in temperate Australasia. The leaf cells in *B. purpurata* are among the largest in the genus: 34–45(51) μm wide, similar in size to those of *B. asymmetrica*. The marked reduction of the dorsal lobe in *B. purpurata* (6,3) is the extreme expression of a tendency that is general in subg. *Balantiopsis* but also apparent in *B. asymmetrica*. A parallel reduction is seen in *B. diplophylla* var. *hockenii*.

The leaf margins in *B. purpurata* are often unarmed, or nearly so, and the ventral lobe insertion is essentially straight. The displacement of the dorsal lobe to the ventral lobe lamina a short distance above the base is a unique characteristic of this species. At times the keel is almost lacking and represented by a portion of a single cell. The cuticle of this species is unusual in being very densely papillose, the papillae being densely crowded and at times appearing as a more or less continuous, roughened surface.

DISTRIBUTION—Confined to the Valdivian zone of southern South America and Juan Fernández.

SELECTED SPECIMENS SEEN—CHILE, PROV. CHILOE: Isla Chiloé, Cordillera San Pedro, near aserradero at San Pedro, 320 m, *Engel 11848* (F); *ibid.*, Río Pudeto,

abandoned rail cut at Pupelde, near sea level, *Engel 11782* (F). PROV. VALDIVIDA: W slope of Cordillera Pelada, 8.8 km by road W of El Mirador on road between La Union and Punta Hueicolla, 580 m, *Engel 12296* (F); near Río Futa in vicinity of Futa, 5.9 km by road S of junction of Highways T-60 and T-65, near sea level, *Engel 10852* (F); Río El Lingue, between Mehuín and Lleco, *Engel 3863* (F, MSC); 2.1 km by road N of Mehuín, S of Queule, ca. 15 m, *Engel 11398* (F). PROV. MALLECO: Cordillera Nahuelbuta, Parque Nacional Contulmo, along trail from western entrance, 7 km by road E of Contulmo, 330–360 m, *Engel 12490* (F).

Balantiopsis ciliaris Hatt.

Balantiopsis ciliaris Hatt., J. Jap. Bot. 41: 129. f. 1–2. 1966. Holotype: North Borneo (Sabah), Mt. Kinabalu, between Kambaranga Radio Station and Waterfalls, 2000–2150 m, *Mizutani 2347* (NICH!).

DESCRIPTION—Hattori (1966, figs. 1, 2); Piippo (1984, fig. 16a–d).

This paleotropical species exhibits the extreme development of leaf armature in the genus, with up to 30 cilia on the ventral margin in the specimen seen (to 95 on both lobes in subsp. *novoguineensis*, *vide* Hattori, 1966). In general aspect and leaf armature, *B. ciliaris* resembles the New Zealand *B. lingulata* but differs in the extremely narrow keel, only 1–2 cells wide.

This species shares with the species of sect. *Pteridophylla* the condition of 2 oil-bodies per cell but has numerous features characteristic of sect. *Balantiopsis*: straight or comma-like ventral lobe insertion, larger leaf cells, and no intermediate thickenings. The species seems best placed in sect. *Balantiopsis*. The species is divided into two subspecies by Hattori (1966), subsp. *ciliaris* of North Borneo and the Philippines and subsp. *novoguineensis*, endemic to New Guinea (Piippo, 1984).

DISTRIBUTION.—New Guinea (1500–2500 m), Borneo, and the Philippines.

SPECIMEN SEEN—NEW GUINEA, MOROBE PROV.: Cromwell Mts., 7 km SE of Indagen airstrip, 2450–2555 m, *Koponen 30985* (F).

Section *Pteridophylla* (Hatch.) Engel & Merr.

Ventral lobe insertion U-shaped, the lobe often canaliculate to conduplicately folded or plicate; leaf cells with intermediate thickenings; cuticle distinctly papillose (often guttulate, rarely smooth), often with a contrasting border of striate-papillose cells; oil-bodies 2 per cell, at opposite ends of the cell.

This section includes the more specialized species of the genus characterized by a greater elaboration and complexity of leaf form and insertion. In the cladogram, the section is supported by intermediate wall thickenings (18,1) and the strongly recurved, U-shaped insertion of the ventral lobe (8,2). Other features found only in sect. *Pteridophylla* (but not in all species) include ventral lobe longitudinally folded and plicate (10,2), insertion of dorsal lobe transverse to U-shaped (9,2), small leaf cells (17,0), guttulate papillae (19,1), and a leaf border (16,1) accentuated by differentiation of the cuticle. With the exception of *B. convexiuscula* and *B. tumida*, oil-bodies are consistently two per cell, situated in opposite ends of the cell. Intermediate wall thickenings (18,1) are an apomorphy of this section but also occur in other genera of the family.

The origin of the sectional epithet *Pteridophylla* (“fern leaf”) is obscure and was not explained by Hatcher (1960–61), who proposed it as a monotypic section of *Isotachis*, including only *I. splendens* (*Anisotachis splendens*).

Balantiopsis cancellata (Nees) Steph.

Ptilidium cancellatum Nees in G. L. & N., Syn. Hep. 251. 1845. *Balantiopsis cancellata* (Nees) Steph., Hedwigia 32: 145. 1893. Original material: “In Peruvia ad Plagiochilam hookerianam repens . . .,” *sin. coll.* (STR!).

DESCRIPTION—Engel (1968, 1978).

ADDITIONAL DATA—Oil-bodies in all leaf cells, occupying small fraction of cell volume, at opposing ends of cell, tan or buff to pale yellowish, brown, glistening, 2 per cell (even near leaf base), subspherical to ovoid to elliptical to crescentic, coarsely papillose, the globules slightly protruding, 5–7 × 4–5 μm to 8–11 × (4)5, spherical ones 5 μm.

Seta with 25 rows of epidermal cells surrounding an inner core of ca. 40 cells of about equal size, the epidermal layer and the outermost layer of the core moderately thick-walled and with corner thickenings, the inner core cells thin-walled and delicate. Capsule long-cylindrical, with spiral dehiscence, the wall 40–46 μm thick, of 3 layers, the outer layer of cells exceeding thickness of both interior strata combined; outer layer of cells short-rectangular, large, in surface view the longitudinal and transverse walls with localized sheetlike thickenings without nodular or bandlike thickenings, in cross section the cells with short spurlike thickenings extending buttress-like from

radial walls a short distance onto the inner tangential wall; innermost layer of cells with longitudinal and transverse radial walls with strongly thickened, continuous sheets of wall material, with semiannular bands pale, common, very wide, closely spaced and numerous, often forked and anastomosing, the close and forked bands delimiting pitlike fenestrae (resembling scalariform pitted tracheids).

Spores 9.1–10.1 μm , the exine pale yellowish brown, with a network of irregular, coalescing vermiform ridges which freely anastomose to form numerous, shallow, small areolae; spore:elater diameter ratio 0.7–0.9:1. Elaters tortuous, 10.1–12.5 μm wide, bispiral, the spirals 3.8–4.8 μm wide, loosely wound.

DISTRIBUTION—Occurring on the Falkland Islands, the Valdivian and Magellanian zones of southern South America, and on Juan Fernández (see Engel, 1978, 1990).

SELECTED SPECIMENS SEEN—CHILE, PROV. MAGALLANES: Isla Riesco, E side of Bahía Borja, Paso Tortuoso, *Engel 6157B* (F, MSC); Isla Desolación, head of Brazo Lobo, *Engel 5837* (F, MSC); head of Fiordo Peel, *Engel 5494* (F, MSC); Fiordo Peel, N shore of Caleta Amalia, *Engel 5398* (F, MSC); Isla Chatham, N shore of Bahía Wide, *Engel 5349* (F, MSC); S side of Isla Madre de Dios, head of fiord E of Mt. Roberto, *Engel 5143* (F, MSC); near E shore of Isla Pilot (Puerto del Morro, Canal Trinidad), *Engel 4760B* (F, MSC); Puerto Charrúa (S side of Isla Wellington), head of inlet, *Engel 4816* (F, MSC). PROV. AISEN: Near glacier on N side of Fiordo Témpano, *Engel 4376D* (F, MSC). PROV. CHILOE: Isla Chiloé, Cocauque area, across Estero Yaldad from village of Yaldad, sea level, *Engel 11986* (F); *ibid.*, Cordillera San Pedro, near aserradero at San Pedro, 320 m, *Engel 11841* (F); *ibid.*, Cordillera San Pedro, Butalcura, near Río Butalcura, 100 m, *Engel 11801* (F); *ibid.*, Aguas Buenas area, 4.7 km E along Aguas Buenas road from Ancud-Quemchi road, 100 m, *Engel 12185* (F). PROV. OSORNO: Road below Refugio Antillanca, 3000 ft, *Engel 3942* (F, MSC). PROV. VALDIVIA: Cordillera Pelada, summit of El Mirador, ca. 100 m SW of refugio, near road between La Unión and Punta Hueicolla, 1000 m, *Engel 12362* (F); Corral, Quebrada El Boldo, 55 m, *Mahú 11939* (F); near Río Futa in vicinity of Futa, 10.5 km by road S of junction of Highways T-60 and T-65, 10 m, *Engel 11009* (F); Río El Lingue, between Mehuín and Lleco, *Engel 3884* (F, MSC). PROV. MALLECO: Cordillera Nahuelbuta, Parque Nacional Contulmo, along trail from western entrance, 7 km by road E of Contulmo, 330–360 m, *Engel 12528* (F). PROV. MALLECO/PROV. ARAUCO: Parque Nacional Nahuelbuta, Aguas Calientes, 10.2 km W of park entrance, 1240 m, *Engel 12622* (F).

Balantiopsis erinacea (Hook. f. & Tayl.) Mitt.

Jungermannia erinacea Hook. f. & Tayl., London J. Bot. 3: 462. 1844. *Gottschea erinacea* (Hook. f.

& Tayl.) Nees in G. L. & N., Syn. Hep. 624. 1846. *Gymnanthe erinacea* (Hook. f. & Tayl.) Mitt. in Hook. f., Bot. Antarc. Voyage 3(2): 230. 1859. *Balantiopsis erinacea* (Hook. f. & Tayl.) Mitt. in Hook. f., Handb. New Zealand Fl. 753. 1867. Lectotype (Engel, 1968): Falkland Is., *Hooker s.n.* (NY!).

DESCRIPTION—Engel (1968, 1990).

TAXONOMY—This species is remarkable for the detachment of the dorsal lobe of the leaf (5,2) and the dorsal lobe insertion, which appears almost circular, due to the dilated, sinuate-lobulate margins at the base of the lobe. The insertion of both the dorsal and ventral lobes is strongly arched and U-shaped, with at least one stem cortical cell intervening between the long-decurrent insertion lines of the lobes (Fig. 2:7,8).

This species was considered the type of a monotypic sect. *Erinacea* by Engel (1990), but its position in the cladogram (Fig. 17) indicates that it properly belongs in sect. *Pteridophylla*.

DISTRIBUTION AND ECOLOGY—Engel (1990).

SELECTED SPECIMENS SEEN—CHILE, PROV. CHILOE: Isla Chiloé, Cocauque area, across Estero Yaldad from village of Yaldad, sea level, *Engel 11978* (F). PROV. VALDIVIA: Valdivia, Isla Teja, Parque de Exposiciones Saval, sea level, *Engel 10924* (F).

The Systematic Position of *Anisotachis* Schust.

The close relationship between *Anisotachis splendens* and *Balantiopsis* was emphasized by Stephani (1895) when the species was first proposed. For a full discussion of this problematical taxon and the history of its interpretation, see Schuster (1964). Hatcher (1960–61) misinterpreted this plant, treating it as an isolated element within the genus *Isotachis* (cf. his phylogenetic diagram, l.c., fig. 764) and the type and only species of his *Isotachis* sect. *Pteridophylla*. Engel (1968, p. 91) emphasized tiering of cells, complex leaf insertion, and conduplicately bilobed succubous leaves in this species as strongly indicative of a close relationship to *Balantiopsis* but stopped short of making the formal transfer of the species because of the absence of reproductive structures.

No support was found in the cladogram for maintaining *Anisotachis* as a distinct genus. Rather, *A. splendens* is consistently resolved as a member of *Balantiopsis* sect. *Pteridophylla*, underscored by the strongly U-shaped insertion line of both the ventral and dorsal lobes (Schuster, 1972,

fig. 5:4, 6), plication of the ventral lobe (l.c., fig. 5:1, 11, 12), and pronounced tiering of cells (l.c., fig. 5:7), all features shared with its sister taxa *B. rosea* and *B. verrucosa*. This species most closely resembles *B. verrucosa* in its sparsely armed leaves and underleaves, dorsal and ventral lobes subequal in size, rounded to truncate-retuse lobe apices (cf. *A. splendens*, Hässel de Menéndez & Solari, 1975, p. 163; *B. verrucosa*, Figs. 2:9; 6:3, 4), and retuse-bidentate to shallowly bifid underleaves (cf. Hässel de Menéndez & Solari, fig. 37: 1, 4; Figs. 2:9; 6:7). Smooth leaf cuticle (19,2) is a homoplasy, occurring here and in the clade containing *Austroscyphus* and *Eoisotachis*.

The following new combination is required:

Balantiopsis splendens (Steph.) Engel & Merr., comb. nov.

Isotachis splendens Steph., Hedwigia 34: 49. 1895.
Anisotachis splendens (Steph.) Schust., Nova Hedwigia 8: 282. 1964. Original material: Chile, Isla Desolación, Bahía Tuesday, *Cunningham* (*non vidi*).

DESCRIPTION—Hässel de Menéndez & Solari (1975), Hatcher (1960–61), Schuster (1964, 1972).

The aspect of this species is notable for the striking resemblance in size and shape of the leaf lobes to the underleaves. The deeply bilobed nature of the leaves is often not evident without careful dissection, and *in situ* the “leaves” often appear 5-ranked.

DISTRIBUTION AND ECOLOGY—A species of the Magellanian moorland, a region occurring south of 48°S to Cabo de Hornos, and limited by the Magellanian rain forest to the east and Pacific Ocean to the west. The moorland is characterized by being extremely wet, with a permanently saturated peaty soil, and with only scattered and discontinuous forests chiefly on coastal fringes or in sheltered gullies (see Godley, 1960; Engel, 1978). The species occurs in wet depressions and pools, where it is often submerged, and ranges from Tierra del Fuego northward in the wet Patagonian Channel region to 50°39'S (Isla Juan).

SELECTED SPECIMENS SEEN—CHILE, PROV. MAGALLANES: Isla Desolación, Puerto Churruca, head of Brazo Lobo, *Engel 5845B* (F, MSC); Isla Desolación, Puerto Churruca, peninsula on N side of Fondeadero Nassau, *Engel 5909* (F, MSC); Isla Desolación, Bahía Tuesday, head of inner harbor, *Engel 5779* (F, MSC); E side of Puerto Bueno, *Engel 5612* (F, MSC); E side of Isla Juan, Bahía Wide, *Engel 5262* (F, MSC).

The Systematic Position of *Isotachis* subg. *Hypoisotachis* Schust.

The sole species of this monotypic subgenus, *Isotachis multiceps* (Lindenb. & Gott.) Gott., is discussed and illustrated by Schuster (1978; 1985a, figs. 4,5). We have studied a specimen of this plant from Brazil (Parque Nacional do Itatiaia, 2140 m, *Vitt 21587*, F), with both young and mature perigynia. Some additional comments are in order.

This species is remarkable for the production of ♀ and often ♂ gametangia on short ventral-intercalary branches, a feature found in no other member of suborder Balantiopsinae. Terminal, *Frullania*-type, vegetative branches are produced, but sparingly; geotropic, microphyllous stolons are also present.

Other features are also noteworthy. The leaf insertion is weakly succubous, compared to weakly to distinctly incubous (or transverse) in *Isotachis*. The leaf cells have well-developed intermediate wall thickenings and are noticeably tiered, although not as regularly as in some *Balantiopsis* species. The ♂ bracts are monandrous, as in *Austroscyphus*, compared to 2–4 per bract in *Isotachis*.

Hypoisotachis has a slender *Isotachis*-like perigynium that bears *Balantiopsis*-like rhizoidal outgrowths from its surface, as well as a few perigynial bractlets inserted on the distal third to half of the outer perigynium wall. The young perigynium is broadly ovoid, shallowly plicate, and strongly tapered toward the ± contracted mouth; the whole is strikingly perianth-like in appearance. However, a cycle of unfused bractlets is inserted just within the mouth of the perigynium proper, which is pluristratose in the basal half. Additional unfused bractlets, external to this, are distinguishable as bractlets by their different areolation, being made up of ± regularly quadrate cells. The capsule is cylindrical and spirally dehiscent, but the capsule wall is bistratose (or locally 3-stratose) as in *Ruizanthus* and *N. carneus*, rather than uniformly 3-stratose; the latter is the apomorphy supporting the *Isotachis*–*Balantiopsis* clade in Figure 16:2, the majority consensus of the “perianth” data set.

We experimented with including this species in the data set and scoring the same characters and character states as in the other taxa (p. 27), including the perianth. Thirty-seven most parsimonious trees were obtained, each with a length of 120 steps. In the strict consensus of these trees,

Hypoisotachis is resolved as the sister taxon to the *Austroscyphus*–*Eoisotachis* clade. Unfortunately, the most striking feature of this curious plant, the production of gametangia on ventral-intercalary branches, is an autapomorphy and thus uninformative in a cladistic analysis. Schuster (1978, p. 240) calls attention to the numerous distinctive features of *Hypoisotachis*, remarking that “perhaps the plant should be placed into an autonomous genus.” The following nomenclatural changes are required.

Hypoisotachis (Schust.) Engel & Merr., *comb. & stat. nov.*

Isotachis subg. *Hypoisotachis* Schust., *Phytologia* 39: 240. 1978.

Type: *Isotachis coilophylla* Herz.

Hypoisotachis multiceps (Lindenb. & Gott.) Engel & Merr., *comb. nov.*

Jungermannia multiceps Lindenb. & Gott. in G. L. & N., *Syn. Hep.* 687. 1847. *Isotachis multiceps* (Lindenb. & Gott.) Gott., *Mexikanske Levermoser* 105. 1863. Original material: Mexico, “apud Sempoaltepec, Talea et San Jago Amatlan” (not seen).

Isotachis coilophylla Herz., *Feddes Repert.* 21: 25. 1925. Original material: Brazil, Serra dos Orçãos, Morro Assu, *Luetzelburg 6035b* (not seen).

DISTRIBUTION—Mexico, Costa Rica, Antilles (Guadeloupe, Jamaica, Puerto Rico), northern South America (Colombia, Venezuela), and southeast Brazil.

Hypoisotachis is strongly anisophyllous but has evolved an erect stem perigynium of the *Isotachis* type. The relationship of *Hypoisotachis* to *Isotachis* is unclear: the latter includes both radial, subsisophyllous species (e.g., *I. intortifolia*) and prostrate, strongly anisophyllous forms (e.g., *I. minima*, Fig. 11:1). Schuster (1972, p. 355) suggests that the erect, fleshy stem perigynium evolved in plants with an erect radial habit of growth. The question of which habit is plesiomorphic in the genus is largely unsettled, except for the indication that subsisophyllous *I. intortifolia* is derived (p. 44).

Phytogeography and Ancestral Areas

An ancestral area analysis was undertaken as part of this study in an attempt to explain the pres-

ent geographical distribution of *Balantiopsis* and the Balantiopsaceae (Fig. 1). An area cladogram is shown in Figure 18, based on the consensus cladogram (Fig. 17) of the four most parsimonious trees obtained in the core phylogenetic analysis. The area cladogram suggests that the South American continent was the ancestral area for the Balantiopsaceae, since the oldest, most plesiomorphic lineages (*Ruizanthus*, *Neesioscyphus*) are South American. Within *Balantiopsis*, the earliest divergent lineages (subg. *Stereocolea*, *B. purpurata*) are also South American. However, both sections of subg. *Balantiopsis* contain Australasian as well as South American species. Several examples of amphipacific species pairs in *Balantiopsis* are indicated in the area cladogram; of these, *Balantiopsis convexiuscula* (Australia, Tasmania, New Zealand) and *B. cancellata* (southern South America) are resolved as sister taxa in all four most parsimonious cladograms (Fig. 15), as are *B. splendens* (southern South America) and *B. rosea* and *B. verrucosa*, a New Zealand species pair. Two of the three tropical species of the genus (*B. brasiliensis* and *B. philippinensis*) are also consistently resolved as sister taxa.

Reconstructions of past distributions of antipodal taxa rely heavily on assumptions drawn from vicariance biogeography. Groups showing amphipacific distribution patterns of this type are usually regarded as “Gondwanalandic”—the most recent common ancestor is assumed to have been widely distributed in Gondwanaland, with fragmentation of the ancestral range as a result of the breakup of the supercontinent, and subsequent speciation. Dispersal is invoked to explain presumably more recent migration of descendants to lower latitudes (e.g., to New Guinea, Borneo, and the Philippines, and to the northern Andes). In other words, the ancestor was more widely distributed than its descendants, and the direction of dispersal was away from the ancestral area in the south to (often geologically younger) areas to the north. In the case of Balantiopsaceae, however, the area cladogram seems to point to a more restricted ancestral area, and the phylogenetically deepest branches on the cladogram are presently neotropical, implying migration in the opposite direction.

Ruizanthus, the most primitive genus in the family, occurs in high-altitude neotropical páramos from northern Peru to Colombia and Venezuela and extending into Central America (Gradstein et al., 1994). The distribution of *Neesioscyphus* extends from the northern Andes and the

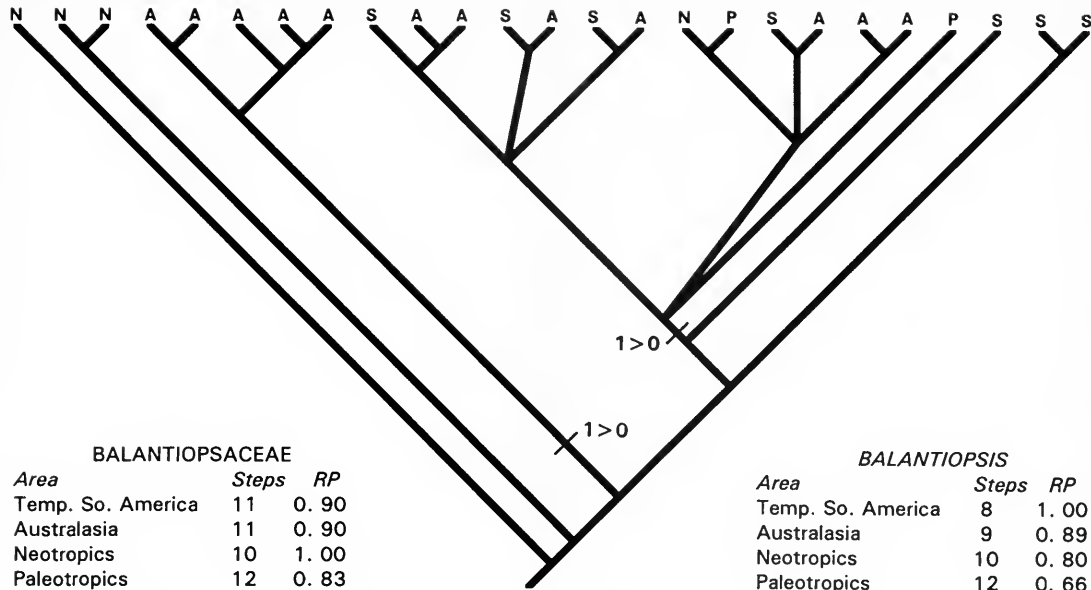


FIG. 18. Area cladogram showing the distribution of each terminal taxon in the data set (based on Fig. 17) with the geographical distribution substituted for the name of the taxon (A = Australasia; N = Neotropics; P = Paleotropics; S = Temperate South America). The tables give the number of steps on the cladogram required to account for the distribution of the terminal taxa and the reversible parsimony (RP) indices (Ronquist, 1994) for each of the putative ancestral areas. Values are given for Balantiopsaceae and for the *Balantiopsis* clade. (The RP index is the reciprocal of the number of steps for a given ancestral area, multiplied by the smallest number of steps for any area on the cladogram.) Bars show the transformation from the “plesiomorphic” South American “state” to Australasia ($1 > 0$), according to a DELTRAN reconstruction of this “character” (see text).

Antilles to Brazil and northern Argentina (Reiner-Drehwald & Drehwald, 1995). The possibility that these taxa (and hence the family as a whole) had an indigenous neotropical origin, however, seems inconsistent with the classic Gondwanalandic pattern shown by the two largest genera in the family (*Balantiopsis*, *Isotachis*), which have their greatest diversity in both southern South America and Australasia (cf. Schuster, 1990, p. 250). Further, at least two elements in the family (*Austroscyphus*, *Eoisotachis*) are restricted to the Australasian sector of former Gondwanaland.

We approached this problem in two ways, the first using the ancestral character state function of PAUP (see p. 44), and the second employing the “reversible parsimony” method proposed by Ronquist (1994). In addition to morphological characters, the geographical distribution of each taxon was entered as part of the data set, although this “character” was excluded when the PAUP search was run. Geographical distribution was treated as a binary character: Australasia (0) or South America (1). A DELTRAN reconstruction of this “character” was then obtained, showing

the ancestral “state” at each of the internal nodes within the tree. The “plesiomorphic” state is South America, changing to Australasia ($1 > 0$) at two points (indicated in Fig. 18), thus supporting a South American ancestral area for the Balantiopsaceae as well as for *Balantiopsis*.

Ronquist (1994) proposed the method of reversible parsimony for determining ancestral areas, based solely on the number of steps on an area cladogram necessary to account for the present distribution of the terminal taxa. It should be emphasized that the method does not examine “the possibility that distribution areas may be historically related to each other” (i.e., p. 273) and is explicitly performed outside the context of vicariance biogeography (see critique in Lavin & Sousa, 1995, pp. 30–32). Ancestors are assumed to have been no more widespread than their descendants, and the direction of dispersal events is assumed to be reversible. This is analogous to treating morphological characters as unordered (see p. 27) to avoid making a priori assumptions as to polarity. The area that requires the smallest

number of steps is the one most likely to have been the ancestral area of the taxon.

For the reversible parsimony analysis we distinguished four putative ancestral areas—temperate South America, Australasia, the Neotropics, and the Paleotropics. The results for each of these areas (Fig. 18) support a neotropical origin for the Balantiopsaceae (i.e., in the present neotropical sector of former Gondwanaland), but also show only a slightly lower probability (RP = 0.90) of a southern South American or Australasian origin. All three of these areas are historically related, so the most likely explanation remains that the overall distribution of the family is due largely to the breakup of formerly continuous areas. Even if parsimony does not provide conclusive evidence as to the area in which the Balantiopsaceae ultimately originated, it is at least strongly suggested that much of the earliest evolution and diversification in the family took place in the South American sector of Gondwanaland, simply because so many basal splits occurred there.

The picture is complicated by the fact that the modern representatives of these earliest divergent lineages occur in high-altitude habitats that only recently came into existence as a result of the uplift of the Andean cordillera in the late Tertiary. Schuster (1985a, p. 52), in discussing the distinctive high-elevation flora of the northern Andes, argues that “few taxa—indeed a very small minority—are clearly derived from subantarctic or Laurasian-temperate antecedents; the majority, clearly, are derived from forest-zone, neotropical ancestors.” Nevertheless, we think it is likely that these taxa (*Ruizanthus*, *Neesioscyphus*) belong to the group of high-altitude neotropical bryophytes of austral origin, which have extended their range northward along the cordillera in relatively recent times, many of which also have outliers in south-eastern Brazil.¹ *Ruizanthus* is said to be “highly

fertile” (Gradstein et al., 1994, p. 75) and hence may be readily dispersable.

The most probable ancestral area for *Balantiopsis* is temperate South America (Fig. 18), a result that is consistent with the present distribution of representatives of the earliest divergent lineages (subg. *Stereocolea*, *B. purpurata*) in the genus. We are postulating an ancestral area for *Balantiopsis* in the sector of Gondwanaland that included present south temperate South America and possibly adjacent Antarctica. The genus has only a limited extension northward to Brazil (*B. brasiliensis*) and is lacking in the Andes. Both sections of subg. *Balantiopsis*, however, contain Australasian as well as American species, indicating that the most recent ancestors of these taxa were probably more widely distributed and that the evolution of sectional diversity in subg. *Balantiopsis* took place before the breakup of Gondwanaland.

Austroscyphus is exclusively Australasian, extending from New Zealand and Tasmania north to New Caledonia (*A. iwatsukii*) and Java (*A. tjiwidiensis* (Sande-Lac.) Schust.; for treatment see Engel, 1980). *Eoisotachis* is also limited in distribution to cold-temperate Australasia (*E. stephanii* of extreme southern South Is., and Stewart Is., New Zealand, and *E. nigella* (Herz.) Schust. of Tasmania). The area cladogram (Fig. 18) shows the *Austroscyphus*–*Eoisotachis*–*Isotachis* clade as an Australasian sister group to *Balantiopsis*. This is obviously an oversimplification, however, since the only *Isotachis* species included in the analysis are Australasian. Schuster (1985b, 1990) places *Austroscyphus* in the Ruizanthoideae. In our classification (see discussion on pp. 47–49), *Austroscyphus* is placed with *Neesioscyphus* in the Neeioscyphaceae, which (if borne out by future study) gives this tribe an amphi-Pacific distribution. It should be emphasized, however, that the cladistic analysis presented in this paper does not support this placement of *Austroscyphus*. The neotropical *Hypoisotachis*, with a distribution similar to that of *Neesioscyphus*, may be the sister taxon to the

¹ For example, *Pseudocephalozia quadriloba* (Steph.) Schust. belongs to a nearly exclusively cool- to cold-temperate Gondwanalandic Lepidoziaceae subfam. Zoopsidoideae but extends northward at high elevations to Costa Rica (Schuster & Engel, 1974). *Clasmatocolea* is exclusively south temperate–subantarctic in range with the exception of *C. vermicularis* (Lehm.) Grolle, which extends north in the neotropics via the high Andes to Costa Rica and north at higher elevations in Africa to Burundi. The species is frequently fertile. The moss genus *Polytrichadelphus* (C. Müll.) Mitt. has its major center of species diversity in the páramos of the northern Andes, with one species (*P. costaricensis* Bartr.) in Central America and another (*P. pseudopolytrichum* (Raddi) G. Sm.) in southeast Brazil (Smith, 1971, fig. 59). How-

ever, the genus is also represented in southern South America (*P. magellanicus* (Hedw.) Mitt.), in Australia and New Zealand (*P. innovans* (C. Müll.) Jaeg.), and in New Guinea (*P. archboldii* Bartr.). *Notoligotrichum* G. Sm. has a similar distribution (i.e., fig. 77), extending northward to Mexico in the New World and to New Guinea (Hyyvönen, 1986). These taxa represent extensions of the “Antarctic radiant” pattern proposed by Smith (1971, 1972).

Australasian *Austroscyphus*–*Eoisotachis* clade (see above).

Isotachis, the most widely distributed genus of Balantiopsaceae, occurs in the neotropics, southern South America, Africa and Madagascar, temperate Australasia, and north in the Old World to Japan (Fig. 1). Unlike *Balantiopsis*, *Isotachis* has a major center of diversity in tropical America (see key in Schuster, 1985a); *Balantiopsis*, however, has only one representative in the neotropics (*B. brasiliensis*, in southeastern Brazil). There are ten species of *Isotachis* in the neotropics, five in southern South America, seven in temperate Australasia; three are Indo-Malayan (*I. japonica* Steph. extends north to southernmost Japan) and, according to Vána (1982), only one occurs in Africa (and that species, *I. aubertii* (Schwaegr.) Mitt., is a tropical alpine species also occurring in tropical America; Gradstein, Pócs & Vána, 1983). The poor representation of *Isotachis* in Africa suggests that the occurrence of the genus there is relatively recent. The total distribution of *Isotachis* (as opposed to that shown in the area cladogram) suggests a history similar to that of *Balantiopsis*, with major diversification occurring prior to the breakup of Gondwanaland.

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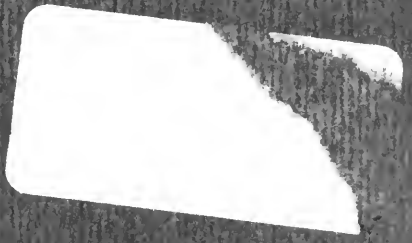
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