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## Botany

NEW SERIES, NO. 44

**Austral Hepaticae. 35. A Taxonomic and Phylogenetic  
Study of *Telaranea* (Lepidoziaceae), with a  
Monograph of the Genus in Temperate Australasia  
and Commentary on Extra-Australasian Taxa**

**John J. Engel  
G.L. Smith Merrill**

**November 30, 2004  
Publication 1531**

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# Austral Hepaticae. 35. A Taxonomic and Phylogenetic Study of *Telaranea* (Lepidoziaceae), with a Monograph of the Genus in Temperate Australasia and Commentary on Extra-Australasian Taxa

John J. Engel and G. L. Smith Merrill

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## Abstract

*Telaranea* is the third largest genus of Lepidoziaceae, after *Bazzania* (over 450 species) and *Lepidozia* (over 300 species). In this monograph, 98 species of *Telaranea* are recognized, 62 of which are extra-Australasian. Included are 11 new species, 2 new varieties, 27 new combinations (25 species and one variety), and one new name. New taxa are fully described and illustrated. Two subgenera of *Telaranea* are recognized (subg. *Acrolepidozia*, subg. *Telaranea*), and 7 sections within subg. *Telaranea* (sect. *Neolepidozia* (Fulf. & J. Tayl.) Engel & Merr. comb. nov., sect. *Cancellatae* Engel & Merr., sect. *Ceraceae* Engel & Merr. sect. nov., sect. *Tricholepidozia* (Schust.) Engel & Merr. comb. nov., sect. *Transversae* Engel & Merr., sect. *Telaranea*, sect. *Tenuifoliae* (Schust.) Engel & Merr. comb. nov.).

A major part of this work is devoted to a phylogenetic study of the genus *Telaranea*, with a discussion of character evolution in the genus and a reconstruction of ancestral character states. An ancestral area analysis was also undertaken, using phylogeny to trace the geographical history of members of the genus. Differing concepts of phylogeny as applied to leafy hepatics are also briefly considered. The phylogenetic analysis included 56 taxa and 32 characters, with representative species of *Lepidozia*, *Kurzia*, and *Arachniopsis* as outgroups. Cladograms obtained from parsimony analyses of the full data set and subsets of taxa, as well as distance (NJ) trees, were strikingly similar in topology. Monophyly of *Telaranea* is supported by the possession of a hyaloderm (enlarged, usually hyaline stem cortical cells) and an undivided first branch underleaf. Progressive reduction in morphological complexity as a central

evolutionary tendency in the genus is strongly supported. The phylogeny indicates that *Kurzia*, as defined by the presence of *Microlepidozia*-type branching, is polyphyletic, and 6 species previously assigned to *Kurzia* are transferred to *Telaranea*. No support was found for maintaining *Arachniopsis* as a distinct genus, and 6 species of the genus are transferred to *Telaranea*. The new genus *Amazoopsis* Engel & Merr. is described, with 3 species: *A. diplopoda* (Pócs) Engel & Merr. comb. nov., *A. dissotricha* (Spruce) Engel & Merr. comb. nov., and *A. gracilis* Engel & Merr. sp. nov. The status of *Monodactyloopsis* (Schust.) Schust. is discussed; the genus includes *M. monodactyla* (Spruce) Schust. and *M. minima* Schust. ex Engel & Merr., sp. nov. *Paracromastigum vastilobum* (Steph.) Engel & Merr. is a new combination. Keys to the subgenera and sections of *Telaranea*, the Australasian species, as well as the southern South American species of *Telaranea*, and the species of *Telaranea* sect. *Tenuifoliae* are included.

## Introduction

Until the mid-1950s, the genus *Telaranea* was frequently understood narrowly to include only the type, *T. chaetophylla* (Spruce) Schiffn., usually treated as a synonym of either *T. nematodes* (Gott. ex Aust.) Howe or *T. sejuncta* (Ångstr.) S. Arnell. With the inclusion of other elements, however, the genus now ranks third among the genera of the family Lepidoziaceae, after *Bazzania*, with over 450 described species and *Lepidozia*, with well over 300. *Kurzia*, with 32–36 taxa (Schuster, 1980) is the next largest genus.

As treated here, *Telaranea* (incl. *Arachniopsis*) comprises 98 species in both the Northern and Southern Hemispheres. The greatest diversity in numbers of species is in western Melanesia and Australasia. Temperate Australasia, and in particular New Zealand, has the largest number of species and the greatest diversity of distinct morphological types. Thirty-six species and 8 varieties of *Telaranea* are treated here from temperate Australasia.

The bulk of the Australasian species now assigned to *Telaranea* were formerly included in the genus *Lepidozia*. Hodgson's (1956) treatment of the New Zealand species of *Lepidozia* is the only revision of the Australasian *Telaranea* taxa to date. Fourteen of the 33 *Lepidozia* species treated by Hodgson are now placed in *Telaranea*. Fulford and Taylor (1959) removed 16 species from *Lepidozia* and placed them in a new genus *Neolepidozia*, with *Jungermannia capilligera* Schwaegr. as its type. Hodgson (1962) treated *Neolepidozia* as a synonym of *Telaranea* and transferred 10 Australasian species of the *Neolepidozia* group to *Telaranea*; Schuster (1963) transferred seven more regional species to *Telaranea*. Engel and Merrill (1996a), added four sections (sect. *Cancellatae*, sect. *Capillares*, sect. *Latifoliae*, and sect. *Transversae*), two new species (*T. hodgsoniae*, *T. pennata*), three new varieties (*T. lindenberghii* var. *complanata*, *T. lindenberghii* var. *melaleuca*, and *T. praenitens* var. *dentifolia*) and nine new combinations (*T. complanata*, *T. elegans*, *T. lindenberghii*, *T. paludicola*, *T. tasmanica*, *T. tetrapila*, *T. tetrapila* var. *roseana*, *T. tetrapila* var. *cancellata*, and *T. tridactylis*), all from Australasia. Engel and Merrill (1999) described three additional species from the region, *T. consobrina*, *T. fragilis*, and *T. palmata*, and transferred one Australasian species, *T. clatritexta*, from *Lepidozia* to *Telaranea*.

The results of our study of the Australasian representatives of the genus *Telaranea* are presented in this monograph. Our conclusions are based on the examination of numerous specimens collected by Engel, Child, Hatcher, Hodgson, Allison, and others, plus all of the relevant type specimens. The result has been a considerable refinement of species concepts, and the acceptance of several additional taxa not previously recognized as belonging to *Telaranea*. The first section of the work deals with taxonomic treatments of the Australasian species. This is followed by a review of the extra-Australasian representatives of the genus. The third portion of the work presents the results

of a phylogenetic analysis of the genus *Telaranea*. The monograph concludes with a discussion of geographical relationships, and a list of excluded taxa.

## Evolution of a Generic Concept

### I. *Telaranea* in the restricted sense

*Telaranea* first appears as a synonym (Spruce, 1885, p. 360, as "*Telaranea nobis nov. gen?*") under subhead 2. of *Lepidozia* subg. *Micro-Lepidozia*, based on a single species, *Lepidozia chaetophylla*, with "*Telaranea chaetophylla* Spruce Mst nov. gen." listed as a synonym (p. 365). *Telaranea* as a genus name dates from 1893, when validly published by Schiffner (1893). It remained essentially monotypic in works published as late as the 1950's (e.g., Schiffner, 1893; Howe, 1902; Stephani, 1909). The detailed study of *T. longifolia* (Howe) Engel & Merr. by Schuster and Blomquist (1955, as *T. nematodes*) included a discussion of the limits of the genus and concluded that "... our present concept of the genus is based largely upon the genotype [i.e., generitype] *T. nematodes*" (p. 592).

The characteristics of *Telaranea* s. str. are those of *T. chaetophylla*, as stated by Spruce: stem cortical cells in 8–10 rows and medulla 4 × 7 cells wide; 3-lobed leaves, the lobes 4–7 cells long, uniseriate (or biseriate) at the base, with their basal cells connate to about ½ their height, half-leaves almost always undivided and underleaves 2- (rarely 3-) lobed, the lobes erect-incurved, from a rhizoid-bearing base.

### II. *Lepidozia* sect. *Capillares* and *Microlepidozia*

Karl Müller (1914) was apparently the first to expand *Telaranea* (as *Lepidozia* subg. *Telaranea*) beyond Spruce's original concept to include other *Lepidozia* species with large-celled, uniseriate leaf lobes and transversely inserted leaves. Among the species included by Müller were *L. blepharostoma*, *L. lawesii*, *L. neesiana* (*T. neesii*), *L. nematodes*, *L. sejuncta*, and *L. trisetosa* (as well as *L. chaetophylla*), all now placed in *Telaranea*. The subgenus was not treated by Müller since it included only extra-European taxa. *Telaranea nematodes* was not reported from Europe until 1936 (Müller, 1956).

Müller's treatment was foreshadowed by the Synopsis Hepaticarum (Gottsche, Lindenberg and Nees, 1845), whose *Lepidozia* sect. *Capillares* included species with deeply divided leaves, capillary (uniseriate) lobes, and a laciniate-ciliate perianth mouth. Four of the 6 species included in the section are now placed in *Telaranea*, namely *T. plumulosa*, *T. neesii*, *T. lindenbergii*, and *T. tetradactyla*; the others are *Kurzia* species (for typification of sect. *Capillares*, see p. 79).

Sect. *Capillares* and two others were adopted by Spruce (1876) as subgenera of *Lepidozia*, the others (sect. *Communes*, *Microphyllae*) having incubous leaves, divided to the middle. Hodgson (1956, p. 589) decried the fact that "with 30 or more years of priority, these names to all intents and purposes have been dropped because Spruce, in addition to ignoring them, replaced them with his own 3 sections . . . and placed these on a permanently higher level by calling them subgenera." Spruce's *Lepidozia* subg. *Microlepidozia* "corresponds nearly to the § *Capillares* of 'Syn. Hep.'" (quoting Spruce, 1876, p. 165), and is "almost distinct enough to form a genus apart." In addition to deeply-divided leaves and ciliate-laciniate perianth mouth (characters of sect. *Capillares*), Spruce adds "leaves transverse, neither succubous nor incubous" and unistratose perianths.

*Telaranea* has had a long history of association with *Microlepidozia* (Spruce) Joerg. (= *Kurzia* v. Mart.), although the two are now generally considered to be distinct. Müller (1956) united the two elements (*Telaranea* and *Microlepidozia*), using Spruce's generic name for the combined genus, distinguished from *Lepidozia* by the nearly transversely inserted leaves, divided up to the base, with setaceous lobes; unistratose perianth; seta cross-section with 8 large, outer cells surrounding 4–16 small, inner cells; and 2-, occasionally 3-stratose capsule valves. Oil-bodies, listed as absent by Müller, are now known to be present in both *Kurzia* and *Telaranea* species. Schuster and Blomquist (1955) distinguished the genus *Telaranea* (sensu Spruce) from *Microlepidozia* primarily by the absence of *Microlepidozia*-type branching in *Telaranea*, and the presence of a distinct hyaloderm. Fulford (1963a) also emphasized *Microlepidozia*-type branching as a character distinguishing *Microlepidozia* from *Telaranea*. Schuster (1969, p. 31) reviewed the distinctions between *Telaranea* and *Microlepidozia* (= *Kurzia*).

### III. *Lepidozia* sect. *Communes* and *Neolepidozia*

*Lepidozia* sect. *Communes* G. L. & N. (Gottsche, Lindenberg and Nees, 1845, = sect. *Lepidozia*, since it included the type of the genus, *L. reptans*) contained species with leaves having a higher disc and non-capillary lobes. Six of the 21 included species are now placed in *Telaranea*, namely *T. capilligera*, *T. centipes*, *T. gottscheana*, *T. patentissima*, *T. praenitens*, and *T. wallichiana*. A seventh species, *T. oligophylla*, was placed in sect. *Microphyllae* by Gottsche, Lindenberg and Nees.

These and similar, *Lepidozia*-like *Telaranea* species remained in *Lepidozia* until Fulford and Taylor (1959) removed 16 species from the genus and placed them in a new genus *Neolepidozia*, with *Jungermannia capilligera* as its type. *Neolepidozia* was distinguished from *Lepidozia* by fewer, larger stem cortical cells forming a distinct hyalodermis, leaves with entire margins, the margins straight or convex and without auricles at the base, a much greater uniformity of leaf cell size than in *Lepidozia*, and a first branch underleaf usually undivided and ventral in position. The relationship between *Neolepidozia* and *Telaranea* was not discussed by Fulford and Taylor.

Fulford (1963b, in key, pp. 17–19) further distinguished *Neolepidozia* from *Lepidozia* by leaf cells tending to be in longitudinal rows and stems with 12 rows of cortical cells, vs. leaf cells not necessarily in rows and cortical cells more numerous in *Lepidozia*. Fulford (1966) added an oblique, nearly longitudinal line of leaf insertion and triangular leaf and underleaf lobes as characters of *Neolepidozia*.

In a review of the *Telaranea* species in South America, Fulford (1963a) distinguished the genus from *Lepidozia* by a stem with 18 to as few as 6 large cortical cells, leaves transversely inserted, 2–6 uniseriate leaf lobes, and a disc "4, 3, 2, 1 or even ½ (or less) rows of cells high." Included were *T. apiahyna*, *T. blepharostoma*, *T. neesii*, *T. plumulosa*, *T. pseudozoopsis*, *T. sejuncta*, and *T. tetradactyla* (the last a *Neolepidozia* in Fulford and Taylor, 1959), all species "which are closely related to one another and which show many characters in common with *T. sejuncta*" (understood by Fulford as synonymous with *T. nematodes*). Fulford's key (1963b, pp. 17–19) separates *Telaranea* from *Lepidozia* by leaves transversely inserted or nearly divided to the base or approximately one-half their length, uniseriate, "capilla-

ceous" leaf lobes, and the margins of the leaves and underleaves entire.

In summary, Fulford's concept of *Telaranea* is ultimately traceable to *Lepidozia* sect. *Capillares* of the Synopsis Hepaticarum, and subg. *Telaranea* of Müller (1914). Subsequently, Piippo (1984) has returned the *Lepidozia*-like species to the parent genus as *Lepidozia* sect. *Neolepidozia*, consisting of species with almost symmetrical leaves, leptodermous cells, and a conspicuous hyaloderm, while maintaining *Telaranea* in the more limited sense of Müller and Fulford.

#### IV. Merging of concepts: *Telaranea* in the modern sense

Hodgson (1962) treated *Neolepidozia* as a synonym of *Telaranea* and transferred 10 Australasian species of the *Neolepidozia* group to *Telaranea*, without according it subgeneric rank. Schuster (1963) combined all three elements discussed above under *Telaranea*, listing *Frullania*-type branching, a stem with a hyaloderm, leaf cells large and pellucid, leaf lobes narrow (1–2, or rarely 3–4 cells broad at base), disc 1–3(4) cells high, capsule-wall 3-stratose (as in *Telaranea* s. str.), and finely areolate spores as characteristics of the combined genus. Schuster recognized 3 subgenera, of which subg. *Telaranea* is "exactly equivalent in concept to [the] genus *Telaranea* of Schuster and Blomquist (1955)." Subgenus *Neolepidozia* comprises the other low-disc, capillary-lobed species of *Telaranea* in the sense of Müller and Fulford, as well as those of *Neolepidozia*. A third element, subg. *Tricholepidozia*, is discussed below.

#### V. Other new elements: *Acrolepidozia*, *Tricholepidozia*, *Chaetozia*

Schuster (1963) proposed the genus *Acrolepidozia*, based on *Lepidozia longitudinalis*, emphasizing a dimorphic mode of growth "quite unlike any of the New Zealand taxa [of *Lepidozia*] known to me." The genus was reduced to a subgenus of *Telaranea* by Schuster (1969, see footnote, p. 30), and considered derived from subg. *Neolepidozia*. Subgenus *Acrolepidozia* is described and discussed in detail in Schuster (1973, p. 389), who called attention to the diminutive half-leaf and first branch underleaves, and deemphasized the mode of growth in this species.

*Telaranea* subg. *Tricholepidozia* was proposed by Schuster (1963) for 4 species with a "*Trichocolea*-like facies" and 8–13-lobed leaves, which had not previously been associated with *Telaranea*. Besides the type, *T. mooreana*, *T. pulcherrima*, *T. radiata*, and *T. trichocoleoides* comprise the subgenus. Schuster (1969, 1973) added a weakly differentiated hyaloderm of ca. 24–28 rows of cortical cells, and a 5-stratose capsule wall as characteristics of this subgenus. Schuster (2000, p. 240) cites relative subisophyly as the chief reason for retaining *Tricholepidozia* as a subgenus.

Grolle (1966) proposed the new subgenus *Chaetozia*, with *T. chaetocarpa* of New Caledonia as its type. This species has the distal portion of the perianth covered with ciliform outgrowths. A second species, *T. trisetosa*, was originally included in the subgenus by Grolle, but it was later found not to have this feature (Grolle, 1968) and was excluded. The subgenus was synonymized with subg. *Telaranea* by Schuster (1969).

#### VI. *Telaranea* and *Arachniopsis*

The striking similarity between *Telaranea* s. str. and *Arachniopsis* Spruce (Spruce, 1882) has been noted since the former was first proposed. Spruce (1885, p. 366) distinguished *Arachniopsis* from *Lepidozia chaetophylla*, citing exclusively postical (ventral-intercalary) branching, leaf lobes quite free from one another (or solitary), and the lack of underleaves in *Arachniopsis*. In fact, underleaves are present in all species, but can consist of as few as 2 adjacent cells, each capped by a slime papilla. In others (*A. diacantha*) they are bilobed and caliper-like, resembling those of e.g., *Telaranea herzogii*. Likewise, terminal, *Frullania*-type branching has since been reported from many *Arachniopsis* species. In more recent times, a 2-stratose capsule wall (already noted by Spruce, 1885, p. 354), 8+4 seta (Schuster, 1965), and the proliferation of rhizoids from near the tips of some leaf lobes (Schuster, 1973, p. 388; illustrated by Fulford, 1968, pl. 96, fig. 2h in *A. coactilis*) have been cited as additional characters distinguishing *Arachniopsis* from *Telaranea*.

Only one species of *Telaranea* (*T. herzogii*) has been transferred formally to *Arachniopsis* (Hodgson, 1964). The supposed lack of terminal branching in *Arachniopsis* and the fact that the genus is rare and poorly represented in herbaria have so far precluded discussion of combining the two

genera, although according to Grolle (1975), the type of *Blepharostoma sejuncta* Ångstr. (*Telaranea sejuncta* (Ångstr.) S. Arnell, a name extensively used in the literature as a synonym of *T. nematodes*) is *Arachniopsis diacantha* (Mont.) Howe.

## VII. Evolutionary speculation

Comments regarding evolutionary development in *Telaranea* and related genera are scattered in the literature and relatively few. *Telaranea* sens. str. has been widely regarded as "reduced" from more structurally complex members of the family, with *Arachniopsis* as a "still further departure along the same lines from the *Lepidozia* type" (Howe, 1902, p. 284). Fulford (1963a) likewise referred to a "drastic reduction which has occurred in the *T. sejuncta* evolutionary line," evidenced by a decrease in the number of rows of cortical cells in the stem, reduction in leaf size and complexity (both in number of lobes and in the height and width of the disc), reduction in the size of underleaves, weaker development of thickening bands on the inner wall of the capsule, and a seta with only 8–10 large outer cells.

Fulford (1963a, p. 80) characterized the genus *Telaranea* as "probably the most clearly defined reduction series among the leafy Hepaticae," a "retrogressive evolutionary series of considerable scope." The South American *T. plumulosa* was identified as the "most primitive condition" by virtue of its radial symmetry, with similar leaves and underleaves, and *T. sejuncta* as "the most reduced and most simple species of the series." Schuster (1965, p. 46) considered *Arachniopsis* as derived by loss of terminal branching from *Telaranea*-like ancestors.

In some cases, an evolutionary progression is implied, as, for example, in the diagrams of axial anatomy in Schuster (1984, p. 813, fig. 15 legend). The leaf of subg. *Tricholepidozia* (*T. pulcherrima*, fig. 7) is shown arising from a quadrifid leaf of *Telaranea* (fig. 6), so that "by an accentuation of this process an 8- or even 12-lobed leaf may ensue." For further discussion see section on phylogenetic relationships (p. 232).

Familial placement is no longer in dispute, although some authors (Evans, 1939; Fulford, 1968) formerly placed *Arachniopsis* in the Cephaloziaaceae. Verdoorn (1932) listed *Arachniopsis* as a genus of Trigonanthaceae, together with *Lepidozia*, *Telaranea*, *Zoopsis*, and other genera of Lepido-

ziaaceae in the modern sense. Schuster (1965) regarded the presence of a "cephalozioid" (8+4) seta in *Arachniopsis* as an instance of "secondary and independent reduction."

## *Telaranea* Spruce ex Schiffn.

*Telaranea* Spruce ex Schiffn. in Engler & Prantl, Die Natürl. Pflanzenfam. 1(3,1): 103. 1893, *nom. cons.* *Telaranea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 358, 360, 365. 1885, *nom. inval.* in syn. *Lepidozia* subg. *Telaranea* (Spruce ex Schiffn.) K. Müll. in Rabenh., Krypt.-Fl. 6(2): 276. 1914. (Type: *Lepidozia chaetophylla* Spruce).

*Arachniopsis* Spruce, On Cephalozia 84. 1882, *nom. rejic.* Lectotype (fide Schuster, 1965): *Arachniopsis coactilis* Spruce.

*Neolepidozia* Fulf. & J. Tayl., Brittonia 11: 81. 1959. Type: *Jungermannia capilligera* Schwaegr.

*Acrolepidozia* Schust., J. Hattori Bot. Lab. 26: 254. 1963. Type: *Lepidozia longitudinalis* Herz.

Plants soft-textured and often lax, to  $\pm$  stiff and wiry, to thread-like and minutely prickly, mostly prostrate or creeping, occasionally ascending to suberect, pale, whitish or yellowish to pure green, rarely brownish yellow to rust brown, often nitid, at times glaucous and water repellent. Branching 1(2)-pinnate, usually rather regularly so, the branches predominantly of *Frullania* type, rarely to frequently becoming flagelliform, rarely absent; *Microlepidozia*-type and *Acromastigum*-type branches in some species; ventral-intercalary branches present, leafy or stoloniform, or absent; lateral-intercalary branches rarely present. Stems with 9–18 rows of cortical cells (as few as 4 in some species of sect. *Tenuifoliae*), mostly thin-walled (the exposed wall rarely thickened), forming a conspicuous hyaloderm (up to 30 rows of weakly differentiated cells in sect. *Tricholepidozia*); medullary cells numerous (as few as 1 in some species of sect. *Tenuifoliae*). Rhizoids from basal and/or distal cells of underleaf. Leaves incubously inserted and oriented, varying to transversely inserted or almost longitudinal in some species, rarely weakly succubous, highly variable in form,  $\pm$  symmetrically lobed, 4-lobed (or 4–6-lobed) in most species, 2–3, as few as 1, or as many as 12-lobed (sect. *Tricholepidozia*), the leaves shallowly to deeply divided; branch leaves similar to those of main axis, typically with 1 lobe fewer than stem leaves, in some species the branches differentiated, the branch leaves (and underleaves) differing from those of the stem in insertion and orientation, and form. Lobes ranging from acute, caudate, acuminate to ciliiform, typi-

cally uniseriate for much of their length, to uniseriate almost or quite to the base. Disc (when present) variable, from 2 cells high (consisting of a single tier of cells along the insertion, plus the basal cells of the lobes) to as many as 6(14) cells high, in some species the “disc” consisting of the connate basal cells of the lobes; margins  $\pm$  straight to slightly curved, normally entire (very rarely denticulate by projecting septae). Cells of disc typically in regular rows and tiers, the number of cell rows equal to twice the number of lobes, often large, usually leptodermous, occasionally firm- to evenly thick-walled, often rather turgid, in a few species collapsing on drying; cuticle mostly smooth, in some species variously papillose, finely scabrous (with minute, sharp prickles), or with a uniform glaucous coating. Oil-bodies hyaline or grayish, the surface variable,  $\pm$  homogeneous in some species, coarsely granular in other species, some species coarsely papillose, (4)5–9(12) per cell. Underleaves small and inconspicuous (rarely rudimentary) to large and similar to leaves in form but with fewer, and often shorter lobes; margins entire. Asexual reproduction rare, by tubers or caducous and fragmenting leaf lobes in a few species.

Dioecious, less commonly autoecious. Androe-  
cia either terminal on short to moderately long *Frullania*-type branches or, more often, on short, spicate ventral-intercalary branches from leading shoots; bracts typically monandrous, the antheridial stalk 1- or 2-seriate; bracteolar antheridia lacking. Gynoecia on short ventral-intercalary

branches lacking normal vegetative leaves. Bracts and bracteoles similar, crenulate to dentate, lobulate to shallowly to deeply lobed. Perianth large for plant size, typically assurgent, ovoid to fusiform to cylindrical, terete below, usually bluntly trigonous to shallowly to deeply plicate above (rarely eplicate), gradually or abruptly narrowed to the mouth; perianth surface smooth (very rarely with prorate cells or ciliate); mouth variable, denticulate to shallowly lobulate to lobulate-ciliate to subfimbriate; perianth 2–4(5)-stratose in basal portion, the median portion (1)2(3)-stratose.

Seta with outer layer of 8 cells or exceptionally as few as 4, the inner cells 15–24(34) to 12 or fewer, rarely as few as 6 or 4. Capsule short- or exceptionally long-elliptic, the wall typically 3-stratose, less often 2-, 4-, or 5-stratose; outer layer of cells in tiers, rectangular, with two-phase development, the longitudinal walls with nodule-like thickenings alternating with primary walls devoid of thickenings; innermost cells usually with semi-annular bands, at times forked and anastomosing and delimiting local fenestrae, the bands complete, less often incomplete, or bands weakly developed or lacking, the radial walls with nodular thickenings and short spinelike extensions onto the exposed tangential wall.

Spores (SEM) reticulate-areolate, with enclosed polygonal areolae bounded by a network of low ridges, or papillose-vermiculate, with short discontinuous ridges formed by coalesced papillae, or the surface irregularly roughened. Elaters little tapered, typically bispiral to tips.

### The Genus *Telaranea* in Australasia

#### Key to Australasian Taxa of *Telaranea*<sup>1</sup>

1. Leaves and underleaves with 2–6 lobes; stem with a distinct hyaloderm formed of 6–18 cell rows; capsule wall normally 2–4-stratose ..... 2
2. Leaves (on main shoots) with 4 or more lobes (or if 3-lobed, then with disc present); leaf disc present and variously developed, 2–6 (to 9) cells high, or in deeply divided leaves, with at least one tier of disc cells along the insertion, plus the basal cells of the lobes; leaf lobes 2–4(8) cells wide at base; half-leaf associated with terminal branches with 2 or more lobes (undivided in *T. fragilifolia* and *T. martinii*) ..... 3
3. Lobes caudate, with a broad triangular base abruptly contracted to a uniseriate row, the cells of the uniseriate row distinctly elongated (ca. 4–5:1) and capillary; lobe cells thick-walled in comparison to the cells of the disc, the septa thickened in the corners and swollen ..... 4

<sup>1</sup> An earlier version of this key was sent to R. M. Schuster ca. 1995 as part of a projected “Flora of New Zealand.” That key was appropriated, with minor modifications, by Schuster (2000, p. 212–226). For example, *T. obscura* Engel & Merr., a manuscript name, appears in the key.



4. Leaf disc 7–9 cells high; plants glaucous and water repellent; first branch underleaf undivided, ciliiform, at times inserted on main axis. Tasmania, Australia (NSW) . . . .  
*T. grossiseta* (p. 39)
4. Leaf disc 4–6 cells high (median sinus); plants not glaucous or water-repellent; first branch underleaf of terminal branches mostly bifid (occasionally 3-fid or undivided), uniformly inserted on base of branch. New Zealand (primarily North Island) . . . . .  
*T. gibbsiana* (p. 37)
3. Lobes acute, gradually attenuate to acuminate, the lobe cells shorter (to 3:1, except *T. elegans*); lobe cell walls  $\pm$  equal in thickness to those of disc cells, the septa often thickened in the corners but not swollen (except *T. praenitens*) . . . . . 5
5. Plants glaucous and water repellent; lobe tips (and sometimes disc) fragmenting . . 6
6. Disc cells thin- to firm-walled, larger, to 54  $\mu$ m wide; disc and lobe margins not denticulate; plants whitish, glaucous, larger (to 1 cm wide with branches) . . . . 7
7. Underleaf disc 3–4 cells high; leaf disc margins entire (cells not bulging). New Zealand (primarily South Island) . . . . . *T. tuberifera* (p. 67)
7. Underleaf disc 1–2(3) cells high; leaf disc margins crenulate by bulging cells . . . . . 8
8. Lobes submoniliform throughout, the lobe cells short, barrel-shaped; leaves 4-lobed (or at times 5–6[7]-lobed), not commonly fragmenting (lobes sometimes missing but disc usually intact). Tasmania, Australia (Victoria, NSW) . . . . . *T. centipes* (p. 64)
8. Lobes straight-sided in distal portion; leaves (3)4-lobed, fragmenting, often only portions of disc present. New Zealand (North Island) . . . . .  
*T. perfragilis* (p. 72)
6. Disc cells uniformly thick-walled, smaller, to 45  $\mu$ m wide; disc and lobe margins finely denticulate by projecting upper ends of cells; plants green to olive,  $\pm$  nitid, often not glaucous (except in youngest parts of plant), small (to 6 mm wide with branches). New Zealand (North Island); Australia (NSW, Queensland) . . . . .  
*T. elegans* (p. 61)
5. Plants not glaucous; lobe tips persistent . . . . . 9
9. Disc 14–16 cells wide at the insertion (or if ca. 8, then the disc more than 6 cells high), the leaves often  $\pm$  horizontally inserted and oriented; leaf lobes (4)5–6(8) cells wide at base; cells of disc and lobes  $\pm$  undifferentiated . . . . . 10
10. Disc narrowing to 8(9) cells wide at the insertion; stem cortical cells in 12–14 rows . . . . . 11
11. Median leaf cells 16–26  $\mu$ m wide, evenly thick-walled and firm; branch leaves subfalcate, appearing as if brushed toward tip of branch; leaves on main axis incubously inserted and obliquely oriented. New Zealand (Westland Prov. only) . . . . . *T. pennata* (p. 18)
11. Median leaf cells 24–38  $\mu$ m wide, thin-walled, lacking trigones; branch leaves not subfalcate, not brushed toward branch tip; leaves on main axis distinctly incubous and almost longitudinally inserted and oriented. Tasmania, Australia (Victoria) . . . . . *T. consobrina* (p. 29)
10. Disc (11)14–16(18) cells wide at insertion; stem cortical cells in ca. 24 rows . . . . . 12
12. Flagelliform terminal branches with at most a few normal leaves at base; leaf disc 8–14 cells high (median sinus), often longer than broad; rhizoids originating from basal cells of underleaf disc; leaf lobes often unequal in size: the dorsal smallest, the two ventral lobes larger. Forest species, on soil. Western Australia . . . . . *T. clatruxia* (p. 11)
12. Flagelliform terminal branches leafy for much of their length; leaf disc 6–8 cells high, broader than high; rhizoids originating from underleaves at bases of lobes and distal cells of disc; leaves  $\pm$  symmetrically lobed.

- Hygic, often in bogs. Auckland Is., New Zealand (South Island, unknown N of Westland Prov.) ..... *T. meridiana* (p. 13)
9. Disc typically 8 cells wide at the insertion (6 cells wide in 3-lobed leaves), the leaves transversely to incubously inserted (if horizontally oriented, then leaves glaucous, cf. couplet 5); leaf lobes 4 cells wide at base or fewer; cells of disc and lobes variously differentiated (in size, shape, wall thickening, and cuticle) ... 13
13. Stem leaves all or predominately 3-lobed (or if 4-lobed then plants distinctly glasslike when dry, and appearing etiolated, the leaves shrunken) ..... 14
14. *Microlepidozia*-type branches present; underleaves asymmetrically 3–4-lobed, with one or more lobes abbreviated ..... 15
15. Leaves with lobes persistent, the leaves of main stems 3(4)-lobed, the disc 2–3 cells high; branch leaves mostly 3-lobed; cuticle smooth or finely striate-papillose. Lateral-intercalary branches occasional. New Zealand ..... *T. trilobata* (p. 89)
15. Leaves with lobes freely fragmenting, the leaves on main stems all 3-lobed, the disc 1–1.5 cells high; branch leaves asymmetrically bifid (dorsal lobe shorter); cuticle striolate. New Zealand (North Island, Little Barrier Is.), Tasmania ..... *T. fragilifolia* (p. 90)
14. *Microlepidozia*-type branches absent; underleaves symmetrically lobed (or if asymmetric, 2-lobed, the longer lobe uniseriate, resembling the lobes of the leaves ..... 16
16. Leaf disc 1.5 cells high, with a single tier of cells along the insertion, plus the partially connate basal cells of the lobes; cuticle of leaf lobes minutely scabrous; first branch underleaf undivided. New Zealand (North Island) ..... *T. granulata* (p. 103)
16. Leaf disc 2–4(5) cells high; cuticle of leaf lobes finely striate papillose (*T. remotifolia*) or smooth; first branch underleaf bilobed, often asymmetrically ..... 17
17. Leaves 3–4-lobed, shrunken and glass-like when dry, the lobes often sharply decurved and clawlike; branch half-leaf bilobed; stems fleshy, with cortical cells in 10–13 rows, the medullary cells in 17–25 rows; dioecious. New Zealand (sporadic on South and North Islands) ..... *T. remotifolia* (p. 73)
17. Leaves on main shoot consistently 3-lobed, the lobes  $\pm$  straight, not clawlike; branch half-leaf undivided; stems slender, with 9 cortical cells, the medullary cells in 9–10 rows; monoecious. New Zealand ..... *T. martinii* (p. 98)
13. Stem leaves 4–6-lobed, never 3-lobed on main shoots; plants not glasslike, not etiolated in aspect, the leaves not appearing shrunken. Lobes not clawlike, about equal in size ..... 18
18. Leaf disc 1.5–3(4) cells high ..... 19
19. Cuticle of leaf lobes smooth ..... 20
20. Basal tier of disc cells small, short-rectangular to quadrate; *Microlepidozia*-type branches present; underleaves asymmetrically lobed, with 1 or more lobes abbreviated. New Zealand, Tasmania ..... *T. pallescens* (p. 87)
20. Basal tier of disc cells narrowly elongate; *Microlepidozia*-type branches not produced; underleaves symmetrically lobed ... 21
21. Disc of stem leaves (incl. basal tier of lobe cells) 2 (rarely 3) cells high; cells of uniseriate row of leaf lobes straight-sided and without or with weakly protruding septa, the cells thicker walled than those of disc; leaves (except var. *complanata*) of both stems and branches widely spreading to squarrose, typically transversely inserted and oriented

- (branch leaves at times weakly incubous); stem medullary cells thick-walled, in 40–67 rows; branches (except var. *complanata*) terete; sporophytes common. New Zealand (common throughout) . . . . . *T. lindenberghii* (p. 80)
21. Disc of stem leaves 3(4) cells high (rarely 2); cells of uniseriate row of leaf lobes typically constricted at the septa, the cells not noticeably thicker walled than those of disc; leaves of both stems and branches obliquely spreading, incubously inserted and oriented; stem medullary cells thin-walled, in 18–36 rows; branches complanate; sporophytes unknown. New Zealand (primarily South Island) . . . . . *T. tetradactyla* (p. 91)
19. Cuticle of leaf lobes scabrous, roughened by minute,  $\pm$  evenly spaced, sharp prickles. Australia (NSW, Queensland) . . . . . *T. quadriseta* (p. 95)
18. Leaf disc 4 or more cells high from medium sinus base to leaf base . . 22
22. Leaves densely areolate, the cells small (18–40  $\mu\text{m}$  wide in median disc), never turgid and pillow-like, typically firm-walled, trigones often present, small to medium . . . . . 23
23. Cells of uniseriate row of leaf lobes with septa thickened and projecting; disc margins (especially the dorsal) minutely serrulate by projecting distal ends of cells. Cuticle of lobe cells finely to distinctly striate-papillose. New Zealand (widespread) . . . . . *T. praeinitens* (p. 32)
23. Cells of uniseriate row of leaf lobes with septa thickened but not distinctly swollen and projecting; disc margins entire . . . . . 24
24. Leaves transversely inserted, palmately divided to 0.6; cells of uniseriate row of lobes elongate (to 2.3:1). Tasmania . . . *T. palmata* (p. 31)
24. Leaves incubously (to almost longitudinally) inserted and oriented, not palmately lobed; cells of uniseriate row of lobes isodiametric to short rectangular (to 1.3:1) . . . . . 25
25. Branch leaves asymmetrically lobed, subfalcate and swept toward the tip of branch, the dorsal lobe smallest . . . . . 26
26. Leaf lobes 4(5) cells wide at base, often with up to 3 additional 4-celled tiers, the lobe tips not caducous; disc 15–16 cells wide in distal portion, the disc cells 16–24  $\mu\text{m}$  wide. Australia (New South Wales) . . . . . *T. quadristipula* (p. 20)
26. Leaf lobes biseriate at the base, at most with an additional biseriate tier, the lobe tips often caducous; disc 8 cells wide throughout, the disc cells 26–32  $\mu\text{m}$  wide. Australia (Queensland) . . . . . [ *T. disparata* p. 147 ]
25. Branch leaves not or only weakly asymmetrically lobed, not subfalcate . . . . . 27
27. Cuticle of leaf disc distinctly papillose, the papillae hemispherical near lobe bases and distinctly elongated and striolate below; branch leaves strongly incubous to almost laterally inserted, the median dorsal cortical cells  $\pm$  exposed. Australia (Queensland) . . . . . [ *T. verruculosa* p. 197 ]
27. Cuticle of leaf disc smooth (except *T. patentissima*

- var. *zebrina*); branch leaves moderately to distinctly incubous, but the insertion reaching the branch midline . . . . . 28
28. Disc cells small, the largest to 25  $\mu$ m wide, the areolation dense, the cells somewhat irregularly arranged; branches complanate, wider than the main shoot, the branch leaves typically closely and regularly shingled. Tasmania, Australia (Victoria, Queensland), Campbell and Auckland Is. (rare) . . . . . *T. tridactylis* (p. 24)
28. Disc cells larger, the largest to 40  $\mu$ m wide, the areolation more ordered and regular (cells in  $\pm$  regular rows and tiers); branches not complanate, the branch leaves not tightly shingled . . . . . 29
29. Lobe cells thin- to moderately thick-walled, with septa thickened in the corners; disc cells with small but distinct trigones; lobes about equal to or shorter than the disc, the uniseriate row 2–4(5) cells long (typically less than half the length of lobe). Cuticle of leaf lobes often striate-papillose. New Zealand, Tasmania, Australia (NSW, rare) . . . . . *T. patentissima* (p. 46)
29. Lobe cells distinctly and evenly thick-walled; disc cells with walls evenly thickened, lacking trigones; lobes longer than the disc, the uniseriate row 4–5(6) cells long (more than half the length of lobe). Cuticle of leaf lobes smooth. Tasmania . . . . . *T. capilligera* (p. 17)
22. Leaves laxly areolate, the cells larger (40  $\mu$ m or more wide in median disc), often appearing turgid and distinctly pillow-like (even under low magnification), typically  $\pm$  thin-walled and with trigones lacking . . . . . 30
30. Leaves (disc)  $\pm$  symmetrical; leaf lobes acute to acuminate, with 1–2 tiers of paired cells at base; disc cells isodiametric . . . . . 31
31. Cells in median sector of disc thin-walled, to (45)50–70  $\mu$ m wide; uniseriate portion of leaf lobe 5–6 cells long; plants varying from medium to robust (to 1.5 cm wide), highly nitid; disc weakly to distinctly cuneate and (9)14–21 cells broad distally (approaching 8 cells wide throughout in var. *roseana*). New Zealand (common) . . . . . *T. tetrapila* (p. 52)
31. Cells in median sector of disc evenly thick-walled and firm, rather dense, to 38  $\mu$ m wide; uniseriate portion of leaf lobe short, 2–3 cells long; plants small and stenotypic in stature, ca. 0.6 cm wide (including branches), rather dull; disc subquadrate, 8(9) cells wide throughout. Auckland Is., New Zealand (South Island and extreme southern sector of North Island) . . . . . *T. hodgsoniae* (p. 45)
30. Leaves (disc) asymmetrical; leaf lobes long attenuate, often falcate and hooked at the tips, with 3–5 tiers of paired cells at base; disc cells  $\pm$  elongate. New Zealand . . . . . *T. paludicola* (p. 60)

2. Leaves with 2–3 lobes, deeply divided; leaf “disc” formed of the partly connate basal lobe cells and lacking a tier of disc cells along the insertion; leaf lobes from a 1-seriate or biseriate base; half-leaf undivided ..... 32
32. Stems appearing fleshy, the cortex in 9–10 cell rows and the medulla in 18–24 rows; leaf lobe bases biseriate, the paired cells elongate, connate for more than 0.5 their length, the cells of the uniseriate row barrel-shaped, constricted at septa; underleaves 3–4 lobed. Alpine tussock grassland plant. New Zealand ..... *T. nivicola* (p. 102)
33. Stems slender and wiry, the cortex in 6–9 cell rows and the medulla in 6–12(18) rows; leaf lobes uniseriate or biseriate at base, the basal cells connate for 0.1–0.4 their length, the cells of the uniseriate row with septa thickened at the corners, feebly swollen; underleaves bilobed. Lowland plants ..... 33
33. Underleaves typically asymmetrically bilobed, the longer lobe resembling a leaf lobe, with a uniseriate row 4(5) cells long, the other abbreviated, with a pair of short basal cells, a  $\pm$  elongated cylindrical cell, capped by a slime papilla; *Microlepidozia*-type and lateral-intercalary branches present. New Zealand .... *T. quinquespina* (p. 109)
33. Underleaves symmetrically bilobed, small and caliper-like; *Microlepidozia*-type and lateral-intercalary branches absent ..... 34
34. Lobes not tapering, flexuous, 6–9 cells long; first branch underleaf equally and symmetrically bilobed; leaves consistently bilobed, the lobes unequal in length; lobe cells about equal in length, the terminal cell small and button-like; cortical cells moderately and evenly thick walled. New Zealand, Tasmania ..... *T. inaequalis* (p. 117)
34. Lobes tapering, stiff, (4)5–6 cells long; first branch underleaf asymmetrically bilobed, one lobed long and divergent, the other short and appressed, resembling an underleaf lobe; leaves 2–3-lobed, when bilobed the lobes  $\pm$  equal in length; lobe cells gradually shorter toward tip, the terminal cell not small and button-like; cortical cells thin walled ..... 35
35. Leaf lobes uniseriate to base (only sporadically with 1 or more lobes biseriate at base), the basal cell 95–120  $\mu$ m long. New Zealand, Tasmania, Australia (Victoria) ..... *T. herzogii* (p. 112)
35. Leaf lobes nearly always biseriate at base, the paired cells of the basal tier 54–74  $\mu$ m long. Tasmania ..... *T. tasmanica* (p. 106)
1. Leaves with 8–12(13) lobes; stem with a weakly differentiated hyaloderm of ca. 24–28 cell rows; capsule wall 5-stratose. New Zealand (Stewart Is., Southland and Westland Prov. of South Is.), Tasmania, Australia (rare in Victoria) ..... *T. pulcherrima* (p. 76)

## Taxonomic Treatments

### *Telaranea* subg. *Acrolepidozia* (Schust.) Schust.

*Acrolepidozia* Schust., J. Hattori Bot. Lab. 26: 254. 1963. *Telaranea* subg. *Acrolepidozia* (Schust.) Schust., J. Hattori Bot. Lab. 36: 389. 1973 (1972). *Telaranea* subg. *Acrolepidozia* (Schust.) Schust., Hep. Anthoc. N. Amer. 2: 30. 1969, *nom. inval. basionym non cit.* Type: *Lepidozia longitudinalis* Herz.  
*Telaranea* sect. *Latifoliae* Engel & Merr., Phytologia 79: 251. 1996 (1995). Type: *Lepidozia meridiana* Hodgs.

Note that “sect. *Meridianae*” (Schuster, 2000, p. 212), was a provisional name for the section published by Engel and Merrill (1996) as Sect. *Latifoliae*.

For a discussion of subgenera and sections and their distinguishing characteristics, see the phylogenetic section which follows (p. 232).

### *Telaranea clatritexta* (Steph.) Engel & Merr.

*Lepidozia clatritexta* Steph., Spec. Hep. 3: 583. 1909. *Neolepidozia clatritexta* (Lindenb.) Fulf. & J. Tayl., Brittonia 11: 85. 1959. *Telaranea clatritexta* (Steph.) Engel & Merr., Novon 9: 339. 1999. Type: Australia, Western Australia, Swan River, Drummond, ex Herb. Kew (G!).  
*Lepidozia whiteleggeana* Steph., Spec. Hep. 3: 584. 1909, *syn. nov.* Type: Australia, Cook River, Botany Bay, *Whitelegge*, comm. F. v. Müller No. 34 (G!).  
*Lepidozia complanata* Herz., Memoranda Soc. Fauna Fl. Fenn. 27(1950–1951): 92. f. 39. 1952, *syn. fide* Engel & Merrill, 1999. *Telaranea complanata* (Herz.) Engel & Merr., Phytologia 79: 251. June,

1996 (1995). Type: Australia, Western Australia, without specific loc., Goebel (M—*non vidi*); isotype: (JE!).

Plants soft and flexuous, complanate and resembling *T. centipes*, loosely creeping, in rather dense mats, pale green, highly nitid when dry, with age becoming dull and opaque brown; plants medium, to 1.0 cm wide, including branches. Branching rather regularly and laxly 1-pinnate, often with numerous long, geotropic flagelliform branches (to 2 cm long), which have few or no normal leaves at the branch base, the branches nearly exclusively of the *Frullania*-type; branch half-leaf shallowly 2(3)-fid, obliquely inserted and in axil of main axis and branch, narrowly rectangular to elliptic; first branch underleaf undivided and subulate (or less often to 3-lobed), longitudinally inserted on ventral-lateral side of main axis at or somewhat below branch base. *Acromastigium*-type branches sporadic, stoloniform, the branch half-underleaf shallowly bifid. Ventral-intercalary branches sporadic, leafy. Stems with cortical cells rather weakly differentiated, thin walled, in 15–26 rows; cortical cells in section moderately larger than the numerous (to ca. 95) medullary cells, the medullary cells moderately thin-walled, the walls finely pitted. Leaves on main shoot rigid, distant to loosely imbricate, when dry with margins revolute (the leaves appearing channelled), when moist the leaves widely spreading, the disc plane or nearly so but the lobes somewhat ventrally decurved, the leaves strongly longitudinally inserted and oriented in well-developed shoot sectors and nearly in same plane as dorsal surface of stem; leaves 455–645  $\mu\text{m}$  wide  $\times$  610–750  $\mu\text{m}$  long, rather asymmetrically 4(6) lobed to (0.25)0.3–0.45, the lobes tending to subdivide, straight to feebly convergent, often distinctly shorter than the disc. Lobes narrowly attenuate, sporadically weakly acuminate, the dorsal lobe at times smallest and the two ventral lobes larger, the largest lobes 5–6(7) (rarely 4) cells wide at extreme base, tapering to a short uniseriate row of 2–3(4) cells; lobe cells  $\pm$  isodiametric to somewhat elongate, thin- to  $\pm$  thick-walled, the cell walls of uniseriate row not much thickened in the corners, the basal cell of the uniseriate portion 20–36  $\mu\text{m}$  wide  $\times$  24–38  $\mu\text{m}$  long (0.9–1.5:1), the next cell slightly narrower and shorter, 18–30  $\mu\text{m}$  wide  $\times$  18–31  $\mu\text{m}$  long (0.8–1.6:1), the terminal cell shorter than the penultimate cell, short conical and rounded at the tip; cuticle smooth. Disc variable:  $\pm$  symmetrically

broad- to narrow-rectangular, (6)8–14 cells high (from median sinus base to leaf base), wider than high to higher than broad, 14–22 cells wide in distal portion narrowing to (10)14–16(18) cells wide in basal portion; dorsal margin gently curved and subcordate at the base, the ventral  $\pm$  straight, entire or rarely with a small accessory lobe or tooth, often strongly decurrent. Cells of disc thin- to slightly and evenly thick-walled or the free wall at margins  $\pm$  thickened, trigones lacking to minute, the median cells elongate, 28–39(43)  $\mu\text{m}$  wide  $\times$  53–65  $\mu\text{m}$  long, the cells in  $\pm$  regular longitudinal rows, not noticeably tiered; basal row of disc cells somewhat larger; cuticle smooth. Underleaves variable in size, ca. 0.8–2 $\times$  the stem in width, strongly spreading, distant, plane or slightly convex, 4(6) lobed to 0.3–0.45, the lobes straight to curved at the tips, weakly divergent, highly variable, the lobes consisting of a base of 2(3) cells, sporadically with a biseriate tier above the base, and a uniseriate row of 2–3(4) not or somewhat elongate cells, or the lobes narrowly acute, 4–5 cells wide at base and resembling the leaf lobes, terminating in a slime papilla; disc symmetrically subrectangular (wider than high), variable in height and width, 3–6(7) cells high (median sinus), 12–15(19) cells wide at widest point; margins entire. Rhizoid initial cells small, subquadrate, forming a bistratose pad or band at the base of the disc. Asexual reproduction by clavate tubers at the tips of stonoliferous branches.

Dioecious. Androecia not seen. Gynoecia strongly dorsally assurgent, slightly swollen and sparsely rhizoidous at base; bracts of innermost series erect to appressed to the perianth, ovoid to elliptic to subrectangular,  $\pm$  regularly but unequally 4(6)-lobed to 0.3–0.4, the lobes narrowly attenuate, 4–6 cells wide at base, ending in a single cell or a short uniseriate row of 2–4 cells, the terminal cell with a rounded tip or surmounted by a slime papilla, the lobe margins sporadically with a 1-several-celled tooth; lamina composed of lax,  $\pm$  regularly elongate-rectangular cells, the marginal cells similar, the margin with several sessile slime papillae, otherwise entire; bracteole of innermost series smaller but similar in form to bracts. Perianth ca. 0.75 emergent, stout cylindric, terete in basal sector, the distal sector trigonous, with 3 distinct plicae, narrowing toward the contracted mouth; mouth shallowly ca. 10–12 lobulate, the cells thin-walled but firm, the lobules ending in a single elongate cell or in a uniseriate row of 2 cells, then with the transverse septa thickened in the corners and weakly swollen and

projecting, the terminal cell broadly rounded, not ending in a slime papilla; perianth 4–5-stratose in basal portion, the median and upper portions 1-stratose.

Sporophyte not seen.

**DIFFERENTIATION AND VARIATION**—The original description and figure of *T. complanata* (Herzog, 1952) gives only a hint of the extreme variability of this species. The impression given is of a plant “aus der Verwandtschaft von *L. centipes*,” as noted by Herzog (ibid., p. 93): subsymmetrical, elongate rectangular leaves, divided to the middle, slender leaf lobes that are 3–4 cells wide at the base, small underleaves with a low disc (2 cells high) and short uniseriate lobes. All of the above features vary considerably. Our study of a number of specimens from several localities in Western Australia has resulted in a considerable broadening of our concept of the species. In particular, the leaves are often distinctly broader than long, shallowly divided, with the lobes 5–6(7) cells wide at the base. The underleaves are often twice the width of the stem, up to 6 cells high (at median sinus), with lobes 4–5 cells wide at the base, and resembling those of the leaves.

Despite a superficial resemblance to *T. centipes*, on closer examination the leaves are strikingly like those of *T. meridiana* in form, areolation, and mode of insertion. In particular, the leaves are typically 14–16 cells wide at the insertion (Fig. 1: 2, 3), with broad lobes, leptodermous cells, and a weakly differentiated hyaloderm (Fig. 1: 11). Unlike *T. meridiana*, however, most plants show at least a tendency toward the curious leaf symmetry seen in *T. pennata*, with the dorsal lobe smallest and the ventral lobes largest and  $\pm$  paired. The similarities between the species of subg. *Acrolepidozia*, with their highly fragmented distribution, argues a considerable antiquity for these very un-*Telaranea*-like species.

A highly unusual feature of this species, apart from its variability, is the production of abruptly long-flagelliform, strongly positively geotropic, terminal branches, which resemble the ventral-intercalary stoloniform branches of many *Bazzania* species (Fig. 1: 1).

This remarkable species has a disjunct distribution in Western Australia and in New South Wales, where it is represented by the type of *L. whiteleggeana*. The latter is a luxuriant plant with stems (as noted by Stephani) to 5 cm long. The leaves are 12–14 cells wide along the insertion, the lobes are 4–5 cells wide at the base, and the

disc is up to 11 cells high. Regrettably, the identity of *L. whiteleggeana* was not known to us at the time the combination based on *L. clatritexta* was made (Engel and Merrill, 1999). The type of *Lepidozia clatritexta* consists of only three stems, and it is a weakly developed expression of the species. The leaves are described as 8 cells wide, but in fact the disc is 10 cells wide at the insertion and 14–17 cells wide in the distal portion. The leaf lobes are 4(5) cells wide at the base. Nevertheless, the distinctive features of this taxon are expressed, namely, the abruptly flagelliform terminal branches, the longitudinally inserted leaves, and underleaves with rhizoids originating from the basal cells of the disc.

**DISTRIBUTION AND ECOLOGY**—Disjunct in New South Wales and in Western Australia. In the west, the species is found from near sea level to 650 m, in forests of *Eucalyptus calophylla*, *Acacia alata*, *Jacksonia*, or of kauri. The species occurs over soil (typically loamy) in humid situations, e.g., shaded banks, stream banks, protected sites near cascades or in boulder fields.

**SELECTED SPECIMENS SEEN**—AUSTRALIA. WESTERN AUSTRALIA: Churchman Brook, off Soldier's Road, Roleystone, just below Churchman Brook Reservoir, SE of Perth, 90 m, *Engel 13319* (F); Darling Range, Little Dandalup Creek, near intersection of Torrens Road with Delpark Road, *Engel 13356* (F); The Cascades, Lefroy Brook, S of Pemberton, *Engel 13418* (F); Walpole-Nornalup Natl. Park, near intersection of Hilltop and Gully Roads, *Engel 13425* (F); ibid., Brainy cutoff near intersection with Tingle Drive East, just beyond bridge over Frankland River, *Engel 18436* (F); Porongurup Natl. Park, Porongurup Range, Devils Slide, 440–650 m, *Engel 13476* (F); Waterfall Beach, Two Peoples Bay Nature Reserve, 30 km E of Albany, *Stoeneburner & R. Wyatt 3680* as *T. centipes* (MELU).

*Telaranea meridiana* (Hodgs.) Hodgs.

*Lepidozia meridiana* Hodgs., Trans. Roy. Soc. New Zealand 83: 611, pl. 2, f. 24. 1956. *Telaranea meridiana* (Hodgs.) Hodgs., Rec. Domin. Mus. 4: 107. 1962. Type: Auckland Is., “Cape Expedition,” No. 2 Camp, 31 Oct. 1944, *Turbott s.n.* (CHR!).

Plants soft and flexuous, brittle, ascending to suberect, in dense cushions, pale green, nitid when dry; shoots medium, to 1.3 cm wide, including branches. Branching somewhat regularly but loosely 1(2) pinnate, often becoming flagelliform, the branches typically flexuous and somewhat contorted, of the *Frullania*-type; branch half-leaf 2-lobed, distinctly obliquely inserted, narrowly rectangular, the lobes  $\pm$  parallel; first

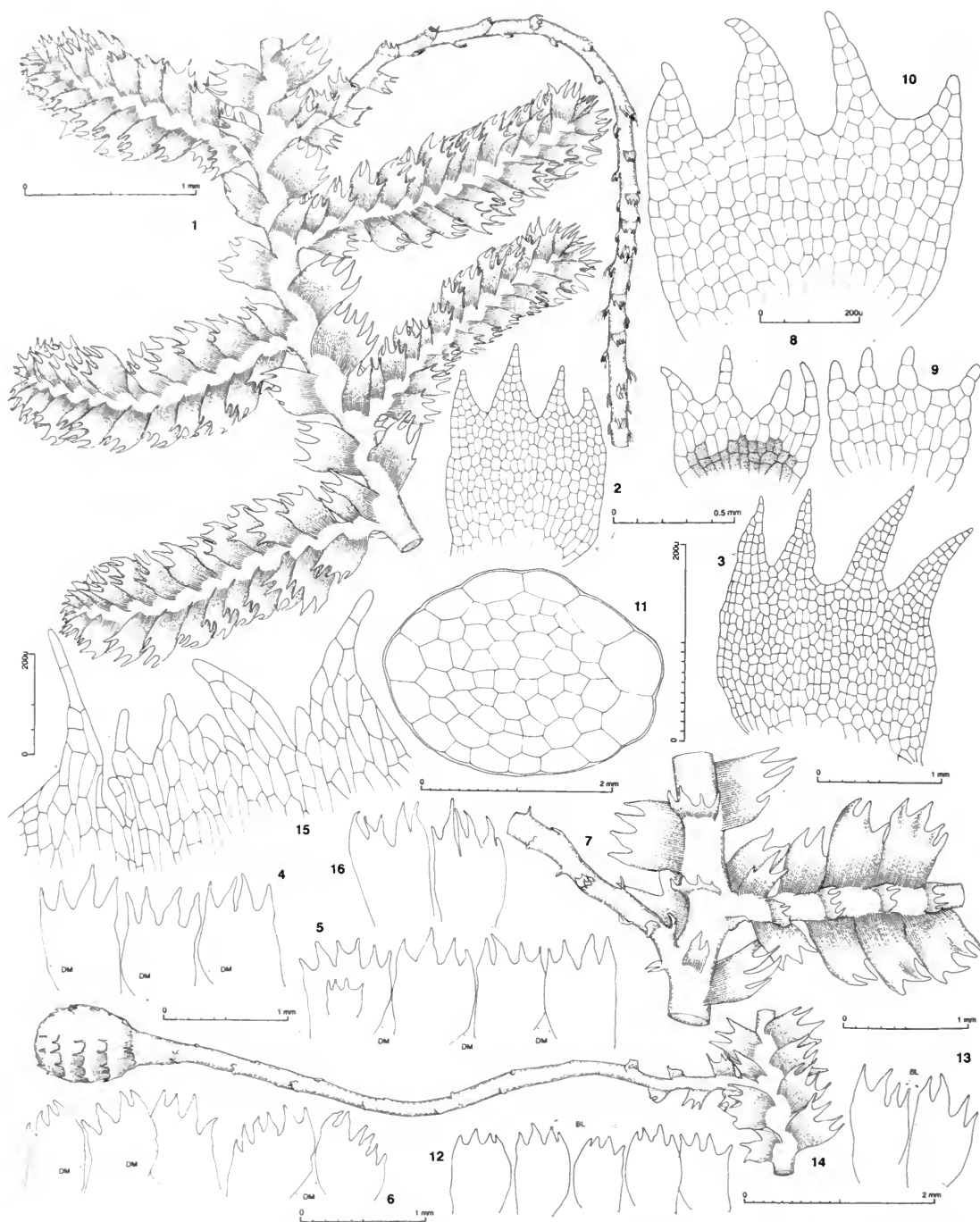


FIG. 1. *Telaranea clatritexta* (Steph.) Engel & Merr. 1. Sector of main shoot with *Frullania*-type branches, one, at upper-right, becoming long flagelliform, dorsal view. 2, 3. Leaves, cellular detail. 4-6. Leaves (dm = dorsal margin; fig. 5 with an underleaf at left at same scale). 7. Main shoot with *Acromastigum*-type stoloniform branch (at left; note half-underleaf) and *Frullania*-type branch (at right). 8-10. Underleaves, cellular detail, showing variation in size and lobe development; stippled cells are those that each give rise to a rhizoid. 11. Stem, cross section. 12-13. Primary branch leaves (= bl). 14. Basal portion of shoot showing stoniferous branch and a tuber. 15. Portion of perianth mouth. 16. Gynoeceal bracts. (Figs. 1-2, 5, 7, 9, 11, 14-16 from Engel 13425, Australia, Western Australia, Walpole-Nornalup Natl. Park, near intersection of Hilltop and Gully Roads; 3-4, 10, 13 from Engel 13446, same loc.; 6, 8, 12 from Engel 13418, Australia, Western Australia, The Cascades, Lefroy Brook.)



branch underleaf undivided, broadly acuminate (rarely bilobed), inserted on ventral-lateral side of branch at juncture of branch and main axis, grading to longitudinally inserted on stem just below the branch. Ventral-intercalary branches not seen. Stems with cortical cells rather weakly (on strongest main axis) to distinctly differentiated, thin walled, in 17–24 rows; cortical cells in section slightly to distinctly larger than the numerous (ca. 120) medullary cells, the medullary cells moderately thin walled, the walls finely pitted. Leaves on main shoot rigid, widely spreading, distant to contiguous (on compact shoots), the disc plane or nearly so, rarely convex, the lobes ventrally decurved and claw-like (not visible in dorsal view), the insertion incubous (on elongated main shoots the leaves often strongly longitudinally inserted and oriented, with the disc broader than high and nearly in same plane as dorsal surface of stem); leaves 520–700  $\mu\text{m}$  wide  $\times$  545–770  $\mu\text{m}$  long, the leaves 4(6) lobed to 0.4–0.6, the lobes straight to feebly divergent, slightly shorter than the disc. Lobes weakly acuminate, the largest leaf lobes (4)5–6(8) cells wide at extreme base, 4–5 cells wide for 4–5 tiers, biseriate for 1–2 tiers, terminating in a short uniseriate row of 2–3(4) cells; lobe cells  $\pm$  isodiametric to short rectangular, thin-walled, the cell walls of the uniseriate row not or very weakly thickened in the corners, the basal cell of the uniseriate portion 18–29  $\mu\text{m}$  wide  $\times$  23–36  $\mu\text{m}$  long (1–1.5:1), the next cell 14–24  $\mu\text{m}$  wide  $\times$  17–26  $\mu\text{m}$  long (1–1.5:1), the terminal cell normally about equal to the penultimate cell in length or a little shorter, tapering to the apex; cuticle smooth, rarely feebly striate papillose. Disc moderately asymmetrically rectangular, the dorsal margin longer than the ventral, 6–8 cells high (from median sinus base to leaf base), 21–24 cells wide in distal portion narrowing to (11)14–16 cells wide in basal portion; margins entire, the dorsal margin straight or weakly subcordate at the base, the ventral straight. Cells of disc thin-walled, trigones lacking, the median cells elongate, 30–42  $\mu\text{m}$  wide  $\times$  38–51  $\mu\text{m}$  long, the cells in  $\pm$  irregular rows; basal row of disc cells somewhat larger; cuticle smooth. Underleaves much smaller than leaves, ca. 1–1.2 $\times$  stem width, firmly inserted, strongly spreading, distant, plane, 4(6) lobed to 0.35–0.65, the lobes straight to curved at the tips, acuminate, 3–4 cells wide for 1–several tiers at base and biseriate for 2–3 tiers, ending in two laterally juxtaposed cells, or more commonly in a uniseriate row formed of 2(3) short cells, terminating in a slime papillae;

disc symmetrically subrectangular (wider than high), 5–6 cells high (median sinus), 15–18 cells wide at widest point, the cells  $\pm$  regularly arranged; margins entire, moderately curved. Rhizoid initial cells small, subquadrate, forming a continuous bistratose pad or band often including the basal portion of the lobes as well as the apex of the disc. Asexual reproduction lacking.

Plants dioecious. Androecia either on short *Frullania*-type branches with a few cycles of reduced leaves prior to androecial formation, or on short, abbreviated, ventral-intercalary branches from leading shoots; bracts closely imbricate, dorsally assurgent, deeply concave, 2-lobed, the lobes acuminate, terminating in a uniseriate row of 2 not or hardly elongated cells; lamina cells irregular in arrangement, the dorsal margin of lamina feebly dilated and slightly incurved, entire or crenulate, devoid of slime papillae; bracts monandrous; antheridial stalk short, ca. 6 cells high, biseriate; bracteolar antheridia absent. Gynoecia not seen.

**DIFFERENTIATION AND VARIATION**—In its most characteristic expression (well represented by the type), *T. meridiana* is a distinctive plant, very un-*Telaranea* like in aspect. Particularly diagnostic are the flexuous, rather loosely pinnate shoots, and the broad-based, longitudinally inserted and oriented leaves (particularly on elongated main shoots, Fig. 2: 1), which may be up to 16 cells wide in the basal sector. Also distinctive are the broad lobes, (4)5–6(8) cells wide at base, which are ventrally decurved and claw-like, and the uniform, dense areolation of the disc and lobes. In more compact expressions (e.g., *Child H3669*), however, the insertion is variable, from distinctly to rather weakly incubous, and the leaves are rather markedly convex (Fig. 2: 6).

**DISTRIBUTION AND ECOLOGY**—Known only from Auckland Is. and South Island, New Zealand (unknown north of Westland Prov.). The species occurs at lower to median elevations, and is primarily terricolous in damp or boggy sites on the forest floor. It less commonly is found in rather open sites, such as in low, mucky niches in swampy areas with *Sphagnum* and scattered *Lepidospermum*, etc., at sea level just north of the Haast River. At Ship Creek (north of the Haast River) it grows in low, wet areas just above the water level in a mature kahikatea (*Dacrycarpus dacrydioides*) swamp forest. In the Lake Kaniere area (125 m, Westland) the species is very common on saturated, rich, peaty soil in and espe-

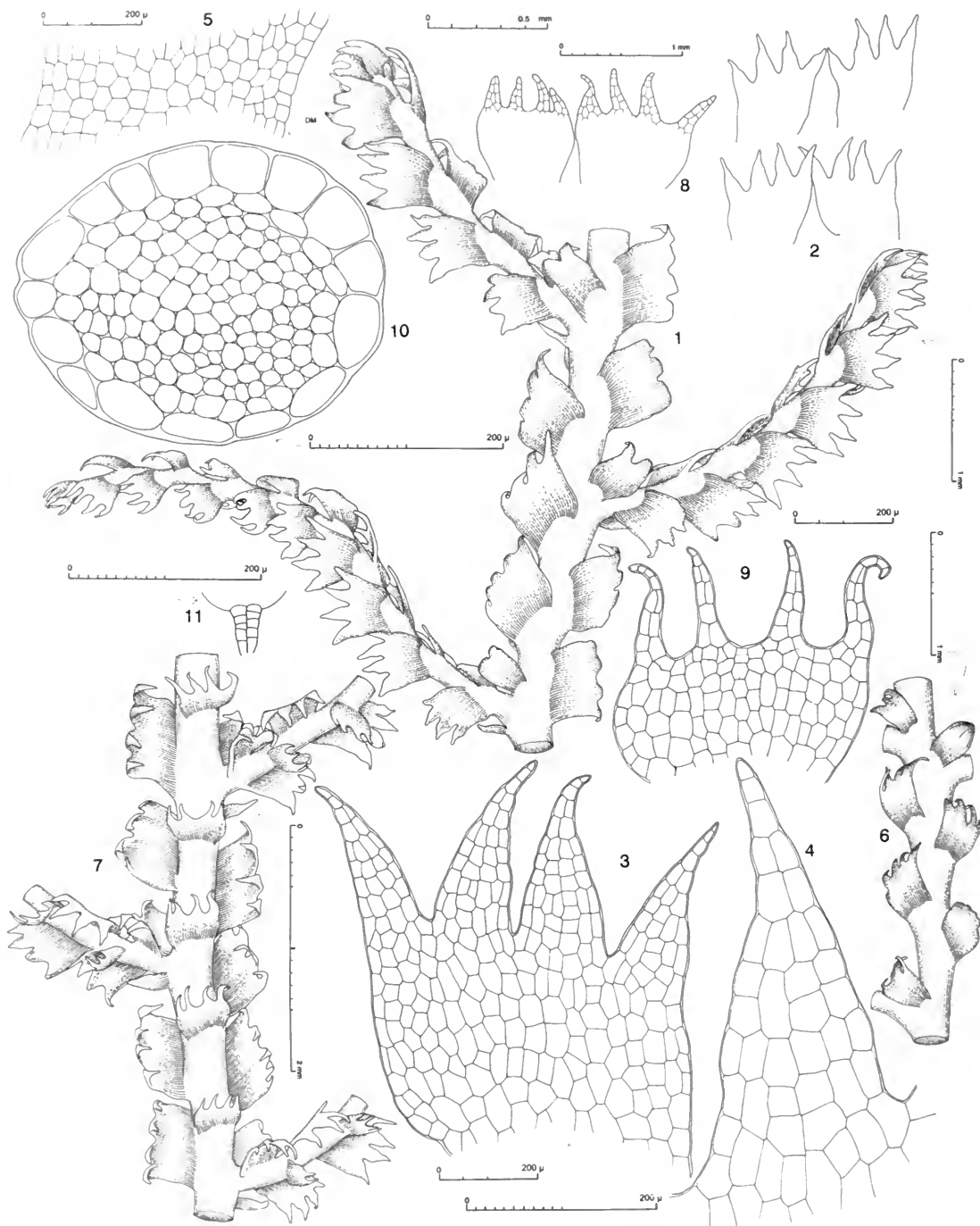


FIG. 2. *Telaranea meridiana* (Hodgs.) Hodgs. 1. Sector of main shoot, dorsal view. 2. Leaves. 3. Leaf, cellular detail. 4. Leaf lobe. 5. Leaf base (dm = dorsal margin). 6. Shoot sector of vigorous plant, dorsal view. 7. Sector of main shoot, ventral view. 8. Underleaves. 9. Underleaf, cellular detail, stippled cell walls indicate rhizoid initials. 10. Stem, cross section. 11. Antheridial stalk. (Figs. 1–4, 7–10 from type; 5 from *Johnson 175*, New Zealand, South Is., Southland Prov., Lake Manapouri; 6, from *Child H3669*, New Zealand, South Is., Westland Prov., Mahinapua; 11 from *Child H3101*, New Zealand, South Is., Otago Prov., Mt. Cargill.)

cially at the edges of narrow, shallow,  $\pm$  stagnant pools in the shade of a mixed podocarp-broadleaf forest. Vegetation at this site consists of *Dacrydium cupressinum*, *Weinmannia racemosa*, *Podocarpus totara*, *Metrosideros umbellata* and an open understory dominated by *Pseudowintera*. It also occurs in pakihis under rushes, etc., associated with *Sphagnum*. The species is associated with a variety of other hepatics that occur in forest niches, e.g., *Telaranea tetradactyla*, *Lepidozia procera*, *L. spinosissima*, *L. laevifolia*, etc.

SPECIMENS SEEN—NEW ZEALAND. SOUTH ISLAND. SOUTHLAND PROV.: Hope Arm, Lake Manapouri, ca. 185 m, *Johnson 175* (CHR); Fiordland Natl. Park, Stuart Mts., W shore of Lake Thomson N of stream draining from Lake Wade, 300 m, *Fife 7782* (F). OTAGO PROV.: Blue Mts., S end, E of Garden Gully Road, ca. 610 m, *Child s.n.153* (F); W slope of Flagstaff, NW of Dunedin, 490–520 m, *Engel 17624* (F); Mt. Cargill, N of Dunedin, ca. 455 m, *Child H3101*—c.  $\delta$  as *Lepidozia laevifolia* (F); Lee Stream, ca. 305 m, *Child H2504* as *T. gottscheana* (F); Lammermoor Range, ca. 610 m, *Child H3855* (F); N of McKerrow River, Martin's Bay, *Hatcher 760, 853* (F). WESTLAND PROV.: Ca. 4 km N of Haast River, sea level, *Engel 21770* (F); Ship Creek, 14.5 km N of Haast River, sea level, *Engel, 21726*, (F); near Lake Paringa, near west coast, ca. 15 m, *Child H1796, 1801* as *Lepidozia microphylla* (F); Mt. Aspiring Natl. Park, Cross Creek, 1.1 km N of Haast Pass, 540 m, *Engel 21876* (F); Mahinapua, S of Hokitika, ca. 60 m, *Child H3669* as *L. microphylla* (F); Lake Kaniere Scenic Reserve, Lake Kaniere Rd, 125 m, *Engel 24881* (F); 10 km S of Greymouth, ca. 150 m, *Child H4947* (F).

### *Telaranea* subg. *Telaranea*

*Telaranea* sect. *Neolepidozia* (Fulf. & J. Tayl.)  
Engel & Merr., comb. nov.

*Neolepidozia* Fulf. & J. Tayl., *Brittonia* 11: 81. 1959.  
*Telaranea* subg. *Neolepidozia* (Fulf. & J. Tayl.)  
Schust., J. Hattori Bot. Lab. 26: 255. 1963. *Lepidozia* sect. *Neolepidozia* (Fulf. & J. Tayl.) Piippo, *Ann. Bot. Fennici* 21: 314. 1984. Type: *Jungermannia capilligera* Schwaegr.

*Telaranea capilligera* (Schwaegr.) Schust.

*Jungermannia capilligera* Schwaegr., *Hist. Musc. Hep. Prodr.* 21. 1814. *Lepidozia capilligera* (Schwaegr.) Lindenb. in G. L. & N., *Syn. Hep.* 204. 1845. *Mastigophora capilligera* (Schwaegr.) Trev., *Mem. Ist. Lomb. Sci. Lett.* III. 4: 416. 1877. *Neolepidozia capilligera* (Schwaegr.) Fulf. & J. Tayl., *Brittonia* 11: 84. 1959. *Telaranea capilligera* (Schwaegr.) Schust., J. Hattori Bot. Lab. 26: 256. 1963. Lectotype (*nov.*): Tasmania, *Labillardière*, hb. Montagne, Lindenberg Hep. no. 4639 (W!); isoelectotypes: (G!, STR!).

Plants rather stiff and wiry, in herbarium clear bronze, shoots small for subgenus, the main shoots to 775  $\mu$ m wide, the plants to 6 mm wide with branches. Branching  $\pm$  regularly pinnate, the branches of the *Frullania* type, rather short, at times flagelliform; branch half-leaf bifid, subtransversely to obliquely inserted, the lobes straight to  $\pm$  divergent; first branch underleaf undivided, biseriate in basal portion, with a uniseriate row of 2–3 submoniliform cells, inserted on ventral side of branch near juncture of branch and main axis. Ventral-intercalary branches present, leafy. Stems with cortical cells in 9–12 rows, rather thick-walled and firm in surface view, in section larger than the medullary cells, rather thick-walled; medullary cells in 40–42 rows, the cells much smaller, with moderately thickened walls. Rhizoids sparse, from distal cells of underleaf disc. Leaves on main axis rigid, obliquely spreading, loosely imbricate, the disc gently incurved, the lobes moderately to distinctly incurved, the insertion moderately to strongly incubous; leaves 330–440  $\mu$ m wide (measured between tips of lobes)  $\times$  290–390  $\mu$ m long, subsymmetric, 4-lobed to 0.5–0.6, the lobes moderately spreading, with some leaves on main shoot with lateral lobes widely and asymmetrically divergent (at times forming an angle of up to 180° with each other), the lobes longer than the disc. Lobes slender, 2–4 cells wide at extreme base followed by 1(2) biseriate tiers, terminating in a uniseriate row of 4–5(6) cells; cells of the uniseriate portion short, submoniliform (lobes constricted at the septa),  $\pm$  isodiametric, evenly and distinctly thick-walled (even the terminal cell decidedly thick walled), the basal cell of the uniseriate portion 31–40  $\mu$ m wide and long (at most 1.3:1), the next cell smaller, 25–31  $\mu$ m wide and 30–34  $\mu$ m long, the terminal cell a little smaller than the penultimate cell, not secondarily divided, broadly rounded at the tip. Disc  $\pm$  symmetrically cuneate, 4(5) cells high (from median sinus to leaf base), 12–15 cells wide in distal portion narrowing to 8 cells wide in basal tier; margins entire,  $\pm$  straight. Cells of disc moderately and evenly thick-walled, lacking trigones, indistinctly tiered; largest cells in median portion of disc 26–36  $\mu$ m wide, (28)35–48  $\mu$ m long, the cells in distal tiers narrower; cuticle smooth. Underleaves much smaller than leaves, erect-spreading to nearly at 90° to stem, distant, plane, 3–4 lobed to 0.45, the lobes rather short, 2 cells wide at the base, terminating in a uniseriate row of 2–3  $\pm$  isodiametric, submonili-

form, somewhat thick-walled cells, sometimes terminating in a slime papilla; disc short cuneate, 3 cells high (median sinus), the cells in  $\pm$  regular tiers, the disc 8–10 cells wide in distal portion (6–8 cells wide in 3-lobed underleaves), narrowing to 8 cells wide at base (6 cells wide in 3-lobed underleaves); margins entire, straight. Asexual reproduction lacking.

Androecia and gynoecia not seen.

**DIFFERENTIATION AND VARIATION**—The type of *Jungermannia capilligera* is a striking plant. We have examined large numbers of New Zealand and Tasmanian specimens, previously named as well as unidentified, and have not found any which match the type of *T. capilligera* in characteristic disc areolation, cell size and wall thickness, and form of the lobes. Accordingly, we have chosen to define *T. capilligera* rather narrowly, so far represented only by the type. More study is needed to understand the variability of this species and its distribution.

The leaves of the main shoot are deeply dissected (to 0.6), with a disc 4 cells high, and at least some leaves have the lobes widely spreading (splayed) as in *T. tridactylis* (Fig. 3: 1, 2). The disc cells, however, are larger, 26–36  $\mu\text{m}$  wide vs. 18–25  $\mu\text{m}$  wide in *T. tridactylis*. The cells are firm, uniformly thick-walled and turgid, and are somewhat more regularly arranged than in *T. tridactylis*. The cells are comparable to those of *T. patentissima* in size, but the leaf lobes are more slender, terminating in a uniseriate row of 4–5(6) cells (Fig. 3: 1–4), vs. 2–4(5) cells in *T. patentissima*. In addition, the disc cells are quite evenly thick-walled (Fig. 3: 3), vs. thinner-walled and with small but distinct trigones in *T. patentissima*. In *T. capilligera*, the lobe cells in particular are evenly and distinctly thick walled (Fig. 3: 4). The terminal cell is also markedly thick walled, more so than in any other Australasian member of sect. *Neolepidozia*.

*Telaranea palmata* (p. 31), another Tasmanian species, is very similar to *T. capilligera*, both species having notably thick-walled leaf cells, particularly in the uniseriate row of the lobes. The most obvious difference is in the leaf insertion, which in *T. capilligera* is distinctly incubous (Fig. 3: 1, 2), vs. subtransverse in *T. palmata*. The cells of the leaf lobes are also more elongate in the latter species, and the septa often weakly projecting.

Oil-bodies of a specimen from Australia (Sydney, leg. Heim, not seen) were described by Jovet-Ast (1949) as botryoidal, 3–4 per cell, 8–10(11)

$\mu\text{m}$  long, composed of 5–8 granules. The specimen in question was determined by Hodgson as this species, but the identity of the specimen should be checked, in light of the more restricted sense of the species used here.

**NOMENCLATURE**—*Telaranea capilligera* is the earliest described species in the genus *Telaranea* (Schwaegrichen, 1814), and is the nomenclatural type of the genus *Neolepidozia* (Fulford and Taylor, 1959), which is treated here as *Telaranea* sect. *Neolepidozia* (see p. 237). The original material of *Jungermannia capilligera* represents a quite different plant from the species as it has previously been understood. We have examined several duplicates of the type (G, STR, W); the W specimen is here designated as the lectotype of the species. Piippo (1984, p. 314) stated that a lectotype of *Jungermannia capilligera* was “chosen by J. Taylor 1958.” The Geneva specimen bears an annotation by Taylor in 1958 as “original,” but to our knowledge this lectotypification was not published.

Schwaegrichen (1814) gives the type locality simply as “Australasia.” Synopsis Hepaticarum (G. L. & N., 1845, p. 204) cites “Insulis australibus (Labillardière); in Terra van Diemen (Hb. M.); in Nova Hollandia (Hb. Berolin.).” The latter, however, refers to the type of *Jungermannia tridactylis*, considered a synonym of *J. capilligera* by G. L. & N. The lectotype designated here is labelled “Hb. Mont.,” and is therefore presumably the Tasmanian plant cited.

The G, STR, and W plants are identical, and almost certainly represent the same collection. All are a clear, bronze color, something like that of *T. lindenberghii* var. *mellea* (p. 86). It is uncertain, however, if this is the natural color of the plant. In the var. *mellea* the color is consistently present in all collections seen.

**DISTRIBUTION**—Stephani (1909, p. 583) listed the distribution as Australia, Tasmania, New Zealand, and Auckland Is., and “ubique communis.” As treated here, the species is apparently endemic to Tasmania and known only from the type. Schuster (2000), however, keyed the species under “Neotropical taxa,” but stated that the species was “doubtfully in Patagonia/Magallanes.” We are discounting records from southern South America (see Engel, 1978).

*Telaranea pennata* Engel & Merr.

*Telaranea pennata* Engel & Merr., Phytologia 79: 252. June, 1996 [1995]. Holotype: New Zealand,

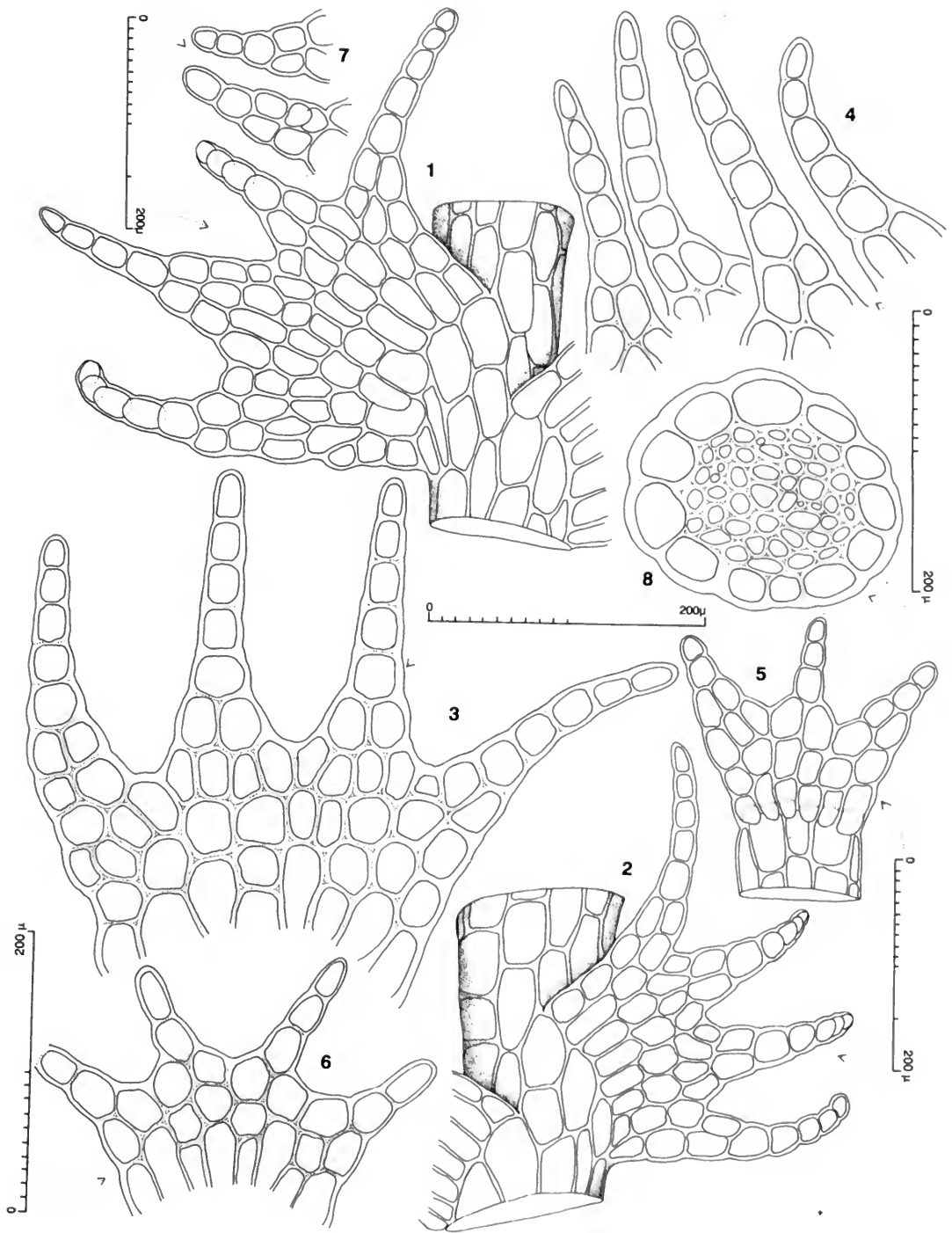


FIG. 3. *Telaranea capilligera* (Schwaegr.) Schust. 1, 2. Leaves, *in situ*. 3. Leaf. 4. Dorsalmost lobes of leaf. 5. Underleaf, *in situ*. 6. Underleaf. 7. First branch underleaves. 8. Stem, cross section. (All from type, hb. W.)

South Island, Westland Prov., Route 73, 8 miles W of Turiwhate, *Engel 6754* (F); isotype: (CHR).

Plants rather stiff, loosely prostrate, loosely matted, pale green to olive-green, nitid when dry; plants medium, to 1 cm wide, including branches. Branching very regularly 1-pinnate, the branches of the *Frullania*-type, rather long for plant size, to 775  $\mu\text{m}$  wide, not becoming flagelliform; branch half-leaf bifid, usually obliquely inserted, narrowly rectangular, the lobes parallel to weakly diverging; first branch underleaf undivided, subulate, (rarely bilobed) inserted on ventral side of branch at juncture of branch and main axis. Ventral-intercalary branches occasional, becoming leading leafy shoots. Stems with cortical cells distinctly differentiated, rather thick walled, in 12–13 rows; cortical cells in section much larger than the numerous (ca. 80) medullary cells, the medullary cell walls moderately and somewhat unevenly thick-walled. Leaves on main shoot rigid, obliquely spreading, contiguous to imbricate, the disc  $\pm$  plane, the lobes somewhat ventrally deflexed, the insertion strongly incubous; leaves 330–390  $\mu\text{m}$  wide  $\times$  315–435  $\mu\text{m}$  long, moderately asymmetric (the dorsal margin shorter), 4(5) lobed to 0.4–0.45, the lobes feebly divergent, shorter than the disc. Leaves on branches closely and regularly imbricate, the ventral lobes subfalcate, appearing as if brushed toward shoot apex. Lobes acute to weakly acuminate, the dorsal lobe shortest, the 2 ventral lobes largest, somewhat paired and often subfalcate (especially on branches), the largest leaf lobes (4)5–8 cells wide at extreme base, terminating in a short uniseriate row of 2–4 cells (ca. half or less the length of lobe); lobe cells short,  $\pm$  isodiametric to short rectangular, thick-walled, the cell walls of uniseriate row somewhat thickened in the corners but the septae not swollen and projecting at the lobe margin, the basal cell of the uniseriate portion 15–20  $\mu\text{m}$  wide  $\times$  17–23  $\mu\text{m}$  long (1.1–1.4:1), the next cell 12–17  $\mu\text{m}$  wide  $\times$  13–21  $\mu\text{m}$  long (1.1–1.4:1), the terminal cell a little shorter than the penultimate cell, the apex  $\pm$  rounded; cuticle smooth to finely striate-papillose at lobe tips. Disc sub-symmetrically quadrate-rectangular to obliquely trapezoidal, 6–9 cells high (8–10 cells high in branch leaves), 16–19 cells wide in distal portion narrowing to 8–9 cells wide in basal portion; margins entire, the dorsal straight to weakly incurved, the ventral margin rounded. Cells of disc small, evenly thick-walled and firm, trigones lacking, the median cells elongate, 16–26  $\mu\text{m}$  wide  $\times$  30–40

$\mu\text{m}$  long, often elongated longitudinally, following the contour of the leaf; basal row of disc cells larger (especially in ventral-basal sector); cuticle smooth. Underleaves much smaller than leaves, 0.9–1  $\times$  stem width, strongly spreading, distant, plane, 4-lobed to 0.5–0.6, the lobes somewhat divergent, narrowly acuminate, the uniseriate portion formed of 3–4 short cells, terminating in a slime papilla; disc symmetrically subrectangular (wider than high), 3(4) cells high (median sinus), the cells  $\pm$  regularly arranged, the disc 8 cells wide; margins entire, usually straight. Asexual reproduction lacking.

Androecia and gynoecia not seen.

**DIFFERENTIATION AND VARIATION**—The highly regular, neatly combed appearance of the branches (Fig. 4: 1), and the characteristic asymmetry of the leaves—the dorsal lobe shortest, and the  $\pm$  paired ventral lobes appearing brushed toward the branch tips (Fig. 4: 3, 4)—will immediately distinguish this apparently rare species. The leaves of *T. clatritexta* of Western Australia are similarly asymmetric, but not to such a marked degree (cf. Fig. 1: 1, 4, 5). Many of our *Telaranea* taxa have asymmetrical *Lepidozia*-like leaves (e.g., *T. paludicola*), with the dorsal lobes paired and often distinctly larger than the ventral. The leaves in *T. pennata*, however, are almost a mirror-image of the typical *Lepidozia*-type leaf.

The leaf lobes in *T. pennata* are broader than in any other New Zealand *Telaranea* (up to 8 cells wide at the base). The disc, however, is shorter than in *T. clatritexta*, 6–9 cells high (Fig. 4: 3) vs. 8–10(14) cells high in *T. clatritexta*.

**DISTRIBUTION AND ECOLOGY**—Known only from the type locality, a dryish forest in Westland Prov., where the species occurs both over rock and on fallen logs in a stream bed.

**SPECIMEN SEEN**—NEW ZEALAND. SOUTH ISLAND. WESTLAND PROV.: Route 73, 8 miles W of Turiwhate, *Engel 6765* (F).

*Telaranea quadristipula* (Steph.) Engel & Merr., comb. nov.

*Lepidozia quadristipula* Steph. in Stephani & Watts, J. & Proc. Roy. Soc. New South Wales 48: 116. 1914. Type: Australia, New South Wales, Rotunda, Neate's Glen, Blackheath, 4 Jan. 1911, *Watts 1009* (G!).

Plants flexuous, in loose mats, pale green, distinctly nitid when dry; plants medium, to 8 mm

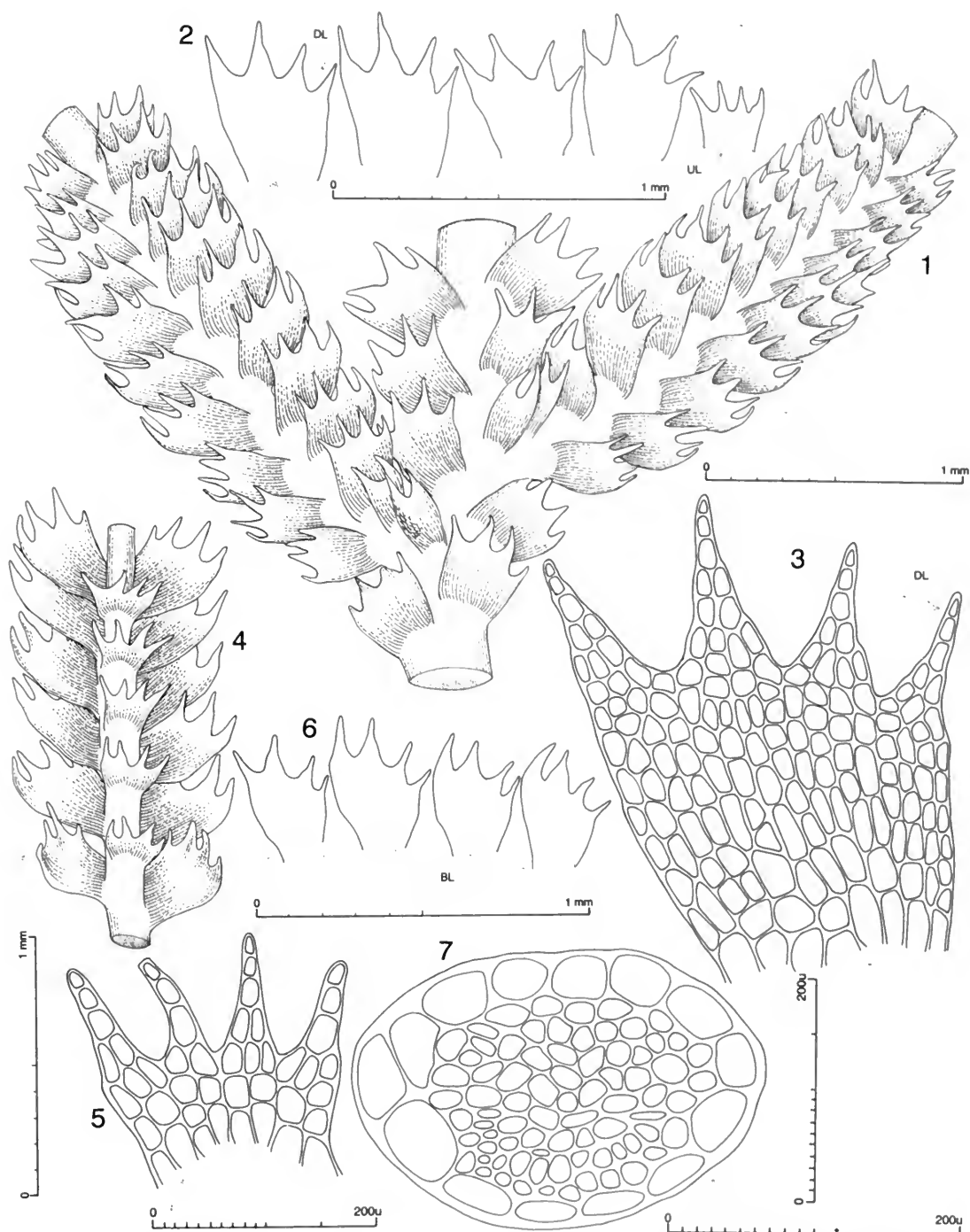


FIG. 4. *Telaranea pennata* Engel & Merr. 1. Sector of main shoot with *Frullania*-type branches, dorsal view. 2. Leaves (dorsal lobe [= dl] at right) and to right an underleaf (= ul). 3. Leaf, cellular detail (dl = dorsal lobe). 4. Sector of branch, ventral view. 5. Underleaf, cellular detail. 6. Branch leaves (= bl; dorsal lobe at right). 7. Stem, cross section. (All from holotype.)

wide, including branches. Branching  $\pm$  regularly 1-pinnate, the branches of the *Frullania*-type, at times abruptly flagelliform; branch half-leaf bifid to 0.4, inserted a little above branch axil; first branch underleaf undivided, subulate, with up to 4 biseriate tiers and a uniseriate row of up to 3 cells, ventral-lateral in position on branch base. Ventral-intercalary branches occasional, leafy. Stem cortical cells thick walled in surface view, in 14 rows, in cross section the outer wall thickened, a distinct cortical layer confined to the dorsal side of stem (ventral cells smaller and thicker walled); medullary cells ca. 37, smaller, firm walled, the outermost medullary cells on ventral side of stem somewhat thicker walled. Leaves on main shoot obliquely spreading, contiguous, the insertion strongly incubous, the leaves  $\pm$  symmetrically 4-lobed to 0.4, the disc cuneate, conspicuously narrowed to the base, complanate, plane to weakly convex, the lobes broadly acuminate, shorter than the disc, the lobe tips ventrally decurved; branch leaves imbricate, subfalcate, appearing "combed" toward the apex, on stronger branches 4-lobed, the dorsal lobe(s) smaller and more slender, the ventral lobe + ventral disc margin broadly arched. Lobes narrowly acute, often  $\pm$  abruptly narrowed in the upper half, 4(5) cells wide at extreme base, with up to 3 additional 4-celled tiers, then contracted to biseriate at the base of the uniseriate row of 3–4 cells; branch leaves with dorsal 1–2 lobes more slender, 2–3 cells wide at base, with 1–2 biseriate tiers or 2 cells wide at the base and otherwise uniseriate; lobe cells isodiametric to short rectangular, firm-walled, about equal to the disc cells or a little smaller, the cells of uniseriate row somewhat thickened in the corners, straight or weakly constricted at the septa, the terminal cell normally about equal to the penultimate cell in length or a little shorter, the apex rounded; cuticle of lobe tips indistinctly papillose. Disc rather broadly cuneate, (4)5–6(7) cells high (from median sinus base to leaf base), 15–16 cells wide in distal portion narrowing to 8 cells wide at the insertion, the margins entire; disc of branch leaves asymmetrically cuneate, (5)6–7 cells high, the dorsal margin longer than the ventral and  $\pm$  straight, the ventral margin broadly arched, not decurrent on the stem. Cells of disc moderately thick-walled, in  $\pm$  irregular rows, 16–24  $\mu\text{m}$  wide  $\times$  23–31  $\mu\text{m}$  long, the basal row of disc cells often conspicuously larger, about twice the width of the cells of the disc proper, which are evidently smaller by vertical subdivisions; cuticle smooth. Underleaves about the

same width as the stem or a little less, obliquely spreading, plane, 4-lobed to 0.5 or a little less; lobes 2–3 cells wide at base, at times with an additional biseriate tier, ending in a uniseriate row of 2–3 short cells, terminating in a slime papilla; disc parallel-sided, 3 cells high, 8 cells wide. Rhizoids originating from distal portion of disc.

Androecia and gynoecia not seen.

**DIFFERENTIATION AND VARIATION**—This apparently rare Australian species has features suggestive of both *T. pennata* and *T. tridactylis*, among them the small cell size (16–26  $\mu\text{m}$  wide) and the flattened, ribbon-like branches, with a characteristic reversed asymmetry of the branch leaves: the dorsal lobe(s) smaller, the ventral larger and broadly arched (Fig. 5: 3, 9), the leaves appearing brushed toward the branch tips. They differ chiefly in the differentiation of the branch leaves from those of the main axis and the height of the leaf disc. In *T. pennata* both the stem and branch leaves show the characteristic asymmetry, but in *T. quadristipula* the leaves on the main shoot are  $\pm$  symmetrically 4-lobed (Fig. 5: 1, 4). The stem leaves of *T. tridactylis* are highly variable, but characteristically include those which are  $\pm$  longitudinally inserted and deeply divided (disc as little as 3 cells high), with distinctive, widely splayed lobes. The lobes of *T. tridactylis* are also more slender: 2–4 cells wide at the base, with 1–2 biseriate tiers. In *T. quadristipula* the leaf disc is (4)5–6(7) cells high (Fig. 5: 1, 4) vs. 6–9 cells high (8–10 cells high in branch leaves) in *T. pennata*. An interesting feature of the leaf lobes of *T. quadristipula* is the often abrupt narrowing from several 4-seriate tiers to biseriate at the base of the uniseriate row (Fig. 5: 1, 5).

*Telaranea disparata* of Queensland has branch leaves with reversed symmetry, but the disc cells are larger (26–32  $\mu\text{m}$  wide), the disc is 8 cells wide throughout, and the lobes are biseriate at the base.

**NOTE**—The specific epithet, "quadristipula," is probably not what Stephani originally intended. The type (Watts 1009, cited in the protologue) is labeled "*Lepidozia quadratistipa*"; the Icones (*Lepidozia* 108, Australia, leg. Watts) is labeled "*Lepidozia quadristipa*." None of these names is particularly informative.

**DISTRIBUTION AND ECOLOGY**—Known only from the type, New South Wales; admixed are *Zoopsis* sp., *Balantiopsis* sp., and the moss *Distichophyllum* sp.



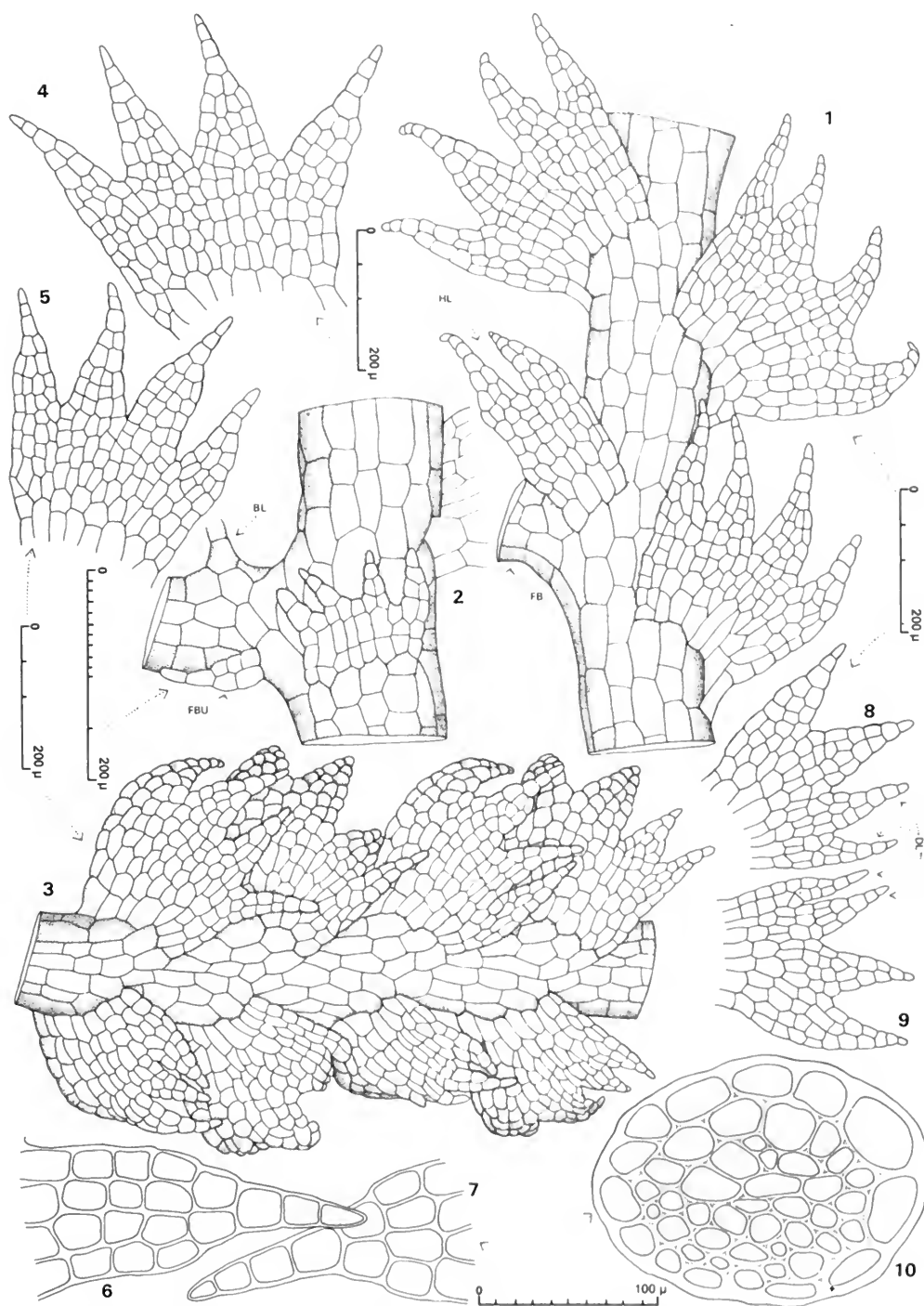


FIG. 5. *Telaranea quadristipula* (Steph.) Engel & Merr. 1. Portion of main shoot with a *Frullania*-type branch (= FB; hl = half-leaf); dorsal aspect. 2. Portion of shoot showing base of terminal branch (fbu = first branch underleaf; bl = branch leaf base); base of main shoot leaf included at right. 3. Portion of primary, *Frullania*-type branch, dorsal aspect; note the dorsal pair of lobes are narrower and often shorter. 4, 5. Leaves of main shoot (both drawn to same scale). 6, 7. Median lobes of leaf, a complete lobe at left, only the distal portion shown at right. 8, 9. Branch leaves; note the two dorsalmost lobes (= dl) are smaller and narrower. 10. Stem, cross section. (All from type.)

*Telaranea tridactylis* (Lehm. & Lindenb.) Engel & Merr.

*Jungermannia tridactylis* Lehm. & Lindenb. in Lehmann, Nov. Min. Cogn. Stirp. Pug. 4: 41. 1832. *Lepidozia tridactylis* (Lehm. & Lindenb.) Mont. in Dumont d'Urville, Voy. Pôle Sud, Bot. 1: 245. 1845. *Telaranea tridactylis* (Lehm. & Lindenb.) Engel & Merr., Phytologia 79: 253. June, 1996 [1995]. Type: "Nova Hollandia," without specific loc., *sin. coll.*, "Hb. Berol[inensis] 46" (W!, Lindenb. Hepat. no. 4636). *Lepidozia oldfieldiana* Steph., Spec. Hep. 3: 581. 1909, *syn. nov.* Lectotype (*nov.*): Tasmania, without specific loc., *Oldfield*, ex hb. Kew (G!—c. ♂).

Plants rather stiff and wiry, prostrate in compact mats, light olive green, highly nitid when dry, not water repellent; shoots very small for subgenus, the main shoots 350–560  $\mu\text{m}$  wide (0.5 cm wide with branches). Branching irregularly to regularly pinnate, occasionally locally 2-pinnate, the branches of the *Frullania* type, rather short (to moderately long but normally determinate), at times flagelliform; branch half-leaf bifid, transversely to obliquely inserted, the lobes sometimes widely divergent; first branch underleaf undivided, subulate, inserted on ventral or ventral-lateral side of branch near juncture of branch and main axis. Ventral-intercalary branches common, leafy or sporadically flagelliform. Stems with cortical cells in 12–13 rows, often rather thick-walled and firm in surface view, in section larger than the medullary cells, the radial walls somewhat thickened, the exposed wall at times distinctly so; medullary cells in ca. 38 rows, the cells much smaller, with thin to very thick walls. Rhizoids sparse, from distal cells of underleaf disc. Leaves on main shoot rigid, fragile, widely spreading, but not at right angles to stem, loosely imbricate to conspicuously distant, plane or slightly concave resulting from occasional gentle incurving of lobes, the insertion variable: subtransverse to strongly incubous to almost longitudinal; leaves (145)265–385  $\mu\text{m}$  wide  $\times$  (120)235–335  $\mu\text{m}$  long, subsymmetric, 4- (rarely 5–6-) lobed to 0.45–0.6, the lobes moderately to widely (and at times asymmetrically) divergent (on more distant leaves on the main axis the lateral lobes often widely spreading, forming an angle of 180° with each other); branch leaves typically closely and regularly imbricate, weakly asymmetrical. Lobes narrowly attenuate, tapering from 2–4 cells wide at extreme base followed by 1–2(4) biseriate tiers, terminating in a uniseriate row of (2)3–5 cells; cells of the uniseriate portion short to weakly elongate, moder-

ately thick-walled, the basal cell of the uniseriate portion 19–26  $\mu\text{m}$  wide, (24)28–34  $\mu\text{m}$  long, (1–1.6:1), the next cell shorter and on the whole narrower, being 14–19(24)  $\mu\text{m}$  wide and 19–25  $\mu\text{m}$  long (1–1.3:1), the terminal cell about the size of the penultimate cell or a little shorter, tapering to the tip. Disc  $\pm$  symmetrically weakly cuneate, 3–5 cells high (disc of branch leaves to 6(7) cells high), 11–16 cells wide in distal portion narrowing to (7)8(9) cells wide in basal tier; margins entire, straight to broadly curved. Cells of disc typically evenly and moderately thick-walled, the areolation rather compact and lacking the regular arrangement of other *Telaranea* species (secondary divisions of disc cells random in both planes); median cells small, 18–23  $\mu\text{m}$  wide, 26–38(42)  $\mu\text{m}$  long; basal cells considerably larger and forming an obvious tier; cuticle with a network of fine irregular striae. Underleaves much smaller than leaves, spreading nearly or at 90° to stem, distant, slightly convex (ventral view), 3–4 lobed to 0.45–0.55, the lobes often gently curved dorsally, narrowly attenuate to subciliiform, 2 cells wide at the base, terminating in a uniseriate row of 2–3 slightly elongated, somewhat thick-walled cells, or consisting entirely of the uniseriate row, terminating in a slime papilla; disc weakly cuneate, 2–3(4) cells high (median sinus), the cells in  $\pm$  regular tiers; disc 9–10 cells wide in distal portion (6–8 cells wide in 3-lobed underleaves), narrowing to 8 cells wide at base (6 cells wide in 3-lobed underleaves), the basal row of cells on the whole longer and forming an obvious tier; margins entire, straight. Asexual reproduction lacking.

Dioecious. Androecia either on short *Frullania*-type branches with a few to several (to 5) cycles of normal vegetative leaves prior to androecial formation, or on short, abbreviated, ventral-intercalary branches lacking normal vegetative leaves; bracts closely imbricate, strongly dorsally assurgent, the entire bract deeply concave, 2(3) lobed, each lobe terminating in a uniseriate row of 2–3 not to hardly elongated cells; lamina cells non-tiered, irregular in shape and arrangement, the lamina margins sometimes denticulate, often with stalked or sessile slime papillae; antheridia 1 per bract, large for bract size, the stalk short, 5–6 cells high, uniseriate; bracteolar antheridia absent. Gynoecia strongly dorsally assurgent, with a vestigial stem perigynium barely present, not swollen, rhizoidous; bracts and bracteoles in 3 series, inserted on the vestigial perigynium; bracts becoming progressively larger and less deeply lobate towards

the perianth, those of innermost series deeply concave, with apices rounded, irregularly denticulate with sporadic 1–2-celled teeth; bract margins crenulate to irregularly repand, with a few sessile slime papillae, the bracts with a border formed of 1 row of cells longer, narrower and more irregular than those within; bracteole nearly identical in size and form. Perianth not extending above vegetative axes and entangled by them, 0.65–0.8 emergent, narrowly fusiform, 5–7.2× longer than wide, terete in basal half, the distal half obscurely trigonous and with 5–6 deep plicae, gradually and distinctly narrowing toward the contracted mouth; mouth with 6 narrowly triangular lobes, each lobe fringed with thick-walled, contorted, coarsely papillose cilia, the cilia consisting of 2–4 elongated cells with thickened and swollen septa, often with a knob-like swelling at the basal end of the cells just above the septa; perianth 2–4 stratose in basal portion, the median portion 2 (locally 1) stratose.

Seta with 8 rows of outer cells (each with their free face bulging), surrounding an inner core of 17–18 much smaller thin-walled cells, with corner thickenings resembling bulging and knotlike trigones. Capsule rather short elliptic, the valves 980–1050  $\mu\text{m}$  long, the wall 24–30  $\mu\text{m}$  thick, of 3 layers, the outer layer subequal to the combined 2 inner layers, or slightly less thick; outer layer of cells in tiers, rather regularly short-rectangular, with 2-phase development, the longitudinal walls with well-defined sheetlike thickenings and nodule-like thickenings (4–6 per cell) alternating with walls that are devoid of thickenings (or with very few sporadic, local, nonpigmented, nodular swellings), the transverse walls devoid of thickenings; intermediate layer thinner than outer or inner layers; innermost layer of cells  $\pm$  tiered, irregularly narrowly to broadly rectangular, with semiannular bands rather narrow,  $\pm$  irregular, short or infrequently complete, rarely forked and anastomosing to delimit ill-defined, local fenestrae.

Spores 14.9–16.8  $\mu\text{m}$ , exine yellow brown, with low, delicate papillae, coalescing to form short ridges that rarely delimit areolae. Elaters rigid, somewhat sinuous, (7.7)8.6–10.1  $\mu\text{m}$  wide, only slightly tapering toward tips, bispiral to tips, the spirals 2.9–3.4  $\mu\text{m}$  wide.

**DIFFERENTIATION AND VARIATION**—This species is the smallest member of sect. *Neolepidozia*. It is distinguished from *T. patentissima* by its smaller size, smaller leaf cells (at most 25  $\mu\text{m}$  wide), and less regular arrangement of disc cells, vs. 25–40  $\mu\text{m}$  wide in *T. patentissima*, with a more *T. tet-*

*rapila*-like areolation of rather regular rows and tiers.

The species shows considerable variation in leaf form and insertion. When optimally developed, the branches are complanate and ribbon-like, and broader than the main shoot, with closely shingled leaves (Fig. 6: 3, 4). The branch leaves have a rather high disc (to 7 cells high) and are often 4-lobed. By contrast, the leaves of the main shoot are often distant, longitudinally-inserted, and deeply divided, with widely splayed lobes, often oriented as much as 180° to each other (Figs. 6: 7; 7: 2). Weaker shoots may have both stem and branch leaves splayed-lobed, and lack the flattened, ribbon-like branches (Fig. 6: 1, 2).

The leaves of the flattened, ribbon-like branches are suggestive of those of *T. pennata* (p. 18) in that the ventral lobes are weakly arched toward the apex of the branch, and the dorsal lobes more slender than the ventral. *Telaranea pennata*, however, is a more robust plant, with the comb-like branches to 775  $\mu\text{m}$  broad, with leaf lobes to 8 cells wide at the base. Both stem and branch leaves tend to show the characteristic asymmetry, and the stems do not have the small, longitudinally inserted, splayed-lobed leaves as in *T. tridactylis*. The disc of *T. pennata* is higher (6–9 cells high), and the disc cells are longitudinally elongate. For further comparisons of *T. tridactylis* with *T. pennata* and *T. quadristipula*, all species with small disc cells in the range of 16–24  $\mu\text{m}$  wide, see comments under *T. quadristipula*.

**DISTRIBUTION AND ECOLOGY**—The type of *T. tridactylis* is from Australia (Nova Hollandia). It is a common species in Tasmania, but in New Zealand is known only from Auckland and Campbell Is. and one station at Milford South on South Island. Reports of this species as *T. capilligera* from mainland New Zealand are based on misdeterminations (confirming Hodgson, 1956, p. 610, sub *Lepidozia gottscheana*). Conversely, *T. patentissima* (p. 46), also a small plant, is common in New Zealand, but rather rare in Tasmania. The species is also known from Victoria, Australia and one station in Queensland. The species was reported for the Strait of Magellan by Montagne (1845) and Kühnemann (1937, 1949). We have not seen the collections on which these reports are based.

*Telaranea tridactylis* is primarily a forest plant. In Tasmania the species occurs, for example, in lower elevation forests such as of *Acacia melanoxylon* and *Leptospermum lanigerum* or of *Leptospermum scoparium*-*Eucalyptus* in the north-

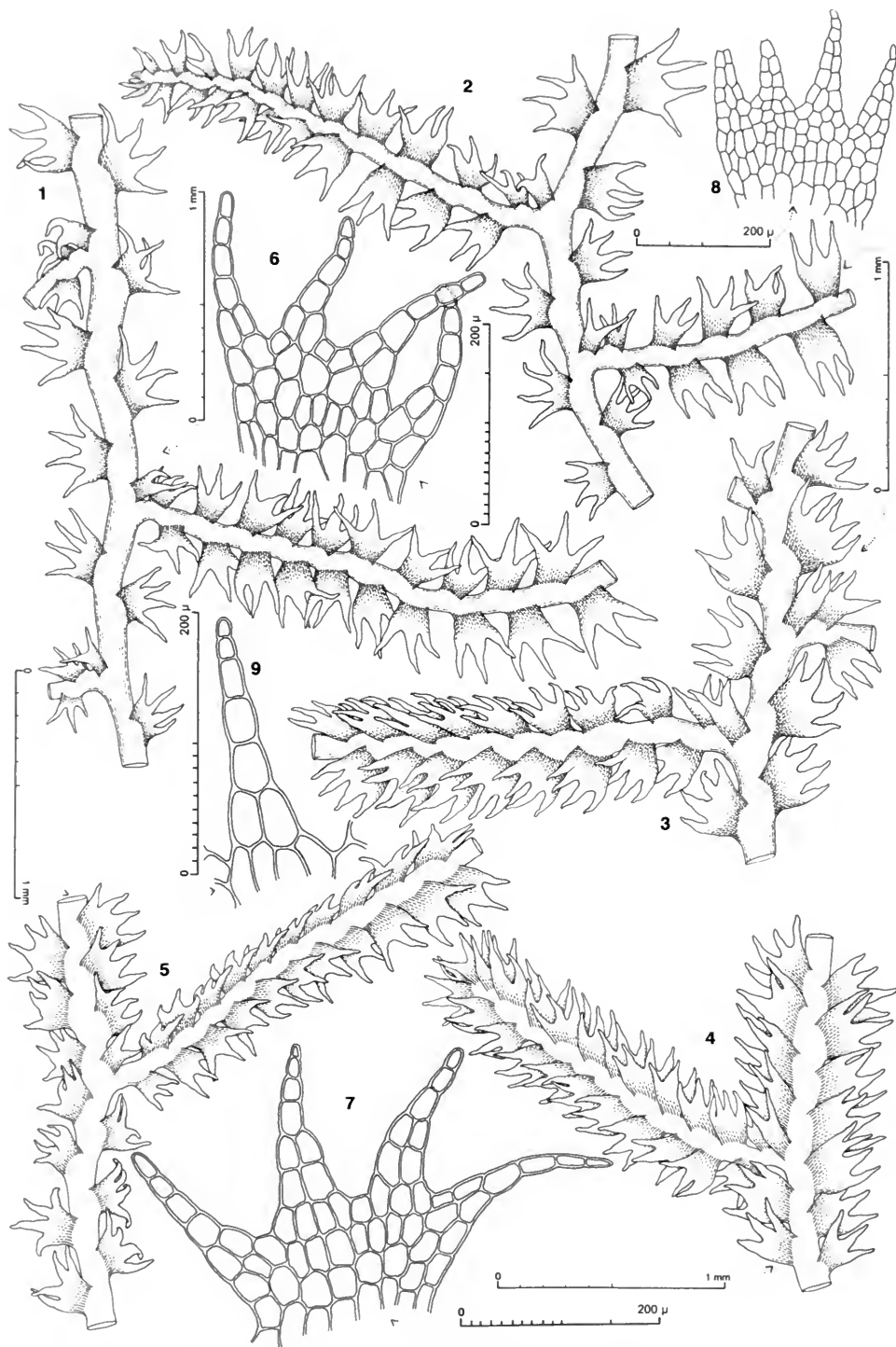


FIG. 6. *Telaranea tridactylis* (Lehm. & Lindenb.) Engel & Merr. 1-5. Portion of main shoot with one or more *Frullania*-type branches, dorsal view (note especially the variation in orientation and planation of branch leaves and the imbrication of main shoot leaves). 6-8. Leaves. 9. Leaf lobe. (Figs. 1, 6, 7, 9 from type of *T. tridactylis*; 2 from Norris 29804, Tasmania, Arve Road; 3, from Norris 27281, Tasmania, above Lake Barrington near Forth Falls; 4, 8 from Engel 19725, Tasmania, Newhaven Road, just S of Doughboy Hill; 5 from Norris 29470, Tasmania, Kermadec River at North Creek.)

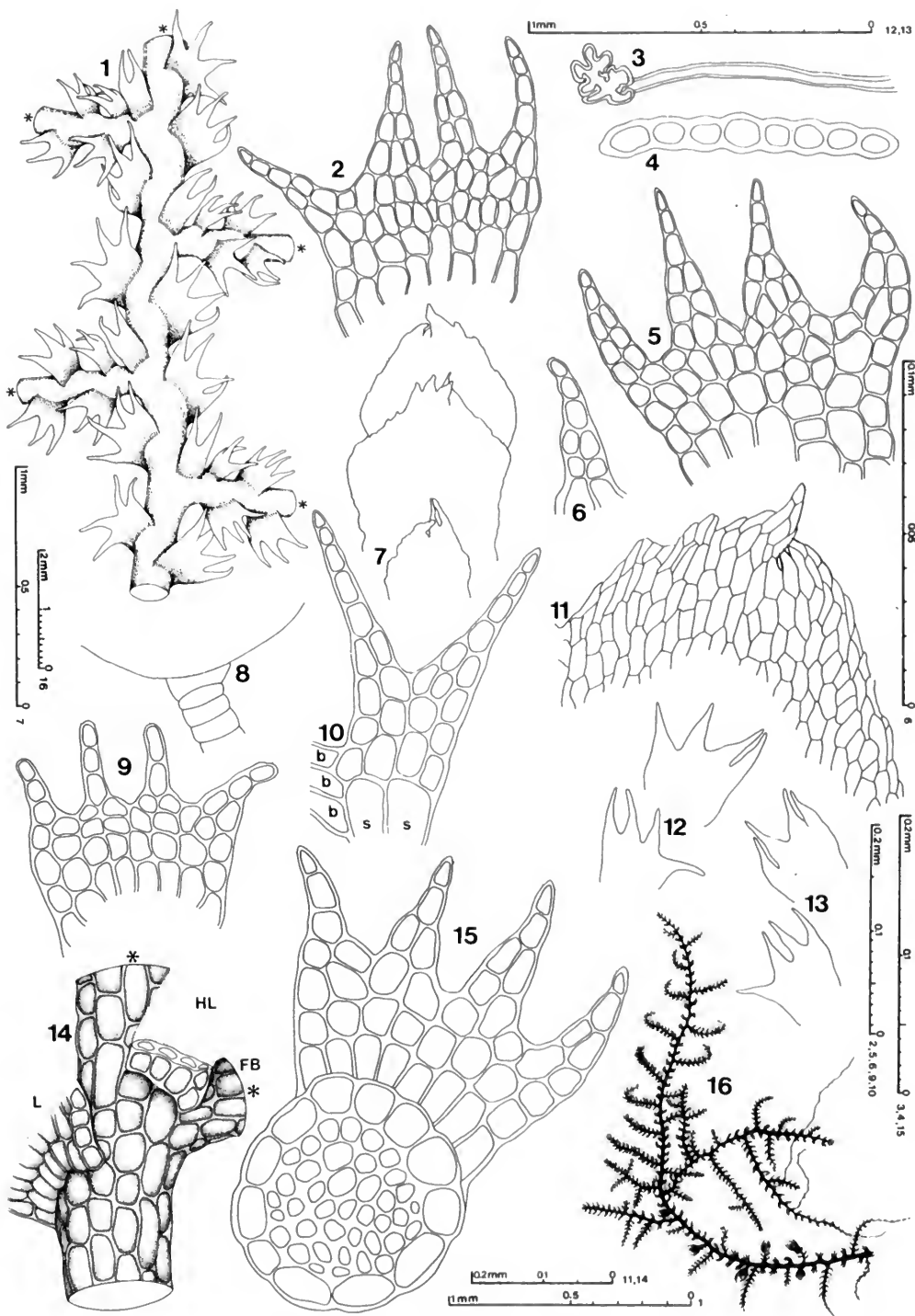


FIG. 7. *Telaranea tridactylis* (Lehm. & Lindenb.) Engel & Merr. 1. Main shoot, with four *Frullania*-type branches, dorsal view. 2, 5. Leaves. 3. Rhizoid with ramified tip. 4. Leaf lamina cross section. 6. First branch underleaf. 7. ♀ Bracts (top to bottom), from innermost, second, and lowermost series. 8. Antheridial stalk. 9. Underleaf. 10. Half-leaf (b = adjoining branch cell; s = adjoining stem cell). 11. Distal portion of innermost female bract. 12, 13. Leaf outlines. 14. Portion of main shoot, dorsal view with only leaf (L) and half-leaf (HL) bases indicated (FB = *Frullania*-type branch). 15. Stem, cross section + underleaf. 16. Portion of main shoot, dorsal view, showing leaf arrangement (note six male branches toward base). (All from Norris 29470, Tasmania, Kermadie River.)

western sector of the state. On the east coast it may occur in forests of *Eucalyptus obliqua* together with varying combinations of other vascular plant forest species. On Mt. Raoul (380 m), for example, it is found in a forest consisting of *E. obliqua* over *Pomaderris apetala*, *Olearia argophylla*, *Bedfordia salicina*, *Hakea lissosperma*, *Pimelea nivea*, *P. drupacea* and *Coprosma quadrifida*. The species also occurs in middle-elevation *Nothofagus-Eucalyptus-Atherosperma* or *Nothofagus cunninghamii-Eucryphia* forests, as well as upper-elevation forests of *Nothofagus-Athrotaxis*. In forests the species often occurs on bryophyte-covered logs (especially where some soil has accumulated), or less frequently, is terricolous or saxicolous on outcrops in niches where soil has accumulated. The species is rare and sporadic in subalpine and alpine zones. For example, it occurs on soil deep under thicket cover in subalpine scrub of *Richea scoparia*, *Nothofagus gunnii*, *Diselma* and *Athrotaxis selaginoides*, etc. In alpine areas it occurs over rock at the margins of creeks or with *Astelium* at margins of seepage areas.

The plant from Youngs Creek, Victoria, occurred in a cool temperate rainforest with *Nothofagus cunninghamii* and *Acacia melanoxylon* co-dominant, *Eucalyptus regnans* emergent, and *Blechnum wattsii* and *Dicksonia antarctica* the main understorey species. At this site the species occurred on the base of *Dicksonia antarctica*. The Scott specimen from Gippsland was found on the trunk of *Nothofagus cunninghamii* in a cool rain forest.

The plant from Milford Sound, New Zealand occurred on exposed, moist, vertical cliffs with a dense bryophyte cover at the forest margin.

SELECTED SPECIMENS SEEN—CAMPBELL IS.: Bee-man Hill, "Meteorological Party" as *T. dispar* (CHR). AUCKLAND IS.: Hooker sub *Jungermannia dispar* (BM, FH); Ewing Is., *Fineran 1358* as *T. patentissima* (CHR). NEW ZEALAND. SOUTH IS., SOUTHLAND PROV.: Fiordland Natl. Park, Milford Sound, track to Bowen Falls, sea level, *Engel 22007* (F). TASMANIA: Waterfall Creek State Reserve, South Bruny Range, 100 m, *Moscal 25217* as *T. praenitens* (HO); E side of Tasman Peninsula, upper slope of Tatnells Hill, S of Waterfall Bay, 500–530 m, *Engel 13164* (F); Cape Raoul State Reserve, Mt. Rauol, 380 m, *Moscal 24890* as *T. tetradactyla* (HO); Sandspit River, 8.5 km WNW of Cape Bernier, 180 m, *Moscal 16838* as *T. tetradactyla* (HO); Humbug Point State Recreation Area, Higginbothams Creek, sea level, *Moscal 25655* as *T. tetradactyla*—c. per. (HO); south coast, Deadmans Bay, 10 m, *Moscal 14180C* (2), both as *T. tetradactyla* (HO); Adamsons Track, 150 m, *Ratkowsky H1540* as *T. gottscheana* (HO); near Manuka Flat on trail to Adamsons

Peak, 300–400 m, *Norris 26878* (F); Adamsons Peak, below hut, *Ratkowsky 80/152* (HO); near Jacques Creek near end of Styx River Road, *Norris 29037* (F); Kermadec River at North Creek, ca. 50 m, *Norris 29470* (F); Arve Road ca. 1 mile W of Willies Saddle, ca. 300 m, *Norris 29804* (F); Tahune Forest Reserve, near Huon River, 70 m, *Engel 19860* (F); E facing slope of Mt. Wellington, O'Grady's Falls, 525 m, *Engel 12752B* (F); Mt. Wellington, 305–365 m, *Rodway s.n.* as both as *L. praenitens* (HO); *ibid.*, 610 m, *Ratkowsky B79e* (F); *ibid.*, "Pipeline," above Silver Falls, *Ratkowsky H1676* as *T. gottscheana* (HO); Glenorchy Water Reserve, 400 m, *Moscal 19900* as *T. praenitens* (HO); Mt. Dromedary, Dean Brook, *Weymouth 851* as *L. praenitens*—c. ♂ (HO); Myrtle Forest, SW of Collinsvale and ca. 2.3 km N of Collins Bonnet, 700 m, *Engel 12773* (F); Mt. Field Natl. Park, Lake Belcher, ca. 900 m, *Norris 28690* (F); Mt. Wedge, *Ratkowsky H1539* as *T. gottscheana* (HO); *ibid.*, Rodway Range, between Rodway Ski Tow and K Col area, 1240–1310 m, *Engel 14415* (F); Mainwaring River, 1 km from mouth, sea level, 1 m, *Moscal 9768A* as *T. praenitens* (HO); near Scotts Peak Road, 2.2 km S of junction with Gordon River Road, E of S end of Lake Gordon, 580 m, *Engel 13800* (F); Serpentine River, below Lake Pedder dam, *Scott & P. Dalton s.n.* as *T. tetradactyla* (MELU); Cradle Mtn.-Lake St. Clair Natl. Park, Overland Track between Watersmeet and Echo Point, W side of Lake St. Clair, 760 m, *Engel 14207* (F); Mt. King William I, 1200 m, *Ratkowsky H1538* as *T. gottscheana* (HO); Surprise Valley, above both Surprise River and Lyell Highway, 2.1 km W of King William Saddle, 750 m, *Engel 19446*—c. sporo. (F); Frenchman's Cap, 1893, *Moore 40*, syntype of *Lepidozia oldfieldiana* (G); Franklin River at Frenchman's Cap Trail crossing, ca. 400 m, *Norris 31157* (F); west coast, Sophia Point, *Moore s.n.* as *L. praenitens* (HO); Zeehan-Renison Bell State Reserve, on Murchison Highway 6.7 km N of intersection with road to Zeehan, 250–320 m, *Engel 20079* (F); Mt. Read, S of Rosebery, 990–1010 m, *Engel 20040* (F); Wilson River, 26 km N of Zeehan, 140 m, *Moscal 21606* as *T. tetradactyla* (HO); Alfred River, 200 m, *Moscal 21869* as *T. tetradactyla* (HO); Mersey River, 2.5 km S of Lewis Falls, 750 m, *Moscal 15267* as *T. praenitens* (HO); Blue Tier, *Rodway s.n.* as *T. praenitens* (HO); Cradle Mt., *Rodway s.n.* (2), both as *L. praenitens* (HO); *ibid.*, near Lake Dove, *Rodway s.n.* as *L. praenitens* (HO); Cradle Mtn.-Lake St. Clair Natl. Park, Weindorfers Forest, along track from Waldheim Chalet to Hounslow Heath Track, 975 m, *Engel 14058* (F); *ibid.*, Cradle Mt. area, Plateau Creek, between Overland Track and Kitchen Hut Track, W of N end of Lake Dove, 1250 m, *Engel 19659* (F); *ibid.*, above Pencil Pine Creek and off track between Quailes Hill and Pencil Pine Lodge, E of Pencil Pine Lodge, 770–800 m, *Engel 19620* (F); above Lake Barrington near Forth Falls, ca. 150 m, *Norris 27281* (F); Foot Mt. Roland, *Rodway s.n.* as *L. praenitens* (HO); Newhaven Road, just S of Doughboy Hill, 0.4 km E of junction with Mawbanna Road, S of Port Latta, 45 m, *Engel 19725* (F); Detention Falls, SSW of Sisters Creek, W of Wynyard, 190 m, *Engel 19673* (F); Ferndene, *Norris 33970* (F); Deadwood, Grafts Tree Hill, *Oldfield 29(H)* (G); Flinders Is., Mileara Valley, Bob Smith's Gully, *Scott s.n.* as *T. dispar* (MELU). AUSTRALIA. VICTORIA: Otway Ranges, Youngs Creek, Phillips Track, *Turner s.n.* as *T. dispar* (F); Gippsland, West

Branch Creek, Gunyah, *Scott s.n.* as *T. patentissima* (F. MELU); Errinundra Plateau, track down to First Creek Falls, *Scott & Chesterfield s.n.* as *T. dispar*—c. sporo. (MELU); Welshpool, near Gunyah Junction, *Scott s.n.* as *T. ?dispar*—c. ♂ (MELU); Marysville, Talbot Drive, *Scott s.n.* as *T. ?dispar* (MELU). QUEENSLAND: Mimos Creek, Blackdown Tableland, *Stone s.n.* (MELU).

### *Telaranea consobrina* Engel & Merr.

*Telaranea consobrina* Engel & Merr., Novon 9: 339. f. 1. 1999. Holotype: Tasmania, eastern slope of Black Bluff just below summit, S of Burnie, 1250 m, Engel 15799 (F); isotype: (HO).

Plants soft and flexuous, ascending to suberect, in soft cushions, pale green, distinctly nitid when dry; plants medium, to 6 mm wide, including branches. Branching rather regularly 1-pinnate, the branches of the *Frullania*-type, at times becoming flagelliform; branch half-leaf 2-lobed, obliquely inserted, narrowly rectangular, the lobes  $\pm$  parallel to slightly diverging; first branch underleaf undivided (very rarely bilobed), broadly acuminate to lanceolate, inserted on ventral side of branch at base of branch. Ventral-intercalary branches not seen. Stems with cortical cells distinctly differentiated, thin-walled, in 13–14 rows; cortical cells in section slightly to distinctly larger than the numerous (49–53) medullary cells, the medullary cells slightly thick walled. Leaves on main shoot obliquely spreading, contiguous, the disc plane or weakly convex, the lobes ventrally decurved, the insertion distinctly incubous, the disc broader than high, nearly in same plane as dorsal surface of stem; leaves 475–600  $\mu\text{m}$  wide  $\times$  440–525  $\mu\text{m}$  long, the leaves 4(5)-lobed to 0.4–0.5, the lobes straight to moderately divergent, slightly shorter than the disc. Lobes narrowly acute to acuminate, 4–5 cells wide at base, often 4 cells wide in basal sector, then biseriate for 2–3 tiers, terminating in a short uniseriate row of 2–3 cells (or sporadically a single cell or 2 laterally juxtaposed cells), the tip sometimes with a slime papilla; lobe cells  $\pm$  isodiametric to short rectangular, thin-walled, the cell walls of uniseriate row not or weakly thickened in the corners, the basal cell of the uniseriate portion 20–25  $\mu\text{m}$  wide  $\times$  24–31  $\mu\text{m}$  long (1–1.3:1), the next cell 17–22  $\mu\text{m}$  wide  $\times$  18–26  $\mu\text{m}$  long (1–1.2:1), the terminal cell normally about equal to the penultimate cell in length or a little shorter, the apex rounded; cuticle smooth. Disc somewhat asymmetrically cuneate, the dorsal margin somewhat longer than the ventral, the disc (5)6–7(8) cells high (from median sinus base to leaf base), 13–

16 cells wide in distal portion narrowing to 8(9) cells wide in basal portion; margins entire, the dorsal margin weakly to broadly arched, the ventral margin  $\pm$  straight to moderately arched, distinctly decurrent on the stem. Cells of disc thin-walled, trigones lacking, the cells of the distal half to one-third smaller by vertical subdivisions or all but the basal row of disc cells smaller, the smaller cells 16–22  $\mu\text{m}$  wide, the largest 24–38  $\mu\text{m}$  wide  $\times$  42–49  $\mu\text{m}$  long, the cells in  $\pm$  irregular rows; cuticle smooth. Underleaves somewhat smaller than leaves, 1.7–2.3 $\times$  stem width, obliquely spreading, distant, plane, 4(5)-lobed to 0.4–0.45, the lobes straight to moderately divergent, narrowly acute, 3–4 cells wide at base and biseriate for 1–2 tiers, ending in a uniseriate row of 2–3 short cells, terminating in a slime papilla; disc symmetrically broadly cuneate (wider than high), 4–5 cells high (median sinus), 14–18 cells wide at widest point, the cells in  $\pm$  irregularly rows; margins entire, moderately arched. Rhizoid initial cells small, subquadrate, in distal portion of disc and basal cells of lobe. Asexual reproduction lacking.

Androeceia and gynoeceia not seen.

**DIFFERENTIATION AND VARIATION**—This rare species of Tasmania and Victoria resembles *T. meridiana* of New Zealand in being rather soft in texture, with broad leaves and ventrally decurved leaf lobes *in situ*, and disc cells arranged in somewhat irregular rows (Fig. 8: 1–3). The epithet *consobrina* (“cousin”) was chosen to evoke this resemblance. It differs most notably in the shape of the leaf disc, which narrows to 8 cells wide at the insertion (Fig. 8: 1) vs. 14–16 cells wide in *T. meridiana* (Fig. 2: 3, 5), and in the narrower lobes, which are only 4–5 cells wide at base (Fig. 8: 1–3), vs. as many as 6(8) cells wide in *T. meridiana* (Fig. 2: 3, 4). The underleaves of *T. consobrina* are larger, roughly twice the width of the stem (Fig. 8: 6), and somewhat shorter (vs. 1.2 $\times$  the stem diameter in *T. meridiana*).

**DISTRIBUTION AND ECOLOGY**—Known only from Tasmania and Victoria, Australia. The species is known from a few stations in Tasmania, two in the northwest, both at 1250 m, occurring in the crevice of a dripping cliff face in an area with alpine vegetation (type) and in the bed toward the side of Plateau Creek, the area within a mosaic of cushion plants, *Diselma*, etc., scattered pools and small streams. The Moore plant is from a considerably lower elevation on the west coast. On Flinders Island the species occurs on creek banks in



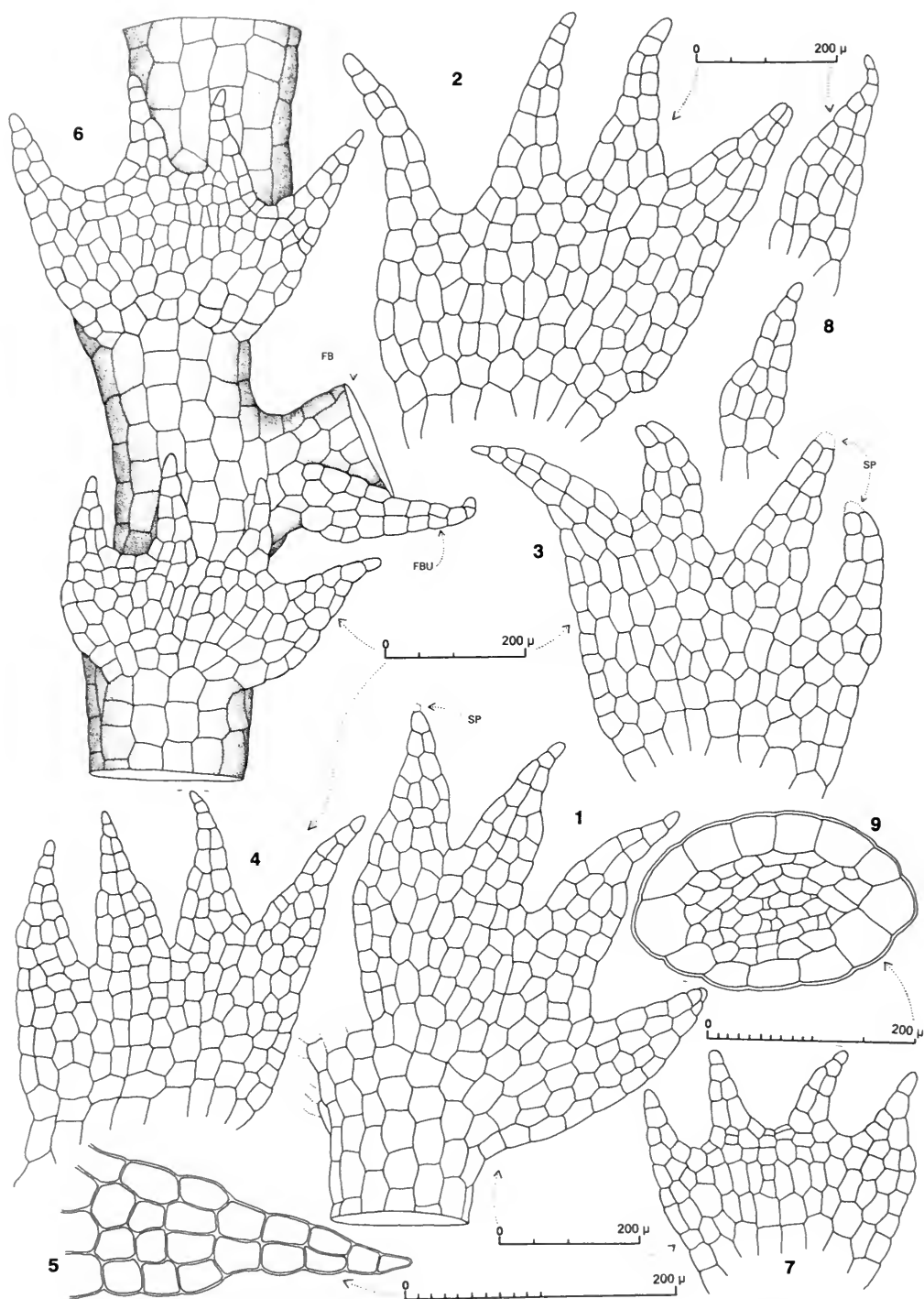


FIG. 8. *Telaranea consobrina* Engel & Merr. 1. Leaf, *in situ*, dorsal view (sp = slime papilla). 2–4. Leaves (sp = slime papilla). 5. Leaf lobe. 6. Sector of main shoot with *Frullania*-type branch (= FB; FBU = first branch underleaf), ventral view. 7. Underleaf; note small-celled rhizoid initials in distal part of disc and in basal portion of a lobe. 8. First branch underleaves. 9. Stem, cross section. (All from holotype.)



a blue gum/tea tree forest. Also known from a single site in Victoria (Grampians Natl. Park), where it is found on wet rocks adjacent to waterfalls.

**SPECIMENS SEEN**—TASMANIA: Cradle Mtn.-Lake St. Clair Natl. Park, Plateau Creek area, between Cradle Plateau and Marions Lookout, NNW of Cradle Mtn., 1250 m, *Engel 13960* (F); Macquarie Harbour, Sophia Point, *Moore 134* (HO); Flinders Is., Bass Strait, Cronley's Creek, foot of Mt. Strzelecki, *Scott s.n.* as *T. patentissima* (F, MELU). AUSTRALIA. VICTORIA: Grampians Natl. Park, Roses Gap, Beehive Falls, *Scott s.n.* as *T. ?patentissima* (F, MELU).

***Telaranea palmata* Engel & Merr.**

*Telaranea palmata* Engel & Merr., Novon 9: 344. f. 3. 1999. Holotype: Tasmania, ridge SE of Black Bluff near junction of access road to plateau area and road to Devonport gold mines, S facing slope, S of Burnie, 1000 m, *Engel 16251* (F); isotype: (HO).

Plants with a rather stiff and wiry appearance, densely to loosely interwoven in compact mats, yellowish green, nitid when dry; shoots small, to 0.6 cm wide, including branches. Branching somewhat irregularly and loosely 1(2)-pinnate, the branches remaining rather short, normally determinate, not much differing in length (rather than plumose), the branches of the *Frullania*-type, occasionally to frequently flagelliform; branch half-leaf 2-lobed, usually obliquely inserted, narrowly rectangular to cuneate, the lobes diverging; first branch underleaf undivided and subulate, inserted on ventral side of branch near base. Ventral-intercalary branches common, leafy, often becoming leading shoots. Stems with cortical cells markedly differentiated, the radial walls thin, the outer wall somewhat thickened, in 12 rows, those on ventral side of stem a little smaller; cortical cells in section larger than the numerous (ca. 50) medullary cells, the medullary cell walls slightly thickened and finely pitted. Rhizoids sparse, from distal cells of underleaf disc. Leaves on main shoot rigid, the disc widely spreading to squarrose, distant to loosely imbricate, moderately concave to hand-like, the lobes erect and incurved, at times subfalcate, the insertion transverse to weakly incubous; leaves 480–665(700)  $\mu\text{m}$  wide (measured between tips of lobes)  $\times$  400–510  $\mu\text{m}$  long, moderately asymmetric,  $\pm$  equally palmately 4-lobed to ca. 0.6, the lobes often widely divergent (the lateral lobe then forming an angle of up to 180° with adjacent median lobe), subequal to somewhat longer than the disc in length. Lobes

attenuate to subcaudate, 2–4 cells wide at base (when 4 cells wide sometimes with an additional 3–4 seriate tier), then biseriate for 1(2) tiers, terminating in a uniseriate row of 4–6 cells (typically more than half the length of lobe); lobe cells  $\pm$  firm, often distinctly thick-walled (to 7  $\mu\text{m}$  thick), the septa thickened in the corners and at times weakly projecting from the lobe margins, the basal cell of the uniseriate row 30–37  $\mu\text{m}$  wide  $\times$  38–54  $\mu\text{m}$  long, the next cell 24–31  $\mu\text{m}$  wide  $\times$  36–48  $\mu\text{m}$  long, the terminal cell shorter than the penultimate cell, tapering to a rounded point; cuticle smooth, the lobe tips rarely weakly striate-papillose. Disc symmetrically to somewhat asymmetrically short cuneate, 4 (rarely 5) cells high (from median sinus base to leaf base), 13–16 cells wide in distal portion, narrowing to 8 cells wide at the insertion; disc margins entire or with feebly projecting septa,  $\pm$  straight. Cells of disc moderately to distinctly thick-walled, trigones minute or none, the cells in  $\pm$  regular tiers, the median and basal disc cells 31–36  $\mu\text{m}$  wide  $\times$  39–48  $\mu\text{m}$  long, the distal tiers often longitudinally divided and 21–25  $\mu\text{m}$  wide (2–2.3:1); cuticle smooth. Underleaves much smaller than leaves, obliquely to widely spreading, distant, plane, 4-lobed to ca. 0.5 or a little more, the lobes divergent, ciliiform, straight, basically 2 cells wide at the base, the uniseriate portion formed of 3(4) slightly elongated,  $\pm$  thick-walled cells with septa thickened in the corners, often terminating in a slime papilla; disc symmetrically subquadrate to weakly cuneate, 3(4) cells high (median sinus), the cells in  $\pm$  regular tiers; disc 8–11 cells wide in distal portion, 8 cells wide at base; margins entire, usually straight. Asexual reproduction lacking.

Plants apparently dioecious. Androecia either terminal on short, primary, *Frullania*-type branches with a few cycles of normal vegetative leaves prior to androecial formation, or on short, exceptionally abbreviated, ventral-intercalary, spicate branches; bracts closely imbricate, strongly dorsally assurgent, deeply concave, bilobed to ca. 0.5, the lobes acute, terminating in a uniseriate row of 2–3 cells, the basal cell not or barely longer than wide, the terminal cell rather sharp and variable in length, to 3:1; dorsal margin of lamina somewhat dilated, crenulate, with slime papillae single and sessile or lacking; bracts monandrous; antheridial stalk short, 6 cells high, uniseriate; bracteolar antheridia absent. Gynoeceia not seen.

**DIFFERENTIATION AND VARIATION**—This species

is similar to *T. patentissima* and *T. capilligera*, but differs from both in the transverse insertion of the leaves (Fig. 9: 1). It differs from *T. patentissima* in several respects: the uniseriate row of the leaf lobes is 4–6 cells long, typically more than half the length of lobe, vs. 2–3(4) cells long in *T. patentissima*; the disc is 4(5) cells high vs. 4–6(7) cells high; the leaves are palmately 4-lobed to 0.6 vs. more shallowly 4(6)-lobed to 0.4–0.5 in *T. patentissima*; and the cells of both disc and lobes are distinctly thick-walled. It resembles *T. capilligera* in the shape of the leaves and in the thick-walled leaf cells, but differs in the elongate cells of the uniseriate row (to 2.3:1; Fig. 9: 4, 5), vs. barrel-shaped (at most 1.3:1) in *T. capilligera* (Fig. 3: 3, 4), and in the weakly projecting septa of lobes (and disc margins) vs. lobe cells barrel-shaped in *T. capilligera*, the lobes contracted at the septa.

*Telaranea palmata*, *T. capilligera* and *T. tri-dactylis* all have at least some leaves with widely spreading lateral lobes (often at an angle of 180° or more), but in the latter two species the leaves of this type are typically almost longitudinally inserted and oriented, whereas all the leaves of *T. palmata* are transversely inserted or only feebly incubous.

The leaves of this species are palmately lobed (to 0.6) like those of *T. praenitens* (p. 32). Both species have protruding septa of the lobe and disc margins, although this character is only weakly developed in *T. palmata*. In addition, the cuticle is smooth vs. distinctly striate papillose in *T. praenitens*.

**DISTRIBUTION AND ECOLOGY**—Endemic to Tasmania, and for the most part a subalpine-alpine species, occurring above 1000 m in protected, moist niches. It is found, for example, on soil under shrubby cover, as well as on the sides of rills, or with *Lophozia* sp., *Pachyschistochila parvistipula*, *Adelanthus* sp. and *Haplomitrium gibbsiae* in seepage channels. The type is from 1000 m in a mosaic of *Gymnoschoenus* (button grass), subalpine shrubs, *Nothofagus cunninghamii*, and rocky outcrops. The Surprise Valley station, however, is at 610 m and heavily forested, with *Nothofagus cunninghamii*, *Eucryphia* and *Anodopetalum* and an understory of *Richea*; *T. palmata* occurred over humus on the forest floor. In the southwest it was collected near sea level (Mainwaring River) in a riverine forest, occurring in carpets of moss, hepatics, and lichens on a downed *Nothofagus cunninghamii*.

**SELECTED SPECIMENS SEEN**—TASMANIA: Mt. Field Natl. Park, Tarn Shelf, below and E of Rodway Range, 1270 m, *Engel 14358* (F); Mt. Field, Clemes Tarn, 1220 m, *Moscal 23024* as *T. tetradactyla* (HO); Lake Gordon, *Walters* (Ratkowsky 79/182) (F, HO); South West District, Mainwaring River, 2 km E of river mouth, 2 m, *Moscal 9671B* as *T. tetradactyla* (HO); Cradle Mtn.-Lake St. Clair Natl. Park, Lake St. Clair area, between Mt. Rufus and Mt. Hugel, 1120–1130 m, *Engel 19363*—c. ♂ (F); Surprise Valley, above both Surprise River and Lyell Highway, 2.6 km W of King William Saddle, 610 m, *Engel 19427* (F); Cradle Mtn.-Lake St. Clair National Park, Weindorfers Forest, along track from Waldheim Chalet to Hounslow Heath Track, 975 m, *Engel 14046* (F).

#### *Telaranea* sect. *Cancellatae* Engel & Merr.

*Telaranea* sect. *Cancellatae* Engel & Merr., *Phytologia* 79: 250. 1996 (1995). Type: *Lepidozia tetrapila* Hook. f. & Tayl.

*Telaranea* sect. *Capillares* Engel & Merr., *Phytologia* 79: 251. 1996 (1995) non *Lepidozia* sect. *Capillares* G. L. & N., *Syn. Hep.* 211. 1845. Type: *Lepidozia grossiseta* Steph.

#### *Telaranea praenitens* (Lehm. & Lindenb.) Hodgs.

*Jungermannia praenitens* Lehm. & Lindenb. in Lehm. & Lindenb., *Nov. Min. Cogn. Stirp.* Pug. 6: 27. 1834. *Lepidozia praenitens* (Lehm. & Lindenb.) G. L. & N., *Syn. Hep.* 206. 1845. *Mastigophora praenitens* (Lehm. & Lindenb.) Trev., *Mem. Ist. Lomb. Sci. Lett.* III. 4: 416. 1877. *Telaranea praenitens* (Lehm. & Lindenb.) Hodgs., *Rec. Domin. Mus.* 4: 107. 1962. Type: New Zealand, South Is., Dusky Bay, *Menzies* (G!, S! [3 seen]).

Plants with a rather spiny appearance, soft, flexuous yet firm, loosely prostrate, often in dense, compact mats, dirty yellowish green, nitid when dry; shoots small to medium, to 0.9 cm wide, including branches. Branching mostly regular and loosely to less often quite densely 1-pinnate, the branches remaining rather short, normally determinate, not much differing in length (rather than plumose), the main axis often bearing only 2–4 normal leaves (on each side) between branches, the branches of the *Frullania*-type, occasionally flagelliform; branch half-leaf bilobed, usually obliquely inserted, narrowly rectangular to cuneate (then with lobes diverging), entire (or with one or both margins toothed in var. *dentifolia*); first branch underleaf undivided and ciliiform, inserted on ventral side of branch near juncture of branch and main axis. Ventral-intercalary branches occasional, often becoming leading shoots and leafy throughout. Stems with cortical cells markedly differentiated, the radial walls thin, the outer wall somewhat thickened, in 12–13 rows, those

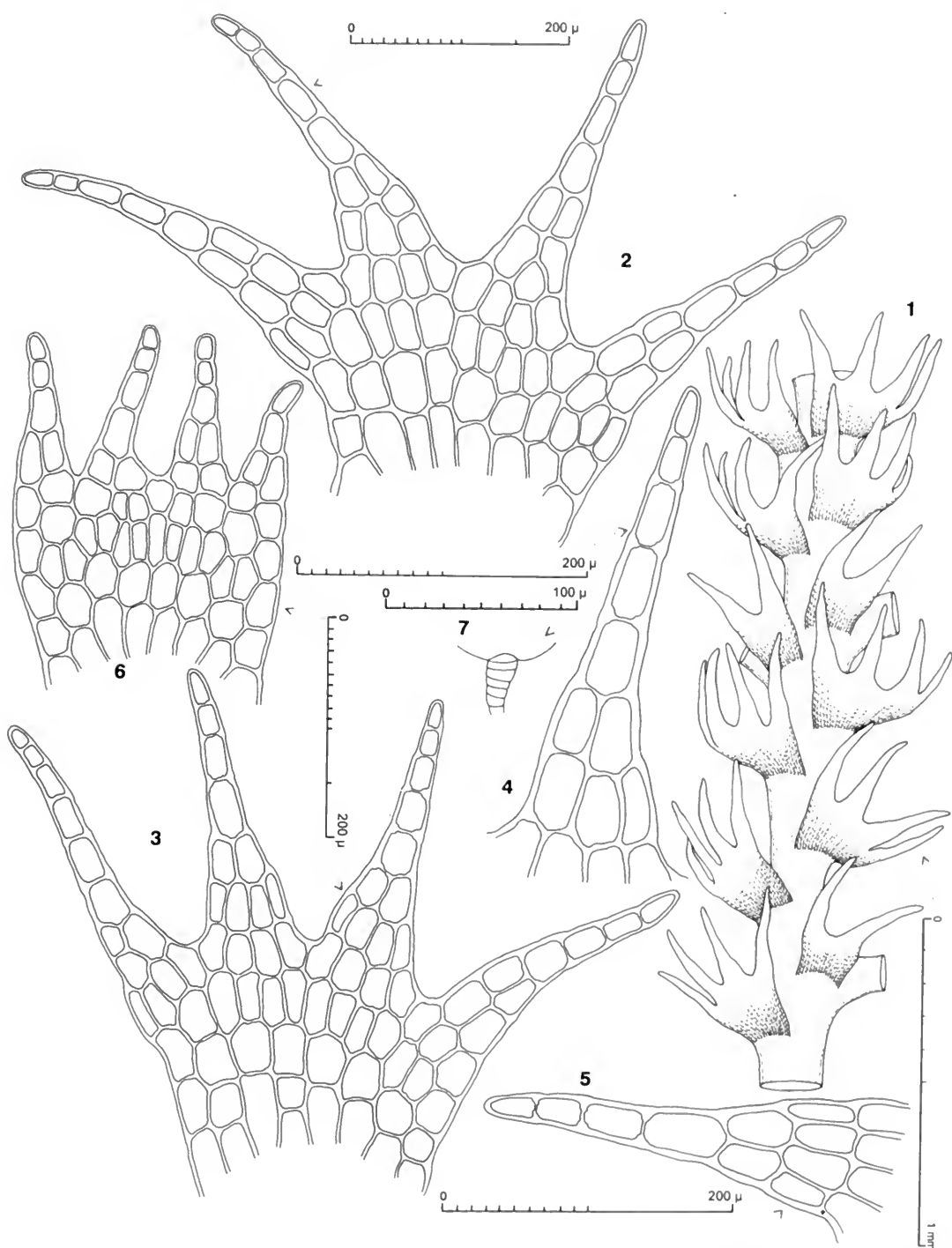


FIG. 9. *Telaranea palmata* Engel & Merr. 1. Portion of main shoot (the terminal branches not shown, but note half-leaves), dorsal view. 2, 3. Leaves. 4, 5. Leaf lobes. 6. Underleaf. 7. Antheridial stalk. (Figs. 1–6 from type; 7 from Engel 19363, Tasmania, Cradle Mtn.-Lake St. Clair Natl. Park, between Mt. Rufus and Mt. Hugel.)

on ventral side of stem a little smaller; cortical cells in section larger than the numerous (ca. 50–65) medullary cells, the medullary cell walls slightly thickened and finely pitted. Rhizoids not seen. Leaves on main shoot rigid, at least the disc widely spreading, distant to loosely imbricate, plane to moderately concave, the lobes somewhat incurved, the insertion moderately to distinctly incubous; leaves 510–870  $\mu\text{m}$  wide  $\times$  455–595  $\mu\text{m}$  long, moderately to distinctly asymmetric (the dorsal lobes paired),  $\pm$  equally and rather deeply palmately 4-lobed to ca. 0.5–0.65 (very rarely [1 population] 5–6-lobed), the lobes often widely divergent, subequal to somewhat longer than the disc in length. Lobes attenuate, 4 cells wide for 1–3 tiers at extreme base (5–6 cells wide at base in var. *dentifolia*), biseriate for much of their length, terminating in a short uniseriate row of 2–4(5) cells (typically less than half the length of lobe), the lobe margins contracted at the transition from 4 cells wide to 2 and from 2 cells wide to 1; lobe cells  $\pm$  firm, moderately thick-walled, the septae thickened in the corners and swollen and projecting from the lobe margins, the lobe cells rectangular and not narrowing distally, the cells in basal portion of lobe 14–20  $\mu\text{m}$  wide  $\times$  20–30  $\mu\text{m}$  long, the cells of the median (biseriate) portion 16–23  $\mu\text{m}$  wide  $\times$  25–40  $\mu\text{m}$  long, the terminal cell of uniseriate row 9–13  $\mu\text{m}$  wide  $\times$  19–23  $\mu\text{m}$  long, tapering to a rounded point; cuticle finely to distinctly striate-papillose. Disc somewhat asymmetrically short cuneate, 4–5 cells high (from median sinus base to leaf base), 15–16(19) cells wide in distal portion narrowing to 8–10 cells wide in basal portion; margins entire (sporadically toothed in var. *dentifolia*), the dorsal margin often bluntly denticulate by projecting septa at the ends of cells,  $\pm$  straight. Cells of disc moderately thick-walled, trigones minute to small, the median disc cells 22–38  $\mu\text{m}$  wide  $\times$  (38)43–60  $\mu\text{m}$  long, in  $\pm$  regular tiers or somewhat irregularly arranged; basal 1–2 rows of disc cells larger; cuticle smooth or faintly striate-papillose distally. Underleaves much smaller than leaves, strongly spreading to subsquarrose, distant, plane, 4(rarely 5)-lobed to ca. 0.5, the lobes divergent, ciliiform, straight, 2–3 cells wide at the base, the uniseriate portion formed of 3–4(5) elongated,  $\pm$  thick-walled cells with thickened septae, often terminating in a slime papilla; disc symmetrically cuneate, 3–4(5) cells high (median sinus), the cells in irregular tiers, the disc 11–17 cells wide in distal portion narrowing to 8–9(12) cells wide at base; margins entire, usually straight.

Plants dioecious. Androeceia either terminal on short to moderately long primary or secondary *Frullania*-type branches or on short, abbreviated, ventral-intercalary, spicate branches; bracts closely imbricate, strongly dorsally assurgent, deeply concave, bilobed to ca. 0.4, the lobes acuminate, terminating in a uniseriate row of 2–4 not to slightly elongated cells; dorsal margin of lamina irregularly crenulate, with a few stalked or sessile slime papillae; bracts monandrous; antheridia large for bract size, the stalk short, 6 cells high, uniseriate; bracteolar antheridia absent. Gynoeceia feebly to strongly dorsally assurgent, slightly swollen and densely rhizoidous at base; bracts small for perianth size, those of innermost series closely ensheathing the perianth, concave, broad ovate to suborbicular,  $\pm$  regularly 3–4-lobulate, the lobules terminating in a pair of laterally juxtaposed cells or a single cell; lamina composed of  $\pm$  regularly subrectangular cells, the margin bordered by cells of variable shape, often long and narrow, the apical or free end of marginal cells often divergent and forming a crenulation, the margins thus irregularly crenulate, otherwise with a sporadic unicellular tooth and a few slime papillae; bracteoles of innermost series similar in form and size to bracts. Perianth long emergent, fusiform, terete in basal and median sectors, the distal sector obscurely trigonous and with 4–5 plicae, the perianth narrowing toward the strongly contracted mouth; mouth cells thick walled, often sinuate, partially or wholly laterally free, occasionally with a laterally free uniseriate row of 2 cells, the mouth thus denticulate-subciliate, the surface cells immediately below mouth often with their apical end projecting as a blunt, thick-walled tooth; perianth 2–3-stratose in basal portion, the median portion 2-stratose.

Seta with 8 rows of outer cells (each with their free face bulging), surrounding an inner core of 19–20 much smaller cells. Capsule rather long elliptic, 980–1260  $\times$  420–560  $\mu\text{m}$ , the wall 26–34  $\mu\text{m}$  thick, of 3 layers, the outer layer subequal to the combined 2 inner layers, or slightly less thick; outer layer of cells in tiers, rather regularly short-rectangular, with 2-phase development, the longitudinal walls with well-defined sheetlike thickenings and nodule-like thickenings (4–6 per cell) alternating with walls that are devoid of thickenings (or with sporadic, local, nonpigmented, nodular swellings), the transverse walls devoid of thickenings; intermediate layer thinner than both outer and inner layers; innermost layer of cells  $\pm$  tiered, irregularly narrowly to broadly rectangular,

with semiannular bands common, rather narrow, close, usually complete, at times forked and anastomosing to delimit ill-defined, local fenestrae.

Spores 12–13  $\mu\text{m}$ , exine yellow brown, areolate (with a low, delicate, close network of furcate ridges that coalesce and delimit areolae). Elaters rigid, nontortuous, 9.6–12  $\mu\text{m}$  wide, only slightly tapering toward tips, bispiral to tips, the spirals 2.4–3.8  $\mu\text{m}$  wide.

**DIFFERENTIATION AND VARIATION**—Judging from identifications of herbarium specimens, *T. praeinitens* has been widely misunderstood. It is, however, one of the easiest of our species to recognize, marked by the rather deeply palmately-lobed leaves (to 0.6), and the minute denticulations formed by the swollen projecting septa on the lobes and disc margins (Fig. 10: 5, 6). In addition, the cuticle of the lobes is almost always distinctly papillose (Fig. 10: 5, 6). *Telaranea verruculosa* (Fig. 60, p. 197), a recently discovered species from Queensland, also has a distinctly papillose cuticle, although in that species the disc is also papillose.

A noteworthy feature of this species is the scabrous condition of the perianth surface. The cells immediately below the mouth are prorate, their apical ends projecting as blunt, thick-walled teeth (Fig. 10: 9). Other species with similarly roughened perianths are *T. mamillosa* (p. 166), and *T. jowettiana* (p. 161). *Telaranea chaetocarpa* (Pears.) Grolle of New Caledonia may represent an extreme of this condition. There, the surface of the perianth bears numerous simple or bifurcate capillary bristles which are similar in appearance to the leaf lobes (Pearson, 1922, p. 27; pl. 2: 45–47; Fig. 41: 1, 2).

Among the specimens assigned to this species are some which have broader-based leaf lobes and discrete teeth on the disc margins of both leaves and half-leaves, a rather startling anomaly in *Telaranea*, a genus thought to have perfectly entire leaves. These are recognized here as a variety, var. *dentifolia*.

#### Key to Varieties of *T. praeinitens*

1. Margins of leaves and half-leaves devoid of teeth; leaf lobes 4 cells wide at base, the cells in basal portion of lobe elongate (ca. 2:1). Throughout New Zealand . . . var. *praeinitens*
1. Margins of leaves and half-leaves (and rarely the lobes) sporadically with 1(2) multicellular

teeth; leaf lobes (at least the median) often 5–6 cells wide at base, the cells of lobe bases somewhat shorter, at times  $\pm$  isodiametric. Local, southern half of South Island . . . . . var. *dentifolia*

*Telaranea praeinitens* (Lehm. & Lindenb.) Hodgs.  
var. *praeinitens*

*Lepidozia beckettiana* Steph., Spec. Hep. 3: 593. 1909. Lectotype (nov.): New Zealand, South Is., Westland, Kellys Range, 30 Jan. 1903, *Beckett 4310*—c. per. (G!).

Leaf and half-leaf margins devoid of teeth; leaf lobes 4 cells wide at base, the cells in basal portion of lobe elongate (ca. 2:1); margins of disc and lobe typically minutely denticulate by protruding end walls of the marginal cells.

**DISTRIBUTION AND ECOLOGY**—Endemic to New Zealand, found on Stewart Island and rather widespread on South and North Islands. The species was reported in the earlier literature from Tasmania (Bastow, 1888; Hooker, 1867; Mitten, 1859; Rodway, 1916; Stephani, 1909) and Western Australia (Lehmann, 1844–47); Ratkowsky (1987) also listed the species for Tasmania. We have seen no collections of the species from Tasmania or Australia.

A species of wet, rich lower- to upper-elevation forests, where often on rotted logs, particularly when largely bryophyte-covered. It occurs, for example, in rich, mixed *Nothofagus* forests with a tree fern understory (Tutoko River, Fiordland); in matai/totara flood-plain forests (Waiho River area in Westland); in *Nothofagus menziesii*-*Dacrydium cupressinum*-*Podocarpus* forests along the Four Mile River (Nelson Prov.); and in *N. menziesii*-*Pseudopanax simplex*-*Podocarpus totora*-*Dracophyllum* forests (Panekiri Range, Urewera Natl. Park). It only sporadically inhabits soil or humus of the forest floor, or moist banks, etc.

The species rarely is subalpine. It was recently found at 1520 m on Mt. Arthur in communities of subalpine cushion vegetation, rocky herb fields, and *Dracophyllum*, where it occurred over decaying blades at the base of a grass immediately adjacent to a small, stagnant pool.

**SELECTED SPECIMENS SEEN**—NEW ZEALAND. STEWART ISLAND: Port Adventure, *Schuster, Scott & Taylor* (CHR). SOUTH ISLAND. SOUTHLAND PROV.: Dusky Sound, Supper Cover, *Zotov* as *T. paten-tissima* (CHR); Doubtful Sound, *Simpson* (CHR); Fiord-

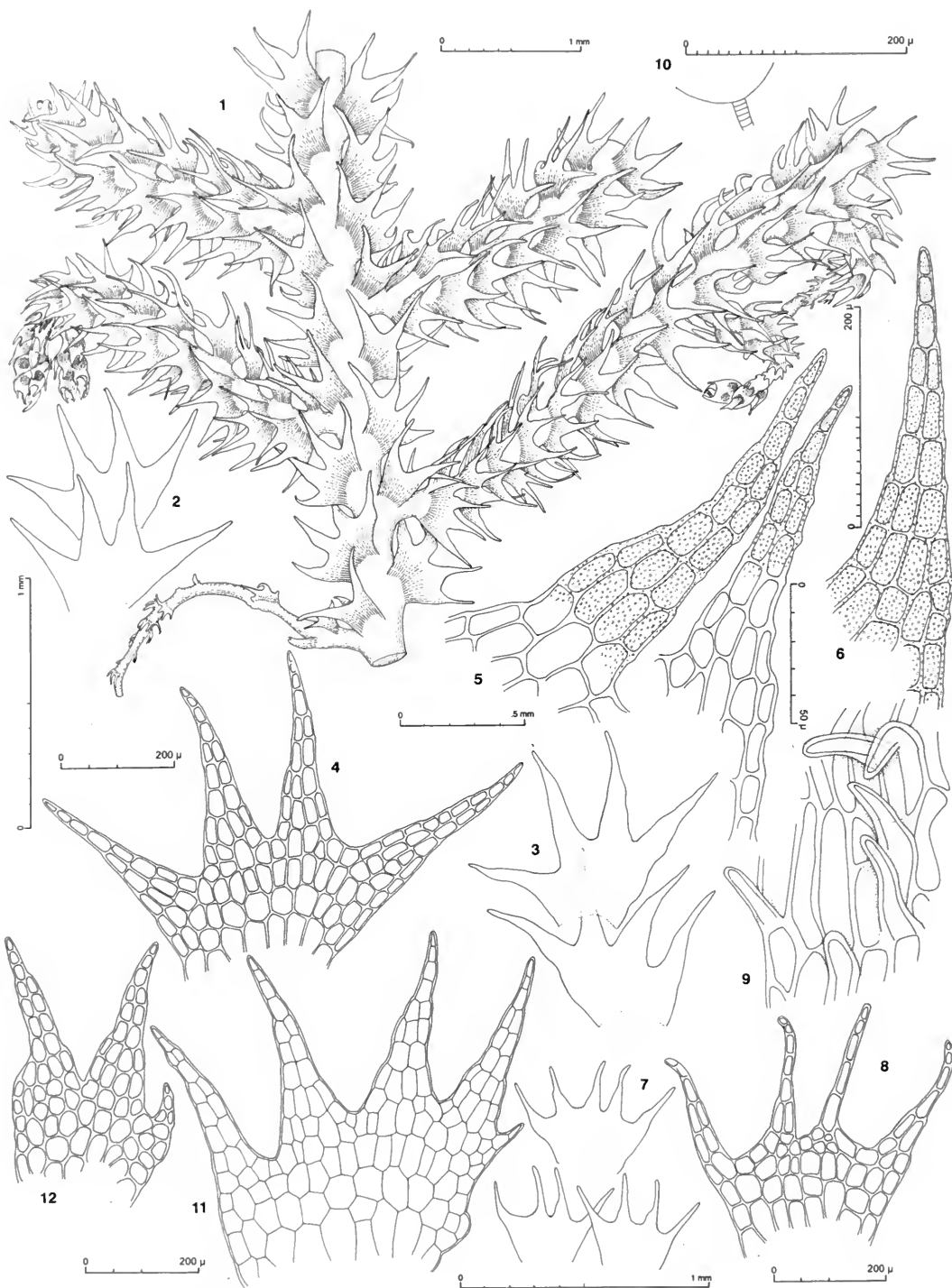


FIG. 10. *Telaranea praenitens* (Lehm. & Lindenb.) Fulf. (Figs. 1–10, var. *praenitens*; 11–12, var. *dentifolia*.) 1. Sector of main shoot showing androecia on primary and secondary terminal branches, dorsal view. 2, 3. Leaves (note symmetry). 4. Leaf, cellular detail. 5, 6. Dorsal lobes of leaves. 7. Underleaves. 8. Underleaf, cellular detail. 9. Sector of perianth surface immediately below mouth. 10. Antheridial stalk. 11. Leaf. 12. Half-leaf. (Figs. 1–2, 4, 6–8, 10 from Engel 18935, New Zealand, South Is., Westland Prov., near Waiho River between Wombat Terrace and Canavans Knob; 3, 5 from Engel 6667B, New Zealand, South Is., Westland Prov., Lake Wombat; 9 from Reif C63B, New Zealand, South Is., Westland Prov., Camp Creek; 11, 12 from type of var. *dentifolia*.)

land Natl. Park, Stillwater River, *Zotov* (CHR); *ibid.*, Cleddau Valley, The Chasm, *Burrell, Scott & Taylor* (CHR); *ibid.*, Tutoko River, W of Milford Sound, 50 m, *Engel 18841* (F). OTAGO PROV.: Fiordland Natl. Park, near head of Lake McKerrow, *Hatcher 727* (F); N of McKerrow River, Martin's Bay, *Hatcher 735b* (F). WESTLAND PROV.: Cascade Road, just W of Jackson River, ca. 8–12 km SW of confluence of Jackson and Arawata Rivers, 25–90 m, *Engel 22992*—c. ♂ (F); Lake Ellery, ca. 30 m, *Child H4569* (F); Haast Pass Road, Robinson Creek, between Haast Pass and gates of Haast bridge, ca. 305 m, *Child H1852* (F); Haast, 5 miles N of bridge, ca. 30 m, *Child H521* (F); Westland Natl. Park, Fox Glacier, S side of Fox River, *Engel 6618A* (F); Weheka, near Fox Glacier Hotel, *Whitehouse 2970A* (F); Westland Natl. Park, Franz Josef Glacier Valley, Roberts Point, SW of Mt. Gunn, ca. 620–670 m, *Engel 18087* (F); *ibid.*, Lake Wombat, 250 m, *Engel 6667B* (F); near Waiho River between Lake Wombat Terrace and Canavans Knob, NW of town of Franz Josef Glacier, off Hwy 6, 110 m, *Engel 18935*—c. ♂ (F); Arthur's Pass Natl. Park, N of Kellys Creek near Hwy 73, N of Otira, 420–475 m, *Engel 18340*—c. sporo. (F); Otira Gorge, *Berggren 3012* (S); Lake Kaniere Scenic Reserve, Lake Kaniere Rd, 125 m, *Engel 24857*—c. per. (F); along Route 73, 8 miles W of Turiwhate, *Engel 6746* (F); Camp Creek, W of Alexander Range, 190–840 m, *Reif C9C, C11G*—c. sporo., *C170C* (F); 2 km N of White Horse Creek, ca. 305 m, *Child H5429* (F). CANTERBURY PROV.: Arthur's Pass Natl. Park, near Bealey Glacier Vista, *Engel 6843* (F). NELSON/WESTLAND PROV. BOUNDARY: Paparoa Range, S side of Porarari River, up river from gorge and ca. 500 m WSW of ford on inland track to Bullock Creek, 10–20 m, *Engel 19172* (F). NELSON PROV.: Paparoa Natl. Park, Bullock Creek Road, along Bullock Creek, NE of Punakaiki, ca. 25 m, *Engel 21616* (F); Four Mile River (Tiropahi) Track, 215 m, *Fife 4674* (F); track to German Terrace, 6 km SSE of Westport on Nine Mile Road, 90 m, *Engel 21554* (F); Nelson Lakes Natl. Park, off Lakehead Track, near juncture with southern end of Loop Track, NE end of Lake Rototiti, 630 m, *Engel 22729* (F); Kahurangi Natl. Park, Mt Arthur, track to summit of Mt. Arthur, 1520 m, *Engel 24943* (F). NORTH ISLAND. WELLINGTON PROV.: Oroua Valley, Western Ruahine State Forest, ca. 670 m, *Hodgson s.n.* (CHR); Mt. Arawaru, *Zotov* (CHR); Tararua Mts., Orongorongo River, ca. 610 m, *Zotov* (CHR); *ibid.*, Mangahao Downs, *Hodgson 10645* (CHR); *ibid.*, N of Field Hut, ca. 795 m, *Zotov* (CHR); Ruahine Mts., above Upper Pohangina Valley, *Allison H7590* (CHR); near E border of Tongariro Natl. Park along road to Tree Trunk Gorge, ca. 0.5 km W from gorge, 750 m, *Engel 21213* (F). GISBORNE PROV.: Urewera Natl. Park, Panekiri Range, summit area of Pukenui in vicinity of Puncikiri Bluff, S of Lake Waikaremoana, 1180 m, *Engel 23341* (F); Urewera Natl. Park, Huiairau Range, summit area of Te Rangaakapua, 1230–1320 m, *Engel 23476* (F). TARANAKI PROV.: Below North Egmont Mt. Hut, *Hodgson 10243* (CHR); Mt. Egmont, 915 m, *Hodgson* (S); Pukeiti Bush, near New Plymouth, *Hatcher 336* (F). SOUTH AUCKLAND PROV.: Pukerimu Bush, E of Taupo, ca. 760 m, *Allison H5908* (CHR); Paeroa Range, S of Rotorua, ca. 915 m, *Allison H3035* (CHR); Ohau-iti River, *Zotov* (CHR).

*Telaranea praenitens* var. *dentifolia* Engel & Merr.

*Telaranea praenitens* var. *dentifolia* Engel & Merr., *Phytologia* 79: 253, June, 1996 [1995]. Holotype: New Zealand, South Island, Fiordland, Dusky Sound, Supper Cove, 11 Feb. 1946, *Allan*, as *Lepidozia gottscheana* (CHR); isotype: (F).

Leaves, half-leaves, and rarely lobes with disc margins sporadically armed with 1(2) multicellular teeth; leaf lobes (at least the median) often 5–6 cells wide at base; cells of lobe bases at times  $\pm$  isodiametric; end walls of marginal cells of disc and lobes often indistinctly or not swollen and protruding.

DIFFERENTIATION AND VARIATION—This variety and the typical expression of the species both have rather deeply divided, palmately lobed leaves, which distinguish *T. praenitens* from other members of the sect. *Neolepidozia*, although the septa between cells are not so distinctly swollen and protruding as in var. *praenitens*. The combination of rather broad leaf lobes, marginal teeth (Fig. 10: 11), and papillose cuticle is reminiscent of *Temnoma* spp.; the well-developed stem hyaloderm, however, marks this plant as a *Telaranea*.

DISTRIBUTION AND ECOLOGY—Known only from a limited number of collections, all from the wet, southwestern sector of South Island. The type occurred intimately intermixed with *Riccardia* sp., and the Simpson collection is mixed with *Sematophyllum amoenum*. The variety appears to be a lower-elevation forest plant.

SELECTED SPECIMENS SEEN—NEW ZEALAND. SOUTH ISLAND. SOUTHLAND PROV.: Fiordland, Doubtful Sound, Hall Arm, *Simpson 1328* as *T. gottscheana* (CHR). WESTLAND PROV.: Westland Natl. Park, 250 m, *Engel 6662* (F); near Lake Parina, W coast, cf. 15 m, *Child H1798* (F).

*Telaranea gibbsiana* (Steph.) Hodgs.

*Lepidozia gibbsiana* Steph., Spec. Hep. 6: 328. 1922. *Telaranea gibbsiana* (Steph.) Hodgs., Trans. Roy. Soc. New Zealand, Bot. 3: 70. 1965. Type: New Zealand, North Is., without specific loc., *Gibbs 1041* (G!).

Plants subisophyllous, soft, with a hairy appearance, flexuous yet firm, prostrate to ascending, in dense, compact mats, pale green to (deep olive green in herb.), highly nitid when dry; plants medium, to 0.8 cm wide, including branches.



Branching regularly rather densely and closely pinnate, occasionally locally 2- or 3-pinnate, nearly exclusively of the *Frullania* type, the branches short to moderately long but normally determinate, sometimes flagelliform; branch half-leaf 2–4-lobed, usually obliquely inserted, cuneate (the lobes diverging, even when bifid); first branch underleaf undivided and ciliiform or 2(3)-fid, inserted on ventral or less often ventral-lateral side of branch near or at juncture of branch and main axis. Ventral-intercalary branches occasional, often becoming leading shoots and leafy throughout. Stems with cortical cells distinctly differentiated, thin-walled, in 13–15 rows, those on ventral side of stem a little smaller; cortical cells in section much larger than the numerous (34–47) medullary cells, the medullary cell walls uniformly slightly thickened. Rhizoids observed only on stoloniform axes. Leaves on main shoot rigid, suberect to widely spreading, loosely to closely imbricate, concave reflecting the incurving of lobes, the insertion moderately to distinctly incubous; leaves 720–1275  $\mu\text{m}$  wide  $\times$  630–890  $\mu\text{m}$  long, subsymmetric to less often asymmetric, 4–6(7) lobed to (0.6)0.65–0.75, the lobes widely divergent, longer than the disc. Lobes ciliiform, rigid, the base subtriangular, (3)4(5) cells wide at extreme base, terminating in a uniseriate row of 5–7(8) cells; cells of the uniseriate portion  $\pm$  thick-walled, the septa thickened in the corners and swollen, the basal cell of the uniseriate portion 36–46  $\mu\text{m}$  wide  $\times$  84–108  $\mu\text{m}$  long ([1.6]2.4–4.1:1), the next cell narrower but of about the same length, 29–36  $\mu\text{m}$  wide  $\times$  84–118  $\mu\text{m}$  long ([2.3]3–4.4:1), the terminal cell normally about the size of the penultimate cell, or a little smaller. Disc  $\pm$  symmetrically cuneate, 4–6 cells high (from median sinus base to leaf base), 15–22 cells wide in distal portion narrowing to 8–15 cells wide in basal portion; margins entire,  $\pm$  straight to less often slightly curved. Cells of disc thin-walled but not delicate, trigones minute to small, the median cells large, 36–65  $\mu\text{m}$  wide, 50–72(78)  $\mu\text{m}$  long; basal 1–2 rows of disc cells considerably larger (wider and on the whole a little longer), often not in regular tiers; cuticle with network of fine irregular, elongate striae. Underleaves somewhat smaller than leaves, strongly spreading to subsquarrose, contiguous to loosely imbricate, plane, 4–6(8)-lobed to 0.6–0.8, the lobes  $\pm$  symmetrically divergent, ciliiform, straight to arched, the uniseriate portion formed of 5–7(8) elongated,  $\pm$  thick-walled cells with swollen septa, not terminating in a slime papilla;

disc symmetrically cuneate, 3–4(5) cells high (median sinus), the cells often not in regular tiers, the disc 9–17 cells wide in distal portion narrowing to (8)10–12 cells wide at base; margins entire, usually straight. Asexual reproduction lacking.

Plants dioecious. Androecia on short, abbreviated, ventral-intercalary, spicate branches from main shoot or primary, *Frullania*-type branches; bracts closely imbricate, strongly dorsally assurgent,  $\pm$  cucullate, bilobed to ca. 0.3, the lobes acuminate, terminating in a uniseriate row of 2–3(4) cells, the basal cell isodiametric to rather elongated, the terminal cell  $\pm$  thick-walled, often curved, rather elongated, to 3.5:1; dorsal margin of lamina somewhat dilated and incurved, entire, bordered by 1–2 rows of elongated, very thin-walled cells, no slime papillae; bracts monandrous; antheridial stalk rather long, ca. 9 cells high, uniseriate; bracteolar antheridia absent. Gynoecia oriented laterally and at best only weakly dorsally assurgent, with a vestigial stem perigynium present, swollen, rhizoidous; bracts becoming progressively larger and less deeply lobate towards the perianth, those of innermost series ensheathing the perianth, deeply concave, the apical portion canaliculate, the bracts  $\pm$  suborbicular, with apices irregularly 4-lobulate, the lobules terminating in a uniseriate row of 1–2 cells; bract margins crenate to dentate, the armature frequently sharply inflexed, often terminating in a slime papilla, the bracts with an obscure border formed of 1 to several rows of cells longer, narrower and more irregular than those within; bracteoles of innermost series nearly identical in form to bracts although a little smaller. Perianth not extending above vegetative axes, 0.5–0.55 emergent, ovoid-cylindrical, terete in basal half, the distal half obscurely trigonous and with 6–9 plicae, the sulci shallow to deep; perianth narrowed toward a decidedly contracted mouth, the mouth with 6 narrowly triangular lobes, each lobe fringed with slightly thick-walled, contorted, crowded, sparingly papillose cilia, the terminal cell of each cilium coarsely papillose.

Seta seen only in collapsed state. Capsule wall 32–40  $\mu\text{m}$  thick, of 3–4 layers, the outer layer subequal to 2 of inner layers; outer layer of cells weakly tiered, rather regularly short-rectangular, with 2-phase development, the longitudinal walls with well-defined sheetlike thickenings and nodule-like thickenings (4–6 per cell) alternating with walls that are devoid of thickenings (or with occasional local, not or weakly pigmented, nodular swellings), the transverse walls devoid of thick-



enings or with 1–2 nodular swellings; innermost layer of cells in weakly defined tiers, irregularly narrowly rectangular; semiannular bands common, rather wide, close, usually complete, at times forked and anastomosing to delimit ill-defined, local fenestrac.

Spores and elaters not seen.

**DIFFERENTIATION AND VARIATION**—*Telaranea gibbsiana* is one of our largest *Telaranea* species, and is most closely allied to *T. grossiseta* of Tasmania. Both are relatively robust plants (for the genus), with a high disc, ciliiform leaf lobes, and the cells of the uniseriate row distinctly elongated and capillary. The septa are thickened in the corners and swollen and projecting (Fig. 11: 7). Similar projecting septa occur in *T. praenitens*. The most obvious differences between *T. gibbsiana* and *T. grossiseta* are the lower disc (4–6 cells high vs. 7–9 cells in *T. grossiseta*), and the characteristic asymmetry of the disc and decidedly water-repellent cuticle in *T. grossiseta*.

**DISTRIBUTION AND ECOLOGY**—The protologue and the type at G give no specific locality within New Zealand, other than North Island. Gibbs (1911), however, stated that the type was collected at Te Aroha, Thames District, south of Auckland, 2500 ft. on stones and rotten wood, in forest in November, 1907.

The species appears to be locally and sporadically distributed on North Island, New Zealand. Known from several sites in the Lake Waikaremoana-Urewera area of North Island; there it occurs on ground, exposed roots, rotted stumps, and bryophyte-covered logs, etc., in forests between 540 and 1320 m (where recorded). It is also locally abundant in the Waipoua Kauri forests, where it occurs associated with *Hymenophyllum*, *Dicranoloma* and *Trichocolea* over rotten logs. The plant is known from a single station on South Island, occurring abundantly on humus in a *Podocarpus-Nothofagus* forest (280–350 m, Nelson Prov.).

**SELECTED SPECIMENS SEEN**—NEW ZEALAND. SOUTH ISLAND. NELSON PROV.: Maimai State Forest, 3 m NW of Reefton, 280–350 m, *Macmillan* 76/12, 76/154 both as *T. gottscheana* (CHR). NORTH ISLAND. GISBORNE PROV.: Lake Waikaremoana, 610 m, *Hodgson s.n.* (F); *ibid.*, Ngamoko Track, *Hodgson* 402 (CHR); *ibid.*, *Hatcher* 1301—c. ♂, 1310 (F); near Lake Waikaremoana, trail to Lake Waikare-iti, *Whitehouse* 29196 (F); Urewera Natl. Park, Waikareiti Track between track entrance and Lake Ruapani, N of eastern extremity of Lake Waikaremoana, 650–920 m, *Engel* 20513—c. sporo. (F); *ibid.*, Maungapohatu, ca. 1100 m,

*Moore* H131 (CHR); *ibid.*, Huiarau Range, summit area of Te Rangaakapua, 1230–1320 m, *Engel* 23503 (F). SOUTH AUCKLAND PROV.: Colomandel Peninsula, Waihi, “ex herb. D. Petrie No. 73”—c. ♂ (CHR). NORTH AUCKLAND PROV.: Track to Mahuta, Waipoua State Forest, ca. 305 m, *Child* H 2137—c. ♂, H2153 (F); SE corner of Waipoua Forest, just N of Tutamoe, 540 m, *Engel* 21136 (F); Waima Forest, Hauturu Highpoint Track in vicinity of summit area of Hauturu Trig, off Waiotemarama Track, 650–680 m, *Engel* 22609 (F).

*Telaranea grossiseta* (Steph.) Engel & Schust.

*Lepidozia grossiseta* Steph., Spec. Hep. 3: 584. 1909.  
*Neolepidozia grossiseta* (Steph.) Fulf. & J. Tayl., Brittonia 11: 85. 1959. *Telaranea grossiseta* (Steph.) Engel & Schust., Fieldiana, Bot. n.s. 14: 3. 1983. Type: Tasmania, West Coast, near Moore’s Lookout, Mar. 1900, *T. B. Moore* 5794 (G!).

Plants subisophyllous, with a rather hairy appearance, flexuous yet firm, prostrate in loose mats, glaucous, whitish green to ceraceous, the surface dull, waxy and water repellent, the old shoots brownish and subnitid; plants large, the main shoot to 2.2 mm wide, to 1.1 cm wide, including branches. Branching loosely to somewhat irregularly 1-(sporadically 2) pinnate, mostly of the *Frullania* type, frequently becoming flagelliform; branch half-leaf bifid, transversely to incubously inserted, the lobes often divergent; first branch underleaf undivided, ciliate to subulate, (rarely bilobed), inserted on ventral-lateral side of stem at or somewhat below the juncture of branch and stem. *Acromastigum*-type branches present but rare. Ventral-intercalary branches common, either leafy throughout or stoloniform, the stolons normally present toward shoot base. Stems with cortical cells distinctly differentiated, in 12–17 rows, much larger than the numerous (ca. 40–90 rows) medullary cells, both the cortical and medullary cells thin or evenly and slightly thick walled. Rhizoids from distal cells of underleaf disc. Leaves on main shoot rigid, widely spreading, nearly but normally not at right angles to the stem, contiguous to loosely imbricate, plane or essentially so, distinctly incubously inserted and oriented, 1135–1650  $\mu\text{m}$  wide  $\times$  1160–1650  $\mu\text{m}$  long, moderately asymmetric, 4(6)-lobed to 0.5–0.65, the lobes somewhat divergent, often asymmetrically so, the dorsal lobe typically stiffly dorsally assurgent and out of plane of leaf, often oriented toward shoot apex, the other lobes  $\pm$  parallel with the disc margins, the lobes about as long as the disc. Lobes ciliiform, rigid, consisting of a short subtriangular base 4–6 cells wide at extreme

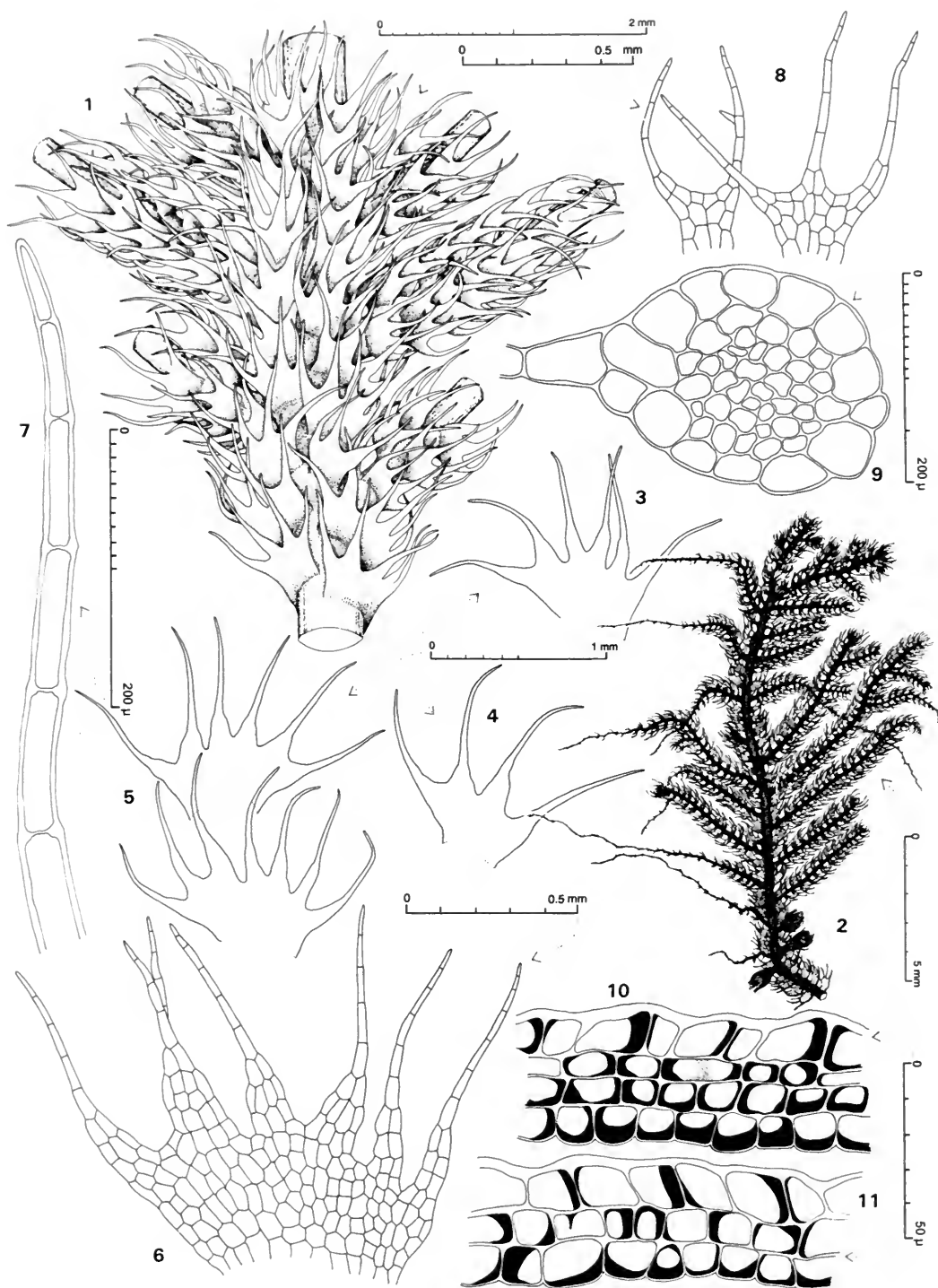


FIG. 11. *Telaranea gibbsiana* (Steph.) Hodg. 1. Shoot with 6 *Frullania*-type branches, dorsal view (note 2-, 3- and 4-lobed half-leaves). 2. Shoot with 3 young gynoecia toward base, dorsal view. 3–6. Leaves. 7. Distal portion of leaf lobe. 8. First branch underleaves. 9. Stem, cross-section. 10, 11. Capsule wall cross sections. (Figs. 1–9 from Hodgson s.n., New Zealand, North Is., Lake Waikaremoana [F]; 10, 11 from Engel 20513, New Zealand, North Is., Gisborne Prov., Urewera Natl. Park, Waikareiti Track.)

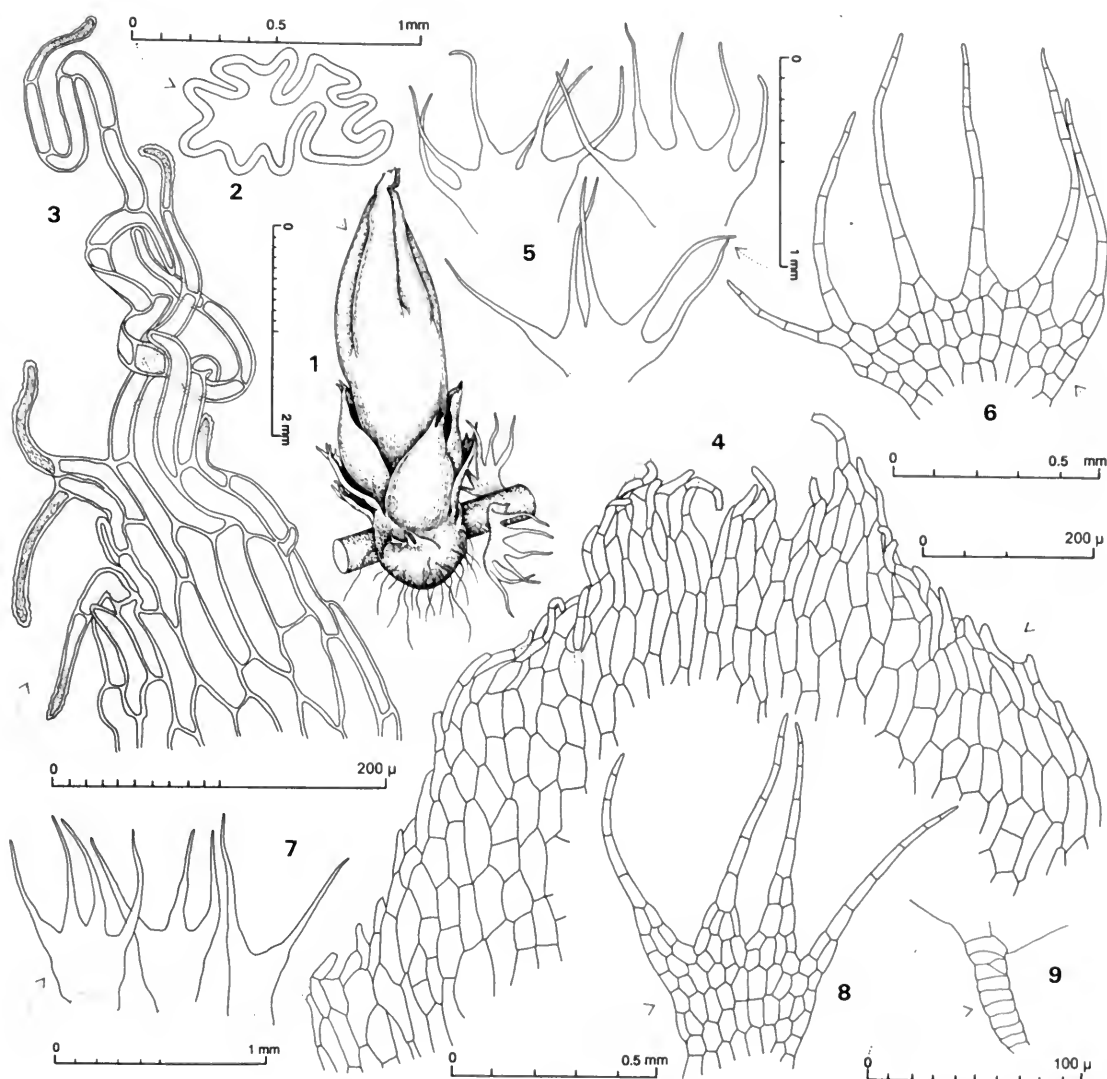


FIG. 12. *Telaranea gibbsiana* (Steph.) Hodg. 1. Gynoecium. 2. Cross section through distal portion of perianth. 3. Portion of perianth mouth. 4. Distal portion of innermost bract. 5. Underleaves of main shoot. 6. Underleaf. 7. Half-leaves. 8. Four-lobed half-leaf. 9. Antheridium. (Figs. 1–8 from Hodgson s.n., New Zealand, North Is., Lake Waikaremoana [F]; 9 from Hatcher 1301, same loc.)

base and abruptly contracted to a bristle-like uniseriate portion 6–7(8) cells long; dorsal lobe often widely divergent, 1–2-seriate at base (if uniseriate to base, then “embedded” in disc), often appearing displaced midway onto the dorsal margin of disc; cells of the uniseriate row thick-walled (in comparison with disc cells), elongated, subcapillary, the septa thickened at the corners and typically swollen, the basal cell of the uniseriate portion  $36\text{--}48\text{ }\mu\text{m}$  wide  $\times$   $137\text{--}168\text{ }\mu\text{m}$  long, the next cell narrower and longer,  $26\text{--}34\text{ }\mu\text{m}$  wide  $\times$   $149\text{--}180\text{ }\mu\text{m}$  long, the longest cells of the uni-

seriate row up to  $7.5:1$ , the terminal cell very short, tapering to a sharp point. Disc asymmetrically cuneate to short rectangular, the dorsal margin (insertion to dorsal lobe base) distinctly shorter than the ventral, the disc 7–9(10) cells high (from median sinus base to leaf base), 14–19 cells wide in distal portion narrowing to 8–12 cells wide in basal portion; margins entire,  $\pm$  straight to slightly curved, sometimes asymmetrically so. Cells of disc thin-walled but not delicate, trigones minute or lacking, median disc cells large,  $46\text{--}60\text{ }\mu\text{m}$  wide,  $77\text{--}94\text{ }\mu\text{m}$  long; cells of disc margins

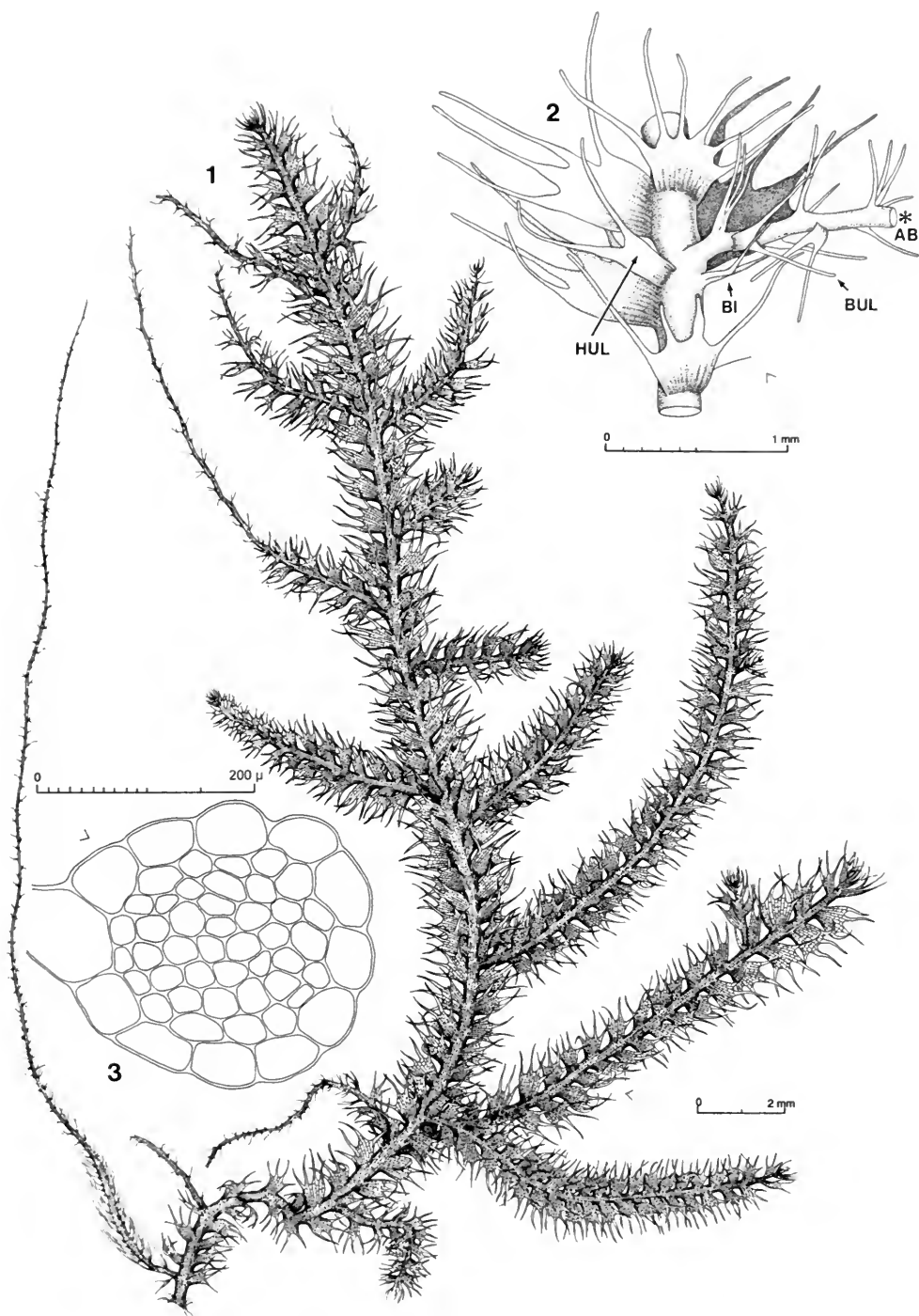


FIG. 13. *Telaranea grossiseta* (Steph.) Engel & Schust. 1. Plant, dorsal view. 2. Portion of main shoot with *Acromastigium*-type branch (= AB), ventral view; note 6-fid underleaf (rare), (HUL = half-underleaf; BL = first branch leaf; BUL = branch underleaf). 3. Stem, cross section. 4. Uniseriate portion of leaf lobe. (All from Engel 14728, Tasmania, Gordon River.)

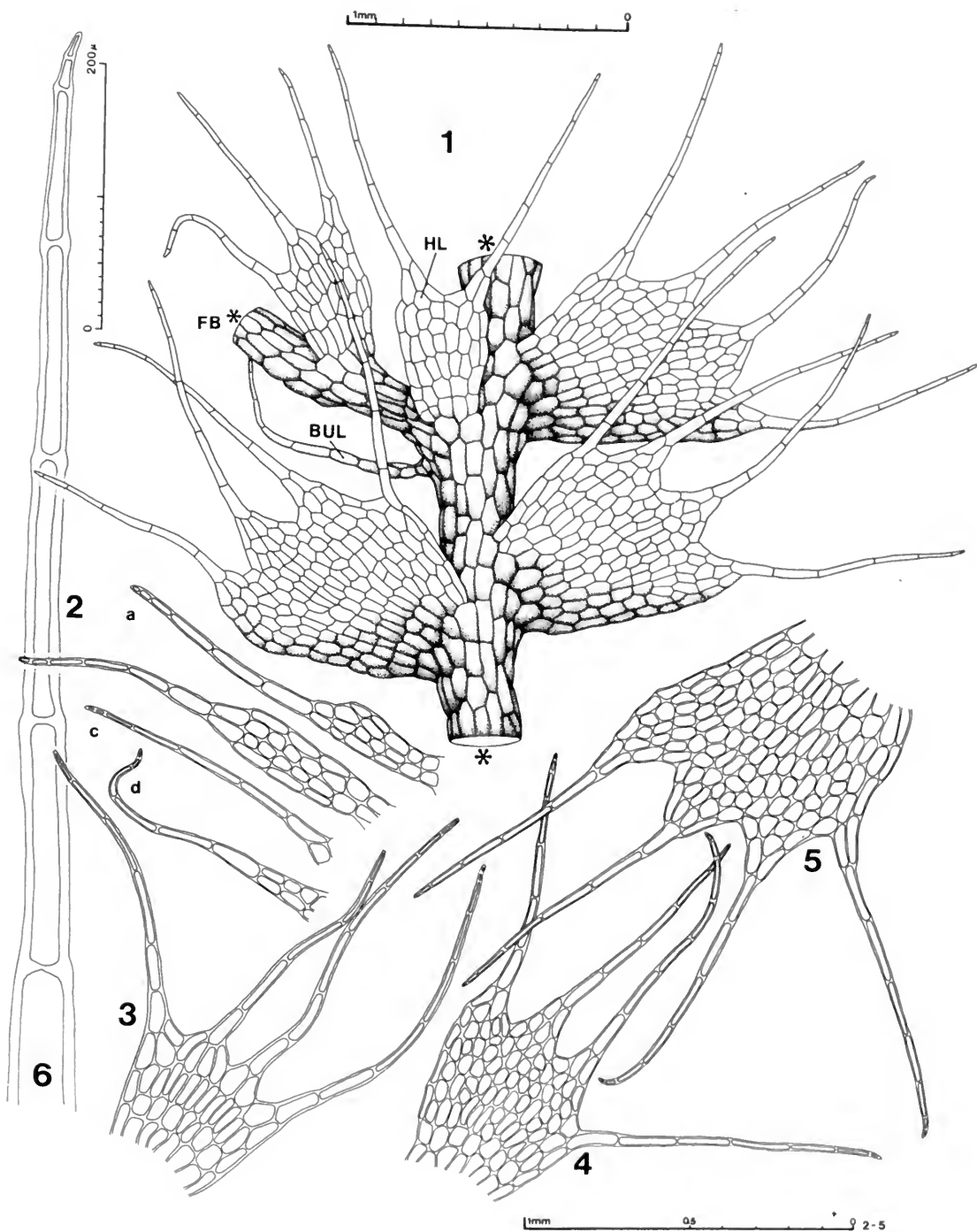


FIG. 14. *Telaranea grossiseta* (Steph.) Engel & Schust. 1. Portion of main shoot with *Frullania*-type branch (= FB), dorsal view (HL = half-leaf; BUL = first branch underleaf). 2. First branch underleaves. 3. Underleaf. 4-5. Leaves. 6. Dorsal lobe of leaf. (All from Engel 14728, Tasmania, Gordon River.)

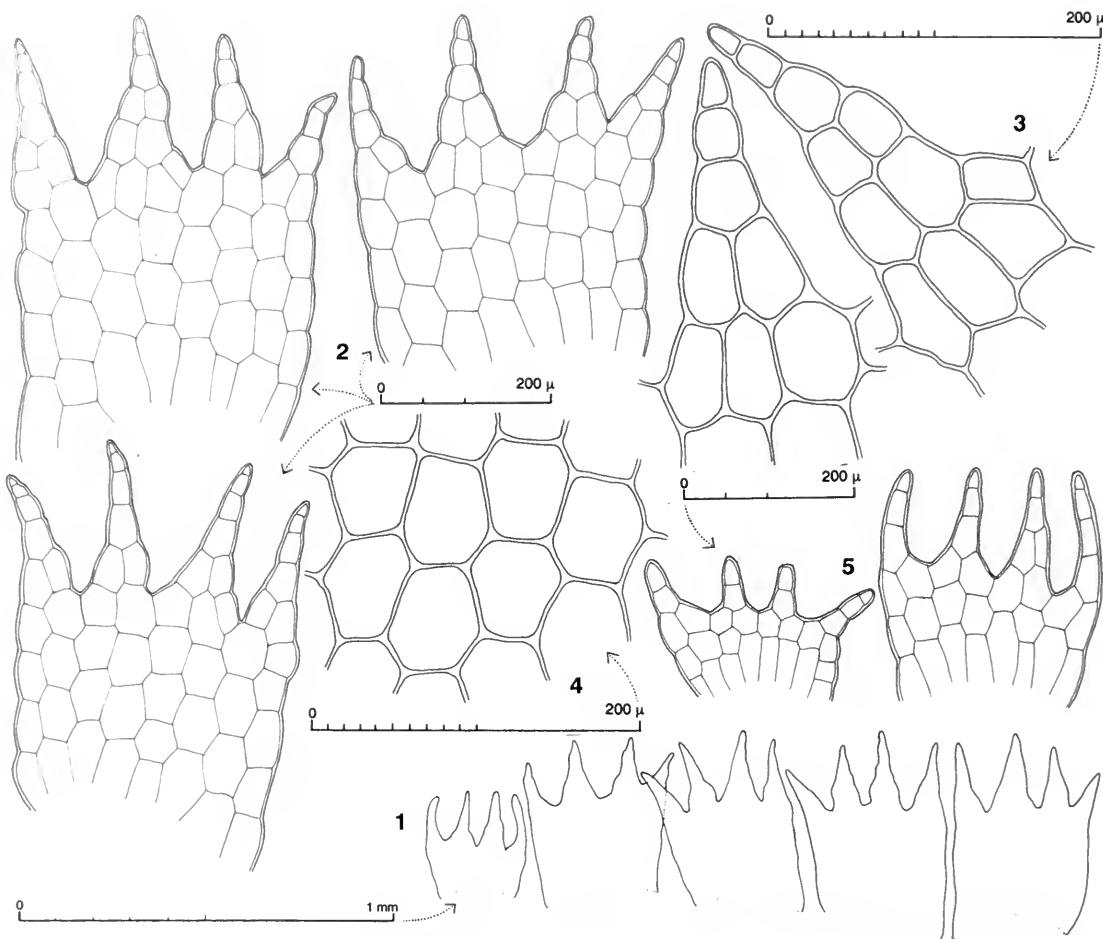


FIG. 15. *Telaranea hodgsoniae* Engel & Merr. 1. Leaves and to left, an underleaf. 2. Three leaves, cellular detail. 3. Median leaf lobes. 4. Median disc cells. 5. Underleaves, cellular detail, stippled walls indicate formation of rhizoid initials. (All from holotype.)

often narrowly elongate, forming an indistinct border; disc cells in  $\pm$  regular tiers to irregularly arranged; cuticle with a hazy to faintly granular appearance caused by the continuous waxy, water-repellent coating, eventually developing a network of fine, irregular lines. Oil-bodies (*fide* Ratkovsky 81/14) ca. 4–6 per cell, botryoidal, small, located around cell periphery, the chloroplasts likewise located. Underleaves somewhat smaller than the leaves, strongly spreading, distant to weakly imbricate, plane, 4–6(8)-lobed to (0.6)0.65–0.7; lobes symmetrically divergent, ciliiform, rigid to tortuous, the uniseriate portion formed of 5–9 elongate,  $\pm$  thick-walled cells, the distal cells often secondarily divided, the lobes commonly terminating in a slime papilla; disc symmetrically cuneate, 3–4 cells high (from me-

dian sinus base to underleaf base), the cells in regular or irregular tiers; disc 13–23 cells wide in distal portion narrowing to 8–13 cells wide at the base; margins entire, usually straight, sometimes gently curved. Asexual reproduction lacking.

Androecia and gynoecia not seen.

**DIFFERENTIATION AND VARIATION**—*Telaranea grossiseta* is a handsome plant, immediately distinguishable by the regularly incubously shingled, dull, glaucous leaves, with divergent, bristle-like lobes. This species has no close relatives in Tasmania, but is closely allied to *T. gibbsiana* of New Zealand. They both have a distinctive “hairy” aspect, and leaf lobes of similar form and orientation. The New Zealand plant, however, is not glaucous, but highly nitid, at least when dry. For

additional comparisons between these species, see under *T. gibbsiana*.

As in other glaucous members of the Lepidoziaceae (e.g., *Bazzania tayloriana*, *Lepidozia glaucophylla*, *Telaranea tuberifera*) the leaves have a waxy, water-repellent coating, although the surface is not as evidently coarsely granular as in some of the foregoing species.

**DISTRIBUTION AND ECOLOGY**—Limited to Tasmania and New South Wales, Australia; in the former confined to the wet, western sector of the state. The species typically occurs over soil in cool, shaded niches of lower to middle-elevation forests. The species is rare and sporadic in distribution, and nowhere, in our experience, common, with one exception. It is locally common on the sides of yabby (crayfish) holes in the Trowutta Caves area (Engel 19760). At Kelly Basin Road it forms large, cushion-like, pure patches on the shaded, vertical rock walls of an abandoned railroad line (Engel 14969).

**SELECTED SPECIMENS SEEN**—TASMANIA: Cradle Mtn.-Lake St. Clair Natl. Park, W shores of Lake St. Clair about 1 mile N of Echo Hut, ca. 750 m, Norris 28050 (F); Franklin River at Frenchman's Cap Trail crossing, ca. 400 m, Norris 31194 (F); Gordon River, vicinity of Sir John Falls, just up river from Butler Is., ca. 50 m, Engel 14728 (F); Kelly Basin Road, between junction with Franklin River Road and Kelly Basin, above Nora River, 90 m, Engel 14969 (F); King River, 11.3 km by road from Regatta Point and 13.3 km by road from Strahan Harbour, sea level, Engel 14927 (F); Mt. Lyell, Ratkovsky 81/14 (HO); near Zeehan, up Dunkley's tram line, 185 m, Weymouth 1445 (F); road from Melba Flats to Confidence Saddle, 200–400 m, Norris 31643 (F); Murchison River at Murchison Hwy, Norris 33735 (F); vicinity of Trowutta Caves (Arch), 4.5 km by road from intersection of Reynolds Road and Reids Road and 6.9 km from Trowutta Post Office, ca. 180 m, Engel 19760 (F); Dismal Swamp, between Brittons Swamp and W coast along Bass Hwy. (2), 34.4 km by road SW of Smithton, 30 m, Engel 16176 (F). AUSTRALIA. NEW SOUTH WALES: Macquarie River, Jan. 1836, Ball (mixed with *Jungermannia procumbens*, nom. hb. [*Balantiopsis*]) (FH).

***Telaranea hodgsoniae* Engel & Merr.**

*Telaranea hodgsoniae* Engel & Merr., Phytologia 79: 251. June, 1996 [1995]. Holotype: New Zealand, South Is., Canterbury Prov., Peel Forest, ca. 1500 ft., Child H2084—c. ♂ (F); isotype: (CHR).

Plants rather stiff and firm, prostrate, in compact mats, glaucescent, whitish green, the surface rather dull and water repellent, subnitid when dry; plants  $\pm$  stenotypic in stature, small, to 0.6 cm wide, including branches. Branching irregu-

larly to rather regularly once-pinnate, the branches of the *Frullania* type, short, hardly tapering, sporadically to rather commonly flagelliform for much of their length; branch half-leaf 2-lobed, strongly obliquely inserted, linear-rectangular, the lobes parallel to weakly diverging; first branch underleaf undivided, subulate, inserted on ventral side of branch at juncture of branch and main axis. Ventral-intercalary branches sporadic, leafy, becoming leading shoots. Stems with cortical cells distinctly differentiated, thin-walled, in 13 rows; cortical cells in section much larger than the numerous (ca. 52) medullary cells, the medullary cell walls slightly thickened and minutely pitted. Leaves on main shoot rigid, obliquely spreading, rather closely imbricate, moderately convex (especially when dry), the insertion distinctly incubous; leaves 315–350(420)  $\mu\text{m}$  wide  $\times$  350–525  $\mu\text{m}$  long, subsymmetric, (3)4-lobed to 0.4–0.5, the lobes straight, much shorter than the disc. Lobes narrowly acute, 2–3(4) cells wide at extreme base, terminating in a short uniseriate row of 2–3 cells; lobe cells short,  $\pm$  isodiametric to short rectangular, bulging, moderately thick-walled, the cell walls weakly thickened in the corners but the septae not swollen and projecting, the basal cell of the uniseriate portion 32–42  $\mu\text{m}$  wide  $\times$  34–48  $\mu\text{m}$  long (1.1[1.3]:1), the next cell 22–32  $\mu\text{m}$  wide  $\times$  22–40  $\mu\text{m}$  long (0.9–1.3:1), the terminal cell normally about equal to the penultimate cell in length or a little shorter, secondary divisions occasional, the apex narrowly rounded; cuticle as in disc. Disc symmetric, subquadrate, 4–5 cells high (from median sinus base to leaf base), 8(9) cells wide in both distal and basal portion; margins entire,  $\pm$  parallel to less weakly curved; cells of margins often bulging. Cells of disc evenly and moderately thick-walled and firm, trigones minute, the cells  $\pm$  isodiametric, those in median sector 38–50(55)  $\mu\text{m}$  wide  $\times$  43–62(70)  $\mu\text{m}$  long, the cells in  $\pm$  regular longitudinal rows, but somewhat offset transversely; cuticle with a hazy, granular appearance. Underleaves much smaller than leaves, ca. 1.3 $\times$  stem width, patent to strongly spreading, distant, plane, 4-lobed to 0.5–0.6, the lobes straight, consisting of a uniseriate row of 3(4) short cells (the lobes 2 cells wide at extreme base) terminating in a slime papilla; disc subquadrate to weakly cuneate, 3 cells high (median sinus), the cells  $\pm$  regularly arranged, the disc 8 cells wide, the cells in distal tier sporadically secondarily divided to

form rhizoid initials; margins entire, usually straight.

Asexual reproduction lacking.

Plants apparently dioecious. Androecia on short, abbreviated, ventral-intercalary branches from leading shoots or from flagelliform branches; bracts closely imbricate, dorsally assurgent, deeply concave, 2-lobed, each lobe terminating in a single cell or a uniseriate row of 2–3 not to hardly elongated cells; lamina cells irregular in shape and arrangement, the dorsal lamina margin feebly dilated, feebly and irregularly crenulate, no slime papillae seen; bracts monandrous; antheridial stalk uniseriate; bracteolar antheridia absent. Gynoeceia not seen.

**DIFFERENTIATION AND VARIATION**—Plants of *T. hodgsoniae* often appear somewhat dull under the dissecting microscope but are never glaucous as in *T. tuberifera* and *T. centipes*. Under the compound microscope the cells have a hazy, granular appearance, rather like frosted glass.

The plant resembles a diminutive *T. tetrapila*. The parallel-sided leaf disc (Fig. 15: 1, 2) is reminiscent of the var. *roseana* of that species, being only 8 cells wide throughout, although only 4–5 cells high (Fig. 15: 2). However, the cells appear small and firm-walled, and the lobes are rather stout and stubby, and not attenuate. The plants are rather uniform in size, small, and not more than 0.6 cm wide, including the branches.

Our concept of this species apparently coincides with *T. roseana* sensu Hodgson (1956, p. 606), since all of the specimens identified as *T. roseana* by Hodgson in the Christchurch Herbarium (CHR) are this taxon. The true *T. roseana*, however, is a different plant, treated here as a variety of *T. tetrapila* (p. 57).

“*Telaranea obscura*” (Schuster, 2000, p. 213) was our provisional name for this species, subsequently published as *T. hodgsoniae* (Engel and Merrill, 1996).

**DISTRIBUTION AND ECOLOGY**—Known only from Auckland Is. and scattered sites on South Island, and the extreme southern sector of North Island (Taranua Range). It apparently is a forest species, where it may cover many square yards on steep, shaded, silty, damp banks in, for example, manuka or mahoe bush (Otago Prov.) or *Nothofagus fusca*-*N. solandri* forest (Nelson Prov.).

**SELECTED SPECIMENS SEEN**—AUCKLAND IS.: Musgrave Peninsula, *Dawbin* as *T. roseana* (CHR). NEW ZEALAND. Without specific loc., ex hb. Petrie (Allison

no. H3063 as *T. roseana*) (CHR). SOUTH ISLAND. OTAGO PROV.: Near Outram, Taieri Plains, S of Dunedin, Allison H3208 as *T. roseana* (CHR); Lake Waihoia, S of Dunedin, ca. 30 m, Allison H3207 as *T. roseana* (CHR); Town Belt, Morningson, Dunedin, Allison H3206 as *T. roseana* (CHR). NELSON PROV.: Nelson Lakes Natl. Park, Pinchgut Track, W of southern sector of Lake Rotoiti, SSW of St. Arnaud, ca. 1280–1390 m, Engel 21390 (F). NORTH ISLAND. WELLINGTON PROV.: Upper Hut, N of Wellington, Druce 914 as *T. roseana* (CHR); Taranua Range, Mt. Holdworth, above Mountain House, ± 850 m, Butler 2584 as *T. roseana* (CHR).

*Telaranea patentissima* (Hook. f. & Tayl.) Hodgs.

*Jungermannia patentissima* Hook. f. & Tayl., London J. Bot. 3: 386. 1844, (3: 286 [sic] in errore pro 386). *Lepidozia patentissima* (Hook. f. & Tayl.) G. L. & N., Syn. Hep. 204. 1845. *Mastigophora patentissima* (Hook. f. & Tayl.) Trev., Mem. Ist. Lomb. Sci. Lett. III. 4: 416. 1877. *Telaranea patentissima* (Hook. f. & Tayl.) Hodgs., Rec. Domin. Mus. 4: 107. 1962. Type: Auckland Is., Hooker (BM! [seen 4], FH!).

Plants soft, often spinescent, flexuous yet firm, prostrate, in loose to compact mats, pale green to yellowish green, nitid when dry; plants rather stenotypic in stature, small, to 0.8 cm wide, including branches. Branching irregularly to somewhat regularly 1-pinnate, never 2-pinnate, the branches of the *Frullania* type, short and hardly tapering to long and flagelliform; branch half-leaf bifid, usually obliquely inserted, narrowly rectangular, the lobes parallel to weakly diverging; first branch underleaf undivided and ciliiform to subulate, inserted on ventral side of branch at juncture of branch and main axis. Ventral-intercalary branches occasional to common, leafy, often becoming leading shoots. Stems with cortical cells distinctly differentiated, thin-walled, in 11–12 rows, the outer walls somewhat thicker; cortical cells in section larger than the numerous (ca. 25–45) medullary cells, the medullary cell walls uniformly slightly thickened. Rhizoids from distal cells of underleaf disc. Leaves on main shoot rigid, obliquely spreading, distant (esp. in small phases) to imbricate, plane to moderately convex, noticeably narrowing to the base, the insertion typically distinctly incubous; leaves 335–545 µm wide × 345–580 µm long, subsymmetric to moderately asymmetric, 4(6)-lobed to 0.4–0.5, the lobes usually somewhat divergent, about equal to or shorter than the disc. Lobes narrowly acute to attenuate, 2–4(5) cells wide at extreme base, the two median lobes typically somewhat larger (and at times 3–4 cells wide in basal sector), often bi-



seriate for 1–2(3) tiers, terminating in a uniseriate row of 2–4(5) cells, typically less than half the length of lobe (exc. var. *zebrina*); lobe cells short,  $\pm$  isodiametric to short rectangular, thin- to moderately thick-walled, the septa somewhat thickened in the corners but not swollen and projecting, the basal cell of the uniseriate portion 22–36  $\mu\text{m}$  wide  $\times$  26–46  $\mu\text{m}$  long (1–1.8:1), the next cell 17–30  $\mu\text{m}$  wide  $\times$  18–34  $\mu\text{m}$  long, the terminal cell at times secondarily divided, tapering to a rounded summit; cuticle smooth to finely striate-papillose (at least the distal half of lobes). Disc symmetrically to somewhat irregularly cuneate, 4–5 cells high from median sinus base to leaf base (up to 6[7] cells high in var. *ampliata*), 10–15 cells wide in distal portion (8 cells wide in smaller leaves) narrowing to (5)8(12) cells wide in basal portion; margins entire,  $\pm$  straight to broadly curved, cells of disc and lobe margins often bulging. Cells of disc thin- to moderately and evenly thick-walled and firm, with small but distinct trigones, the cells in median sector of disc subquadrate to somewhat elongate, 25–42  $\mu\text{m}$  wide  $\times$  38–55  $\mu\text{m}$  long; cuticle smooth (coarsely striolate-papillose in var. *zebrina*). Underleaves somewhat to much smaller than leaves, variable in size, ca. 1–1.5 $\times$  stem width, strongly spreading, distant to less often contiguous, plane, (3)4-lobed to 0.35–0.45, the lobes weakly divergent, biseriate at base (exc. var. *zebrina*), with a uniseriate row of 2–4 rather short cells, terminating in a slime papilla; disc symmetrically subquadrate to weakly cuneate, 3–4 cells high (median sinus), (8)10–14 cells wide in distal portion narrowing to 8 cells wide at base (8 cells wide throughout in var. *zebrina*); margins entire, usually straight to somewhat curved. Asexual reproduction lacking.

Plants dioecious. Androeceia mostly on short, abbreviated, ventral-intercalary, spicate branches from main shoot or, occasionally, from primary, flagelliform *Frullania*-type branches; bracts closely imbricate, dorsally assurgent, deeply concave, bilobed to ca. 0.35, the lobes short acuminate, terminating in a uniseriate row of 2(3) cells, the basal cell slightly longer than wide, the terminal cell to ca. 2:1; dorsal margin of lamina somewhat dilated, crenulate, with a few slime papillae; bracts monandrous; antheridial stalk 8 cells high, uniseriate; bracteolar antheridia absent. Gynoeceia feebly to strongly dorsally assurgent, swollen and densely rhizoidous at base; bracts small for perianth size, those of innermost series closely ensheathing the perianth, concave, oblong to suborbicular, very shallowly and irregularly 3–4-lob-

ulate, the lobules terminating in single curved cell or several sinuous, laterally juxtaposed cells, sometimes irregularly denticulate; lamina composed of  $\pm$  regularly subrectangular cells, the margin bordered by narrower elongated cells, the apical or free end of marginal cells often divergent and forming a blunt tooth, especially distally, the margins otherwise with a sporadic unicellular tooth and a few slime papillae; bracteoles of innermost series smaller but similar in form to bracts. Perianth long emergent, fusiform, terete in basal and median sectors, the distal sector obscurely trigonous and with 3-plicae, the perianth narrowing toward the contracted mouth; mouth cells thick-walled, often sinuate, partially or wholly laterally free, occasionally with a laterally free uniseriate row of 2 cells, the mouth thus indistinctly denticulate-subfimbriate; perianth 2- to locally 3-stratose in basal portion.

Seta with 8 rows of outer cells surrounding an inner core of 21–24 much smaller cells. Capsule rather short elliptic, 1070  $\times$  525  $\mu\text{m}$ , the wall 41–46  $\mu\text{m}$  thick, of 4 layers, the outer layer equivalent to 1.5–1.8 $\times$  thickness of any one of the interior layers; outer layer of cells rather regularly short-rectangular, with 2-phase development, the longitudinal walls with well-defined sheetlike thickenings and nodule-like thickenings (4–6 per cell) alternating with walls that are devoid of thickenings (or with sporadic, pigmented or non-pigmented, nodular swellings), the transverse walls often with thickenings; intermediate layer thinner than outer or inner layers; innermost layer of cells  $\pm$  tiered, irregularly narrowly to broadly rectangular, with semiannular bands common, rather wide, close, usually complete, rarely forked and anastomosing to delimit ill-defined, local fenestrae.

Spores 12–13.9(15.4)  $\mu\text{m}$ , exine pale brown, with low but sharply defined, close papillae and short-vermiculate markings which at times coalesce. Elaters rigid, nontortuous, 8.6–10.6  $\mu\text{m}$  wide, only slightly tapering toward tips, bispiral to tips, the spirals 2.4–3.8  $\mu\text{m}$  wide.

**NOMENCLATURE**—The type of *Jungermannia patentissima*, as stated in the protologue, was “creeping on other *Hepaticae* or on *Musci*,” namely *Bazzania adnexa*, *Heteroscyphus sinuosus*, *Lepidozia* sp., a hypnoid moss, and a hymenophylloid fern. A portion of the type is present in Thomas Taylor’s herbarium (FH) under the manuscript name *Jungermannia patentispina*, with the same admixture of cryptogamic species.

Examination of the type of *Lepidozia gottscheana* discloses that this widely used name is a synonym of *T. patentissima* and has been misapplied to the plant that is properly called *T. tetrapila* (p. 52). The protologue of *Lepidozia gottscheana* states only that the plant came from New Zealand. The type (W, "no. 28") is labelled "Dusky Bay," and therefore was presumably collected by Menzies. Both perianths and mature sporophytes are present, as per the original description. The specimen at Geneva ("Original," ex herb. Bescherelle) also bears the notation "Dusky Bay," and is a probable isotype, although gynoeceia are not present.

**DIFFERENTIATION AND VARIATION**—*Telaranea patentissima* is a relatively common plant in New Zealand, but its variability may cause difficulties in determination. At times the species can resemble a smaller *T. tetrapila*. The leaf disc is  $\pm$  regularly cuneate, with the disc cells arranged in regular rows and tiers (Fig. 16: 4). Another feature shared with *T. tetrapila* and its varieties is the occasional occurrence of secondary cell divisions at the tips of the lobes (Fig. 16: 3). However, the smaller plant size, the relatively small cells (40  $\mu$ m in width or less), and the firm, rather evenly thickened cell walls with small but distinct trigones ally this species with sect. *Neolepidozia*. Hodgson (1956, p. 609) says, "cells 30–40  $\mu$ , showing as large in such a small plant." Hodgson provided a description based on the type, although the plant is considerably more common than her discussion would indicate. The concept of *T. patentissima* in Allison & Child (1975, p. 79) also appears to be correct.

*Lepidozia gracillima* Carr. & Pears. (1888) of New South Wales is a synonym of *T. patentissima*, as shown by the type (G!). The disc cells are 23–28  $\mu$ m wide, somewhat smaller than in typical *T. patentissima*. *Telaranea quadristipula*, also of New South Wales, has disc cells 16–24  $\mu$ , and has lobes 4(5) cells wide at the base, often with up to 3 additional 4-celled tiers, often somewhat abruptly contracted to the uniseriate row (Fig. 5: 1, 5). Stephani (1909, p. 581) remarks that the illustration of the leaves of *L. gracillima* in the original publication is "missglückt und irreführend." In particular, the lobes are shown as terminating in a single cell, rather than uniformly ending in a uniseriate row of 2–3 cells as in the type, and the leaf outlines filled in with oddly shaped cells.

Three expressions of *T. patentissima* are recognized here at the varietal level:

## Key to the Varieties of *T. patentissima*

1. Leaf disc typically 4 cells high,  $\pm$  regularly cuneate, the areolation regular, the cell divisions in distal sector mostly longitudinal, preserving a regular tiered arrangement; disc and lobe margins straight; leaves 4-lobed . . . . . 2
2. Cells of disc coarsely striolate-papillose; uniseriate portion of leaf lobes (4)5 cells long; underleaf disc 8 cells wide throughout, the lobes uniseriate, 2–3 cells long . . . . . var. *zebrina*
2. Cells of disc smooth; uniseriate portion of leaf lobes 2–4(5) cells long; underleaf disc (8)10–14 cells wide in distal portion narrowing to 8 cells wide at base . . . . . var. *patentissima*
1. Leaf disc typically 5–6(7) cells high, becoming irregularly and often asymmetrically cuneate, the areolation (esp. in distal sector)  $\pm$  irregular due to divisions in various planes; disc and lobe margins irregular, with bulging cells; leaves often 5–6-lobed . . . . . var. *ampliata*

## *Telaranea patentissima* (Hook. f. & Tayl.) Hodgson, var. *patentissima*

*Lepidozia gottscheana* Lindenb. in G. L. & N., Syn. Hep. 206. 1845, syn. nov. *Mastigophora gottscheana* (Lindenb.) Trev., Mem. Ist. Lomb. Sci. Lett. III. 4: 416. 1877. *Neolepidozia gottscheana* (Lindenb.) Fulf. & J. Tayl., Brittonia 11: 85. 1959. *Telaranea gottscheana* (Lindenb.) Hodgson, Rec. Domin. Mus. 4: 106. 1962. Type: New Zealand, Dusky Bay, "(Hb. Hk., L. et Lg. n. 28)," sin. coll.—c. per. + sporo. (G!, W!, Lindenberg Hepat. no. 4748).

*Lepidozia gracillima* Carr. & Pears., Proc. Linn. Soc. New South Wales ser. 2. 2: 1045. pl. XXVII. 1888, syn. nov. Type: Australia, New South Wales, "New Sydney," Botany Bay, *Whitelegge*—c. ♂ (G!).

*Lepidozia corticola* Steph., Spec. Hep. 3: 591. 1909, syn. nov. *Neolepidozia corticola* (Steph.) Fulf. & J. Tayl., Brittonia 11: 85. 1959. *Telaranea corticola* (Steph.) Hodgson, Rec. Domin. Mus. 4: 107. 1962. Type: New Zealand, South Is., Mt. Winterslow, (Canterbury), Mar. 1906, Beckett 457 (G!).

Leaves 4-lobed, the disc  $\pm$  regularly cuneate, the disc and lobe margins straight; disc typically 4 cells high, with areolation regular, the cell divisions in distal sector mostly longitudinal, preserving a regular tiered arrangement.

## *Telaranea patentissima* var. *ampliata* Engel & Merr., var. nov.

Folia saepe 5–6 lobata, lobis anguste acutis (ad basin

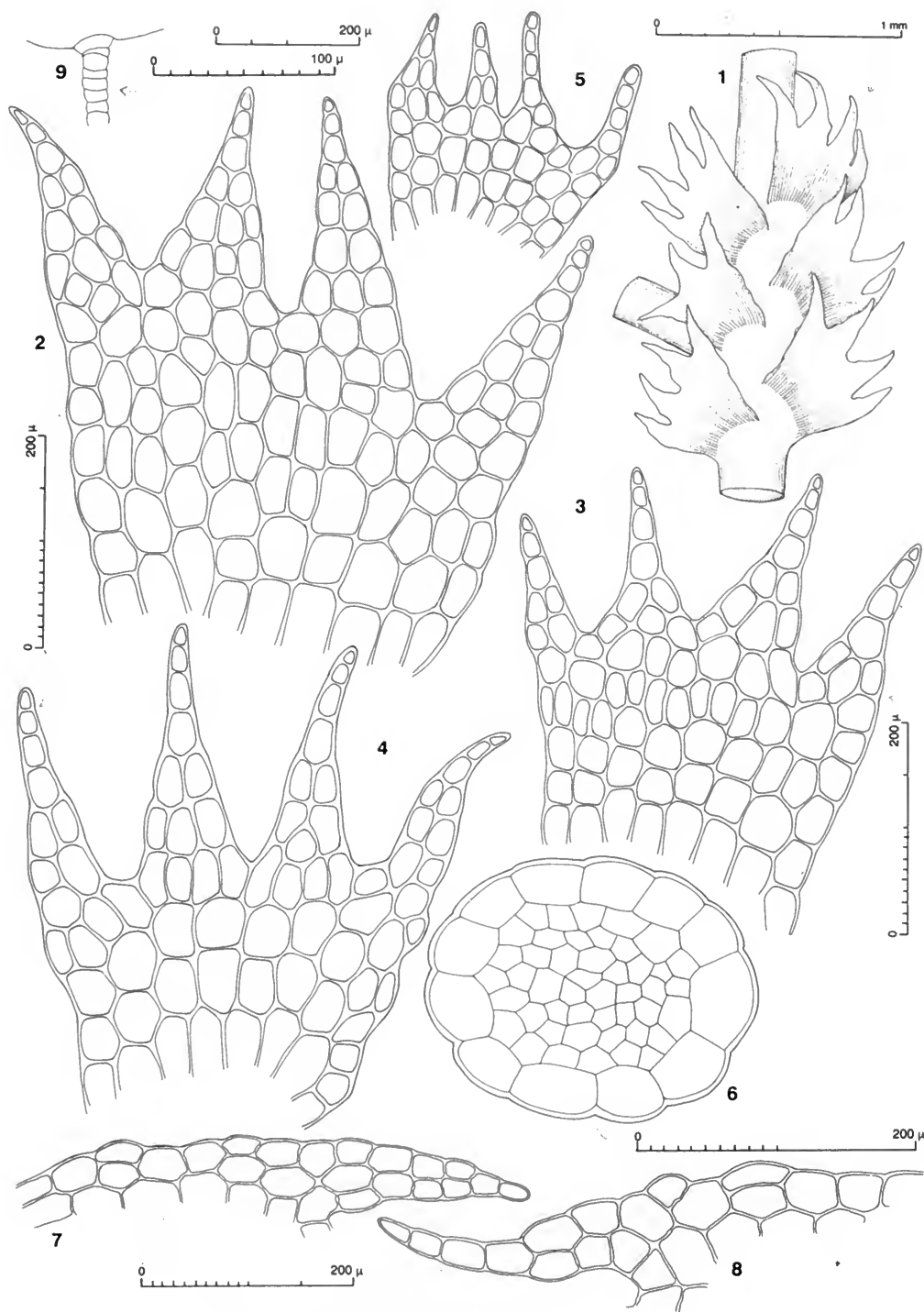


FIG. 16. *Telaranea patentissima* (Hook. f. & Tayl.) Hodg. (Figs. 3-5, 9, var. *patentissima*; 1, 2, 6-8, var. *ampliata*.) 1. Sector of main shoot, dorsal view. 2-4. Leaves, cellular detail. 5. Underleaf, cellular detail. 6. Stem, cross section. 7, 8. Dorsal lobe and dorsal margin of disc. 9. Antheridal stalk. (Figs. 1-2, 7 from holotype of var. *ampliata*; 3 from Kirk 183, New Zealand, Great Barrier Is.; 4-5, 9 from Zotov New Zealand, North Is., Wellington Prov., Tararua Mts., Field Hut; 6, 8 from Hatcher 29, New Zealand, North Is., South Auckland Prov., Rotorua.)

3–4 cellulas latis), disco plerumque 5–6(7) cellulas alto, asymmetricae irregulariterque cuneato, disco lobisque margine cellulis tumidis.

HOLOTYPE—New Zealand, Otago Prov., Mt. Maungatua, W of Mosgiel, 500 m, *Engel 17777*—c. sporo. (F); isotype: (CHR).

Leaves often 5–6-lobed, the disc becoming irregularly and often asymmetrically cuneate, the disc and lobe margins irregular, with bulging cells; disc typically 5–6(7) cells high, with areolation (esp. in distal sector)  $\pm$  irregular due to divisions in various planes.

This distinctive expression of the species has broad, somewhat irregularly cuneate leaves, with the cells of the lobe and disc margins often bulging (Fig. 16: 7, 8). The leaf disc is rather high (to 6 or 7 cells, Fig. 16: 2), the cells are somewhat irregularly arranged, and the lobes are narrowly acute (often 3–4 cells wide for several tiers above the extreme base).

The distal broadening of the cuneate leaf disc results from additional cell divisions, which are mostly confined to the distal portion of the disc; the remainder of the disc has  $\pm$  regular rows and tiers of comparatively large,  $\pm$  isodiametric to slightly elongated cells.

Specimens referable to the var. *ampliata* include *Engel 22818* from Nelson Lakes Natl. Park and *Hatcher 29* from Rotorua, both New Zealand, and *Engel 13783* from near Lake Gordon, and *Engel 14016* from Lake St. Clair Natl. Park, Tasmania.

*Telaranea patentissima* var. *zebrina* Engel & Merr., var. nov.

Var. *patentissima* simile, differt cellulis disci striatulo-papillois, disco ubique 8 cellulas lato, lobis foliorum parte uniseriata (4)5 cellulas longa, lobis amphigastrium 2–3 cellulas longis uniseriatis.

HOLOTYPE—New Zealand, North Island, Puketi Forest, 6 Dec. 1993, *Braggins 93/172* (AKU); isotype: (F).

Leaves distinctly papillose, the dorsal half of disc coarsely striolate-papillose, the lobes with a uniseriate row (4)5 cells long (more than half the length of lobe); underleaf disc 8 cells wide throughout, the lobes uniseriate, 2–3 cells long.

This variety is similar to var. *patentissima* in

almost all respects but has a more pronounced development of cuticle on the leaves. Papillae are not confined to the tips of the lobes but occur also on the disc (Fig. 17: 1), which is conspicuously striolate (Fig. 17: 9). Among the other Australasian species of the genus, only *T. verruculosa* of Queensland (Fig. 60: 6, p. 197) has a striolate disc. The variety also differs by the underleaves with uniseriate lobes 2–3 cells long and disc 8 cells wide throughout (Fig. 17: 11), and the somewhat longer leaf lobes, with a uniseriate portion (4)5 cells long (Fig. 17: 1, 2).

The varieties of *T. patentissima* are not distinguished in the discussions of ecology and distribution and specimens cited.

DISTRIBUTION AND ECOLOGY—*Telaranea patentissima* occurs on Auckland, Campbell, and Stewart Islands, and is rather common throughout the South Island and North Island, New Zealand. Also present (but much less common) in Tasmania, as well as in New South Wales, at present represented by a single collection, the type of *L. gracillima*. In New Zealand the species occurs in middle- to upper-elevation forests (typically above 400 m) to the subalpine-alpine zone. In the forest zone (often *Nothofagus*) it often occurs on very rotted logs, typically on the side or lower half of prostrate, bryophyte-covered logs, or in moist, sheltered niches such as cliff faces and soil of boulders of stream edges, etc. In the subalpine and alpine zones it occurs under snow tussock cover or over soil in protected niches of cliffs, etc. In the southern extremity of South Island (Milford Sound) it may be found at sea level with *Treubia lacunosa*, *Pellipsis*, *Verdoornia succulenta*, and *Geocalyx novaezealandiae*, etc. It also, though rarely, occurs at lower elevations in pakihis (under *Gleichenia*).

In Tasmania the species has a similar altitudinal range to that of New Zealand; for example, it occurs in *Nothofagus-Eucalyptus-Atherosperma*- or *Nothofagus-Athrotaxis* forests. In forests the plant occurs on bryophyte-covered logs and stumps, and in rock crevices of dryish stream beds; in subalpine scrub it occurs over soil at edges of tarns.

SELECTED SPECIMENS SEEN—AUCKLAND IS.: *Horning SA444* (CHR); *Kirk 559* (BM). CAMPBELL IS.: *Poppleton M14* (CHR). NEW ZEALAND. SOLANDER IS.: East Bay, 10 m, *Johnson* as *T. gottscheana* (CHR); SE Peninsula, 100 m, *Johnson* as *T. gottscheana* (CHR); SE Ridge, 160 m, *Johnson* as *T. gottscheana* (CHR). STEWART ISLAND: Rakiura Natl. Park, directly behind Belltopper Falls, ca. 30 m, *Engel 24164*; *ibid.*, Port Pegasus, ca. 200 m, *Engel 24178* (F). SOUTH ISLAND.

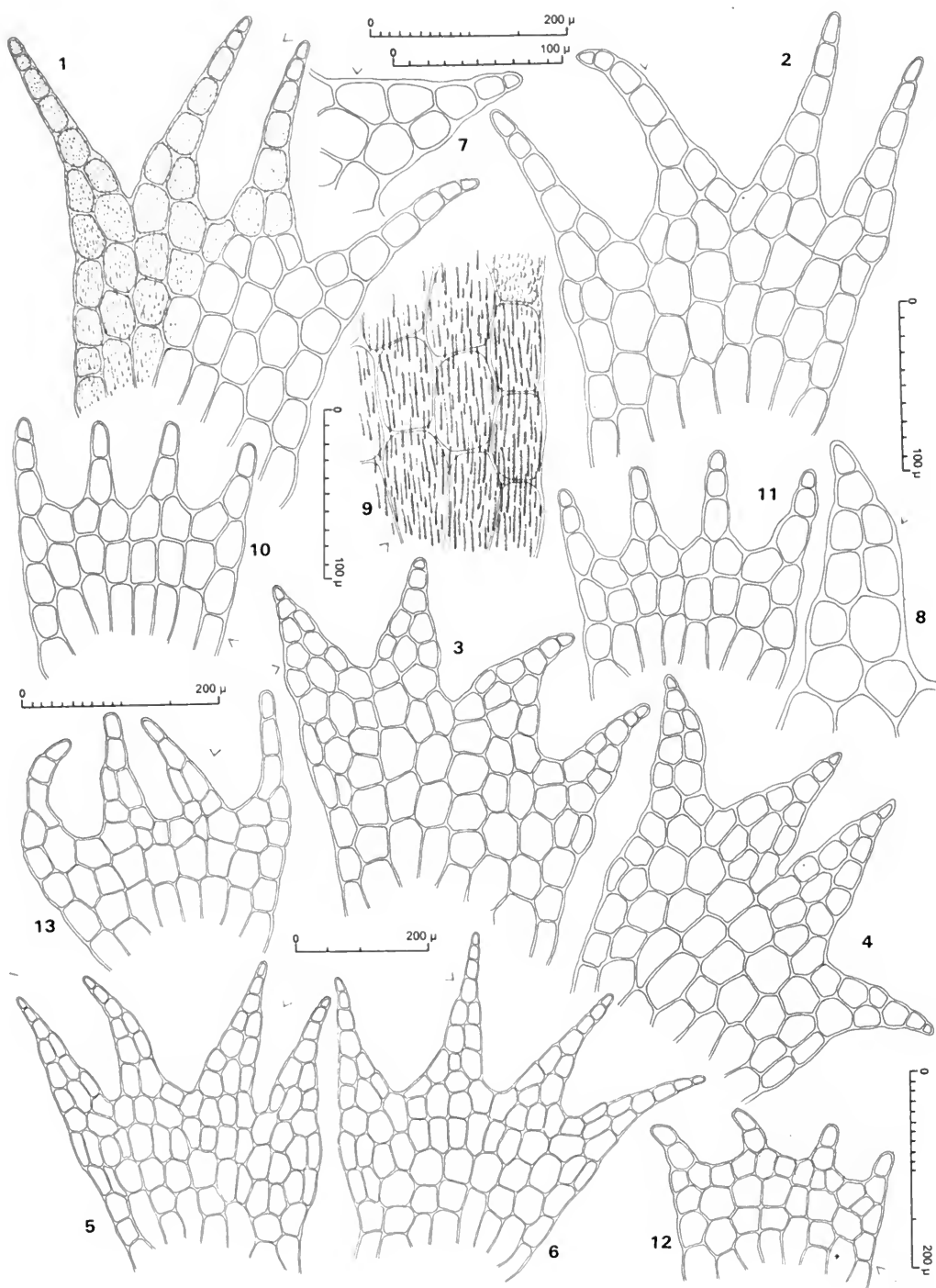


FIG. 17. *Telaranea patentissima* (Hook. f. & Tayl.) Hodg. (Figs. 1, 2, 9-11, var. *zebrina*; 3-8, 12, 13, var. *patentissima*). 1-6. Leaves, the leaf of fig. 1 with cuticle shown in part. 7, 8. Leaf lobes. 9. Marginal cells of leaf base showing papillae. 10-13. Underleaves (all drawn to scale of fig. 10). (Figs. 1, 2, 9-11 from type of var. *zebrina*; 3, 4, 7, 8, 12 from type of *T. patentissima* (BM); 5, 6, 13 from type of *T. gottscheana* [W].)

SOUTHLAND PROV.: Waikaia State Forest, junction of Waikaia River Track and Tison Peak Track, upstream from Piano Flat Recreational Area, ca. 260 m, *Engel* 24705 (F); Dusky Bay, 1791 [*Menzies*] (BM); Lake Hauroko, ca. 215 m, *Child* H1559 (F); Mt. Burns, ca. 1280 m, *Child* H5051 (F); near road between Homer Tunnel and Te Anau, *Hatcher* 1528 (F); Cascade Creek, near Lake Gunn, tributary of Eglington River, ca. 365 m, *Child* H2597 (F); Fiordland Natl. Park, Lake Gunn, *Zotov* as *T. gottscheana* (CHR); *ibid.*, Central Earl Mts., Mistake Creek, between Triangle Peak and Melita Peak, 740–800 m, *Engel* 18785 (F); *ibid.*, Gertrude Valley, off track to Gertrude Saddle, NE of Homer Tunnel, 1880–1900 m, *Engel* 18899 (F); *ibid.*, Milford Sound, along path to lower end of Bowen Falls, sea level, *Schuster* 55548b as *Lepidozia concinna* (F); *ibid.*, Moraine Creek Track, area N of Moraine Creek, W of Hollyford River, 610 m, *Engel* 23210 (F). OTAGO PROV.: Mt. Cargill, just below summit, N of Dunedin, ca. 670 m, *Engel* 17576 (F); *ibid.*, W of summit road, ca. 455 m, *Child* H2044 as *Lepidozia tetradactyla* (F); Silver Peaks Range, N of Dunedin, *Allison* H5911 (CHR); Lee Stream, Hindon Road, ca. 305 m, *Child* H929 (F); near Herbert, Oamaru District, *Allison* H5907 as *T. praenitens* (CHR); Rock and Pillar, ca. 915 m, *Child* H2751 as *Tennnoma palmatum* (F); Paradise, Dart Valley, N of N end of Lake Wakatipu, ca. 365 m, *Child* H1193 as *T. meridiana* (F); trail between Gunn's Hut and Hidden Falls, ca. 30 m SE of Lake McKerrow, *Hatcher* 580 as *Lepidozia meridiana* (F); Mt. Aspiring Natl. Park, below and W of Mt. Shrimpton, 1370–1470 m, *Engel* 17874 (F); Makarora River, near base of Haast Pass, *Allison* H5968—c. sporo. as *T. gottscheana* (CHR). OTAGO/WESTLAND PROV. BOUNDARY: Mt. Aspiring Natl. Park, summit area of Haast Pass, 570 m, *Engel* 17984—c. sporo. (F). WESTLAND PROV.: Kellys Range, *Beckett* 4304, 4599, syntypes of *Lepidozia beckettiana*—(both) c. per. (G); Turiwhare Falls on Route 73, *Engel* 6531A (F); Mt. Aspiring Natl. Park, Blue Valley Track, above Blue River just N of confluence with Makarora River, 430–480 m, *Engel* 21919 (F); *ibid.*, Cross Creek, 1.1 km N of Haast Pass, 540 m, *Engel* 21871 (F); Camp Creek, W of Alexander Range, 630 m, *Reif* C270B (F); Paparoa Range, ridge immediately N of Sewell Peak, 910 m, *Engel* 19042 (F). WESTLAND/CANTERBURY PROV.: Arthur's Pass Natl. Park, Arthur's Pass area, Upper Twin Creek Valley, 930 m, *Engel* 18528 (F); *ibid.*, Halpin Creek, at junction with main road, *Hair & Beuzenberg* (CHR). CANTERBURY PROV.: Arthur's Pass, *Moore* H77 (CHR); *ibid.*, *Hair* 3&4pp (CHR); Arthur's Pass Natl. Park, Bealey River, off Bealey Valley Track, 830–850 m, *Engel* 18509 (F). NELSON PROV.: Big Totara River, ca. 60 m, *Child* H5448 (F); Nelson Lakes Natl. Park, NE margin of Lake Rotorua, W of St. Arnaud, 520 m, *Engel* 21500 (F); *ibid.*, E slope of Robert Ridge in vicinity of Mt. Robert Skifield, W end of Lake Rototiti, 1400–1480 m, *Engel* 22828 (F); *ibid.*, Upper Travers River, *Simpson* 3332 (CHR); Kahurangi Natl. Park, Mt. Arthur, Mt. Arthur Hut Track, 1050 m, *Engel* 24927 (F). NORTH ISLAND. WELLINGTON PROV.: Tararua Mts., Field Hut, ca. 825 m, *Zotov* as *L. praenitens*—c. ♂ (CHR); Tararua Range, Ohau Stream, *Moore* H171 as *T. gottscheana* (CHR); *ibid.*, Mt. Holdsworth, *Wormald* 14pp as *T. gottscheana* (CHR); Te Matawai, *Zotov* as *L. capilligera*; Tongariro Natl. Park, Soda Springs, Mangatepopo Stream, NE of Whakapapa Vil-

lage, 1350 m, *Engel* 22491 (F). SOUTH AUCKLAND PROV.: Ruahakune Bush, E of Taupo, ca. 760 m, *Allison* H5893 as *T. gottscheana* (CHR); Rotorua, hot springs area, *Hatcher* 29 (F); Whareorino Forest, start of track to Leitch's Hut, 278 m, *Engel* 23766 (F); Mt. Te Aroha, ca. 3 km E of Te Aroha, 900–940 m, *Engel* 22146 (F). NORTH AUCKLAND PROV.: NE Waitakere Ranges, Swanson University Reserve, Tram Valley Road, 95 m, *Engel* 20470 (F); Waitakere, ca. 120 m, *Child* H2234 (F); SE corner of Waipoua Forest, just N of Tutamoe, 540 m, *Engel* 21119 (F); *ibid.*, Mataraurau Plateau, Waoku Road, *Braggins* 94/240 (AKU). LITTLE BARRIER IS.: *Hynes* as *T. gottscheana* (CHR). GREAT BARRIER IS.: *Kirk* 176, 183, both as *L. gottscheana* (CHR). TASMANIA: Trail to Adamsons Peak between Manuka Flat and the hut, 500–800 m, *Norris* 27048 (F); along Old Hartz Trail about 1 mile beyond Kermadec Plains, ca. 650 m, *Norris* 29674 (F); Geeveston Forestry District, just S of Spur 2 on Hermans Road, 410 m, *Blanks* (HO); Mt. Wellington, Deep Creek, *Rodway* n.s.—c. sporo. as *L. praenitens* (HO); same loc., 490 m, *Weymouth* 1516—c. sporo. as *L. praenitens* (HO); Manuka Road, W of Tahune Bridge, 130 m, *Jarman* 99/4—c. ♂ + per. (HO); near Scotts Peak Road, 2.2 km S of junction with Gordon River Road, E of S end of Lake Gordon, 580 m, *Engel* 13783 (F); plateau region E and SE of Mt. Eliza summit, E of Lake Pedder, ca. 1225 m, *Engel* 13668G (F); Cradle Mtn.-Lake St. Clair Natl. Park, Ballroom Forest, SW side of Lake Dove, 950–1050 m, *Engel* 14016 (F); Paddys Lake, below and E of Black Bluff, SW of Nietta, 1090 m, *Engel* 19784 (F); Flinders Is., Mt. Strzelecki, Cronley's Ck, *Scott* s.n. (MELU).

*Telaranea tetrapila* (Hook. f. & Tayl.) Engel & Merr.

*Lepidozia tetrapila* Hook. f. & Tayl. in Taylor, London J. Bot. 5: 370. 1846. *Mastigophora tetrapila* (Hook. f. & Tayl.) Trev., Mem. Ist. Lomb. Sci. Lett. III. 4: 416. 1877. *Telaranea tetrapila* (Hook. f. & Tayl.) Engel & Merr., Phytologia 79: 253. June, 1996 [1995]. Lectotype (*nov.*): New Zealand, Hooker "n. 119. 1844" (FH!); isolectotype: (W!), Lindenberg Hep. no. 4739).

Plants soft, flexuous yet firm, loosely prostrate to suberect, in dense, compact mats, pale green to yellowish green to olive green (to pale amber in var. *cancellata*), nitid when dry, often somewhat water-repellent; plants variable in stature, small to medium, to 1.5 cm wide, including branches. Branching regular and rather densely pinnate, sometimes 2-pinnate, the main axis often bearing only 2–4 normal leaves (on each side) between branches, the branches of the *Frullania* type, short to moderately long but normally determinate, of about equal length or (especially in robust plants) gradually becoming longer from shoot apex to base (e.g., plumose), hardly tapering, sporadically flagelliform; branch half-leaf 2(4)-lobed, usually

obliquely inserted, narrowly rectangular, the lobes parallel to weakly diverging; first branch underleaf undivided and ciliiform or, less often, bifid, sporadically trifid, inserted on ventral side of branch near or (often) at juncture of branch and main axis. Ventral-intercalary branches occasional, leafy, often becoming leading shoots. Stems with cortical cells distinctly differentiated, thin walled, in 11–18 rows, those on ventral side of stem a little smaller; cortical cells in section much larger than the numerous (35–65) medullary cells, the medullary cell walls uniformly slightly thickened. Rhizoids from distal cells of underleaf disc. Leaves on main shoot rigid, obliquely spreading, distant (small phases) to loosely to closely imbricate, plane to moderately convex, the insertion weakly to distinctly incubous; leaves 630–980  $\mu\text{m}$  wide  $\times$  630–840  $\mu\text{m}$  long, subsymmetric, 4–6(8) lobed to 0.4–0.55, the lobes straight to widely divergent, typically shorter than the disc (longer than the disc in var. *cancellata*). Lobes typically subcaudate, the base subtriangular, 2–4 cells wide at extreme base, terminating in a uniseriate row of (4)5–6(8) cells (typically more than half the length of lobe); cells of the uniseriate portion short, often  $\pm$  barrel shaped (longer cells of the uniseriate portion to 2.5:1 in var. *cancellata*), rather thin-walled, the septae thickened in the corners but the septa not swollen and projecting, the basal cell of the uniseriate portion 34–52  $\mu\text{m}$  wide  $\times$  48–72  $\mu\text{m}$  long (1.1–1.6:1), the next cell narrower but of about the same length, 28–40  $\mu\text{m}$  wide  $\times$  41–62  $\mu\text{m}$  long (1.2–2.2:1), the terminal cell normally smaller than the penultimate cell, the distal lobe cells often short quadrate and more numerous resulting from secondary cell divisions; cuticle of at least the distal half of lobes finely to  $\pm$  distinctly striate-papillose. Disc symmetrically to somewhat asymmetrically broadly subrectangular to cuneate, 4–6(7) cells high (from median sinus base to leaf base), (9)14–21 cells wide in distal portion narrowing to 8–12 cells wide in basal portion (disc typically 8 cells wide throughout in var. *roseana*); margins entire,  $\pm$  straight to less often curved; cells of disc margins often bulging. Cells of disc thin-walled but firm, trigones lacking or minute, large, convex, “pillow-like” (obvious even under low magnification), the largest cells (in median sector of disc) large, often  $\pm$  isodiametric, (45)50–70  $\mu\text{m}$  wide  $\times$  55–90  $\mu\text{m}$  long; basal 1–2 rows of disc cells considerably larger (wider), irregularly arranged or in  $\pm$  regular tiers; cells of disc margins (especially the dorsal) sometimes forming an indistinct border of elongate,

narrower cells; cuticle smooth. Oil-bodies grayish (var. *tetrapila*) or hyaline (var. *cancellata*), coarsely papillose, the spherules protruding beyond membrane, the median disc cells with 5–11 oil-bodies per cell (8–9 per in lobe cells), narrowly to broadly elliptic to subrescentic and 8.3–11.6  $\times$  5.5–5.8  $\mu\text{m}$ , less often ca. 14.7  $\times$  5.3  $\mu\text{m}$ , the subspherical ones 5.9–6.6  $\mu\text{m}$  in diam. Underleaves normally smaller than leaves (subequal to leaves in var. *cancellata*), strongly spreading, contiguous to loosely imbricate, plane, 4–6-lobed to 0.4–0.6, the lobes somewhat divergent, ciliiform, the uniseriate portion formed of 3–5(8) somewhat elongated cells; disc symmetrically cuneate, (3)4–5 cells high (median sinus), the cells in  $\pm$  regular tiers or irregularly arranged, the disc (10)12–19 cells wide in distal portion narrowing to 8–10 cells wide at base; margins entire, usually straight. Rhizoid initial cells small, subquadrate, at bases of lobes or forming a continuous bistratose band across the apex of the disc. Asexual reproduction lacking.

Plants dioecious. Androecia on short, abbreviated, ventral-intercalary branches from leading shoots, as well as from flagelliform or stoloniform branches; bracts closely imbricate, dorsally assurgent, deeply concave, 2–3 lobed, each lobe terminating in a single cell or a uniseriate row of 2 not to hardly elongated cells; lamina cells irregular in shape and arrangement, the dorsal margin of lamina feebly dilated and slightly incurved, irregularly crenulate, at times with a few sessile slime papillae; bracts monandrous; antheridia large for bract size, the stalk short, ca. 7 cells high, uniseriate; bracteolar antheridia absent. Gynoecia oriented laterally and at best only weakly dorsally assurgent, with a vestigial stem perigynium present, swollen, rhizoidous; bracts and bracteoles in 2–3 series, inserted on the vestigial perigynium, becoming progressively larger and less deeply lobate towards the perianth, those of innermost series ensheathing the perianth, deeply concave, the apical portion canaliculate; bracts of innermost series  $\pm$  suborbicular, irregularly 4-lobulate, the lobules terminating in a uniseriate row of 1–2 cells; bract margins crenate to dentate, the armature frequently sharply inflexed, often terminating in a slime papilla, the bracts with an obscure border formed of 1 to several rows of cells longer, narrower and more irregular than those within; bracteoles of innermost series nearly identical in form to bracts although a little smaller, free from bracts. Perianth not extending above vegetative axes, 0.5–0.55 emergent, ovoid-cylindrical.

dricul, terete in basal half, the distal half obscurely trigonous and with 6–9 plicae, the sulci shallow to deep; perianth narrowed toward a decidedly contracted mouth, the mouth with 6 narrowly triangular lobes, each lobe fringed with slightly thick-walled, contorted, crowded, sparingly papillose cilia, the terminal cell of each cilium coarsely papillose.

Seta with 8–9 rows of outer cells, surrounding an inner core of 20–34 much smaller cells. Capsule short-cylindric, 1204–1470  $\mu\text{m}$   $\times$  560–805  $\mu\text{m}$ , the wall 41–50  $\mu\text{m}$  thick, of 4 layers (locally 3), the outer layer subequal to the combined thickness of the inner layers, or slightly less thick; outer layer of cells in tiers,  $\pm$  regularly short-rectangular, with 2-phase development rather indistinct, the longitudinal secondary walls with sheet-like thickenings and nodule- to spine-like thickenings (4–6 per cell) alternating with primary walls also with similar thickenings, the transverse walls almost devoid of thickenings, or with local, nonpigmented, nodular swellings; intermediate layers (when 2 in number) thinner than the outer or innermost layers; innermost layer of cells  $\pm$  tiered, rather regularly narrowly rectangular, with semiannular bands common, rather narrow, complete, only rarely forked to delimit local fenestrae.

Spores 12–13.4  $\mu\text{m}$  in diam., exine rather thick in optical section, dark yellow brown, areolate (with a low, close network of well-defined, rather thick, furcate ridges that anastomose to form areolae). Elaters rigid,  $\pm$  straight, 9.1–12.5  $\mu\text{m}$  wide, only slightly tapering toward tips, bispiral to tips, the spirals 3.8–5.3  $\mu\text{m}$  wide.

**NOMENCLATURE**—The original specimen of *Lepidozia tetrapila* in Taylor’s herbarium (FH) includes plants of *Telaranea tridactylis* and a larger *Telaranea* with prominent, pillow-like disc cells. The statements in the protologue, “cells remarkably large and strongly defined” and “stems about 1 one inch long,” and the reference to “flagelliform shoots” can only apply to the larger plant. This element is therefore selected as the lectotype. Also admixed with the type are *Lepidozia pendulina*, *Chiloscyphus spiniferus*, *Haplomitrium gibbsiae*, and *Isotachis lyallii*, the last three segregated by Taylor into separate micropackets.

The type locality of *T. tetrapila* is not given in the protologue, however the presence of *T. tridactylis*, a species known to occur only on Campbell Is., Auckland Is. and Tasmania, strongly suggests that the plant came from the subantarctic

islands. Hodgson (1956, p. 597), who had not seen the type, mentioned this name in passing as a possible older name for *Lepidozia laevifolia*.

**DIFFERENTIATION AND VARIATION**—*Telaranea tetrapila* is the oldest name for the species which has generally been called *Telaranea* (or *Lepidozia*) *gottscheana* in the New Zealand literature (e.g., Hodgson, 1956; Allison & Child, 1975). The type of the name *L. gottscheana*, however, is *T. patentissima*. At its best, *T. tetrapila* is one of the most handsome of our *Telaranea* species, and is common throughout New Zealand. The plants are highly variable in size, color, and general aspect, as well as leaf form and number of lobes. The most useful features for distinguishing the species are the large, pillow-like, almost geometrically hexagonal disc cells (Figs. 18: 4; 19: 3), which are conspicuous and easily observed, even under the dissecting microscope, the bulging cells of the lobe bases and the short, secondarily divided cells at the lobe tips (Figs. 18: 5, 6; 19: 9). One marked expression of *T. tetrapila* (var. *roseana*) bears a strong resemblance to *T. tuberifera*, due to its widely spreading, parallel-sided leaves (Fig. 19: 1). Another (var. *cancellata*) somewhat resembles *T. gibbsiana* in the finely elongated leaf lobes, and large, ciliiform-lobed underleaves.

Examination of herbarium specimens indicates that *T. tetrapila* has often been confused with *T. praenitens*, which differs by its more deeply-lobed, palmate leaves and the characteristic minute denticulations formed by the swollen projecting end-walls on the lobes and disc margins.

**Key to the Varieties of *T. tetrapila***

- 1. Leaves rather flat and widely spreading, the disc parallel-sided and somewhat higher than wide (resembling *T. tuberifera*), 8 cells wide in both distal and basal portions; lobes often straight and aligned with the disc margins . . . . . var. *roseana*
- 1. Leaves weakly to distinctly convex, and obliquely spreading, the disc weakly to distinctly cuneate, (9)14–21 cells broad distally, the margins often curved; lobes divergent . . . 2
- 2. Lobes typically shorter than the disc, the cells of the uniseriate row short, often  $\pm$  barrel-shaped; underleaves smaller than leaves; oil-bodies greyish, 5–8 per cell. Common throughout New Zealand . . . . . var. *tetrapila*



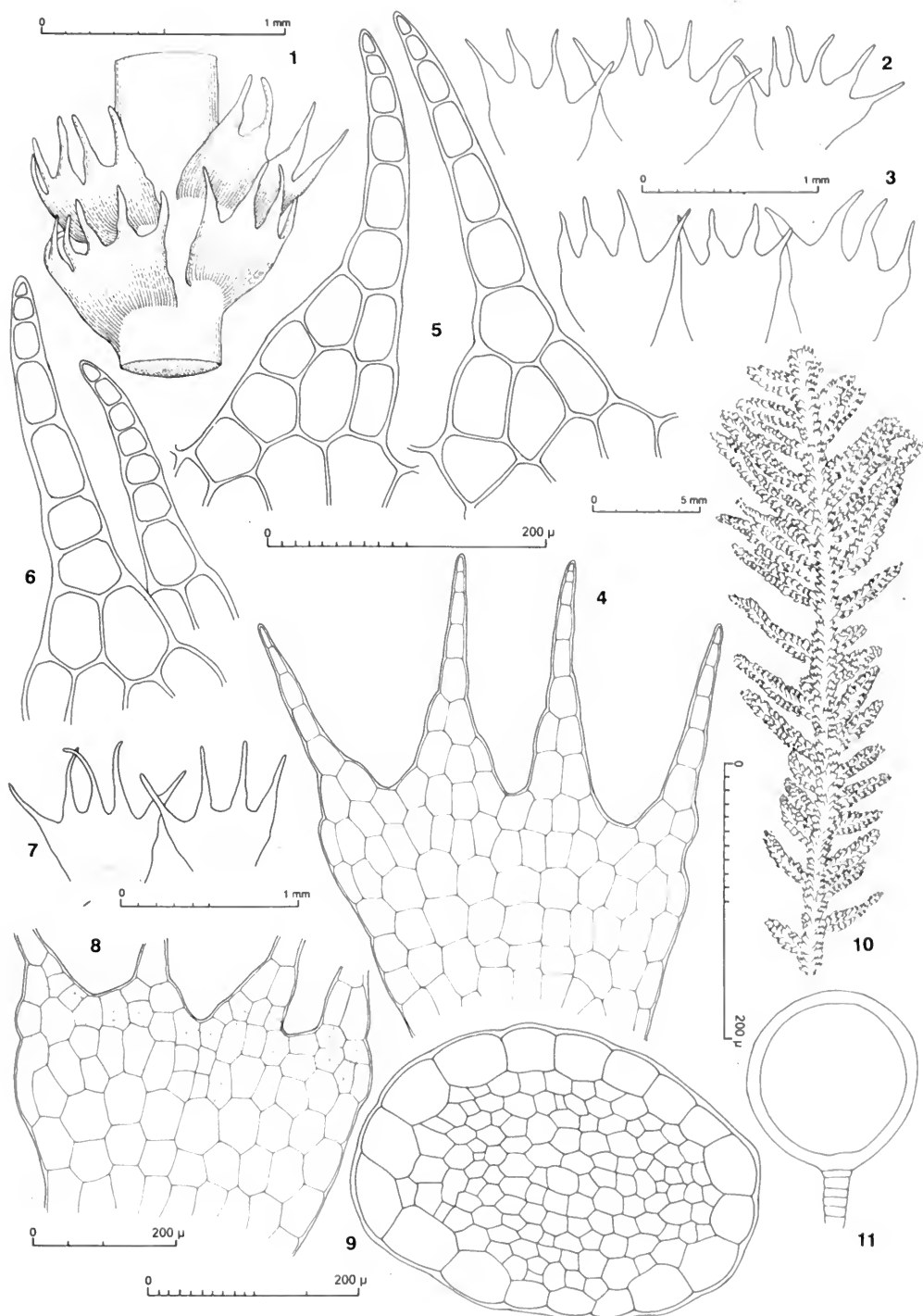


FIG. 18. *Telaranea tetrapila* (Hook. f. & Tayl.) Engel & Merr. var. *tetrapila*. 1. Sector of leading shoot, dorsal view. 2, 3. Leaves. 4. Leaf, cellular detail. 5, 6. Median lobes of leaf; note secondary septa. 7. Underleaves. 8. Underleaf disc, cellular detail, stippled cell walls indicate rhizoid initial cells. 9. Stem, cross section. 10. Plant, dorsal view. 11. Antheridium (as seen in optical section). (Figs. 1, 3, 6-7, 10 from Engel 18029, New Zealand, South Is., Otago/Westland Prov. boundary, Mt. Aspiring Natl. Park, summit area of Haast Pass; 2, 5, 8 from Reif C151A; 4, from Reif C93E; 9, from Reif C80F, all Reif coll. from New Zealand, South Is., Westland Prov., Camp Creek; 11 from Engel 19298, New Zealand, South Is., Westland Prov., Paparoa Range, Croesus Track.)

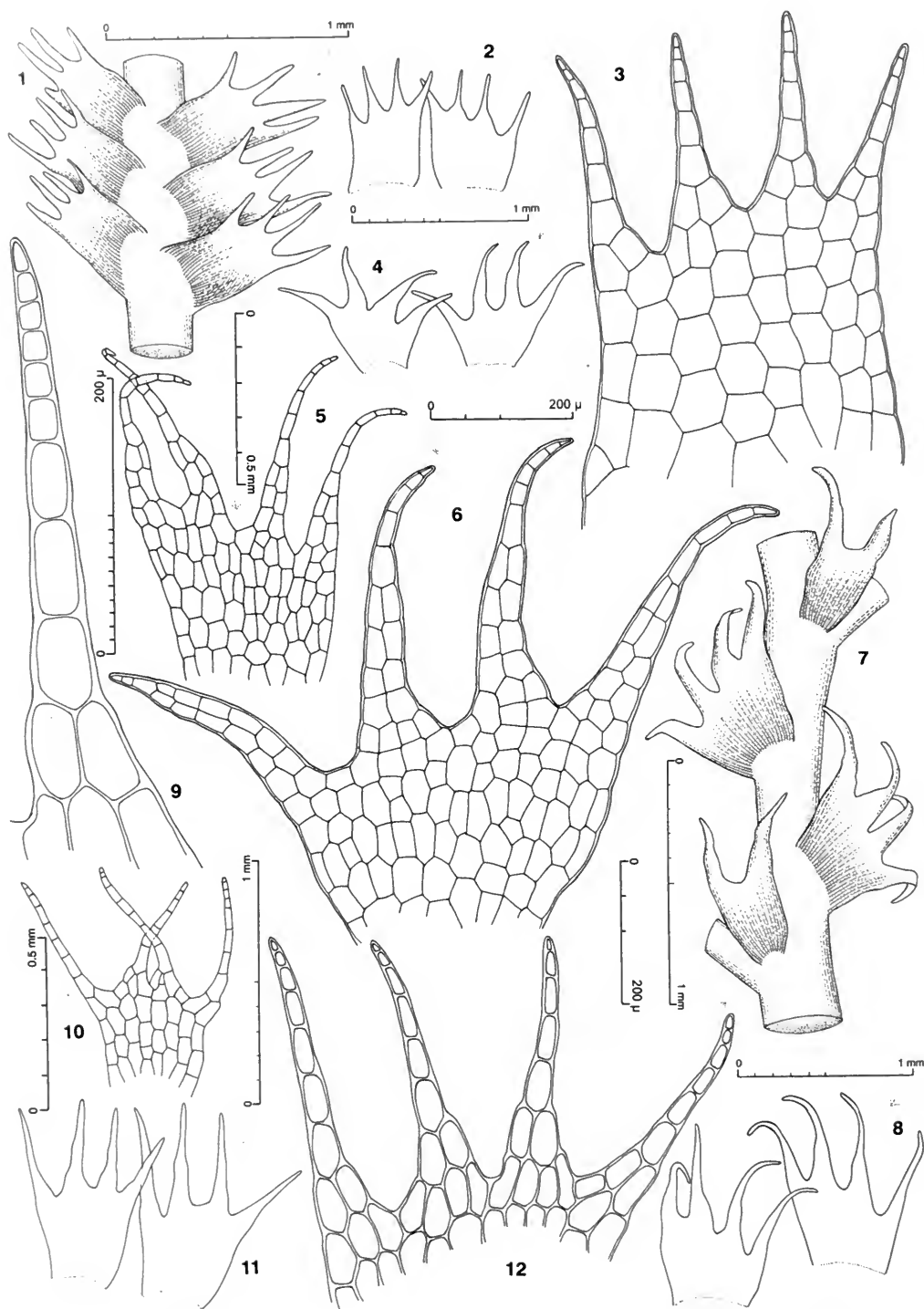


FIG. 19. *Telaranea tetrapila* (Hook. f. & Tayl.) Engel & Merr. Var. *roseana* (Steph.) Engel & Merr. (1-3); var. *cancellata* (Col.) Engel & Merr. (9-12); *Telaranea paludicola* (Hodgs.) Hodgs. (4-8). 1. Sector of main shoot, dorsal view. 2. Leaves. 3. Leaf, cellular detail. 4. Leaves. 5, 6. Leaves, cellular detail. 7. Sector of main shoot with branch bases and associated half-leaves, dorsal view. 8. Leaves of extreme. 9. Leaf lobe showing secondary cell divisions in distal portion. 10. Underleaf. 11. Leaves (note, figure drawn at 50% larger than other leaf outlines). 12. Distal sector of leaf. (Figs. 1-3 from Fife 4964, New Zealand, South Is., Nelson Prov., Fox River; 4, 6-7 from type of

2. Lobes longer than the disc, the cells of the uniseriate row  $\pm$  elongate (to 2.5:1), not barrel-shaped; underleaves subequal to leaves in size; oil-bodies hyaline, 8–11 per cell. Scattered sites on North Island . . . . .  
 . . . . . var. *cancellata*

*Telaranea tetrapila* var. *roseana* (Steph.) Engel & Merr.

*Lepidozia roseana* Steph., Spec. Hep. 3: 590. 1909. *Neolepidozia roseana* (Steph.) Fulf. & J. Tayl., Brittonia 11: 85. 1959. *Telaranea roseana* (Steph.) Hodgs., Rec. Domin. Mus. 4: 106. 1962. *Telaranea tetrapila* var. *roseana* (Steph.) Engel & Merr., Phytologia 79: 253. June, 1996 [1995]. Type: New Zealand, without specific loc., 1898, Petrie, "com. Rose" (G!).

Plants resembling *T. tuberifera*; leaves rather flat and widely spreading; leaf lobes typically shorter than the disc, subcaudate,  $\pm$  parallel with the disc margins; leaf disc parallel-sided and somewhat higher than wide, typically 8 cells wide in both distal and basal portions, the cells conspicuously large, hexagonal (as in var. *tetrapila*).

**DIFFERENTIATION AND VARIATION**—Plants assigned to this variety often bear a striking resemblance to *Telaranea tuberifera*, but differ by not having the glaucous cuticle or the strongly horizontal leaf orientation of that species; it also differs by the nonfragmenting lobe apices, and the absence of tubers at the tips of flagelliform stolons. The leaves are obliquely oriented, as in var. *tetrapila*, but are typically rather flat, and diverging at a wider angle with the stem. As indicated in the species description, *T. tetrapila* is very variable, and even well-developed plants will have some leaves which are only 8 cells wide throughout the disc, particularly on the branches. The var. *roseana*, when well developed, has a very characteristic appearance, due to the conspicuously parallel-sided disc (somewhat higher than wide), which is typically 8 cells wide in both distal and basal portions (Fig. 19: 3), and the lobes are often straight and aligned with the disc margins.

The var. *roseana* differs from *Telaranea paludicola* by the more slender lobes, which are 2 (and only sporadically 3–4) cells wide at the base, and

the very prominent, hexagonal disc cells are arranged in precise geometrical fashion.

Hodgson (1956, p. 608) treated this plant as *T. corticola*, describing the leaf cell size as 50–60  $\mu$ m, but referring to Stephani's (1909) measurements as "much smaller, being only  $27 \times 36 \mu$ ." Examination of the type of *T. corticola*, however, reveals that this species' is a synonym of *T. patentissima* (p. 46).

**DISTRIBUTION AND ECOLOGY**—The var. *roseana* is known primarily from South Island, New Zealand in lower- to middle-elevation forests, especially on damp, clayey banks. Known in the North Island only from Wellington, South and North Auckland Provinces.

**SELECTED SPECIMENS SEEN**—NEW ZEALAND. SOUTH ISLAND. SOUTHLAND PROV.: Waikaia State Forest, junction of Waikaia River Track and Tison Peak Track, upstream from Piano Flat Recreational Area, ca. 260 m, Engel 24721 (F); Fiordland Natl. Park, Stuart Mts., W shore of Lake Thomson N of stream draining from Lake Wade, 300 m, Fife 7729 as *T. cf. patentissima* (F). OTAGO PROV.: Bluc Mts., ca. 455 m, Child Hs.n.159 (F); Waipori Gorge, S of Dunedin, Allison H7809 (CHR); Paradise, Dart Valley, N of N end of Lake Wakatipu, ca. 365 m, Child H1248 as *T. praenitens* (F). WESTLAND PROV.: Lake Kaniere Scenic Reserve, Lake Kaniere Rd, 125 m, Engel 24826 (F); Rapahoe Range (or Twelve Apostles Range), N of Greymouth, ca. 150 m, Child H5393 as *T. centipes* (F); Paparoa Range, along Croesus Track, ESE of Barrytown, between Granite Creek and Fagan Creek watersheds, 250 m, Engel 19287 (F); Hari Hari, Langridge as *T. praenitens* (CHR). NELSON PROV.: Track on N bank of Fox River, ca. 1.5 km E of Route 6 Fife 4964—c. per. (F). NORTH ISLAND. WELLINGTON PROV.: Tongariro Natl. Park, Mangawhero River near juncture of Rimu Track and Forest Walk, just NE of Ohakune, 625 m, Engel 22711 (F). SOUTH AUCKLAND PROV.: Whareorino Forest, start of track to Leitch's Hut, 280 m, Engel 23746 (F); Coromandel State Forest Park, Kaureranga River, just SE of suspended footbridge, 150 m, Engel 22287 (F); ibid., Mt. Moehau, below summit of "Little Moehau," ca. 800 m; Engel 23670 (F). NORTH AUCKLAND PROV.: Waipoua Forest, Lookout Track between Lookout Road and Waipoua River Road, above forest headquarters, ca. 240 m, Engel 21082 (F); Waipoua Kauri Forest, Hatcher 441 (F); Omahuta Forest Sanctuary, E of Mangamuka Bridge, 320 m, Engel 21035 (F).

*Telaranea tetrapila* var. *cancellata* (Col.) Engel & Merr.

*L. paludicola*; 5, 8 from Child 5446, New Zealand, South Is., Nelson Prov., Big Totara River; 9–12 from Zotov 7083, New Zealand, North Is., Wellington Prov., Ohau-iti River.)

*Lepidozia cancellata* Col., Trans. & Proc. New Zealand Inst. 18: 244. 1886. *Telaranea tetrapila* var. *cancellata* (Col.) Engel & Merr., Phytologia 79: 253. June, 1996 [1995]. Type: New Zealand, Waipawa Co., near Norsewood, edge of Bartramia Creek, 1885, *Colenso a.1418* (BM!, WELT!).

*Psiloclada digitata* Col., Trans. & Proc. New Zealand Inst. 18: 243. 1886, *syn. nov.* Type: New Zealand, Waipawa Co., near Norsewood, 1885, *Colenso a.1378* (BM!, WELT = 0).

Plants resembling *T. gibbsiana*, often pale amber in color; plants medium, to 1.1 cm wide, including branches; branching somewhat irregularly to regularly 1-pinnate; leaf lobes longer than the disc, subcaudate, rather abruptly tapering to a uniseriate row of cells,  $\pm$  straight, the cells of the uniseriate row  $\pm$  elongate (to 2.5:1), not barrel-shaped; leaf disc at most moderately asymmetric, the disc cells mostly isodiametric; oil-bodies grayish, 5–8 per cell; underleaves subequal to the leaves in size, with long ciliiform lobes, the terminal cells often secondarily divided.

**DIFFERENTIATION AND VARIATION**—Colenso (1886, p. 245) aptly described this as “a truly elegant plant.” It is chiefly distinguished by the rather regularly 1-pinnate shoots; the often pale amber pigmentation; the slender leaf lobes, which are subcaudate as in the var. *tetrapila*, but with a uniseriate row composed of elongated (to 2.5:1) cells; and the rather large underleaves, with long, ciliiform lobes, rather like those of *T. gibbsiana*. It differs from *T. paludicola* in the  $\pm$  isodiametric cells of the disc and lobe bases, and the abruptly tapering lobes, with a long, uniseriate row, which are  $\pm$  straight, versus lobes biseriate, often falcate and hooked at the tips in *T. paludicola*.

**DISTRIBUTION AND ECOLOGY**—Known only from several scattered sites on North Island, “on trees and logs, forming large and thick patches” (Colenso, l.c., p. 245). A slip of newspaper with the type (WELT) indicates that the plant was associated with the moss *Cyathophorum*. On Mt. Te Aroha, plants occurred at 880–890 m loosely on the floor as well as over soil deep in a protected niche under the lip of the forest overhang, both populations in a stunted *Nothofagus menziesii* forest associated with *Dracophyllum* and *Quintinia serrata*. In the Herangi Range the species occurred at ca. 720–750 m on an exposed plateau with a mosaic of subalpine bog vegetation, stunted *Quintinia serrata*, *Dracophyllum*-heath (to 1 m tall), rocky outcrops and small water channels. At this site plants were found in moist niches, e.g., on the floor or beneath blades of *Poa* sp.

**SELECTED SPECIMENS SEEN—NEW ZEALAND.** NORTH ISLAND. WELLINGTON PROV.: Ohau-iti R. (Ohauite Stream), *Zotov 7083* (CHR!—c. per.); Tararua Mts., Akatarawa Saddle, *Zotov 9294* (CHR—c. sporo.). GISBORNE PROV.: Waikaremoana, Wairoa, *Hodgson 111* (CHR). NEAR GISBORNE/SOUTH AUCKLAND PROV. BOUNDARY: Urewera Natl. Park, track to Whakataka Hut from Lake Waikaremoana, N of western extremity of Lake Waikaremoana, 1160 m, *Engel 23284* (F). SOUTH AUCKLAND PROV.: Southern extent of Herangi Range, plateau area S of Te Whakapatiki, W of Te Kuiti township, ca. 720–750 m, *Engel 25127* (F); Kaimai-Mamaku Forest Park, Mt. Te Aroha, S facing slope, 880–890 m, *Engel 23828*—c. ♂ (F). GREAT BARRIER IS.: Coffin's Creek Camp, 245 m, *Lloyd 260pp* (CHR).

*Telaranea tetrapila* (Hook. f. & Tayl.) Engel & Merr. var. *tetrapila*

Plants with shoots to 1.5 cm wide (including branches); branching regularly and rather densely pinnate (often plumose in well-developed plants); leaf lobes typically shorter than the disc, subcaudate,  $\pm$  straight, the cells rather short, barrel-shaped; leaf disc at most moderately asymmetric, often distinctly cuneate, (9)14–21 cells broad distally, composed mostly of large, hexagonal cells, except for distal tier at base of lobes; oil-bodies hyaline, 8–11 per cell.

**DISTRIBUTION AND ECOLOGY**—The typical variety is common throughout New Zealand in low-to middle-elevation, forests (typically below 700 m), where it can be particularly luxuriant. It can occur in the upper limits of *Nothofagus menziesii* forests or in subalpine scrub, but at these upper elevations the plants often represent a small or weak phase of the species (it nevertheless may produce sporophytes and androecia and may be well developed in such niches). It grows on an array of substrates, but typically can be found on the forest floor, on soil of mossy banks, on rotted logs, or, at times, on upright tree trunks. It is able to tolerate some degree of exposure and can occur, for example, in open boggy areas with *Juncus squarrosus*, *Coprosma*, *Leptospermum*, *Cassinia*, etc. (Mt. Cargill area), or in pakihis, with *Gleichenia*, *Lycopodium*, *Juncus*, *Drosera* spp., *Schizaea* and *Leptospermum*, etc. (Tiropahi River area).

**SELECTED SPECIMENS SEEN—NEW ZEALAND.** SO- LANDER IS.: Summit, 330 m, *Johnson* (CHR); *ibid.*, plateau, 300 m, *Johnson* (CHR); *ibid.*, SW Bay, 100 m, *Johnson* (CHR). STEWART ISLAND: *Cockayne 8383* as *L. remotifolia* (CHR); Rakiura Natl. Park, Port Pegasus, immediately adjacent Belltopper Falls, ca. 10–80 m, *Engel 24137* (F); Pegasus, *Schuster, Scott & Taylor*

(CHR); Mt. Rocky summit area, 530 m, *Engel* 24292 (F); Ulva Is., Paterson's Inlet, *Hatcher* 1589 (F); near Oban, Half Moon Bay, *Hatcher* 1635 (F); Christmas Village, Mt. Anglem, 170 m, *Scott* as *T. roseana* (CHR). SOUTH ISLAND. SOUTHLAND: Bluff Hill, 90–120 m, *Allison* H5163 (CHR); *ibid.*, *Kirk* 527 (CHR); Fiordland Natl. Park, Mt. Burns, Burns Creek, ca. 1280 m, *Child* H5117 (F); *ibid.*, Stuart Mts., W shore of Lake Thomson N of stream draining from Lake Wade, 300 m, *Fife* 7607, 7726 both as *T. cf. patentissima* (F); *ibid.*, off track along East Branch of Eglinton River, SE of Mt. Eglinton, 440 m, *Engel* 18748 (F). OTAGO PROV.: Lake Wilkie, Catlins District, *Burrell* (CHR); Catlins River area, near Purakanui, NE of Macleennan, ca. 150 m, *Child* 794—c. ♂ (F); Blue Mts., S end, E of Garden Gully Road, *Child* Hs.n.158 (F); near Akatore Stream, coastal, S of Dunedin, *Allison* H5898 (CHR); S of Taieri River, S of Dunedin, ca. 180 m, *Allison* H5897 (CHR); saddle W of road to Mt. Cargill, N of Dunedin, 500 m, *Engel* 17529 (F); immediately N of Mt. Cargill, N of Dunedin, 525 m, *Engel* 17593—c. sporo. (F); Mt. Cargill, Mt. Holmes, N of Dunedin, ca. 550 m, *Child* H1075 as *T. corticola* (F); W slope of Flagstaff, NW of Dunedin, 560 m, *Engel* 17634 (F); Silver Peak, *Simpson* as *L. praenitens* (CHR); Leith Valley, near Dunedin, *Child* H102 (F); Route Burn, ca. 520 m, *Child* Hs.n.67 (F); Mt. Aspiring Natl. Park, Blue River near confluence with Makarora River, NNE of Makarora, 310 m, *Engel* 18914 (F). OTAGO/WESTLAND PROV. BOUNDARY: Mt. Aspiring Natl. Park, summit area of Haast Pass, 570 m, *Engel* 17987 (F). WESTLAND PROV.: Between confluence of Jackson River and Arawata River and Lake Ellery, off Jackson River Road, sea level, *Engel* 17944—c. per. (F); Lake Paringa, ca. 15 m, *Child* H1886 (F); Ship Creek, 14.5 km N of Haast River, sea level, *Engel* 12760 (F); Westland Natl. Park, terminal moraine of Fox Glacier, S side of Fox River, *Engel* 6617A (F); *ibid.*, Franz Josef Glacier Valley, Roberts Point, SW of Mt. Gunn, ca. 620–670 m, *Engel* 18089—c. per. (F); *ibid.*, track to Alex Knob just below juncture with track to Louisa Peak, 1150–1170 m, *Engel* 19002 (F); *ibid.*, trail to Lake Wombat, *Engel* 6694 (F); Arthur's Pass Natl. Park, Bealey River, off Bealey Valley Track, 830–850 m, *Engel* 18469—c. sporo. (F); *ibid.*, Upper Twin Creek Valley, 930 m, *Engel* 18529A—c. sporo. + ♂ (F); *ibid.*, N of Kellys Creek near Hwy 73, N of Otira, 420–475 m, *Engel* 18329 (F); Camp Creek, W of Alexander Range, 190–990 m, *Reif* C3F—c. ♂, C260E (F); White Horse Creek, ca. 150 m, *Child* H5411—c. ♂ (F); Paparoa Range, road to Sewell Peak, 710 m, *Engel* 19075 (F); *ibid.*, along Croesus Track, ESE of Barrytown, between Granite Creek and Fagan Creek watersheds, 450 m, *Engel* 19298—c. ♂ (F); Mt. Aspiring Natl. Park, Cross Creek, 1 km N of Haast Pass, 510 m, *Engel* 23114 (F). WESTLAND/CANTERBURY PROV. BOUNDARY: Arthur's Pass Natl. Park, Bridal Veil Track, E side of Bealey River and just N of town of Arthur's Pass, 760–825 m, *Engel* 22939 (F); *ibid.*, Bealey Valley Track, ca. 875–900 m, *Engel* 22875 (F). NELSON/WESTLAND PROV. BOUNDARY: Paparoa Range, S side of Porarari River, up river from gorge and ca. 500 m WSW of ford on inland track to Bullock Creek, 10–20 m, *Engel* 19209 (F); Lower Basin (Syncline area) of Porarari River, 30–45 m, *Fife* 6667 (F); track between Punakaiki and Porarari Rivers, 150 m, *Fife* 6078 (F). NELSON PROV.: Paparoa Natl. Park, Bullock Creek Road, along

Bullock Creek, NE of Punakaiki, ca. 25 m, *Engel* 21578 (F); Paparoa Range, upper slopes of N side of Tiropahi or Four Mile River, between sea and Route 6, S facing side of gorge, 130–170 m, *Engel* 19246 (F); Maimai State Forest, 3 m NW of Reefton, 280–350 m, *Macmillan* 76/169 as *T. praenitens* (CHR); upper Buller River gorge, near Lyell, *Allison* 6464 (CHR); track to German Terrace, 6 km SSE of Westport on Nine Mile Road, 90 m, *Engel* 21551 (F); Nelson Lakes Natl. Park, NE margin of Lake Rotoroa, 520 m, *Engel* 21496 (F); *ibid.*, off Lakehead Track, near juncture with southern end of Loop Track, NE end of Lake Rotoiti, 630 m, *Engel* 22736 (F); Big Bush State Forest 48, Donald Creek, 480–600 m, *Macmillan* 77/40 (CHR); Able Tasman Natl. Park, Mt. Evans, 1067 m, *Child* 4703B (F); *ibid.*, Porters Rock Track, ca. 915 m, *Child* H4680 as *L. cf. concinna* (F). NORTH ISLAND. WELLINGTON PROV.: Orongorongo River, ca. 610 m, *Zotov* 7148 as *L. praenitens* (CHR); Taranua Mts., Field Hut, 825 m, *Zotov* 7633, 7374 as *L. praenitens* (CHR); *ibid.*, Table Top, *Moore* H175 (CHR); *ibid.*, Akatarawa Saddle, *Zotov* 9295 as *L. praenitens* (CHR); *ibid.*, Ruamahanga Valley, *Zotov* 9267 as *L. praenitens* (CHR); Ohau-iti River, *Zotov* 7090 as *L. praenitens* (CHR); Ruahine Range, Pohangina Valley, ca. 855 m, *Child* H194—c. sporo. (F); Tongariro Natl. Park, ca. 8 km from Ohakune on Ohakune Mt. Road, ca. 950 m, *Engel* 21326 (F); *ibid.*, near Ohakune Mt. Hut, Mt. Ruapehu, 1370 m, *Sainsbury* (CHR); *ibid.*, Mt. Hauhungatahi, Mt. Ruapehu, *Moore* (CHR); *ibid.*, Mahuia Track, *Barr* (CHR). HAWKES BAY PROV.: "Kiwi," Wairoa, *Hodgson* 203 (CHR). TARANAKI PROV.: Mt. Egmont, Ngaroto Track, *Barr* 385 (CHR); Pukeiti Bush, near New Plymouth, *Hatcher* 293—c. per. (F); Mt. Messenger, ca. 185 m, *Allison* H5905 (CHR). NEAR GISBORNE/SOUTH AUCKLAND PROV. BOUNDARY: Urewera Natl. Park, crest trail from highway 38 towards Whakataka summit, N of northern extremity of Lake Waikaremoana, 930–1030 m, *Engel* 20665 (F). GISBORNE PROV.: Lake Waikaremoana, *Hodgson* as *L. praenitens* (F); Urewera Natl. Park, Huiarau Range, summit area of Te Rangaakapua, 1230–1320 m, *Engel* 23461 (F). SOUTH AUCKLAND PROV.: W of Lake Taupo, *Matthews* (CHR); Mamaku Plateau, W of Lake Rotorua on Rt. 5, 400 m, *Engel* 20507 (F); southern extent of Herangi Range, vicinity of plateau area S of Te Whakapatiki, W of Te Kuiti township, ca. 720–750 m, *Engel* 25158 (F); Herangi Range, Whareorino Forest, near tributary of Awakino River, W of Leitchs Road, and SW of Te Kuiti township, 285 m, *Engel* 23934 (F); Kaimai Range, network of tracks at the end of Wrights Rd. off the Katikati-Tauranga highway, Swimming Holes Track, 60 m, *Engel* 23537 (F); Mt. Te Aroha, ca. 3 km E of Te Aroha, 900–940 m, *Engel* 22150 (F); Coromandel State Forest Park, summit of Table Mt., 835 m, *Engel* 22378 (F). NORTH AUCKLAND PROV.: Waitakere Hills, W of Auckland, *Hatcher* 207—c. per. (F); NE Waitakere Ranges, Swanson University Reserve, Tram Valley Road, 95 m, *Engel* 20447 (F); Auckland, N shore, Kauri Point Centennial Park, up from W end of Kendalls Bay, *Cameron* 5562 as *T. praenitens* (F); Auckland, *Kirk* 559 (CHR); Kauri Grove Track, upper Piha Valley, near Auckland, *Barr* 223 (CHR); Waipoua Forest, Lookout Track between Lookout Road and Waipoua River Road, above forest headquarters, ca. 240 m, *Engel* 21067; *ibid.*, track from Lookout to forest headquarters, *Braggins* 94/278B

(AKU); *ibid.*, track to Te Matua Ngahere, ca. 340 m, *Engel* 22560 (F); Waipoua State Forest, *Allison* H763 (F); Omahuta Forest Kauri Sanctuary, E of Mangamuka Bridge, 260 m, *Engel* 21012 (F); Tributary of Mangamuka River, Maungataniwha Range, SE of Kaitaia on State Highway 1, 200 m, *Engel* 20812 (F).

*Telaranea paludicola* (Hodgs.) Hodgs.

*Lepidozia meridiana* var. *paludicola* Hodgs., *Trans. Roy. Soc. New Zealand* 83: 611. *pl.* 2, *f.* 21. 1956. *Telaranea paludicola* (Hodgs.) Hodgs., *Trans. Roy. Soc. New Zealand, Bot.* 3: 69. 1965; *Engel & Merr.*, *Phytologia* 79: 252. 1996 (1995). Type: New Zealand, North Is., Tararua, Oriwa Lake Hollow, bog, 3300 ft., 15 April 1933, *Zotov* (CHR!; "No. 6619 in Bot. Divn. Herb.").

Plants with a rather spinose appearance, resembling *T. praenitens*, soft, flexuous yet firm, loosely prostrate, often in dense, compact mats, pale green to olive-green or at times brownish yellow to rust-brown, nitid when dry; shoots medium, to 0.9 cm wide, including branches. Branching somewhat irregularly to regularly 1-pinnate, the branches rather short, normally determinate, of the *Frullania* type, often flagelliform; branch half-leaf 2(3–4)-lobed, usually obliquely inserted, narrowly rectangular to linear, the lobes parallel to slightly diverging; first branch underleaf undivided and ciliiform or less often 2–3-lobed, inserted on ventral or ventral-lateral side of branch near base. Ventral-intercalary branches occasional, often becoming leading shoots and leafy throughout. Stems with cortical cells markedly differentiated, the radial walls thin, the outer wall slightly thickened, in 12–14 rows, those on ventral side of stem a little smaller; cortical cells in section larger than the numerous (ca. 65) medullary cells, the medullary cell walls in ventral half of stem slightly thickened, those in dorsal half of stem distinctly thicker. Leaves on main shoot rigid, distant to loosely imbricate, widely spreading, moderately concave, the lobes incurved, the insertion moderately incubous; leaves 770–980(1260)  $\mu\text{m}$  wide (from lobe tip to lobe tip)  $\times$  700–1050  $\mu\text{m}$  long, usually distinctly asymmetric, or less often subsymmetric,  $\pm$  equally 4(5–6)-lobed to ca. 0.4–0.6, the lobes typically somewhat longer than the disc, often distinctly falcate and hooked at the tip. Lobes slender, long attenuate, divergent, the dorsal lobes often  $\pm$  paired, the lobes 3–4 cells wide for 1–2 tiers at extreme base, biseriate for 2–4(5) tiers, terminating in a long uniseriate row of (4)5–7(8) cells (at times more than half the length of lobe); lobe cells  $\pm$  firm, thin to moderately thick-

ened, the septa thickened in the corners but not swollen and projecting from the lobe margins (the lobes at times somewhat constricted at the septa), the lobe cells all elongated (to 2.5:1), the basal cell of uniseriate row (28)34–50  $\mu\text{m}$  wide  $\times$  78–88  $\mu\text{m}$  long, the next cell 36–42  $\mu\text{m}$  wide  $\times$  76–78  $\mu\text{m}$  long, the terminal cell normally about equal to the penultimate cell in length but sometimes secondarily divided, the terminal cell of uniseriate row tapering to a blunt tip; cuticle smooth or finely striate-papillose at lobe tips. Disc often distinctly asymmetric, typically longer than broad and narrowing to the base, 5–7 cells high (from median sinus base to leaf base), 15–16 cells wide in distal portion narrowing to 8–11 cells wide in basal portion; disc margins  $\pm$  straight, entire, or the marginal cells somewhat bulging. Cells of disc moderately thin-walled, trigones small or lacking, median disc cells longitudinally elongate, (38)45–52  $\mu\text{m}$  wide  $\times$  65–110  $\mu\text{m}$  long, in  $\pm$  regular, somewhat obliquely arranged tiers; cuticle smooth. Underleaves much smaller than leaves, strongly spreading to subsquarrose, distant, plane, 4(5)-lobed to ca. 0.6, the lobes divergent, ciliiform, straight to subfalcate and hooked at tip, 2 cells wide at the base, often with an additional biseriate tier at base of lobe, the uniseriate portion formed of (3)5–8 short to elongated cells with septae thickened at the corners; disc symmetrically cuneate, 4–5(6) cells high (median sinus), the cells in  $\pm$  regular tiers; disc 9–12 cells wide in distal portion narrowing to 8 cells wide at base; margins entire, usually straight. Rhizoid initial cells small, subquadrate, at bases of lobes or forming a continuous bistratose, dense band across the apex of the disc.

Gametangia and sporophytes not seen.

DIFFERENTIATION AND VARIATION—*Telaranea paludicola* is a striking plant when well developed. Although described as a variety of *T. meridiana* (Hodgson, 1956), *T. paludicola* has little to do with that species. It is more likely to be confused with *T. tetrapila* but is distinguished primarily by the pronounced leaf asymmetry (Fig. 19: 5, 6, 8), the longitudinally elongated disc cells (Fig. 19: 5, 6), and the slender, caudate leaf lobes, which are often falcate and hooked at the tips (Fig. 19: 6–8).

Hodgson (1956) referred to the "3–5 rows of twin cells [biseriate tiers] below the 5 single ones" of the lobes. In this, it resembles *T. praenitens*, but lacks the characteristic swollen, projecting septa of that species and has larger leaf cells

(median disc cells (38)45–52  $\mu\text{m}$  wide vs. 22–38  $\mu\text{m}$  in *T. praenitens*).

**DISTRIBUTION AND ECOLOGY**—This plant is sporadic in distribution in middle and upper elevations (usually not below 500 m) of both North and South Islands, New Zealand. As the specific epithet suggests, the plants typically occur in boggy sites, at times creeping among *Sphagnum* (for example, on the sides of old *Sphagnum* mounds, or mixed with *Chiloscyphus spiniferus* deep in shaded pockets among bryophyte masses). At Omoroeroa Saddle it occurred in a bog with dwarf/shrub heath vegetation including *Juncas* sp., *Carex* sp., and stunted *Libocedrus bidwillii* surrounded by mature *Dacrydium cupressinum* forest. In subalpine areas it occurs in sheltered, protected pockets, particularly in moist sites, such as rills in scrub consisting of *Chionochloa*, *Dracophyllum* and *Hebe* or of *Dracophyllum* and *Olearia*; also found under cover of tussock blades in mosaic areas of stunted *Olearia colensoi* and *Chionochloa*. Also at the lips of tarns in low alpine vegetation (Mt. Robert Skifield).

The species also is present on Stewart Island, but as is the case with a number of vascular and nonvascular plants, it occurs at considerably lower elevations on this island as compared to counterparts on the South and North Islands (see Wardle, 1991). *Telaranea paludicola* was found at 5 m (track to Mason's Bay) in a mosaic of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium*-*Dracophyllum* heath (to 1–2 m tall), and dense communities of *Gleichenia dicarpa* and *Empodisma*. At this site the species occurs in  $\pm$  protected, moist niches, e.g., on the floor (particularly in pockets), on vertical, shaded small banks under *Leptospermum* or at the margin of bryophyte-covered mounds beneath *Leptospermum*.

**SELECTED SPECIMENS SEEN**—NEW ZEALAND. STEWART ISLAND: Rakiura Natl. Park, Fresh Water Swamp, track to Mason's Bay, ca. 1 km W of Freshwater Hut, 5 m, *Engel* 24405 (F). SOUTH IS. SOUTHLAND PROV.: Fiordland Natl. Park, Moraine Creek Track, area N of Moraine Creek, W of Hollyford River, 610 m, *Engel* 23217 (F). OTAGO PROV.: Ajax Swamp, ca. 1 km N of Ajax Hill, Catlins River area, ca. 610 m, *Child* H5505 (F); Lee Stream, Hindon Road, ca. 305 m, *Child* H931 (F); between Waitati and Dunedin, ca. 365 m, *Allison* H5907 (CHR); E slopes of Mt. Cargill, Dunedin, ca. 520 m, *Allison* H5826 as *T. praenitens* (CHR); Mt. Cargill, N of Dunedin, ca. 610 m, *Child* H677 (F); Bethune's Gully, Dunedin, ca. 490 m, *Allison* 4683 (CHR); Mt. Maungatua, W of Mosgiel, 760 m, *Engel* 17762 (F); Mt. Aspiring Natl. Park, below and W of Mt. Shrimpton, 1370–1470 m, *Engel* 17906 (F). OTAGO/WESTLAND PROV. BOUNDARY: Haast Pass, ca. 610 m, *Child*

H4507 (F). WESTLAND PROV.: Westland Natl. Park, track to Alex Knob just below juncture with track to Louisa Peak, 1150–1170 m, *Engel* 18998 (F); *ibid.*, Omoroeroa Saddle, Highway 6, 330 m, *Engel* 24812 (F); 2 km N of White Horse Creek, *Child* H5426 (F). WESTLAND/CANTERBURY PROV. BOUNDARY: Arthur's Pass Natl. Park, Bealey Valley Track, ca. 875–900 m, *Engel* 22882 (F). NELSON PROV.: Big Totara R., ca. 60 m, *Child* 5446 (F); Mt. Richmond Forest Park, Red Hills, track to Maitland Hut, NE of St. Arnaud, ca. 700–920 m, *Engel* 21469 (F); Nelson Lakes Natl. Park, E slope of Robert Ridge in vicinity of Mt. Robert Skifield, W end of Lake Rotoiti, 1400–1480 m, *Engel* 22827 (F). NORTH IS.: WELLINGTON PROV.: Taranaki Mts., Field Hut, 825 m, *Zotov* as *L. praenitens* (CHR); Tongariro Natl. Park, Mt. Ruapehu, off Ohakune Mountain Road, ca. 890 m, *Braggins* 92/88A (F); *ibid.*, ca. 7 km from Ohakune on Ohakune Mt. Road, 900 m, *Engel* 22708 (F); *ibid.*, Blyth Track, along small stream ca. 0.5 km from Ohakune Mt. Road, ca. 1230 m, *Engel* 21308 (F); *ibid.*, Taranaki Falls Track, E of Whakapapa Village, 1080 m, *Engel* 22429 (F). GISBORNE PROV.: Urewera Natl. Park, Huiarau Range, summit area of Te Rangaakapua, 1265–1320 m, *Engel* 23452 (F); *ibid.*, Waipai Swamp, Waikareiti Track between track entrance and Lake Ruapani, N of eastern extremity of Lake Waikaremoana, 720 m, *Engel* 20600 (F). TARANAKI PROV.: Pukeiti Bush, near New Plymouth, *Hatcher* 274 (F). SOUTH AUCKLAND PROV.: Plateau E of Waiotapu Valley, Rotorua Region,  $\pm$  550 m, *Allison* H5896 (CHR); near Atiamuri, S of Rotorua, ca. 305 m, *Allison* H3026 (CHR); Whakarewarewa, Rotorua, *Allison* H5913 (CHR).

*Telaranea* sect. *Ceraceae* Engel & Merr., sect. nov.

Plantae in omnes partes glaucedinae insignis, folia  $\pm$  longitudine inserta, discus foliorum altus marginibus parallelibus, lobi foliorum plerumque fragiles atque caduci, amphigastrium primum ramorum plerumque distans, pedicellus antheridialis 2-seriatus.

Type: *Lepidozia centipes* Tayl. in G. L. & N., Syn. Hep. 204. 1845.

*Telaranea* sect. *Glaucolopidozia* Schust., Beih. Nova Hedwigia 118: 212. 2000, *nom. nud.*

For a discussion of this section and its distinguishing characteristics, see p. 238.

*Telaranea elegans* (Col.) Engel & Merr.

*Lepidozia elegans* Col., Trans. & Proc. New Zealand Inst. 21: 65. 1889 (1888). *Telaranea elegans* (Col.) Engel & Merr., Phytologia 79: 251. June, 1996 [1995]. Type: New Zealand, Great Barrier Is., Frith of Thames, 1888, *Winkelmann* (Colenso a.1355) (BM!, WELT!).

*Lepidozia tripilosa* Steph. in Stephani & Watts, J. & Proc. Roy. Soc. N. S. W. 48: 116. 1914, *syn. nov.*



Type: Australia, New South Wales, Centennial Glen, Blackheath, 10 Jan. 1911, *Watts 1043* (G!).

Plants delicate, flexuous, prostrate in loosely creeping, thin mats, faintly glaucous and water repellent (particularly shoot tips), yellowish green to olive-green and  $\pm$  nitid, becoming brownish with age; shoots medium, to 6 mm wide, including branches. Branching loosely but  $\pm$  regularly and often sparingly pinnate, the branches of the *Frullania* type, at right angles to the shoot, often becoming leading shoots, rarely becoming flagelliform; branch half-leaf bifid, linear, obliquely to almost longitudinally inserted; first branch underleaf undivided, subulate, inserted on ventral-lateral side of branch near juncture of branch and main axis. Ventral intercalary branches occasional, both stoloniform and leafy and becoming leading shoots. Stems with cortical cells thin-walled but firm, in 12 rows, in section much larger than the numerous (26–29) medullary cells. Rhizoids from distal cells of underleaf disc. Leaves on main shoot spreading at right angles to stem, approximate to contiguous but scarcely overlapping, plane, strongly horizontally oriented, the disc in the same plane as the dorsal surface of the stem or nearly so, the insertion almost longitudinal, the lobe tips often broken; leaves 200–285  $\mu\text{m}$  wide  $\times$  385–575  $\mu\text{m}$  long, longer than broad, (3)4-lobed to 0.4, the lobes strictly parallel with disc margins, shorter than the disc. Lobes setaceous, 2–3(4) cells wide at extreme base, uniseriate or biseriate in basal tier, the uniseriate portion 3–4 cells long, the lobe cells successively narrower in width (the cells scarcely tapered); cells of uniseriate portion elongate-rectangular, the walls straight-sided and not bulging, the basal cell 22–34  $\mu\text{m}$  wide  $\times$  36–55  $\mu\text{m}$  long, the next cell of similar length but narrower, 14–20  $\mu\text{m}$  wide  $\times$  35–46(60)  $\mu\text{m}$  long, the terminal cell slender, 8–14  $\mu\text{m}$   $\times$  24–40  $\mu\text{m}$ , rounded at the tip. Disc  $\pm$  symmetrically rectangular, parallel-sided, 5–6 cells high (from median sinus base to leaf base), 8 cells wide throughout; margins entire or finely serrulate by projecting distal ends of the marginal cells (esp. the dorsal margin); ventral margin  $\pm$  straight, the dorsal weakly arched. Cells of disc firm, in regular longitudinal rows, uniformly and often distinctly thick-walled, trigones none; me-

dian disc cells isodiametric to short rectangular, 23–36  $\mu\text{m}$  wide, 33–49  $\mu\text{m}$  long; basal row of disc cells considerably longer and forming an obvious tier; cuticle with a hazy to faintly granular appearance, rarely glaucous. Underleaves much smaller than leaves, widely spreading, 4-lobed to 0.75–0.85, the lobes divergent, ciliiform, consisting of a uniseriate row of 2–3 elongated, thin- to slightly thick-walled cells, inserted on 2 disc cells, terminating in a slime papilla; disc abbreviated, 2(3) cells high, 8 cells wide. Asexual reproduction probably by broken tips of leaf lobes.

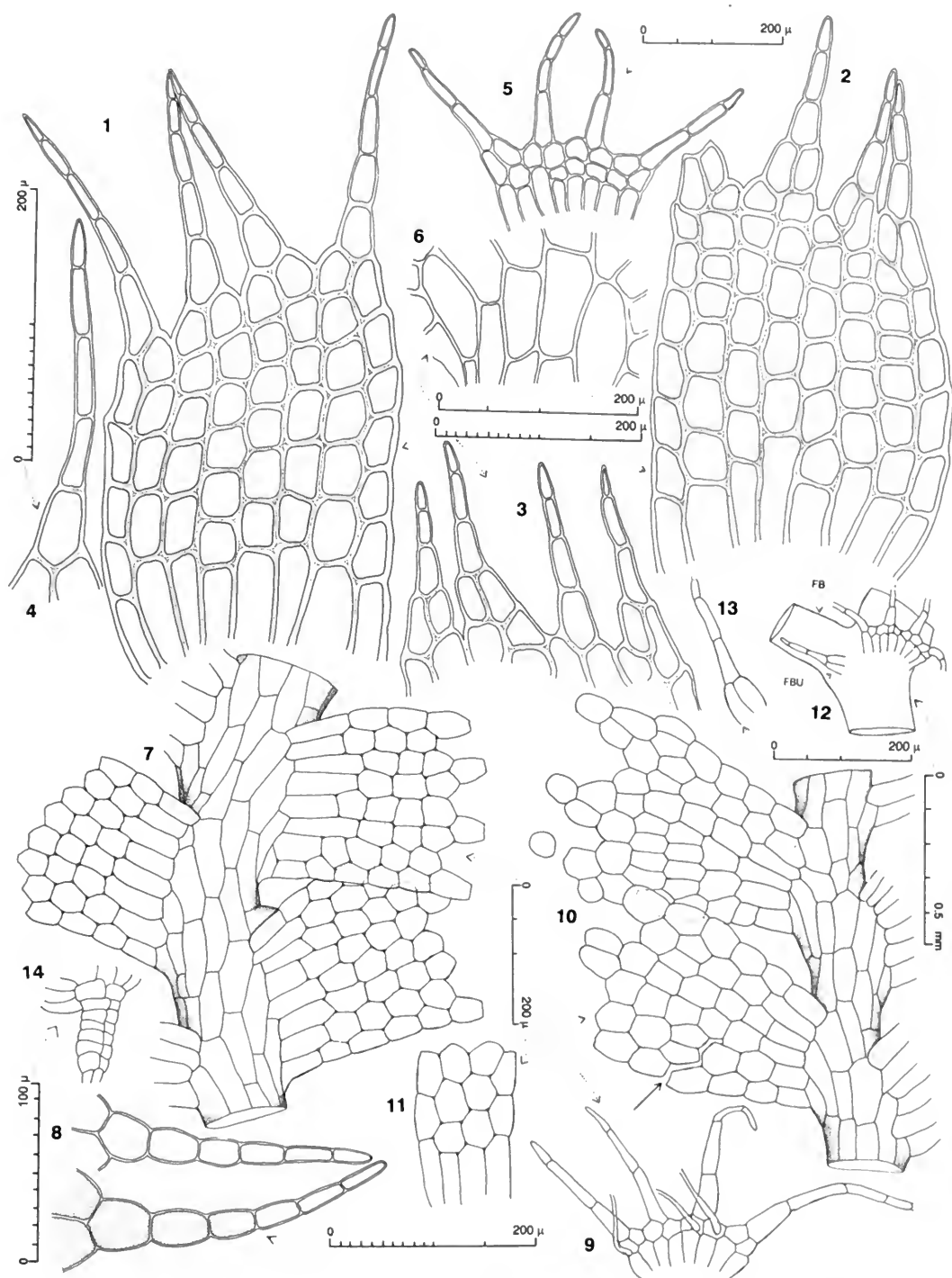
Gametangia and sporophytes not seen.

**DIFFERENTIATION AND VARIATION**—This is an interesting species, both in its morphology and its disjunct geographical distribution. In overall aspect, leaf shape, and slender, bristle-like leaf lobes it resembles a small *T. tuberifera* (p. 67), but the lobes in *T. elegans* are typically shorter, only 3–4 cells in length (Fig. 20: 2, 3) vs. (4)5–6(7) cells in *T. tuberifera*, and the disc cells are smaller, 36–45  $\times$  42–55  $\mu\text{m}$  vs. 41–54  $\times$  60–74  $\mu\text{m}$  in *T. tuberifera*. Its most notable features are the evenly thick-walled cells of the disc and the finely serrulate disc margins (Fig. 20: 1, 2). *Telaranea elegans* also typically lacks the conspicuous glaucous, water-repellent cuticle characteristic of *T. centipes*, *T. perfragilis* and *T. tuberifera*. The Queensland specimen cited below (*Windolf 689*) is distinctly glaucous and whitish. Typically, however, the plants are only faintly glaucous, most evident in the youngest portions of the plant. In herbaria the plants are yellowish-green to olive-green in color and somewhat nitid (on the label of the Waipoua specimen cited below, K. W. Allison notes “glaucous when fresh”). *Telaranea elegans*, as used in the key in Schuster (2000, p. 212), is equivalent to *T. tuberifera*, and is not *T. elegans* sensu the type.

*Lepidozia elegans* Col. was put in the synonymy of *L. centipes* by Stephani (1892). They differ chiefly in the disc margins, which in *T. elegans* are entire or finely serrulate by projecting distal ends of the marginal cells, vs. distinctly crenulate by bulging marginal cells in *T. centipes*. In both *T. centipes* and *T. elegans* the leaf disc is rather low, 5–6 cells high vs. 6–9(10) cells in *T. tuber-*

FIG. 20. *Telaranea elegans* (Col.) Engel & Merr. (1–6) and *T. perfragilis* Engel & Merr. (7–14). 1, 2. Leaves. 3. Distal portion of leaf. 4. Leaf lobe. 5. Underleaf. 6. Stem, surface view. 7. Sector of main shoot, dorsal view. 8. Leaf





lobes (cuticle shown in part). 9. Underleaf. 10. Sector of branch showing (top leaf) fragmenting of leaf tip forming a gemma-like body (at arrow) and (lower leaf) a disc in process of partially breaking away (fracture at arrow). 11. Half-leaf. 12. Branch base (FB = *Frullania*-type branch; FBU = first branch underleaf), the underleaf of main shoot shown in part. 13. First branch underleaf shown in fig. 12. 14. Antheridial stalk. (Figs. 1, 4–6 from type of *T. elegans*, WELT; 2–3, from *Engel 17216*, Australia, New South Wales, Morton Natl. Park, Fitzroy Falls; 7–14 from type of *T. perfragilis*.)

*ijera*. The underleaf disc in *T. elegans* is only 1–2 cells high, as in *T. centipes*.

*Lepidozia tripilosa* Steph. (Stephani & Watts, 1914) of New South Wales is a synonym of *T. elegans*. Stephani's illustration (Icones, *Lepidozia*, 111) shows a leaf with 3 lobes and a disc 6 cells wide throughout, and probably represents a branch leaf. The protologue describes the leaves as 3-lobed. Our examination of the type (G!) reveals that the leaves of the main shoot are 4-lobed.

**DISTRIBUTION AND ECOLOGY**—Known from a few stations in the northern sector of North Island, New Zealand and from New South Wales and Queensland, Australia. The New Zealand populations occur in *Nothofagus menziesii*-*Griselinia littoralis* forests or *Leptospermum*-*Weinmannia silvicola*-*Dacrydium cupressinum* scrub forests or (Waipoua area) *Agathis* forests with *Weinmannia silvicola*. At the Aongatete River site, the species occurred in a mixed *Dacrydium cupressinum* and *Beilschmedia tawa* forest with *Cyathea* understorey. Plants occur in shaded, moist, protected niches, often with only marginal light, as, for example, within pockets on  $\pm$  vertical stream banks. Plants for the most part are very loosely creeping, and form thin,  $\pm$  pure, feltlike sheets that hardly touch the substrate. At Waikohatu Stream in Waipoua Forest the species occurs not only over soil under overhanging vertical banks well above the stream, but also, at this hyperhumid site, growing epiphytically on fronds of *Trichomanes elongatum*. The Waipoua plant collected by Allison formed a pure colony on very shady bare ground above a creek in the forest; the niche was "too shady for other plants" (label data). In New South Wales the species occurs in shaded niches in forests between 475 and 640 m. The plant from Fitzroy Falls occurred over soil among exposed fibrous roots of a vertical bank; the plant from Tobys Glen on soil over a boulder near a waterfall. In Queensland, the plant was collected at 80 m on the bank of small stream in a wet sclerophyll forest.

**SPECIMENS SEEN**—NEW ZEALAND. NORTH ISLAND: SOUTH AUCKLAND PROV.: Kaimai Range, network of tracks at the end of Wrights Rd. off the Kaitiaki-Tauranga highway, Swimming Holes Track, 60 m, *Engel* 23539 (F); *ibid.*, Aongatete River, upstream from intersection of North-South Track and river, 425 m, *Engel* 23638 (F); Mt. Te Aroha, ca. 3 km E of Te Aroha, 900–940 m, *Engel* 22124 (F); Coromandel State Forest Park, ridge between Webb Creek Track and Billy Goat Track, 510–540 m, *Engel* 22338 (F). NORTH AUCK-

LAND PROV.: Waipoua Forest, Waikohatu Stream at Waikohatu Kauri Bridge, 290 m, *Engel* 22657, 22662 (F); Waipoua Forest, Allison H3202 as *T. centipes* (CHR). AUSTRALIA. NEW SOUTH WALES: Morton Natl. Park, Fitzroy Falls, 530–640 m, *Engel* 17216 (F); Blue Mts. Natl. Park, Tobys Glen, W of Glenbrook, 475 m, *Engel* 17226 (F); Sydney, [Gore Cove], Jul. 1885, *Whitelegge*, com. Pearson (BM). QUEENSLAND: Cooroora, 80 m, *Windolf* 689 as *T. centipes* (MELU).

### *Telaranea centipes* (Tayl.) Schust.

*Lepidozia centipes* Tayl. in G. L. & N., Syn. Hep. 204. 1845. *Mastigophora centipes* (Tayl.) Trev., Mem. Ist. Lomb. Sci. Lett. III. 4: 416. 1877. *Neolepidozia centipes* (Tayl.) Fulf. & J. Tayl., Brittonia 11: 85. 1959. *Telaranea centipes* (Tayl.) Schust., J. Hattori Bot. Lab. 26: 256. 1963. Type: Terra van Diemen (Tasmania), 1824, *Spence* (FH!).

Plants soft, flexuous, prostrate and loosely creeping in noncompact mats, glaucous, commonly greenish white, dull and distinctly water repellent; shoots medium, to ca. 1 cm wide, including branches. Branching normally loosely and somewhat irregularly pinnate, the branches of the *Frullania* type, frequently elongating and remaining leafy, rarely stoloniform or becoming flagelliform; branch half-leaf bifid, linear, obliquely inserted and bisecting the angle between the branch and main axis; first branch underleaf undivided, ciliate to subulate (rarely asymmetrically bilobed), inserted on ventral-lateral side of branch near juncture of branch and main axis, or displaced toward lateral or ventral-lateral side of stem, often somewhat below the branch. Ventral intercalary branches common, both leafy and stoloniform. Stems with cortical cells distinctly differentiated, in 12 rows, those on ventral side of stem somewhat smaller, the dorsal cortical cells much larger than the ca. 25–27 medullary cells, both the cortical and medullary cells evenly and slightly thick walled. Rhizoids issuing from distal cells of underleaf disc, or basal cell(s) of first branch underleaf. Leaves on main shoot rigid, fragile (the lobes at times partly broken off), widely spreading, at times nearly at right angles to stem, distant to loosely imbricate (more densely shingled in plants growing in drier conditions), plane, strongly horizontally oriented, the disc in the same plane as the dorsal surface of the stem or nearly so, the insertion distinctly incubous; leaves 390–525  $\mu$ m wide  $\times$  410–575  $\mu$ m long, subsymmetric, mostly 4-lobed to ca. 0.35–0.45 (leaves on robust main shoots at times 5–6(7) lobed, somewhat distant and wider than high), the lobes  $\pm$  parallel with disc margins or only slightly divergent, shorter

than the disc. Lobes attenuate to subcaudate, 2–4 cells broad at base, often biseriate for 1(2) tiers, terminating in a uniseriate row of (2)3–4(5) cells that are distinctly constricted at the septa; lobe cells thin- to somewhat thick-walled, short to somewhat elongated, barrel-shaped and bulging lending the lobes a submoniliform aspect, the basal cell of the uniseriate portion 25–42  $\mu\text{m}$  wide  $\times$  37–59  $\mu\text{m}$  long (ca. 1.1–1.8:1), the next cell narrower and shorter, 18–26  $\mu\text{m}$  wide  $\times$  34–49  $\mu\text{m}$  long (ca. 1.5–2.2:1), the terminal cell variable, short to somewhat elongate. Disc  $\pm$  symmetrically quadrate to subrectangular to distinctly cuneate, 5–6(7) cells high (from median sinus base to leaf base), 8–15 cells wide in median portion of disc, the basal tier consisting of 8–12 cells; margins about equal in length, entire to crenulate due to the bulging marginal cells, the ventral  $\pm$  straight, the dorsal often distinctly arched and contracted to the insertion (esp. seen *in situ*). Cells of disc in regular longitudinal rows, the walls moderately thickened, trigones minute or absent; median disc cells large, subquadrate grading to subrectangular, 36–54  $\mu\text{m}$  wide, 60–84  $\mu\text{m}$  long, the basal row somewhat larger (much longer but only occasionally a little wider) and forming an obvious tier; cuticle a dense granular and faintly striate coating. Underleaves much smaller than leaves, widely spreading, distant, often gently curved dorsally, 4(6) lobed to 0.75–0.85, the lobes divergent, ciliiform, consisting of a uniseriate row of 2–4 elongated, thin- to slightly thick-walled cells, inserted on 2(3) disc cells, terminating in a slime papilla; disc abbreviated, 1–2 cells high, (7)8(10) cells wide. Asexual reproduction probably by caducous tips of leaf lobes.

Plants dioecious. Androecia either on short *Frullania*-type branches with a few to several cycles of normal vegetative leaves prior to androecial formation or on short, abbreviated, ventral-intercalary branches lacking normal vegetative leaves; bracts closely imbricate, strongly dorsally assurgent, deeply concave, (2)3–4-lobed, each lobe terminating in a uniseriate row of 2–3 not to hardly elongated cells; lamina cells irregular in shape and arrangement, the lamina margins somewhat incurved, irregularly crenulate to denticulate, often with stalked or sessile slime papillae, occasionally with a cilium near the base; bracts monandrous; antheridia large for bract size, wide ovoid, the stalk short, 6–7 cells high, biseriate; bracteolar antheridia absent. Gynoecia strongly dorsally assurgent, slightly swollen and densely rhizoidous at base; bracts small for perianth size,

those of innermost series closely ensheathing the perianth, the tips somewhat spreading, the bracts bistratose at extreme base but soon thinning to unistratose and remaining so, concave, orbicular to suboblate; apices irregularly 4–6 ciliate-lobulate, the lobules consisting of a uniseriate row of (2)3–4 cells, inserted on a base of 2–4 cells, terminating in a slime papilla; margins irregularly repand, with a few short cilia and several sessile slime papillae; bracteoles of innermost series nearly identical in form and size to bracts. Perianth ca. 0.75 emergent, narrowly obovoid-cylindrical to fusiform, terete in basal half, the distal half obscurely trigonous and with 4–8 plicae, the sulci shallow to deep, the perianth narrowing toward the mouth; mouth short ciliate, the cilia formed of 1–3 rather elongate, coarsely striolate-papillose cells; cells immediately below the mouth with well defined long striae; perianth 3–4 stratose in basal portion, the median portion 2(3) stratose.

Seta not examined. Capsule rather short elliptic, the valves 735  $\mu\text{m}$  long, the wall 24  $\mu\text{m}$  thick, of 3 layers, the outer layer  $\pm$  equal to the thickness of the combined 2 inner layers, or slightly less thick; outer layer of cells in tiers, rather regularly short-rectangular, with 2-phase development, the longitudinal walls with well-defined sheetlike thickenings and nodule-like thickenings (4–6 per cell) alternating with walls that are devoid of thickenings (or with sporadic, local, nonpigmented, nodular swellings), the transverse walls devoid of thickenings; intermediate layer thinner than outer or inner layers; innermost layer of cells  $\pm$  tiered, irregularly narrowly to broadly rectangular, with semiannular bands common, rather narrow, close, usually complete, at times forked and anastomosing to delimit ill-defined, local fenestrae.

Spores not seen. Elaters rigid, nontortuous, 8.6–10.6  $\mu\text{m}$  wide, only slightly tapering toward tips, bispiral to tips, the spirals 4.3  $\mu\text{m}$  wide.

**DIFFERENTIATION AND VARIATION**—Examination of numerous Tasmanian specimens of *Telaranea centipes* has shown them to be distinct from the New Zealand plants referred here to *T. tuberifera*. Three species of sect. *Ceraceae* with a distinctly glaucous appearance are recognized here: *T. centipes*, *T. perfragilis* and *T. tuberifera*. True *T. centipes* appears to be confined to Australia (Tasmania, Victoria, New South Wales). Particularly diagnostic of *T. centipes* are the short (to 2.2:1), bulging, bead-like (submoniliform) cells of the lobes (Fig. 20: 11). The dorsal margin of the disc

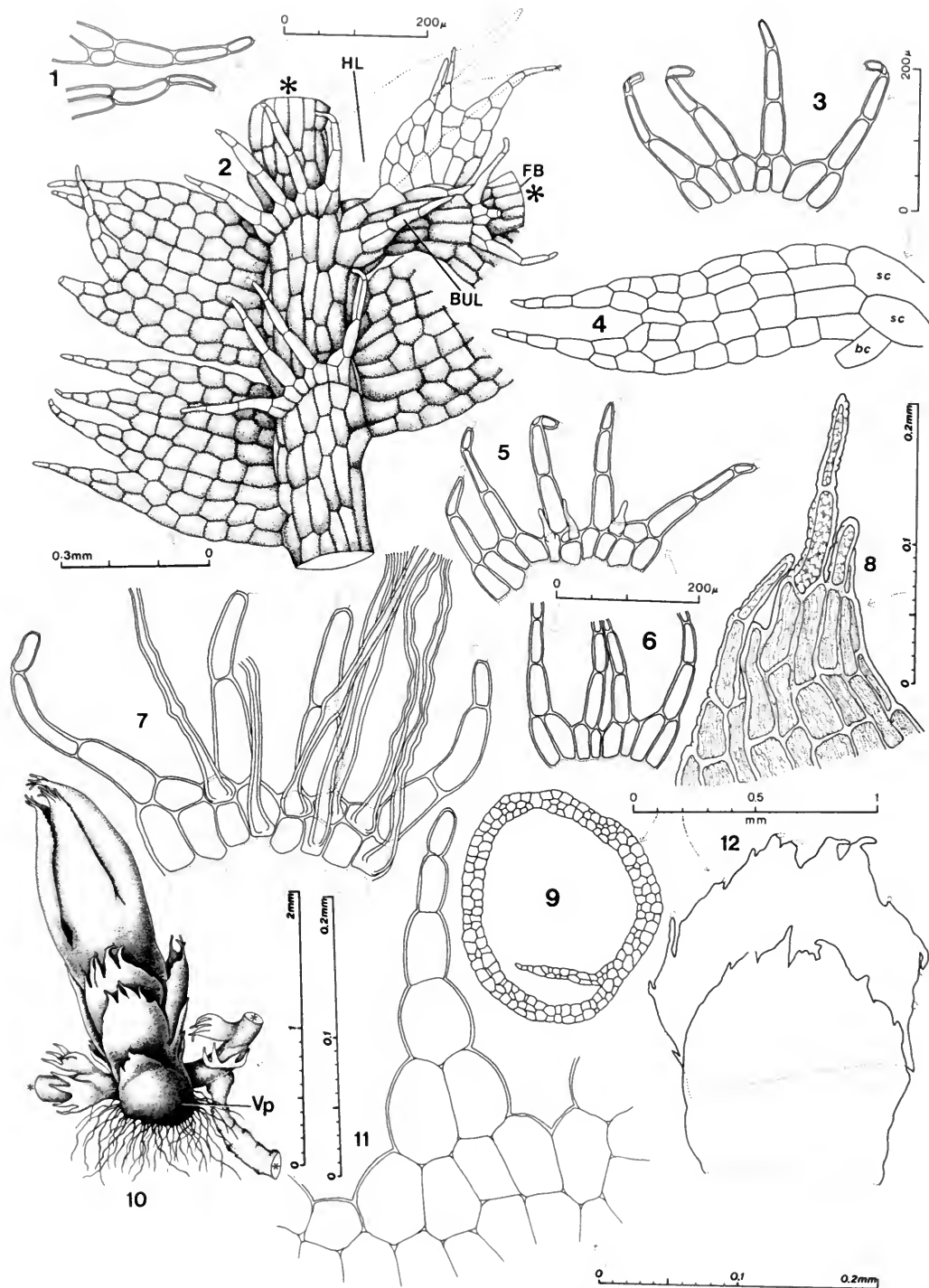


FIG. 21. *Telaranea centipes* (Tayl.) Schust. 1. First branch underleaves. 2. Portion of main shoot with branch, ventral view (BUL = first branch underleaf; FB = *Frullania*-type branch; HL = half-leaf, shown in outline). 3, 5-7. Underleaves from leading shoots, stem cells stippled (note insertion of 3 young rhizoids in fig. 5 and of mature rhizoids in fig. 7). 4. Half-leaf (sc = subtending stem cell; bc = subtending branch cell). 8. Portion of perianth mouth showing cuticular detail. 9. Perianth, cross section through median third. 10. Perianth bearing shoot. 11. Median lobe of leaf. 12. Female bract and (below) bracteole of innermost series. (Figs. 1-7 from *Engel 15593*, Tasmania, track from Ferndene to Mt. Dial; 8-12 from *Engel 15191*, Tasmania, Lillydale Falls.)

is often crenulate, due also to the bulging marginal cells. Compared to *T. tuberifera*, the leaf disc in *T. centipes* is lower, 5–6(7) cells high vs. 6–9(10) cells high, and the underleaf disc is also lower, 1–2 cells high vs. 3–4 in *T. tuberifera*. The leaves of well-developed leading shoots differ from those of the branches in being much broader than high, up to 12 cells wide at the insertion, and at times 5–6(7)-lobed (Fig. 22: 2, 3), with the dorsal margins broadly arched and contracted to the insertion. In *T. tuberifera*, the leaves are (3)4-lobed and tend to be parallel-sided, with the disc longer than wide (Fig. 23: 5–7).

The rare *T. perfragilis* (p. 72) of North Island, New Zealand also has bulging cells of the leaf margins, but has parallel-sided leaves which are highly fragmented and broken—typically not only the lobes but also much of the disc is missing. The basal cells of the lobes are barrel-like and bulging as in *T. centipes*, but the intact lobes taper to a slender distal portion, with narrower, elongate, nonbulging cells.

Oil-bodies of *T. centipes* from Australia were described by Jovet-Ast (1949) as botryoidal, 3–4 per cell, composed of 6(7–9) very large granules. The specimen, from Sydney, determined by Hodgson, was probably this species.

**DISTRIBUTION AND ECOLOGY**—Occurring in Tasmania and in Australia (Victoria, New South Wales). In Tasmania the species occurs sporadically in lower- to middle-elevation, dry *Eucalyptus* forests (usually under 400 m). It occurs nearly exclusively in the drier, eastern half of the island, and in the wet, southern and central sectors it apparently is rare or lacking west of ca. 146° 30' E (we have seen only 1 specimen west of that longitude—Engel 16509 from the Williamsford-Rosebery area). It extends west only in the northern sector of the island (e.g., Ferndene-Mt. Dial area). It occurs on soil, particularly of banks and shaded, moist, cliff faces, particularly where soil has accumulated. It rarely occurs in wet *Nothofagus* forests or in the subalpine zone. Scott (1985) stated that the species is common in wet sclerophyll forests of Victoria. In Victoria (as in Tasmania) the species can occur rarely in upper elevations (1450 m on Mt. Buffalo, Engel 17084).

**SELECTED SPECIMENS SEEN**—TASMANIA: E coast of Tasman Peninsula, Waterfall Bay, Camp Falls, 150–240 m, Engel 12720 (F); Freycinet Natl. Park, trail to Mt. Amos, 100–500 m, Norris 30603 (F); Mt. Cameron, 300–350 m, Norris 28484 (F); Lilydale Falls, 2.6 km by road N of Lilydale, NNE of Launceston, ca. 200 m, Engel 15191—c. per. + ♂ (F); Kermadie River, 140 m,

Ratkowski H1546 (HO); Kermadie River at North Creek, ca. 50 m, Norris 29380 (F); Huon River near Codeine Creek, ca. 150 m, Norris 30157 (F); Mt. Wellington, Silver Falls pipeline, 580 m, Ratkowski 1545 (HO); E slope of Mt. Wellington, McRobies Gully, ca. 100–300 m, Norris 29291 (F); *ibid.*, headwaters of New Town Rivulet, ca. 600–800 m, Norris 29337 (F); Mt. Field Natl. Park, Tyenna River, ca. 200 m, Norris 28825 (F); Styx River Road at intersection with Gordon River Road, Norris 28858 (F); North East Dundas Tramway (abandoned), W of Williamsford and SW of Rosebery, ca. 400 m, Engel 16509 (F); Great Western Tiers, plateau near Lake Salome, W of Walls of Jerusalem, 1050 m, Engel 15991 (F); Leven Gorge, along River Leven, 10 km by road from Nietta, 400 m, Engel 15741—c. ♂ (F); above Cethana Dam, ca. 200–300 m, Norris 27348 (F); above Lake Barrington near Forth Falls, ca. 150 m, Norris 27242 (F); near Devil's Gate Dam, ca. 150 m, Norris 27219 (F); track from Ferndene to Mt. Dial, SSW of Penguin, 30–60 m, Engel 15593—c. ♂ (F). AUSTRALIA, VICTORIA: Mt. Buffalo Natl. Park, Dickson's Falls, ENE of The Horn (Mt. Buffalo), 1450 m, Engel 17084 (F); Mackley Creek Road, which leads N from road between Powelltown and Noojee, just E of Powelltown, Engel 16832 (F); Great Dividing Range, Watts River near Fernshaw, NE of Melbourne, Engel 16775 (F); Marysville, Olsens Track, Meagher.689 (F). NEW SOUTH WALES: Monga, Scott s.n. (MELU 1300).

### *Telaranea tuberifera* Engel & Schust.

*Telaranea tuberifera* Engel & Schust., Fieldiana, Bot. n.s. 14: 2, fig. 1. 1983. Holotype: New Zealand, South Island, Fjordland Natl. Park, Falls Creek, Upper Hollyford River Valley, along Milford Road, Schuster 48775 (F!).

Plants soft, flexuous, prostrate, often in interwoven, ± thick mats, glaucous, greenish white to ceraceous, becoming light brown with age, distinctly water repellent; shoots medium, to 1 cm wide, including branches. Branching loosely and somewhat irregularly pinnate, occasionally 2–3 pinnate, the branches of the *Frullania* type, frequently elongating and remaining leafy, rarely stoloniform or becoming flagelliform; branch half-leaf bifid, linear, obliquely inserted; first branch underleaf undivided, ciliate to subulate, inserted on ventral side of branch base, at times displaced toward the ventral-lateral side of the stem-branch juncture. Ventral intercalary branches common, leafy or stoloniform and rooting in the substrate. Stems with cortical cells thin-walled, with a granular coating like that of the leaves, in 12–14 rows, those on ventral side of stem somewhat smaller, in section much larger than the numerous (ca. 25), evenly and slightly thick-walled medullary cells. Rhizoids from distal cells of underleaf disc. Leaves on main shoot rig-

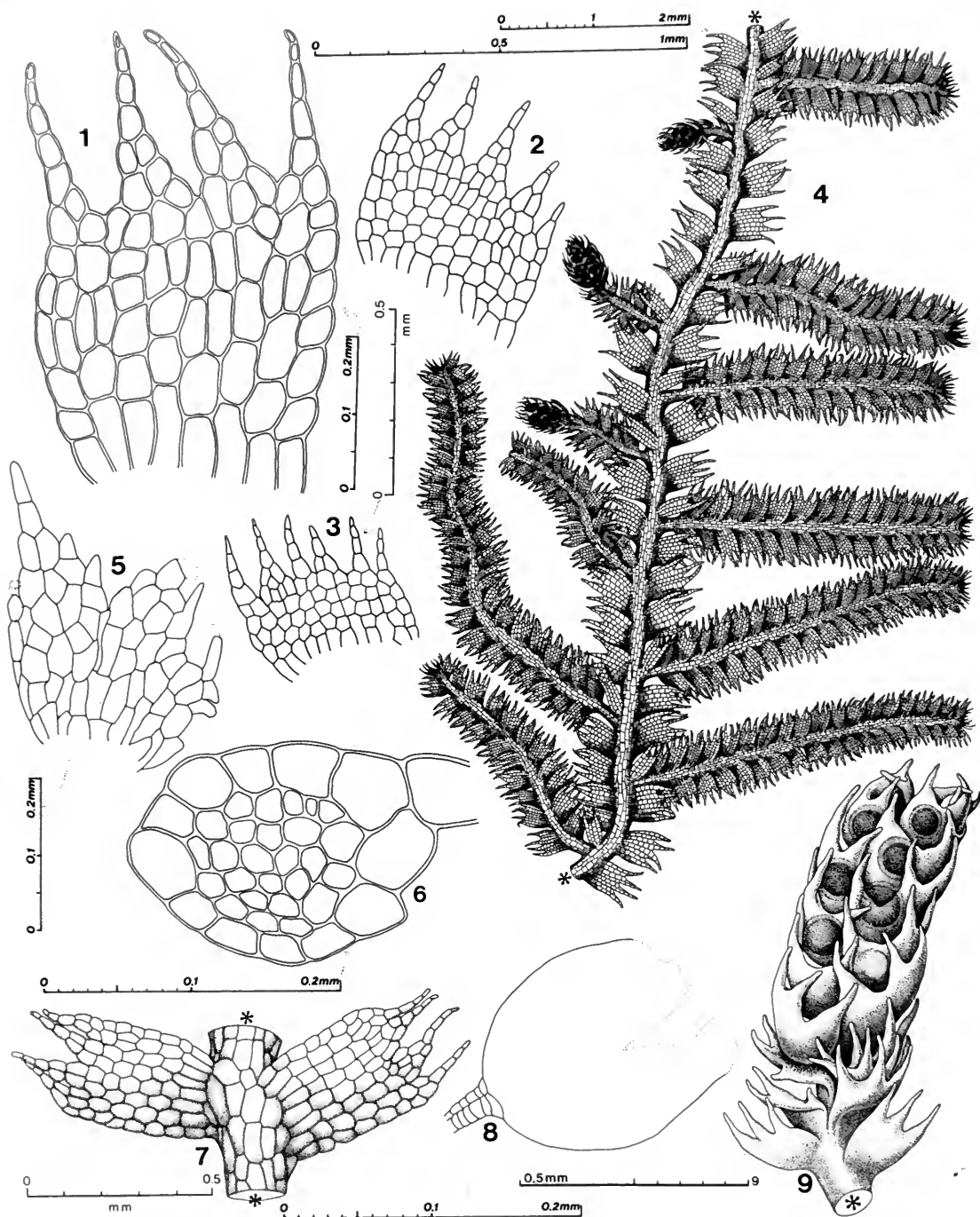


FIG. 22. *Telaranea centipes* (Tayl.) Schust. 1. Leaf of main shoot. 2, 3. Leaves of main shoot. 4. Plant with 3 androecia-bearing *Frullania*-type branches. 5. Male bract. 6. Stem, cross section. 7. Opposing leaf pair of main shoot, dorsal view. 8. Antheridium. 9. Androecial branch. (Figs. 1, 4–9 from *Engel 15593*, Tasmania, track from Ferndene to Mt. Dial; 2, 3 from *Engel 15191*, Tasmania, Lillydale Falls.)

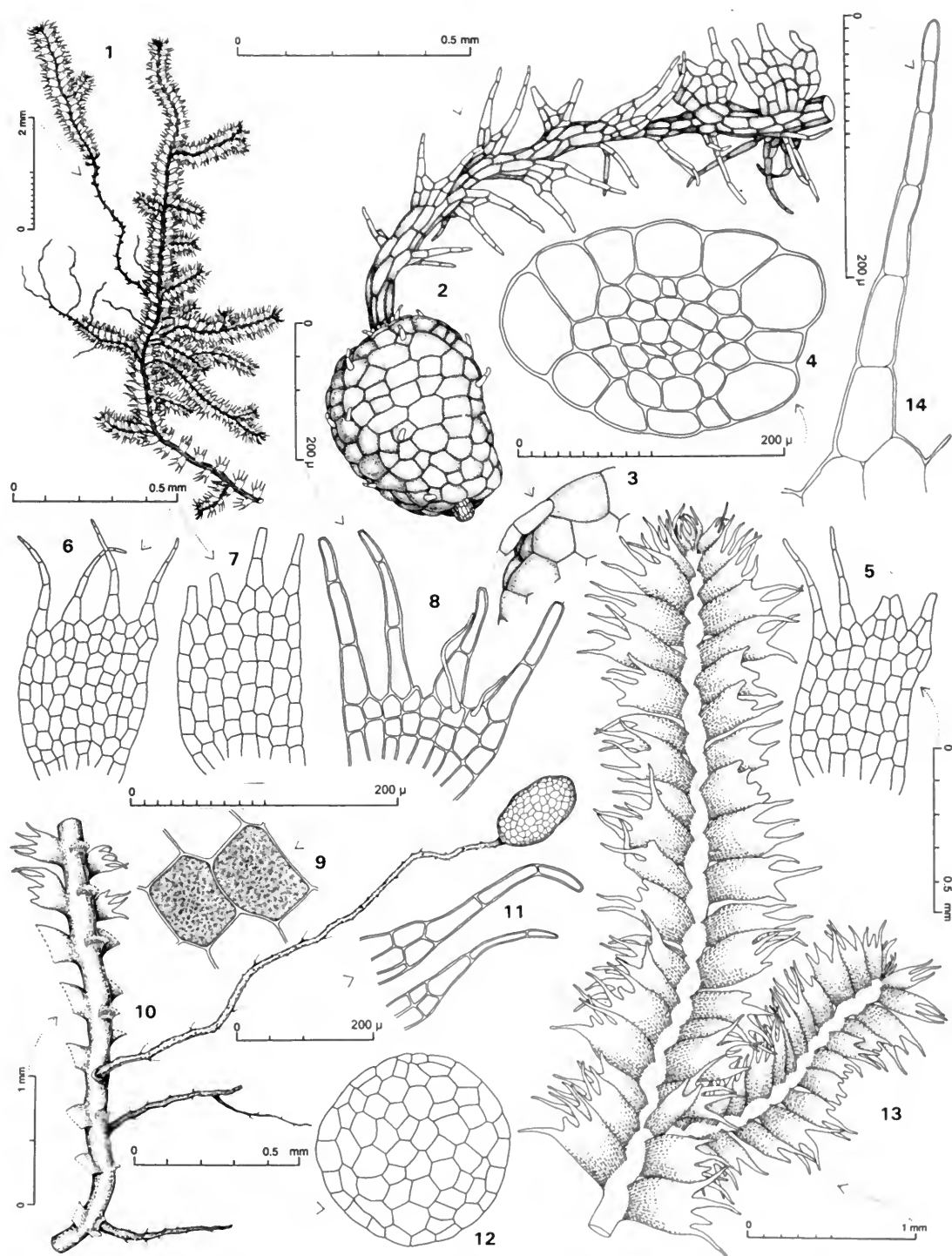


FIG. 23. *Telaranea tuberifera* Engel & Schust. 1. Plant, dorsal view. 2. Germinating tuber; note scattered leaf rudiments and previous point of attachment of tuber to stolon at opposing end of tuber. 3. Portion of tuber surface showing a leaf rudiment. 4. Stem, cross section. 5-7. Leaves. 8. Underleaf; note rhizoid position. 9. Median discus cells showing cuticular detail in part. 10. Old, basal portion of shoot showing stoloniferous branches and a tuber. 11. First branch underleaves. 12. Tuber, cross section. 13. Portion of main shoot; note ragged leaf apices. 14. Median lobe of leaf. (All from type of *T. tuberifera*.)



id. fragile (the lobe tips frequently caducous), spreading  $\pm$  at right angles to stem, imbricate, plane, strongly horizontally oriented, the disc in the same plane as the dorsal surface of the stem or nearly so, the insertion strongly incubous; leaves 595–770  $\mu\text{m}$  wide  $\times$  775–840  $\mu\text{m}$  long, subsymmetric, longer than broad, (3)4-lobed to 0.4–0.5, the lobes strictly parallel with disc margins, equal to or shorter than the disc. Lobes setaceous, typically 2 cells wide at extreme base (or rarely 4 cells wide, and then biseriate for 1[2] tiers), terminating in a uniseriate portion of (4)5–6(7) cells only weakly constricted at the septa; cells of uniseriate portion thin- to somewhat thick-walled, elongated, the walls not bulging, the basal cell 35–42(–50)  $\mu\text{m}$  wide  $\times$  60–92  $\mu\text{m}$  long (1.8–2.4:1), the next cell much narrower and of similar length, 20–30  $\mu\text{m}$  wide  $\times$  72–94  $\mu\text{m}$  long (3–4.6:1), the terminal cell very thin-walled and often collapsed, variable in size, short to somewhat elongate. Disc  $\pm$  symmetrically rectangular, often rather narrowly so, 6–9(10) cells high (from median sinus base to leaf base), 8–10(11) cells wide in distal portion, 8(11) cells wide at base; margins entire, the ventral  $\pm$  straight, the dorsal curved (esp. as seen *in situ*). Cells of disc in regular longitudinal rows, the cell walls thin to slightly thickened, trigones minute or absent; median disc cells large, short rectangular to somewhat elongated, 41–54  $\mu\text{m}$  wide, 60–74  $\mu\text{m}$  long; basal row of disc cells considerably larger (much longer and generally a little wider) and forming an obvious tier; cuticle a dense granular and faintly striate coating. Underleaves much smaller than leaves, strongly spreading, distant, often gently curved dorsally, 3–4-lobed to 0.55–0.7, the lobes divergent, ciliiform, consisting solely of a uniseriate row of (2)3(4) elongated, thin-walled cells, the lobes terminating in a slime papilla; disc narrowed toward base, (2)3–4 rows of cells high and 8(9) cells wide, the basal tier of cells larger. Rhizoid initials in a band at base of underleaf lobes. Asexual reproduction by elliptic to ovoid tubers at the tips of stoloniform branches and probably by caducous leaf lobes.

Plants apparently dioecious. Androecia not seen. Gynoecea feebly to strongly dorsally assurgent, weakly swollen and rhizoidous at base; bracts small for perianth size, those of innermost series closely ensheathing the perianth, the tips somewhat spreading, the bracts concave, broad ovate,  $\pm$  regularly 4–6 ciliate-lobulate, the lobules 2(4) cells wide at base, with a uniseriate row of 2(3) cells, terminating in a slime papilla; lamina

composed of  $\pm$  regularly subrectangular cells, the margins each with 1–several weak teeth formed by the apical or free divergent end of marginal cells, terminating in a slime papilla, otherwise entire; bracteoles of innermost series similar in form and size to bracts. Perianth long emergent, fusiform, terete in basal and median sectors, the distal sector obscurely trigonous and with 3(4) plicae, the perianth narrowing toward the strongly contracted mouth; mouth cells thin-walled, often sinuate, partially or wholly laterally free, occasionally with a laterally free uniseriate row of 2 cells, the mouth thus shortly denticulate-subciliate; perianth 2–3-stratose in lower portion, the median portion 2-stratose.

Seta with 5–7 rows of outer cells (each with their free face bulging), surrounding an inner core of 9–17 much smaller cells. Capsule short elliptic, 910–980  $\times$  476–497  $\mu\text{m}$ , the wall 24  $\mu\text{m}$  thick, of 3 layers, the layers of  $\pm$  equal thickness; outer layer of cells in tiers, rather regularly short-rectangular, with 2-phase development, the longitudinal walls with well-defined sheetlike thickenings and nodule-like to spinose thickenings (4–6 per cell) alternating with walls that are devoid of thickenings (or with sporadic, local, nonpigmented to pigmented, nodular swellings), the transverse walls devoid of thickenings, or rarely with a few nodular swellings; innermost layer of cells  $\pm$  tiered, irregularly narrowly rectangular, with semiannular bands common, rather narrow, close, usually complete, at times short and spinose, or rarely forked.

Spores 13.9–15.8  $\mu\text{m}$ , exine yellow brown, areolate (with a network of sharply defined furcate ridges that coalesce and delimit areolae). Elaters rigid, nontortuous, 8.2–10.6  $\mu\text{m}$  wide, only slightly tapering toward tips, bispiral to tips, the spirals 2.9–4.8  $\mu\text{m}$  wide.

**DIFFERENTIATION AND VARIATION**—This is the common New Zealand glaucous *Telaranea*, which has been known in the New Zealand literature as *T. centipes* (Hodgson, 1956; Allison & Child, 1975). As treated here, however, *T. centipes* sens. str. is confined to Tasmania, Victoria and New South Wales. The chief differences between *T. tuberifera* and *T. centipes* are in the shape of the disc, the disc margins, and the form of the lobes. The lobes in *T. tuberifera* are setaceous and whisker-like (Fig. 23: 6, 13), composed of a uniseriate row of 5–6 cells, typically inserted on a base of two cells, which are a continuation of the highly regular longitudinal rows of cells of the disc (Fig.



23: 5, 7). The cells of the uniseriate row are elongated (to 4.6:1) and subcapillary (Fig. 23: 14). They are much longer than those of *T. centipes*, and are never bulging, nor are the lobes strongly constricted at the septa (cf. Fig. 21: 11).

The leaf disc of *T. tuberifera* is parallel-sided, and the lobes strictly aligned with the disc margins as in *T. tetrapila* var. *roseana* (p. 57), but *T. tuberifera* is distinctly glaucous, greenish white to ceraceous, and almost tediously water repellent, whereas *T. tetrapila* and its varieties are never so. As in *T. tetrapila*, the disc cells of *T. tuberifera* are large and prominent, even under the dissecting microscope, but unlike *T. tetrapila*, the leaves are horizontally oriented, with the disc lying in essentially the same plane as the stem. For additional differences, see comments under *T. tetrapila*.

Conspicuously glaucous leaves are also seen in other regional Lepidoziaceae, for example *Bazania tayloriana* and *L. glaucophylla*. Interestingly, these glaucous species also have strongly horizontally-oriented leaves, spreading at nearly right angles with the stem, suggesting a possible adaptive significance to this combination of features.

*Telaranea tuberifera* was described as a new species by Engel and Schuster (1983), citing the presence of caducous leaf lobes, and the production of tubers at the tips of prostrate, microphyllous intercalary stolons, issuing from older sectors of the plant (Fig. 23: 2, 10). Caducous, fragmenting leaf lobes are even more strongly developed in another glaucous species, *T. perfragilis* (p. 72). We have observed tubers in several additional collections of *T. tuberifera*. Two other regional *Telaranea* species are now known to produce tubers: *T. clatritexta* (Fig. 1: 14; subg. *Acrolepidozia*) and *T. tasmanica* (Fig. 32: 1, 2; sect. *Telaranea*). *Telaranea europaea* (p. 150) also produces tubers. Hässel de Menendez (1984) has described similar tubers in several different genera of Lepidoziaceae, as well as in another *Telaranea* species, *T. blepharostoma* (Steph.) Fulf. of southern South America.

**DISTRIBUTION AND ECOLOGY**—Endemic to New Zealand where mostly on Stewart Island and South Island and infrequent and sporadic on North Island. The species is for the most part tercolous in lower to middle to upper elevation forests of, for example, *Podocarpus*, or of *Nothofagus fusca*, *Dacrydium cupressinum*, or of *Nothofagus menziesii* associated with *Dracophyllum* and *Quintinia serrata* or of dense, broadleaf forests of *Coprosma australis*, *Rhipogonum scandens*, *Rhoplostylis sapida* and ferns, etc. It typically oc-

cupies very shaded niches in forests, where it may form pure, at times extensive colonies, often in sites too shaded for other plants. It is often found deep in shaded pockets or holes and on steep-sided banks, as, for example, under the liplike overhang of the forest edge at the top of the bank of Waikohatu Stream (Engel 22653). It is notable, for example, that *Hodgson* 632 from Mt. Drury, was collected on the sides of a cave. It may be subalpine, where it may line deep pockets or deep crevices in ledges in scrub of, for example, *Olearia*, *Dracophyllum longifolium*, *Gaultheria* and *Cassinia vauvilliersii*, etc.

The Butterfield Beach station on Stewart Island is of interest. Plants formed large sheets over a thin layer of sandy, loamy soil on bedrock near the mouth of a sea cave just a few meters above sea level on an exposed shoreline. The niche likely would be exposed to periodic salt spray (see Engel & Schuster, 1973).

**SELECTED SPECIMENS SEEN—NEW ZEALAND.** STEWART ISLAND: Rakiura Natl. Park, Port Pegasus, immediately adjacent Belltopper Falls, ca. 10–80 m, *Engel* 24133 (F); *ibid.*, Fresh Water Swamp, track to Mason's Bay, c. 1 km W of Freshwater Hut, ca. 5 m, *Engel* 24461 (F); Port Pegasus, *Schuster, Scott & Taylor* as *T. centipes* (CHR); Butterfield Beach, 1–2 m above sea level, *Engel* 24109 (F). SOUTH ISLAND: OTAGO PROV.: Fiordland, head of Lake McKerrrow, near McKerrrow Hut, *Hatcher* 1493 (F). WESTLAND PROV.: Monkey Puzzle Gorge, Cascade Road, Martyr River near Martyr Saddle, 120 m, *Engel* 23021 (F); Cascade Road, just NE of Martyr Saddle, N of Jackson River, S of Jackson Bay, 75–110 m, *Engel* 23054 (F); ca. 10 km along Cascade Rd, 45 m, *Engel* 24774 (F); Arthur's Pass Natl. Park, N of Kellys Creek near Hwy 73, N of Otira, 420–475 m, *Engel* 18323 (F); *ibid.*, Otira River Gorge near parking area for track to Mt. Rolleston, 915 m, *Fife* 5409 (F); Camp Creek, W of Alexander Range, 310–800 m, *Reif* C86B, C124D as *T. centipes* (F); Paparoa Range, along Croesus Track, ESE of Barrytown, ridge between Granite Creek and Fagan Creek watersheds, 250 m, *Engel* 19307—c. sporo. (F). WESTLAND/CANTERBURY PROV. BOUNDARY: Arthur's Pass Natl. Park, Arthur's Pass area, Upper Twin Creek Valley, 930 m, *Engel* 18526 (F). NELSON/WESTLAND PROV. BOUNDARY: Paparoa Range, S side of Porarua River, up river from gorge and ca. 500 m WSW of ford on inland track to Bullock Creek, 10–20 m, *Engel* 19193 (F). NELSON PROV.: Big Bush State Forest 48, Donald Creek, 480–600 m, *Macmillan* 77/95 as *T. centipes* (CHR). NORTH ISLAND. WELLINGTON PROV.: Tararua Mts., Ruamahanga, *Zotov* as *T. centipes* (CHR). SOUTH AUCKLAND PROV.: Mt. Drury, Tauranga, sea level, *Hodgson* 632 as *T. centipes* (CHR); Kaimai-Mamaku Forest Park, Mt. Te Aroha, S facing slope, 880–890 m, *Engel* 23858 (F); Coromandel Peninsula, *Matthews* 42 as *T. centipes* (CHR). NORTH AUCKLAND PROV.: Waipoua Forest, Waikohatu Stream at Waikohatu Kauri Bridge, 290 m,

Engel 22653 (F); Waipoua Forest, Waikohatu Stream, Allison H708 as *T. centipes* (CHR).

*Telaranea perfragilis* Engel & Merr., nom. nov.

*Telaranea perfragilis* Engel & Merr., nom. nov. pro *Telaranea fragilis* Engel & Merr., Novon 9: 341. f. 2. 1999 non *T. fragilis* Miz., J. Hattori Bot. Lab. 40: 449. f. 1. 1976 (Philippines). Holotype: New Zealand, North Is., North Auckland Prov., NE Waitakere Ranges, Swanson University Reserve, Tram Valley Road, 95 m, Engel 20465 (F); isotype: (CHR).

Plants delicate, flexuous, prostrate in thin straggling mats or as isolated strands among other bryophytes, glaucous, whitish to bluish green, dull and distinctly water repellent; shoots medium, to ca. 1 cm wide, including branches. Branching loosely and irregularly 1-pinnate, the branches of the *Frullania* type, rarely becoming flagelliform; branch half-leaf bifid, linear, obliquely inserted and bisecting the angle between the branch and main axis; first branch underleaf undivided, subulate, inserted on the ventral side of branch at branch base. Ventral-intercalary branches present, both leafy and stoloniform. Stems dorsiventrally flattened, with cortical cells distinctly differentiated, in 9–12 rows, thin walled, those on ventral side of stem much smaller and similar in size to medullary cells, the dorsal cortical cells much larger than medullary cells; medullary cells ca. 16, moderately thick-walled. Rhizoids issuing from distal tier of underleaf disc cells. Leaves fragile, typically erose-truncate (the lobes all or mostly broken off, and often the distal tiers of disc cells missing), widely spreading, at times nearly at right angles to stem, distant to loosely imbricate, plane, strongly horizontally oriented, the disc in the same plane as the dorsal surface of the stem or nearly so, the insertion distinctly incubous; leaves 260–290  $\mu\text{m}$  wide, the fragmented leaf 280–390  $\mu\text{m}$  long (including basal cell of lobe), 465–505  $\mu\text{m}$  long with lobes, leaves subsymmetric, 4-lobed to ca. 0.4, the lobes  $\pm$  parallel with disc margins or only slightly divergent, shorter than the disc. Lobes (when present) subcaudate, 2 cells broad at base, terminating in a uniseriate row of 6–7 cells, distinctly constricted at the septa (esp. in basal portion); lobe cells thin walled, the basal pair of lobe cells and the basal cell of uniseriate row barrel-shaped and bulging, 42–50  $\mu\text{m}$  wide  $\times$  50–61  $\mu\text{m}$  long (1–1.3:1), the next cell a little narrower but not much longer, 25–31  $\mu\text{m}$  wide  $\times$  40–54  $\mu\text{m}$  long (1.3–2.1:1), the distal cells of uniseriate row slender,  $\pm$  elon-

gate, the terminal cell variable: short to somewhat elongate. Disc  $\pm$  symmetrically quadrate to subrectangular, 5–6(7) cells long (from median sinus base to leaf base), mostly 8 cells wide throughout; margins about equal in length, distinctly crenulate due to bulging marginal cells,  $\pm$  straight to weakly arched. Cells of disc in regular longitudinal rows, thin-walled but firm or moderately thick walled, trigones minute or absent; median disc cells large, subquadrate, 33–45  $\mu\text{m}$  wide, 40–52  $\mu\text{m}$  long, the basal row somewhat longer, forming an obvious tier; cuticle a finely granular and faintly striate coating. Underleaves much smaller than leaves, widely spreading, distant, often gently curved dorsally, 4-lobed to 0.75–0.85, the lobes widely divergent, ciliiform, consisting of a uniseriate row of 3–4 elongated, thin-walled cells, inserted on 2 disc cells, terminating in a slime papilla; disc abbreviated, 2 cells high, 8 cells wide. Asexual reproduction evidently by fragmentation of leaf lobes and disc.

Plants apparently dioecious. Androecia on short, abbreviated, ventral-intercalary branches lacking normal vegetative leaves; bracts rather closely imbricate, strongly dorsally assurgent, deeply concave, 2–3-lobed, each lobe terminating in a uniseriate row of (2)3 moderately elongated, thick-walled cells; lamina margins irregularly minutely crenulate by few cells with the free margin bulging, otherwise with a few slime papillae; bracts monandrous; antheridia large for bract size, the stalk 8 cells high, biseriate; bracteolar antheridia absent. Gynoeceia not seen.

**DIFFERENTIATION AND VARIATION**—Commenting on the North Auckland specimens cited below, Hodgson (1956, p. 606) observed that the leaves “present a curious appearance, in that the apices are either crenulate with protruding cells of the discus, or with 1 or 2 segments showing as reduced to one roundly quadrate cell, sitting as it were on 2 terminal cells of the lengthwise rows,” which aptly describes the leaves of this species. In shoots freshly mounted in water the leaves often can be observed breaking apart (Fig. 20: 10, arrow), and it is likely that detached lobe and disc cells function as gemmae. The populations cited by Hodgson (1956) were included under her treatment of *Lepidozia centipes*.

*Telaranea perfragilis* resembles *T. centipes* in the conspicuously turgid, bulging cells of the disc margins and lobes, but the leaves are 4-lobed in *T. perfragilis* and the disc is typically parallel-sided and 8 cells wide throughout (Fig. 20: 7). In

*T. centipes* the disc is cuneate and up to 15 cells wide in the distal portion, and the leaves are sometimes 5–6(7)-lobed on robust main shoots. In addition, the basal cells of the uniseriate row in *T. perfragilis* are fat and bulging, but the distal portion of the uniseriate row, when present, is slenderly tapering, with narrower, more elongate cells (Fig. 20: 8).

**DISTRIBUTION AND ECOLOGY**—Known from a few scattered sites in North and South Auckland Provinces, New Zealand. The species occurs on moist, clayey banks or at times over rock in forests. The type occurred on a vertical clayey bank above a small stream in an old *Kunzea* forest with *Agathis* and (common) *Phyllocladus trichomanoides*.

**SPECIMENS SEEN**—NEW ZEALAND. NORTH ISLAND: SOUTH AUCKLAND PROV.: Coromandel State Forest Park, ridge just W of summit of Table Mt., 820 m, Engel 22410 (F). NORTH AUCKLAND PROV.: Orakei, Auckland, Langridge (Allison 3197) as *T. centipes* (CHR); Waipoua Forest, Allison H711 (CHR).

*Telaranea* sect. *Tricholepidozia* (Schust.) Engel & Merr., comb. & stat. nov.

*Telaranea* subg. *Tricholepidozia* Schust., J. Hattori Bot. Lab. 26: 256. 1963. Type: *Lepidozia mooreana* Steph.

*Telaranea remotifolia* Hodgs.

*Telaranea remotifolia* Hodgs., Rec. Domin. Mus. 4: 107. 1962. *Lepidozia remotifolia* Hodgs., Trans. Roy. Soc. New Zealand 83: 603, pl. 2, f. 14. 1956, non *L. remotifolia* Horik., J. Sci., Hiroshima Univ., Ser. B, Div. 2, 2: 202. 1934 (Taiwan). Type: New Zealand, North Is., Tararua, Ruamahanga V., 3 Dec. 1933, Zotov 9275 (MPN!); isotype: (CHR!).

Plants soft, appearing etiolated and often rather flaccid, loosely prostrate and straggling, in pure, intermingled loose mats or as isolated wisps among other bryophytes, pale green to grass-green, the plants when dry glasslike, the stems sinuous and the leaves shrunken and inconspicuous; plants stenotypic in stature, small, to 1.2 cm wide, including branches. Branching very irregularly and distantly pinnate, the branches of the *Frullania* type, typically long, weak and filiform; branch half-leaf undivided and subulate or bifid and narrowly rectangular, usually obliquely inserted and bisecting the angle between branch and main axis; first branch underleaf asymmetrically bifid, the dorsal lobe leaf-lobe-like, the ventral lobe shorter and terminating in a slime papilla, the

first branch underleaf inserted on ventral to ventral-lateral side of branch near juncture of branch and main axis. Ventral-intercalary branches rare, leafy. Stems often appearing fleshy and large for plant size, with cortical cells in 10–13 rows, distinctly differentiated, thin-walled, in section much larger than the numerous (17–25[34]), thin-walled medullary cells, the medullary strand distinctly visible in surface view of stem. Rhizoids not seen. Leaves on main shoot delicate, brittle, obliquely to widely spreading, conspicuously remote and alternately arranged, weakly convex, the insertion distinctly incubous to almost longitudinal; leaves 265–385  $\mu\text{m}$  wide  $\times$  440–565  $\mu\text{m}$  long, asymmetric, 3–4-lobed to ca. 0.55, the lobes straight to weakly divergent, about equal to disc or a little longer. Lobes narrowly attenuate, 2–4 cells wide at extreme base, terminating in a uniseriate row of 2–3(4) cells, the dorsal lobe(s) typically somewhat stronger and with 1(2) biseriate tiers between the uniseriate portion and the extreme base, the ventral lobe typically weaker; cells of the uniseriate portion somewhat elongate, thin-walled, the septa neither thickened nor swollen, the basal cell of uniseriate portion 36–50  $\mu\text{m}$  wide  $\times$  60–79  $\mu\text{m}$  long, the next cell 24–38  $\mu\text{m}$  wide  $\times$  43–67  $\mu\text{m}$  long, the terminal cell hardly tapering, rounded at the tip; cuticle of lobe tips finely striate-papillose, otherwise smooth. Disc somewhat asymmetric, parallel-sided to weakly cuneate, 2–3(4) cells high (from median sinus base to leaf base), 6–11 cells wide in distal portion narrowing to 6–8 cells wide in basal portion; margins entire,  $\pm$  straight. Cells of disc thin-walled, trigones lacking, the basal tier of disc cells at times considerably longer (particularly when disc 2 cells high), the distal tier(s) shorter,  $\pm$  elongated, (35)42–53  $\mu\text{m}$  wide  $\times$  72–90  $\mu\text{m}$  long; cuticle smooth. Oil-bodies hyaline, coarsely papillose, the spherules somewhat protruding beyond membrane, the median disc cells with 6 oil-bodies per cell, globose to subglobose and 5–5.9  $\mu\text{m}$  in diam., the cells at sinus base with 5–6 oil-bodies per cell, elliptic to subfusiform, 5.3–6.4  $\times$  9.5–12.2  $\mu\text{m}$ , a few ca. 6.4  $\times$  14.2  $\mu\text{m}$ . Underleaves much smaller than leaves, roughly equal in width to the medullary strand of the stem, spreading, distant, slightly convex (ventral view), 3–4-lobed to 0.45–0.55, the lobes straight to weakly divergent, consisting of a uniseriate portion of 1–2(3) somewhat elongated cells, terminating in an elongate slime-papilla, and a base of 2 laterally juxtaposed cells; disc rectangular (broader than high) to weakly cuneate, 2 cells high (median sinus), 6–

8 cells wide in distal and basal portions; margins entire, straight. Asexual reproduction lacking.

Plants dioecious. Androecia delicate and easily detached, either on short primary *Frullania*-type branches with a few cycles of normal vegetative leaves prior to androecial formation, or on short, abbreviated, ventral-intercalary branches from leading shoots, the androecium exceptionally long for genus, with up to 9 pairs of bracts; bracts closely to rather loosely imbricate, dorsally assurgent, deeply concave, bilobed to ca. 0.5, the lobes acuminate and terminating in a single cell or a uniseriate row of 2 cells, the tip cell of the lobe rather elongated (to 84  $\mu$ m long, to 3.2:1); dorsal margin somewhat dilated and with a large tooth/lobule with its free margin crenulate, at times with a slime papilla; ventral margin with a conspicuous tooth; bracts monandrous; antheridial stalk short, ca. 5 cells high, biseriate; bracteolar antheridia absent. Gynoecia not seen.

**DIFFERENTIATION AND VARIATION**—*Telaranea remotifolia* has a lax, etiolated aspect when dry. The pale green, loosely matted stems appear fleshy and out of proportion to the leaves, which are distant, shrunken, distinctly glasslike and strongly convex. The leaf lobes are often sharply decurved and clawlike. Another of our species with a similar lax, etiolated appearance is *T. nivicola* (p. 102), but this has a greatly reduced disc, consisting only of the partially united paired basal cells of the leaf lobes.

Optimally developed shoots have the aspect of an etiolated *T. tetrapila*. Leaves on such shoots are frequently 4-lobed, and the disc is 3–4 cells high (Fig. 24: 1, 4, 5), and the lobes are biseriate, at least in part (Fig. 24: 4, 5). The leaves of somewhat weaker shoots have a disc 2–3 cells high and are mostly 3-lobed (Fig. 24: 2). In all cases, however, the ventral leaf lobe is the smallest. Also distinctive are the underleaves, which are particularly small and are about equal in width to the medullary strand of the stem (Fig. 24: 8), which is clearly visible through the cells of the hyaloderm.

Plants with abbreviated leaf discs (2 cells high) could be confused with *T. tetradactyla*, which also has a rather glasslike appearance, but even when suboptimal, the transverse leaf insertion of this species will distinguish it from *T. remotifolia*.

Hodgson (1956) stated that perianths are present in the type material. Careful examination of the type revealed only a single, old, decayed perianth.

**DISTRIBUTION AND ECOLOGY**—Sporadically occurring on Stewart Island as well as South and North Islands, New Zealand. The species seems to have a rather broad ecological amplitude, at least with respect to elevation. For example, on Stewart Island (Fern Gully Track) the species was found at 20–30 m on very old wood of a long-abandoned bridge in dense shade of a forest dominated by *Fuchsia excorticata* and *Griselinia littoralis* canopy with a *Blechnum discolor* understory. Yet it occurs above tree line on stream banks and submerged boulders (915 m, Lake Shirley) as well as over peaty soil in shallow pools at bog edges (having abundant *Sphagnum*) in an area of tussock grassland with a mosaic of scattered bogs and patches of *Dracophyllum*, *Dacrydium bidwillii*, *Hebe* and *Donatia* (825 m, summit of Mt. Maungatua, Otago Prov.). The species also occurs in mixed *Nothofagus* forests (310 m, Blue River), as well as in dense *Nothofagus* forests of the southern portion of South Island, where it is terrestrial or on rotted logs, occurring at times with *Acromastigum cunninghamii*, *Telaranea tuberifera*, *Lepidozia kirkii*, etc. At the Kaimai Range station it is found over thin soil on vertical bedrock along the Aongatete River within a mixed *Dacrydium cupressinum* and *Beilschmedia tawa* forest with *Cyathea* understory (425 m). In the Waipoua area (290 m) it occurs in *Agathis* forests (with *Weinmannia silvicola*) over soil of stream-bed rocks or of stream banks within the steep-sided valley of Waikohatu Stream (290 m).

**SELECTED SPECIMENS SEEN**—SOLANDER IS.: SE Peninsula, W side, 100 m, *Johnson* (CHR). LONG IS. (Taukiepa Is.), Murders Cove, *Fineran* 889 (CHR). NEW ZEALAND. STEWART ISLAND: Rakiura Natl. Park, Fern Gully Track, 20–30 m, *Engel* 24055 (F). SOUTH ISLAND. SOUTHLAND PROV.: Dusky Sound, Supper Cove, *Zotov* (CHR); SE of head of Lake Shirley, 915 m, *Given* 69459 as *T. gottscheana* (CHR); Milford Track, Sutherland Falls, *Morice et al.* (CHR). OTAGO PROV.: Leith Valley, *Allison, Scott & Taylor* (CHR); summit plateau of Mt. Maungatua, W of Mosgiel, 825 m, *Engel* 17736 (F); Maungatua, W of Mosgiel, ca. 915 m, *Child* H4099 (F); Fiordland, beyond Lake Howden, *Burrell, Scott & Taylor* (CHR); trail between Gunn's Hut and Hidden Falls, ca. 30 miles SE of Lake McKerrow, *Hatcher* 539 (F); near McKerrow Hut, head of Lake McKerrow, *Hatcher* 1431 (F); Martins Bay, N of McKerrow River, *Hatcher* 858 (F); Mt. Aspiring Natl. Park, Blue River near confluence with Makarora River, NNE of Makarora, 310 m, *Engel* 18921—c. ♂ (F). WESTLAND PROV.: Cascade Road, just W of Jackson River, ca. 8–12 km SW of confluence of Jackson and Arawata Rivers, 25–90 m, *Engel* 22982 (F); Haast Pass Road, Robinson Creek, between Haast Pass and gates of Haast bridge, ca. 305 m, *Child* H1838

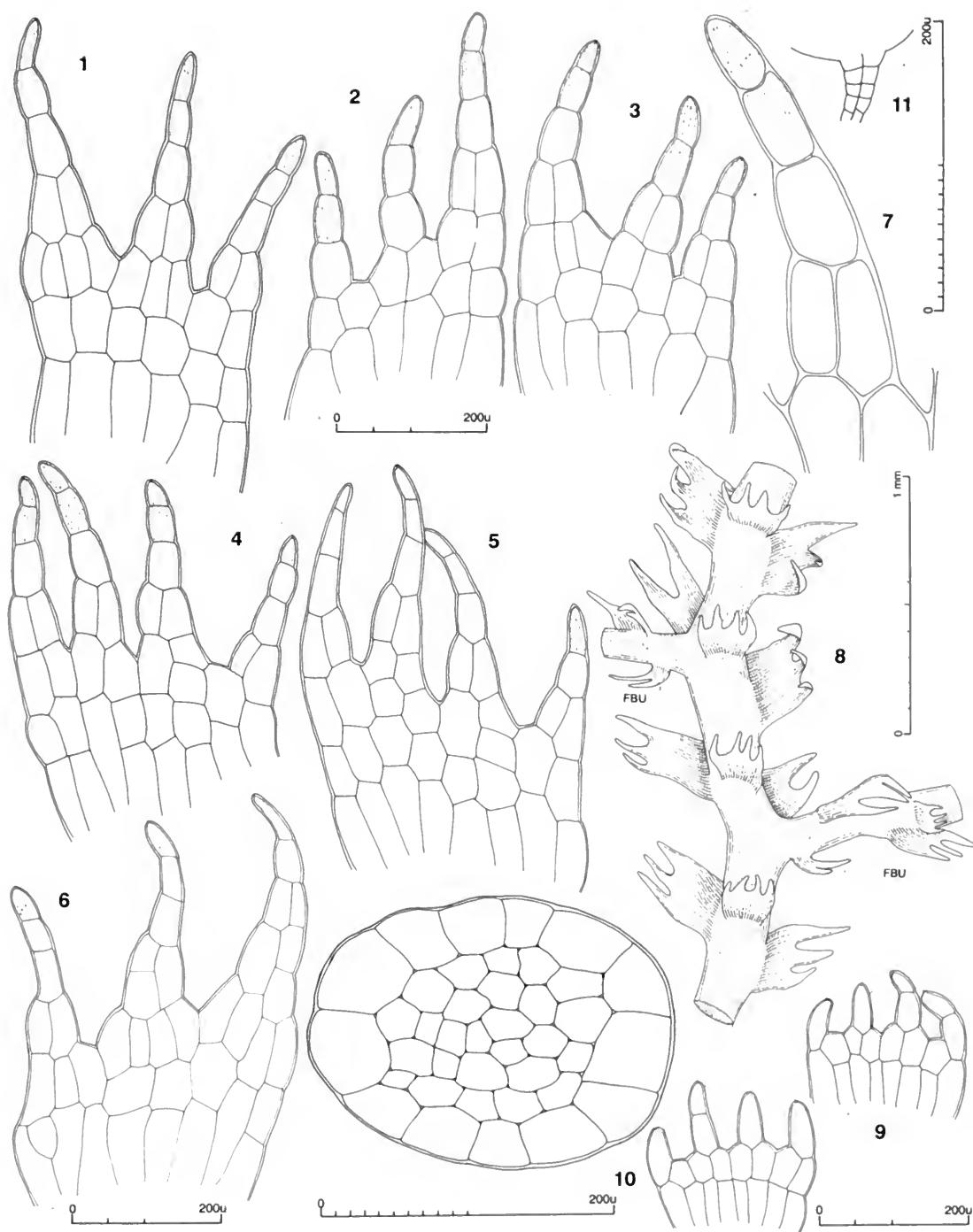


FIG. 24. *Telaranea remotifolia* Hodgs. 1–6. Leaves, cellular detail. 7. Dorsal lobe of leaf. 8. Main shoot (fbu = first branch underleaf), the medullary strand shown with stipple; ventral view. 9. Underleaves, cellular detail. 10. Stem, cross section. 11. Antheridial stalk. 12, 13. First branch underleaves (both at same scale). (Figs. 1, 5–6, 10, 12, 13 from Engel 18921, New Zealand, South Is., Otago Prov., Mt. Aspiring Natl. Park, Blue River; 2–4, 7–9 from type; 11 from Child 5366, New Zealand, South Is., Westland Prov., 5 km N of Runanga.)

(F); Copland Valley, ca. 90 m, *Child H4731* (F); 5 km N of Runanga, ca. 60 m, *Child H5366*—c. ♂ (F). NELSON: Madman's Creek, ca. 2 miles S of Route 6 bridge over Little Totara River, ca. 30 m, *Fife 4645* (F). NEW ZEALAND. TARANAKI PROV.: Pukeiti Bush, near New Plymouth, *Hatcher 219A* (F). SOUTH AUCKLAND PROV.: Kaimai Range, Aongatete River, upstream from intersection of North-South Track and river, 425 m, *Engel 23628* (F). NORTH AUCKLAND PROV.: Waipoua River, ca. 70 m upstream from State Highway 12 bridge, ca. 95 m, *Engel 21061* (F); Waipoua Forest, Waikohatu Stream at Waikohatu Kauri Bridge, 290 m, *Engel 22652* (F).

*Telaranea pulcherrima* (Steph.) Schust.

*Lepidozia pulcherrima* Steph., Spec. Hep. 3: 600. 1909. *Telaranea pulcherrima* (Steph.) Schust., J. Hattori Bot. Lab. 26: 256. 1963. Type: New Zealand, Okarito, *Kirk 588* (G!, CHR!—Bot. Div. Herb. no. 4844).

Plants subsisophyllous, with a soft and woolly appearance, flexuous, prostrate, superficially appearing like *Trichocolea mollissima*, markedly pale green, distinctly nitid when dry; shoots medium, to 1.3 cm wide (including branches). Branching regularly and rather densely pinnate, 2-pinnate in broadest portion of plant, the main axis often bearing only 2(–4) normal leaves (on each side) between branches, the branches of the *Frullania* type, rather short, determinate, rarely becoming flagelliform; branch half-leaf 4–5(6)-lobed, often obliquely inserted, cuneate, the lobes diverging; first branch underleaf 3–4-lobed, inserted on ventral-lateral side of juncture of branch and main shoot. Ventral-intercalary branches frequent, leafy, often becoming leading shoots. Stems with cortical cells poorly differentiated, in 24–30 rows of thin-walled cells, the dorsal and lateral somewhat larger than the exceedingly thin-walled medullary cells but hardly forming a differentiated hyaloderm, the 6–8 or more ventral cortical cells not or scarcely larger than medullary cells; medullary cells numerous (ca. 75), thin-walled, in 8–9 vertical tiers medially. Rhizoids originating from basal tier of underleaf cells. Leaves soft yet firmly attached, the disc spreading, the lobes becoming suberect, the leaves closely imbricate, feebly convex due to slight decurving of lobes, the insertion subtransverse to weakly incubous; leaves 1015–1825  $\mu\text{m}$  wide  $\times$  1015–1400  $\mu\text{m}$  long, very slightly asymmetric,  $\pm$  equally (7)9–12(13)-lobed to 0.55–0.65, the lobes  $\pm$  symmetrically spreading, longer than the disc. Lobes ciliiform, widely spreading, uniseriate throughout, inserted on a triangular base com-

posed of 2 disc cells, the uniseriate portion 6–9(10) cells long, the cells  $\pm$  thin-walled, the septa somewhat thickened in the corners, moderately to distinctly constricted, the basal cell 40–66  $\mu\text{m}$  wide  $\times$  (110)120–140  $\mu\text{m}$  long (1.7–3.3:1), the longest cells 86–130(160)  $\mu\text{m}$  long and 3.6–5.5(6.3):1 in var. *pulcherrima*, 125–160  $\mu\text{m}$  long and 7.4–9.6:1 in var. *mooreana*, terminal cell shorter than penultimate cell, rather sharply tapering to a point. Disc  $\pm$  symmetrically to slightly asymmetrically short cuneate, 4–5 cells high in dorsal sector (including intermediate cells and paired cells at bases of lobes), 3–4 cells high in ventral sector, 18–20(24) cells broad at midpoint of disc; disc margins entire,  $\pm$  straight. Cells of disc in  $\pm$  regular tiers, thin-walled but not delicate, with no trigones, the median disc cells large, 38–48  $\mu\text{m}$  wide  $\times$  62–84  $\mu\text{m}$  long; basal row of disc cells (intermediate cells) narrower; cuticle smooth. Oil-bodies (*vide* Schuster, 2000), 9–12 per cell, finely granular. Underleaves similar to leaves, the disc spreading to subsquarrose (the lobes erect), imbricate, plane, symmetrically 6–10-lobed to 0.8, the lobes symmetrically spreading; disc short cuneate, 4–5(6) cells high (median sinus), (15)19–23 cells broad in median portion, the cells in  $\pm$  regular tiers; margins entire; cuticle as in leaves. Asexual reproduction lacking.

Diocious. Androecia either terminal on short, secondary *Frullania*-type branches or on short, abbreviated, ventral-intercalary subspicate branches; bracts rather closely imbricate, strongly dorsally assurgent, 3 lobed, the dorsal somewhat inflexed (and  $\pm$  oriented toward shoot apex), the lobes 3–4 cells wide at base, terminating in a uniseriate row of 3–4 elongate cells; lamina with dorsal margin somewhat incurved to form a weak pocket, with a few slime papillae or small teeth (one at times large, lobuliform and inflexed); bracts monandrous; antheridial stalk biserial; bracteolar antheridia absent. Gynoecia strongly dorsally assurgent; bracts very small for perianth size, those of innermost series appressed to perianth, strongly concave and  $\pm$  abruptly involute-tubular forming a subcullate apex, the bracts broad elliptic to broad obovate; apices very shallowly and irregularly 3–4-lobulate, the lobules composed of cells similar to those of lamina, terminating in a short uniseriate cilium of 2–3 elongated cells, often with a terminal slime papilla; lamina composed of  $\pm$  regularly subrectangular cells, the margins curved, the marginal cells obliquely oriented and sinuous, the free apical ends diverging and forming irregular denticula-

tions, with slime papillae frequent; bracteoles of innermost series similar in form to bracts but slightly smaller. Perianth large for plant size, terete for most of its length, trigonous and 3-plicate only near the summit, the perianth gradually tapering toward the mouth; mouth crenate-denticulate by the variably projecting, bluntly rounded, marginal cells.

Capsule (Schuster, 1969, p. 33; 2000, fig. 81) wall 5-stratose, the outer layer  $\pm$  equal in thickness to intermediate layers; outer layer of cells in tiers, with primary cells subdivided by 3 longitudinal walls with sheetlike sinuous thickenings, the transverse walls devoid of thickenings; innermost layer of cells  $\pm$  tiered, narrowly rectangular, with semiannular bands common, mostly complete.

Spores areolate. Elaters rigid, not or weakly tortuous, 8.6–10.6  $\mu\text{m}$  wide, only slightly tapering toward tips, bispiral to tips, the spirals 4.3  $\mu\text{m}$  wide.

NOMENCLATURE—Stephani's *L. pulcherrima* and *L. mooreana* were published in the same work (Stephani, 1909). *Telaranea pulcherrima* is the name which is current in the Australasian literature (Hodgson, 1956; Scott, 1985; Glenny, 1998), and is the most expressive and appropriate name for this truly beautiful plant.

DISTRIBUTION AND ECOLOGY—Present in New Zealand (Stewart Is. and Southland and Westland Prov. of South Island), Tasmania, and Australia (rare in Victoria). The species is much more common in Tasmania than in New Zealand, where it is apparently somewhat frequent only on Stewart Is. This species forms pure, translucent light yellow-green to whitish green mats in very wet sites. On Stewart Is. it is associated with quiet pools and small, quiet rills or narrow creek systems where it occurs within the pools or loosely over very deep humus at the creek margins. The humidity is always very high in such sites, which are in the shade of podocarp-hardwood forests of *Dacrydium cupressinum* and *Weinmannia racemosa*, with a subcanopy of *Dicksonia squarrosa* and woody liane of *Ripogonum scandens* (Engel 24201) or of stunted and dense *Leptospermum scoparium*-*Dracophyllum*-*Weinmannia* forest (to 3–4 m tall) (Engel 24357). In the Haast River area the plant occurs at sea level in open swampy areas with *Sphagnum* and scattered *Leptospermum*, etc., in low areas between hummocks (Engel 21771). Among the most hygrophytic of the *Telaranea* species, usually confined to sites (damp rocks near

water, perhaps subject to inundation, and peaty ground where submersion could occur) where never subject to drying out. In Tasmania the species is confined to forests in the wet western half of the island (the sole exception being the Mt. Arthur station).

DIFFERENTIATION AND VARIATION—The pale yellowish green, soft-textured, rather spongy, regularly 2(3)-pinnate, plumose shoots, and the multiple leaf lobes, radiating fan-like from the disc (Fig. 25: 1–3) will immediately distinguish this species. In all these respects, the plants have the aspect of a small, delicate *Trichocolea*.

Based chiefly on Stephani's (1909) descriptions, *T. pulcherrima* and *T. mooreana* have previously been maintained as separate species (Schuster, 1963). The latter has been regarded as a somewhat weaker plant with 8-lobed rather than 12-lobed leaves, but this distinction is not borne out by examination of collections. The New Zealand and Tasmanian plants are distinguishable, however, in the form of the lobes, and are treated here as varieties of the species (see below).

An extreme form of *T. pulcherrima* is possibly represented by an illustration in Stephani's *Icones* (*Lepidozia* 122), Tasmania, leg. Weymouth, as *Lepidozia multipila*, an unpublished name. The stem leaf is strongly asymmetric and 16-lobed, but the plants we examined, labeled *T. multipila* in Stephani's herbarium (G), are fairly typical of the Tasmanian var. *mooreana*. In our experience, the common run of lobe numbers in *T. pulcherrima* is 8–12, and never as many as 16. In the related *T. trichocoleoides* of Borneo and New Guinea (p. 194), the strongly asymmetric leaves are associated with a distinct ventral decurrency of the leaf, a condition which we have not observed in *T. pulcherrima*. Stephani's figure of *L. multipila* shows a disc which is 6–7 cells high in the dorsal sector, diminishing to only 2–3 cells high in the attenuated ventral portion, whereas the most we have seen in *T. pulcherrima* is 4–5 cells high dorsally and 3–4 cells ventrally; his figure of *T. mooreana* (ibid., 102) is of a 13-lobed, symmetric leaf with a disc 3 cells high throughout.

Key to Varieties

- 1. Cells in distal half of leaf lobes shorter and larger in diam., the longest 86–130(160)  $\mu\text{m}$  long and 3.6–5.5(6.3):1. New Zealand . . . . . var. *pulcherrima*
- 1. Cells in distal half of leaf lobe slender and cap-



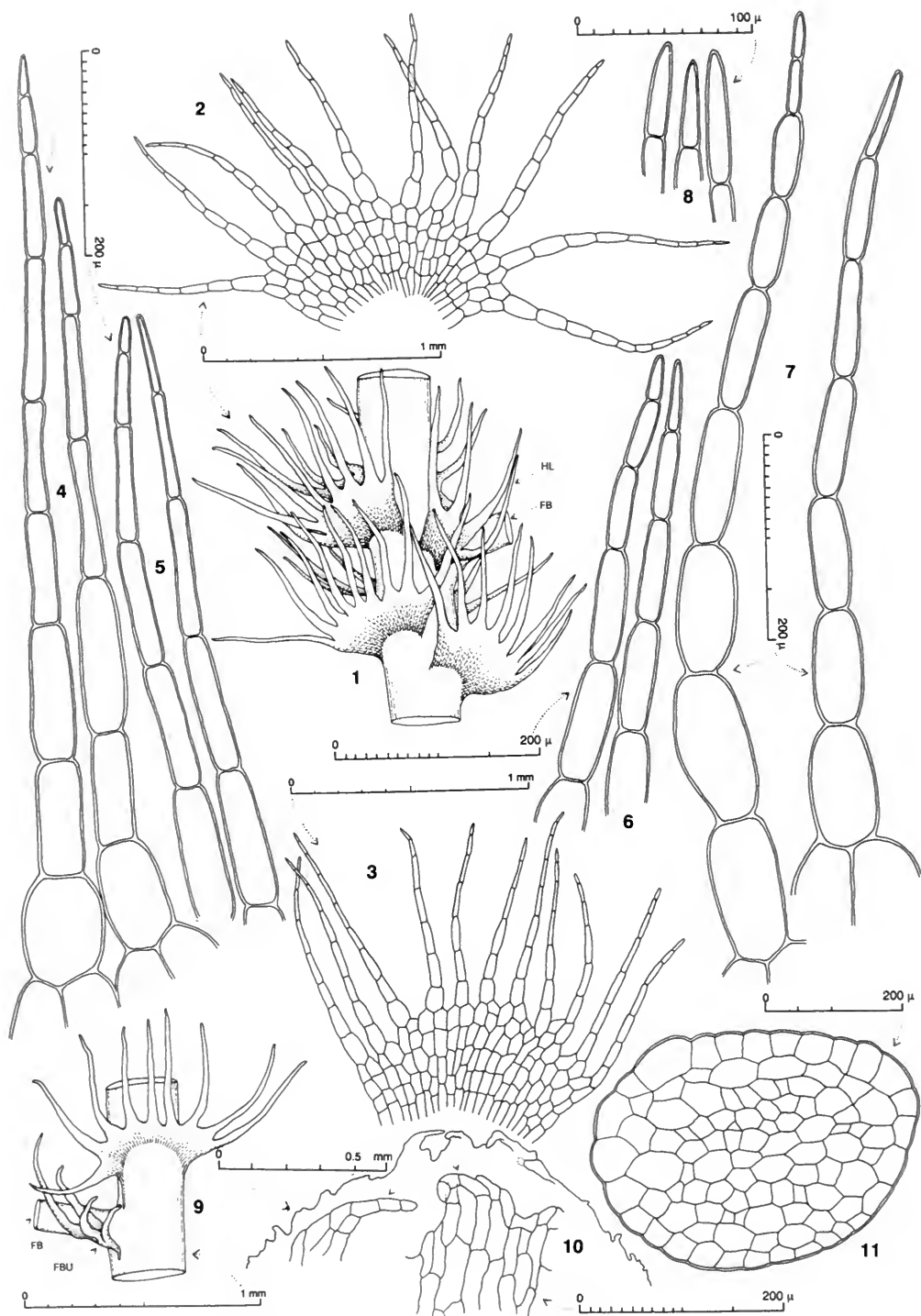


FIG. 25. *Telaranea pulcherrima* (Steph.) Schust. Var. *pulcherrima* (1, 2, 6, 7, 9); var. *mooreana* (Steph.) Engel & Merr. (3-5, 8, 10, 11). 1. Sector of main shoot, dorsal view (FB = *Frullania*-type branch; HL = half-leaf). 2, 3. Leaves. 4-7. Leaf lobes. 8. Terminal cells of leaf lobes. 9. Sector of main shoot, ventral view (FB = *Frullania*-type branch; FBV = first branch underleaf). 10. Apex of innermost ♀ bract, with (at arrows) 2 of lobules shown in detail. 11. Stem, cross section. (Figs. 1, 6, 9 from Engel 21771, New Zealand, South Is., Westland Prov., ca. 4 km N of Haast River; 2, 7 from type of *Lepidozia pulcherrima*; 3, 4, 8 from type of *Lepidozia mooreana*; 10, 11 from Engel



illary, the longest 125–160  $\mu\text{m}$  long and 7.4–9.6:1. Tasmania, Australia . . . var. *mooreana*

***Telaranea pulcherrima* (Steph.) Schust. var. *pulcherrima***

Longest cells in distal portion of lobes shorter than in var. *mooreana*, 86–130(160)  $\mu\text{m}$  long, 3.6–5.5(6.3):1 (see Fig. 25: 6, 7). Stephani's illustration (Icones *Lepidozia*, 199) gives the dimensions of the lobe cells as  $36 \times 108 \mu\text{m}$ .

NOTE—The protologue (Stephani, 1909) and Icones (*Lepidozia*, 199) cite the collector as Kirk. A specimen from Okarito at CHR determined as *Lepidozia lindenberghii* bears the number 588 (as does the type at G); the plants are labeled "A. H." but are strikingly similar in appearance to the type, and are probably parts of the same collection (see also Hodgson, 1956, p. 614).

DISTRIBUTION—Confined to New Zealand.

SELECTED SPECIMENS SEEN—NEW ZEALAND. STEWART ISLAND: Rakiura Natl. Park, Port Pegasus, ca. 100–200 m, *Engel* 24201 (F); *ibid.*, Mt Rocky Track, 390–475 m, *Engel* 24357 (F); Pegasus, track to tram line, *Schuster, Scott & Taylor* (CHR); Rakiuhua Flat, *Moore* (CHR). SOUTH ISLAND. SOUTHLAND PROV.: Supper Cove, *Zotov s.n.* (CHR). WESTLAND PROV.: Ca. 4 km N of Haast River, sea level, *Engel* 21771 (F).

***Telaranea pulcherrima* var. *mooreana* (Steph.) Engel & Merr., comb. & stat. nov.**

*Lepidozia mooreana* Steph., Spec. Hep. 3: 585. 1909.  
*Telaranea mooreana* (Steph.) Schust., J. Hattori Bot. Lab. 26: 256. 1963. Type: Tasmania, West Coast, King River, *T. B. Moore s.n.* (G!).

Lobe cells in distal half of lobe slender and capillary, the longest 125–160  $\mu\text{m}$  long (7.4–9.6:1) (see Fig. 25: 4, 5).

DISTRIBUTION—Confined to Tasmania and Australia (Victoria).

SELECTED SPECIMENS SEEN—TASMANIA: Without specific loc., *Moore* as *Lepidozia multipila* [*nom. herb.*] (G); N slope of Mt. Victoria, ca. 800 m, *Norris* 28324 (F); along tributary of Styx River about 10 miles W of Maydena, *Norris* 28933 (F); Tahune Forest Reserve, off Pine Track, along Huon River, 70 m, *Engel* 19927 (F); Florentine River, near Gordon River Road, 1 km W of

junction with Scotts Peak Road, *Engel* 15084 (F); Clear Hill Road, 0.9–9.2 km N of Gordon River Road on E side of Lake Gordon, 350–425 m, *Engel* 16718 (F); Gordon River just E of confluence with Serpentine River, WNW of Strathgordon, 350 m, *Engel* 13885—c.  $\delta$  (F); Gordon River, Sir John Falls, just up river from Butler Is., sea level, *Engel* 14696 (F); Gordon River, across river and slightly W of Gorge Creek and Pine Landing, sea level, *Engel* 14849 (F); Cradle Mtn.-Lake St. Clair Natl. Park, Pine Valley, between Pine Valley Hut and Cephisus Falls, NNW of Lake St. Clair, 850 m, *Engel* 14233 (F); Surprise Valley, above Surprise River and below Lyell Highway, 2.6 km W of King William Saddle, 610 m, *Engel* 19424 (F); Franklin River at Frenchman's Cap Trail crossing, ca. 400 m, *Norris* 31195 (F); Kelly Basin Road, between junction with Franklin River Road and Kelly Basin, above Nora River, 90 m, *Engel* 14952 (F); Allans Creek, NE slope of Mt. Darwin, off Kelly Basin Road (Crotty Track), 410 m, *Engel* 16575 (F); King River, 11.3 km by road from Regatta Point and 13.3 km by road from Strahan Harbour, sea level, *Engel* 14938 (F); road between Zeehan and Trial Harbour, 250 m, *Engel* 16407—c. per. (F); Dubbilbarril, *Weymouth s.n.*, 1098, as *Lepidozia multipila* (G); North East Dundas Tramway (abandoned), W of Williamsford and SW of Rosebery, ca. 400 m, *Engel* 16477 (F); Cradle Mtn.-Lake St. Clair Natl. Park, Weindorfers Forest, along track from Waldheim Chalet to Hounslow Heath Track, 975 m, *Engel* 14059 (F); S shore of Lake Lea, ca. 800 m, *Norris* 27459 (F); southern spur of St. Valentines Peak, SSW of Burnie, 700–790 m, *Engel* 15680 (F); Emu (Companion) River near Guildford Road, SSW of Burnie, 500 m, *Engel* 15833 (F); between Arthur River and Julius River along Sumac Road, S of Roger River West, S of Smithton, 100 m, *Engel* 16114 (F); vicinity of Trowutta Caves (Arch), 4.5 km by road from intersection of Reynolds Road and Reids Road and 6.9 km from Trowutta Post Office, ca. 180 m, *Engel* 19761 (F); Newhaven Road, 9.4 km by road E of junction with Mawbanna Road, S of Detention River mouth, 70 m, *Engel* 19708 (F). AUSTRALIA. VICTORIA: Otway Ranges, headwaters of Calder River, *Turner s.n.* (F).

***Telaranea* sect. *Transversae* Engel & Merr.**

*Telaranea* sect. *Transversae* Engel & Merr., Phytologia 79: 251. 1996 (1995). Type: *Lepidozia lindenberghii* Gott.

*Lepidozia* sect. *Capillares* G. L. & N., Syn. Hep. 211. 1845, "IV. *Capillares*." Lectotype (nov.): *Lepidozia lindenberghii* Gott. non *Telaranea* sect. *Capillares* Engel & Merr., Phytologia 79: 251. 1996 (1995). Type: *Lepidozia grossiseta* Steph.

*Kurzia* subg. *Leucolepidozia* Schust., J. Hattori Bot. Lab. 48: 356. 1980. Type: *Kurzia quadriseta* Grolle.

Note that "sect. *Gibbsianae*" (Schuster, 2000, p. 214) was our provisional manuscript name for

E16407, Tasmania, road between Zeehan and Trial Harbour; 5 from *Engel* E19927; Tasmania, Tahune Forest Reserve, along Huon River.)

the section later published by Engel and Merrill (1996) as sect. *Capillares*. "*Lepidozia* IV. *Capillares*" G. L. & N. was first treated as a section ("§ *Capillares*") by Spruce (1876).

*Telaranea lindenbergii* (Gott.) Engel & Merr.

*Lepidozia lindenbergii* Gott. in G. L. & N., Syn. Hep. 213. 1845. *Mastigophora lindenbergii* (Gott.) Trev., Mem. Ist. Lomb. Sci. Lett. III. 4: 416. 1877. *Telaranea lindenbergii* (Gott.) Engel & Merr., Phytologia 79: 252. June, 1996 [1995]. Type: "Nova Zeelandia inter *L. praenitentem* (Hb. Hk.)" (W!, Lindenberg Hepat. no. 4849).

For synonymy, see under varieties.

Plants delicate, often with a bristly appearance, soft, flexuous yet firm (straight and  $\pm$  wiry in var. *mellea*), prostrate, pale green to pale yellow-green (or brownish yellow to rust brown in var. *mellea*), nitid when dry; plants small, to 5 mm wide, including branches. Branching rather regularly 1–2 pinnate, the branches rather closely spaced, often at right angles to main axis, often  $\pm$  equal in length or the branching pattern  $\pm$  plumose, with branches becoming gradually longer toward shoot base, terete (complanate-foliate in var. *complanata*), scarcely tapering (long-flagelliform in var. *mellea*); branch leaves transversely inserted (incubous in var. *complanata* and var. *papillata*); branch half-leaf 2-lobed; first branch underleaf undivided and ciliiform, inserted on ventral side of branch at juncture of branch and main axis. Ventral-intercalary branches occasional, leafy. Stems flexuous, often appearing stout for plant size; cortical cells distinctly differentiated, somewhat thick-walled, in 12–18 rows; cortical cells in section much larger than the numerous (ca. 40–67), moderately to distinctly thick-walled medullary cells. Rhizoids often copiously produced from cells of underleaf disc. Leaves on main shoot rigid, widely spreading to squarrose, rather distant on main stems to closely imbricate on the branches, plane or somewhat handlike due to incurving of lobes, typically transversely inserted and oriented (at times weakly incubous), transverse or weakly incubous on branches; leaves 245–280  $\mu\text{m}$  wide  $\times$  175–225  $\mu\text{m}$  long ranging to 390–440  $\mu\text{m}$  wide  $\times$  235–320  $\mu\text{m}$  long (4-lobed) to 525–735  $\mu\text{m}$  wide  $\times$  370–460  $\mu\text{m}$  long (6-lobed), symmetric to weakly asymmetric, 4–6(7)-lobed to 0.65–0.8, the lobes divergent, longer than disc height. Lobes ciliiform, typically uniseriate to the base, inserted on a triangular base composed of 2 disc cells (or sporadically with an

additional biseriate tier between base and uniseriate row), the uniseriate portion 5–6(7) cells long (4–5 cells long in var. *papillata*), with cells moderately thick-walled and firm, straight-sided and without or with weakly bulging septa, the basal cell of the uniseriate portion 20–32  $\mu\text{m}$  wide  $\times$  42–65  $\mu\text{m}$  long (1.8–2:1), the next cell narrower and a little shorter, 17–24  $\mu\text{m}$  wide  $\times$  38–48  $\mu\text{m}$  long (2.6–2.8:1), the terminal cell a little smaller than the penultimate cell, evenly tapered to the tip; cuticle smooth. Disc semicircular, 2 cells high (locally 3, exceptionally 4 in var. *mellea*) (from median sinus base to leaf base), including paired cells at bases of lobes, the basal tier of cells elongate and 8 cells wide in 4-lobed leaves to 12 cells wide in 6-lobed leaves; margins entire, straight to somewhat incurved. Underleaves much smaller than leaves, inconspicuous, 4–5-lobed nearly to base, the lobes ciliiform, the uniseriate portion formed of 3–4 somewhat elongated cells, terminating in a slime papilla; disc abbreviated, 2 cells high, 8 cells wide (in 4-lobed underleaves); margins entire. Rhizoid initial cells small, subquadrate, formed from some or all cells of underleaf disc. Cells of disc somewhat thinner-walled than lobe cells but firm, trigones lacking, the largest cells (in median sector of disc) 17–24  $\mu\text{m}$  wide  $\times$  40–60  $\mu\text{m}$  long (basal tier); basal tier of disc cells often longitudinally elongated; cuticle smooth.

Plants dioecious. Androecia either terminal on short to moderately long primary or secondary *Frullania*-type branches or on short, abbreviated, ventral-intercalary, spicate branches; bracts closely imbricate, strongly dorsally assurgent, deeply concave-subcucullate, 2(3)-lobed to ca. 0.5, the lobes subcaudate, terminating in a uniseriate row of 3–4 rather elongated, moderately thick-walled cells, the terminal cell tapering to summit, to 3:1; dorsal margin of lamina somewhat dilated and incurved, crenulate and with a few slime papillae or with a 1- to several-celled, often sharp tooth; bracts monandrous; antheridial stalk short, 6 cells high, uniseriate; bracteolar antheridia absent. Gynoecia not dorsally assurgent and lying in the same plane as main shoot or feebly to strongly dorsally assurgent, scarcely swollen and often densely rhizoidous at base; bracts small for perianth size, those of innermost series closely ensheathing the perianth, concave, short oblong to ovate; apices shallowly (3)4-lobulate, the median sinus a little deeper, the lobules acuminate, terminating in a uniseriate cilium of 2–4 somewhat elongated cells, often with a terminal slime papil-

la; lamina composed of  $\pm$  regularly subrectangular cells, the margins curved, with a few blunt teeth formed by the divergent apical or free end of marginal cells, or margins subentire or with a few small 1–2-celled teeth; bracteoles of innermost series similar in form to bracts, but 0.5–0.75 their size. Perianth long emergent, terete in basal sector, trigonous above, basically 3-plicate but with several accessory smaller plicae, the perianth narrowing toward the contracted mouth; mouth with 9–13 caudate lobes, the lobes each with a base composed of 2–4 laterally juxtaposed, elongate cells, the lateral cells of base often with the distal end protruding to form a “shoulder,” the lobes each terminating in a flexuous or stiff setose cilium composed of a uniseriate row of 3–5 elongate, rather thick-walled cells, the basal 1–2 cells 13–20  $\mu\text{m}$  wide  $\times$  96–130  $\mu\text{m}$  long, (5.7–8.3: 1) (var. *lindenbergii*) or 14–22  $\mu\text{m}$  wide  $\times$  60–90  $\mu\text{m}$  long, (3.1–4.6:1) (var. *complanata*); perianth 2-stratose in basal portion, the cells in section radially elongate.

Seta with 8 rows of outer cells, surrounding an inner core of 15–18 much smaller cells. Capsule short elliptic, 1120–1295  $\mu\text{m}$   $\times$  553–616  $\mu\text{m}$ , the outer wall undulate in transverse section, the primary walls shorter than the thickened secondary walls, alternatively 29–31  $\mu\text{m}$  to 38–41  $\mu\text{m}$  thick, of 3 layers, the outer layer at its thickest point equivalent to the combined thickness of the two inner layers; outer layer of cells (surface view) in tiers, thin-walled, rather regularly short-rectangular, with 2-phase development, the longitudinal walls with rather weakly developed nodule-like thickenings (4–6 per cell) alternating with walls that are devoid of thickenings, the transverse walls also devoid of thickenings; intermediate layer thinner than outer or inner layers; innermost layer of cells  $\pm$  tiered, somewhat irregularly narrowly rectangular, with semiannular bands common, rather narrow, close, usually complete, sporadically forked and anastomosing to delimit fenestrae.

Spores 13.4–14.9(15.4)  $\mu\text{m}$ , exine pale brown, with a network of low but sharply defined papillae and short-vermiculate markings that coalesce and delimit areolae. Elaters rigid,  $\pm$  sinuous, 7.7–9.6  $\mu\text{m}$  wide, only slightly tapering toward tips, bispiral to tips, the spirals 3.8–4.8  $\mu\text{m}$  wide.

**DIFFERENTIATION AND VARIATION**—This common and widespread species was treated by Hodgson (1956) as a synonym of *T. tetradactyla*. The name *Lepidozia lindenbergii* has been used

extensively for the New Zealand plant. All of the published species in this complex have proved to be *T. lindenbergii*, whereas *T. tetradactyla* s. str. (p. 91) has no synonyms. For a discussion of the differences between these two species, and the typification of *T. tetradactyla*, see the nomenclatural notes under that species.

*Telaranea lindenbergii* is readily distinguishable from other *Telaranea* species by the distant, widely spreading, deeply dissected stem leaves (Fig. 26: 1), with a low disc, for the most part only 2 cells high (Fig. 26: 2, 3). The leaves of the main axis are  $\pm$  transversely inserted and oriented, although the orientation of the branch leaves is variable. Three varieties of the species are recognized, which can be distinguished as follows:

**Key to Varieties of *Telaranea lindenbergii***

- 1. Stems flexuous, often appearing somewhat fleshy for plant size, the branches more closely spaced; branches short, of about equal length, hardly tapering, only exceptionally flagelliform, the secondary branches often frequent; plants pale green . . . . . 2
- 2. Branch leaves  $\pm$  transversely inserted and oriented. Common throughout New Zealand . . . . . var. *lindenbergii*
- 2. Branch leaves incubously inserted and oriented . . . . . 3
- 3. Branches terete; lobe cells papillose . . . . . var. *papillata*
- 3. Branches complanate-foliate; lobe cells smooth . . . . . var. *complanata*
- 1. Stems slender, straight, rather wiry, the branching  $\pm$  distant; branches long, flagelliform, the secondary branches typically few; plants brownish yellow to rust brown. Primarily southern South Is. . . var. *mellea*

*Telaranea lindenbergii* (Gott.) Engel & Merr. var. *complanata* Engel & Merr.

*Telaranea lindenbergii* var. *complanata* Engel & Merr., Phytologia 79: 252. June, 1996 [1995]. Holotype: New Zealand, South Is., Otago Prov., Whare Flat, W of Dunedin, 70 m, Engel 17641—c. sporo. (F).

Branches distinctly complanate-foliate, the branch leaves imbricate, obliquely spreading, incubously inserted and oriented; leaves of main axis variable in insertion, mostly subtransverse to

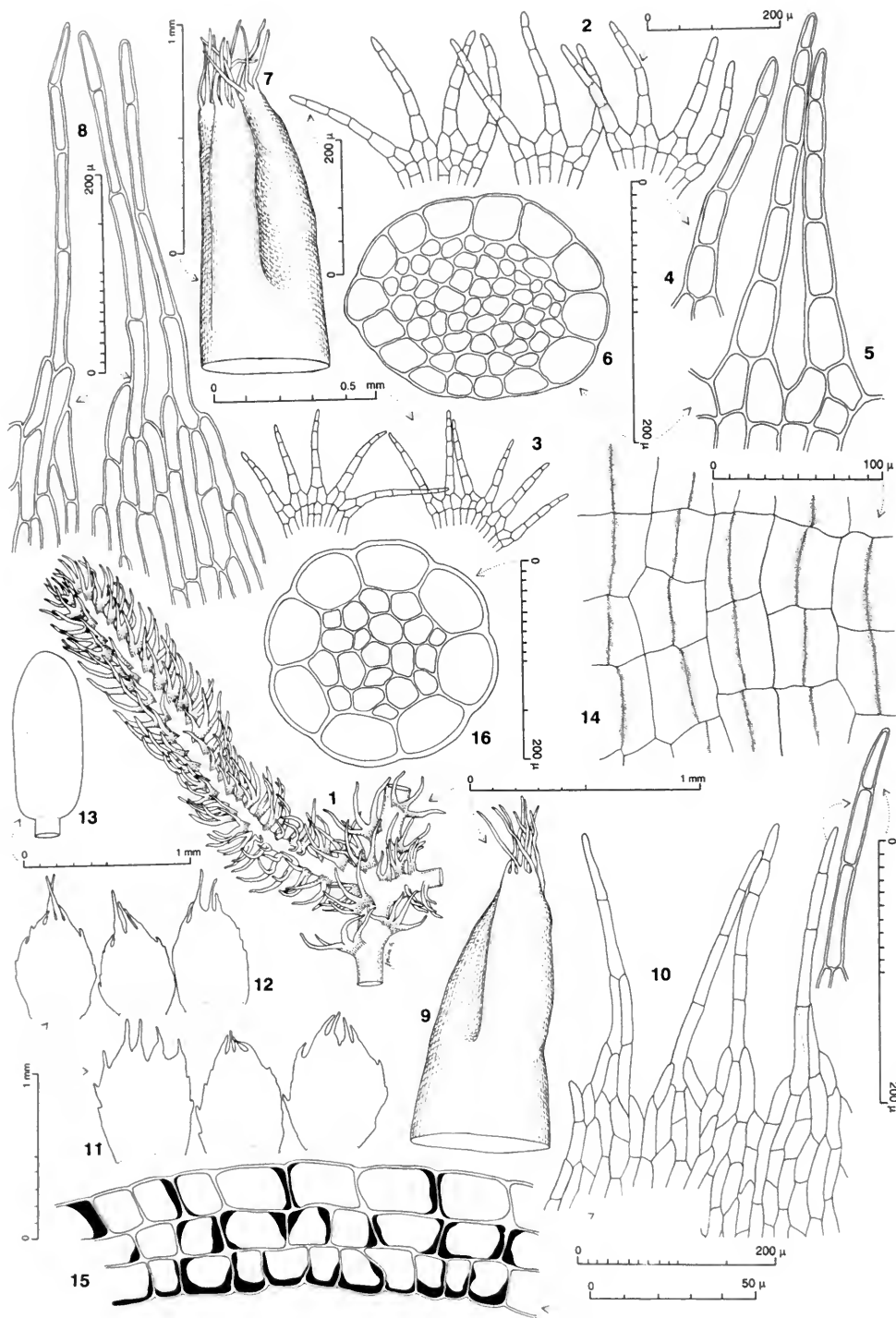


FIG. 26. *Telarannea lindenberghii* (Gott.) Engel & Merr. (1–8, 11, 13–16) + *Telarannea tetradactyla* (Hook. f. & Tayl.) Hodgs. (9–10, 12). 1. Sector of main shoot and primary branch, dorsal view. 2. Three leaves. 3. Two leaves. 4. 5. Leaf lobes. 6. Stem, cross section. 7. Distal sector of perianth. 8. Portion of perianth mouth. 9. Distal half of perianth. 10. Portion of perianth mouth, the uniseriate row at right shown at higher magnification. 11. ♀ Bracts and, in middle, bracteole. 12. ♀ Bracts and bracteole. 13. Capsule profile. 14. Capsule wall, outer layer, showing 2-phase development. 15. Capsule wall, cross section. 16. Seta, cross section. (Figs. 1–2, 4, 7–8, 11 from Engel 19300, New

moderately incubous, sporadically strongly oblique to almost longitudinal.

**DIFFERENTIATION AND VARIATION**—Similar in aspect and branching to var. *lindenbergtii* but differing chiefly in the flattened, comblike branches with obliquely spreading, incubously oriented leaves. This plant is likely to be confused with *T. tetradactyla*, which also has strongly complanate-foliate branches, but differs in the higher disc of the leaves of the main axis, which is typically 3 or often 4 cells high, vs. 2 or only rarely 3 cells high in var. *complanata*. In addition, the stems of var. *complanata* are stouter, with more numerous, thicker-walled medullary cells. *Telaranea tetradactyla* is also a much softer, laxer plant with more irregular branching, and is essentially an extreme southern South Island plant.

The branches of var. *complanata* are complanate-foliate, and the branch leaf insertions extend to the middle of the adjacent cortical cells along the midline, thus lacking a conspicuous median strip. Broad, dorsiventrally flattened branches are also a feature of *T. chaetophylla* (p. 136), the type species of the genus, but there the branch leaves do not extend to the midline, leaving a prominent 2-cell-wide dorsal median strip of quadrate cortical cells (Fig. 42: 2). Several other extraterritorial species (*T. fissifolia*, *T. kogiana*) show this type of branches.

**DISTRIBUTION AND ECOLOGY**—Known from scattered sites at lower elevations on Stewart Island and South and North Islands. The variety occurs in humid niches within forests of various types and may be on rotten logs and on rich humus or clayey soil of banks. It also is present on trunks of *Cyathea dealbata* and *Dicksonia squarrosa* and in such niches may form large colonies; in particularly humid niches it is also found on old, very rotted, prostrate tree fern trunks.

The Lee Bay site on Stewart Island is of interest. Plants occurred over soil of a drainage area just above the shoreline at the edge of very exposed coastal scrub that includes *Brachyglottis rotundifolia*, *Carpodetus serrata* and *Coprosma robusta*; the coastal scrub is at the margin of a podocarp/hardwood forest. The niche likely

would be exposed to periodic salt spray (see Engel & Schuster, 1973).

**SELECTED SPECIMENS SEEN**—NEW ZEALAND. STEWART ISLAND: Rakiura Natl. Park, Port Pegasus, ca. 100–200 m, Engel 24192 (F); Lee Bay, head of Rakiura Track to Christmas Hut, 5 m, directly above shoreline, Engel 24105 (F). SOUTH ISLAND. OTAGO PROV.: Leith Valley Bush, Morrison's Creek Gully, Dunedin, Allison H7713 as *T. tetradactyla*—c. sporo. (CHR); Cosy Dell, Dunedin, ca. 150 m, Child H1509 as *T. tetradactyla*—c. sporo. (F). NORTH ISLAND: SOUTH AUCKLAND PROV.: Puaiti Bush, S of Rotorua, Allison H25—c. per., H3236—c. per. (CHR); Herangi Range, Whareorino Forest, near tributary of Awakino River, W of Leitchs Road, SW of Te Kuiti township, 285 m, Engel 23950—c. ♂ (F); Whareorino Forest, start of track to Leitch's Hut, 280 m, Engel 23752—c. ♂ (F); Mangaotaki Catchment, Waitanguru Scenic Reserve, track to Waitanguru Falls, 180 m, Engel 23794 (F); Kai-mai Range, spur ESE of Ngatamahinerua, headwaters of Poupu Stream, ca. 2 km W of North-South Track, 400–425 m, Engel 23567—c. per. (F).

*Telaranea lindenbergtii* (Gott.) Engel & Merr. var. *papillata* Engel & Merr., var. nov.

Foliis ramulorum incubis sed ramuli vix complanatis, lobis foliorum 4–5 cellulas longis, cellulis loborum papillosis diversa.

Holotype: New Zealand, North Island, South Auckland Prov., Whareorino Forest, track to Leitch's Hut, 280 m, Engel 23773—c. sporo. (F); isotype: (AK).

**DIFFERENTIATION**—Known only from the type, the plants are similar to var. *complanata* in the incubous insertion of the branch leaves, but differ in the terete, not complanate-foliate branches and the roughened cuticle of the leaf lobes (Fig. 26A: 6). The lobes are rather short, 4–5 cells long (Fig. 26A: 1–5) vs. 5–6(7) cells long in var. *lindenbergtii* (Fig. 25: 2–5).

**DISTRIBUTION AND ECOLOGY**—The type and only known plant occurred on clay banks under a *Blechnum novae-zealandiae* overhang, with *Weinmannia* and *Dicksonia squarrosa* as the dominant forest canopy and with occasional *Leptospermum scoparium*.

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←  
Zealand, South Is., Paparoa Range, along Croesus Track; 3, 5 from Allison H79, New Zealand, North Is., South Auckland Prov., Puaiti Bush; 6 from Allison 3236, same loc. as Allison H79; 9–10, 12 from Child H2353, New Zealand, South Is., Otago Prov., Ross Creek; 13–15 from Reif C86E; New Zealand, South Is., Westland Prov., Camp Creek; 16 from type of var. *complanata*.)

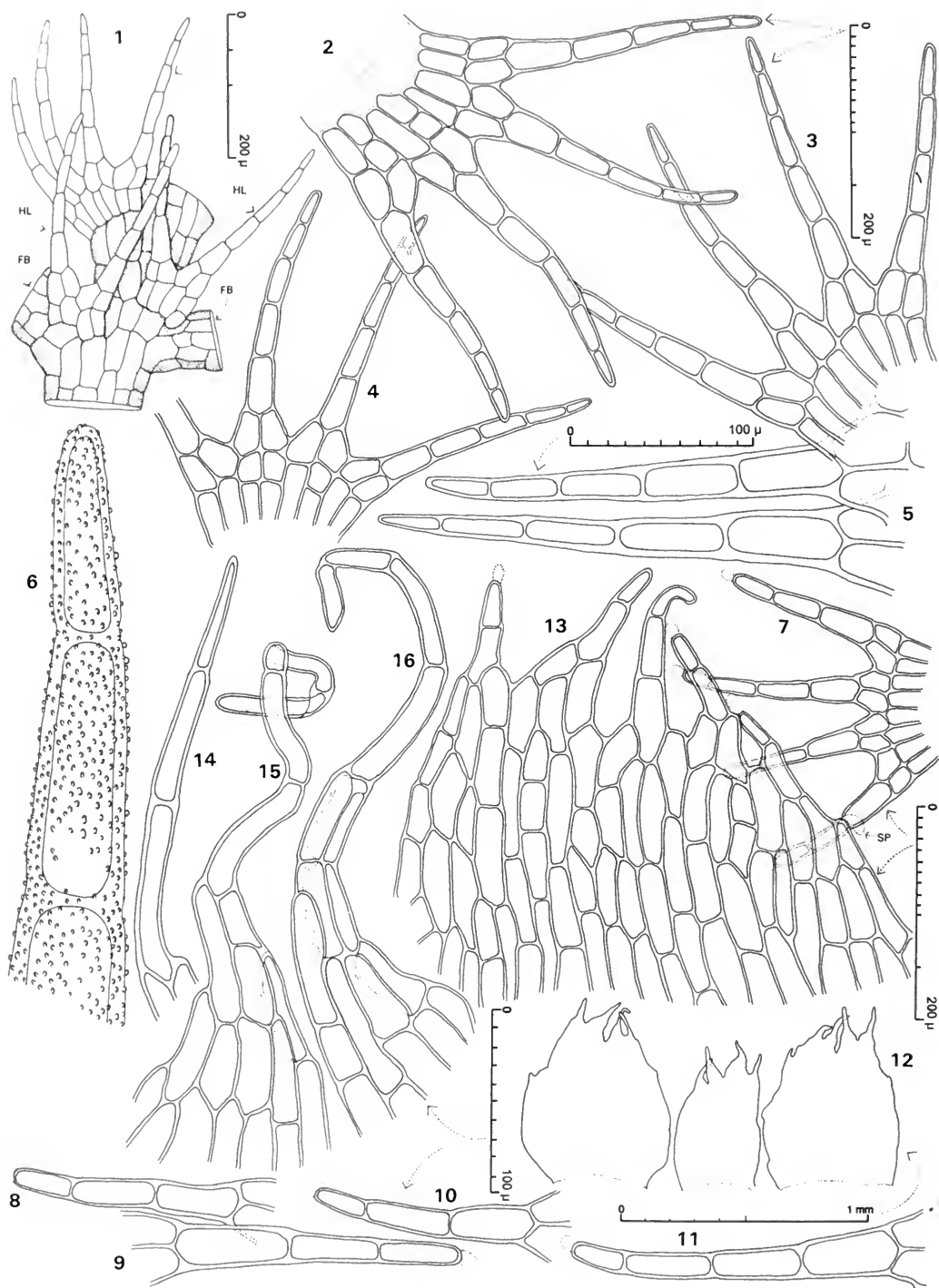


FIG. 26A. *Telaranea lindenberghii* var. *papillata* Engel & Merr. 1. Portion of shoot showing a leaf and 2 half-leaves (= hl) each at the base of a *Frullania*-type branch (= FB), dorsal aspect. 2-4. Leaves (cuticular detail not shown); all drawn to same scale. 5. Two leaf lobes, cuticular detail not shown. 6. Distal portion of leaf lobe showing cuticular papillae ( $\times 1065$ ). 7. Underleaf. 8-11. Underleaf lobes. 12. Innermost  $\varnothing$  bracts and, in middle, bracteole. 13. Distal portion of  $\varnothing$  bract. 14-16. Lobes of perianth mouth, all drawn to same scale. (All from type.)

***Telaranea lindenberghii* (Gott.) Engel & Merr. var. *lindenberghii***

*Lepidozia subverticillata* Col., Trans. & Proc. New Zealand Inst. 18: 245. 1886. Lectotype (*nov.*): New Zealand, Waipawa Co., near Norsewood, 1885, *Colenso a. 1420* (WELT!—c. per. + sporo. + ♂); isoelectotype: (BM!—c. ♂).

*Lepidozia leuocarpa* Col., Trans. & Proc. New Zealand Inst. 21: 65. 1888 (1889). Lectotype (*nov.*): New Zealand, Waipawa Co., near Norsewood, "Shingle splitter's swamp," 1885, *Colenso a. 1320* (WELT!—c. per. + sporo.); isoelectotype: (BM!—c. per. + sporo.).

*Lepidozia minutissima* Col., Trans. & Proc. New Zealand Inst. 21: 66. 1888 (1889). Type: New Zealand, Waipawa Co., near Dannevirke, 1888, *Colenso a. 1319* (BM!, WELT = 0).

*Lepidozia oculata* Col., Trans. & Proc. New Zealand Inst. 22: 456. 1889 (1890). Type: New Zealand, Waipawa Co., South of Dannevirke, 1889, *Colenso a. 1517* (BM!—c. ♂, WELT = 0).

*Lepidozia hepaticola* Steph., Spec. Hep. 3: 592. 1909. Type: New Zealand, without specific loc., *Goebel s.n.* (G!).

*Lepidozia radiata* Steph., Spec. Hep. 6: 339. 1922, *syn. nov.* *Telaranea radiata* (Steph.) Schust., J. Hattori Bot. Lab. 26: 256. 1963. Type: New Zealand, *sin. loc.*, "inter *Colenso 1095*" (G!, WELT!—c. ♂).

Plants pale green; stems flexuous, often appearing fleshy for plant size; branches rather closely spaced, of about equal length, hardly tapering, often at right angles to main axis, with secondary branches often frequent; branches terete, not complanate, with leaves typically transversely inserted and oriented (at times weakly incurving of lobes; leaf disc 2–3(4) cells high; leaf lobes typically uniseriate to the base, the cells of uniseriate row weakly constricted at septa or sometimes with feebly protruding septa.

**DIFFERENTIATION AND VARIATION**—*Telaranea lindenberghii* var. *lindenberghii* has a distinctive aspect due to the  $\pm$  regular 1–2-pinnate branching and the rather short primary branches of roughly equal length. The leaf insertion is typically transverse and the disc is only 2 (locally 3) cells high, consisting of a basal tier of narrowly elongate cells, and a distal tier, formed by the bases of the lobes. The lobe cells are commonly moderately thick-walled, and the lobes are either straight-sided or have weakly protruding septa (Fig. 26: 4, 5) and a firm, subcapillary appearance, suggestive of *T. praenitens*. The var. *lindenberghii* is noteworthy for the high incidence of fruiting, with perianths (and often sporophytes) present in a large number

of the specimens examined, and androecia also commonly present.

Plants of *T. lindenberghii* often bear a striking resemblance to *T. pallescens*. Both species are very pale to whitish green in color, with transversely inserted, deeply dissected, handlike leaves. The branches are, often subopposite, at right angles to the main shoot, with an abundance of secondary branches. The presence of a hyaloderm and absence of *Microlepidozia*-type branching will immediately mark *T. lindenberghii*. In addition, the disc cells of *T. pallescens* are quite small, short-rectangular to quadrate, and the disc is 2–4(5) cells high.

The protologue of *Lepidozia radiata* Steph. (Stephani, 1922) describes a plant with 8-lobed leaves, and a disc only 2 cells high; Stephani's *Icones* 177 also depicts a plant with 8-lobed leaves. Hodgson (1956, p. 614) compared this species to *T. pulcherrima*, but said that "Colenso's specimen No. 1095, ex Herb. Stephani, labeled *T. radiata* is *L. tetradactyla*." Hamlin (1972, p. 284) listed this species as a synonym of *T. tetradactyla*, citing "*Colenso a. 1095* in WELT." The latter specimen is typical *T. lindenberghii* var. *lindenberghii*, with leaves 4–6-lobed and a disc 2 cells high. It is associated with *Symphogyna* sp., *Schistochila balfouriana* and *Heteroscyphus coalitus*, etc., but no other *Telaranea* species are present. We also examined the specimen at G labeled "inter *Colenso 1095*," which is also var. *lindenberghii*, a plant known to occasionally produce 7-lobed leaves but never, in our experience, 8-lobed leaves. *Lepidozia radiata* is treated here as a synonym of *T. lindenberghii*.

**DISTRIBUTION AND ECOLOGY**—Auckland Is. and New Zealand (Stewart Island and South and North Islands). The species was reported as *Lepidozia lindenberghii* in the earlier literature from Tasmania (Bastow, 1888; Hooker, 1867; Mitten, 1859); we have seen no collections of the species from Tasmania or Australia.

The plant is common throughout New Zealand in low- to middle-elevation forests (typically below 700 m, and commonly at sea level). It occurs on a variety of substrates but commonly may be found on rotted, especially decorticated wood (rather frequently on crumbly wood on the forest floor), bryophyte-covered logs, tree fern bases (e.g., *Cyathea*), shaded, clayey, mossy banks, damp leaf litter, or, less commonly corticolous (e.g., bark of *Kunzea*), etc. It often forms yellow-green, feltlike, at times dense mats.



**SELECTED SPECIMENS SEEN—NEW ZEALAND.** Without specific loc., *Cunningham*, ex hb. Pearson as *Lepidozia chaetophylla* var. *tenuis* (BM). AUCKLAND IS.: Ranui Cove, *Fineran* 1967 (CHR). MUTTONBIRD IS.: Long Island, Boat Harbour Gully, *Fineran* 732 (CHR). STEWART ISLAND: Rakiura Natl. Park, Mt Rocky summit area, 530 m, *Engel* 24310 (F); between Half Moon Bay and Deep Bay, *Hatcher* 1581 (F). SOUTH ISLAND. SOUTHLAND: Waikaia, Heriot Rd, ca. 610 m, *Child* 3924a (F); Preservation Inlet, Revolver Cove, *Allan* as *L. hepaticola* (CHR); Doubtful Sound, *Simpson* (F); Bligh Sound, Fiordland, *Simpson* H3221 (CHR); Head of Milford Sound, Fiordland, *Allison* H6594—c. per. (CHR). OTAGO PROV.: Conical Hill State Forest, near Tapanui, *Rawlings* (CHR); Taieri River, south of Dunedin, near Henley, *Allison* H5852 (CHR); Swampy Hill, Dunedin, *Child* H2644 (F); Morrisons Creek, N of Dunedin, ca. 150 m, *Child* H s.n. 146 as *T. gottscheana* (F); trail between Gunn's Hutt and Hidden Falls, ca. 30 miles SE of Lake McKerrow, *Hatcher* 668—c. per. (F); N of McKerrow River, Martin's Bay, *Hatcher* 793 (F). WESTLAND PROV.: Ship Creek, 14.5 km N of Haast River, sea level, *Engel* 21765 (F); Westland Natl. Park, Gillespies Cook River Road, between Tornado Creek and Wheland Creek, *Engel* 6587 (F); *ibid.*, trail to Lake Wombat, *Engel* 6692 (F); *ibid.*, Lake Wahapo, *Engel* 6734 (F); *ibid.*, Franz Josef Glacier Valley, Roberts Point, SW of Mt. Gunn, ca. 620–670 m, *Engel* 18095 (F); Lake Kaniere Scenic Reserve, Lake Kaniere Rd, 125 m, *Engel* 24846—c.  $\delta$  (F); Arthur's Pass Natl. Park, N of Kellys Creek near Hwy 73, N of Otira, 420–475 m, *Engel* 18359 (F); Camp Creek, W of Alexander Range, 280–440 m, *Reif* C88F—c. per., C86E—c.  $\delta$  + sporo., C111C (F); Paparoa Range, along Croesus Track, ESE of Barrytown, between Granite Creek and Fagan Creek watersheds, 450 m, *Engel* 19300—c. per. (F). OTAGO/WESTLAND PROV. BOUNDARY: Mt. Aspiring Natl. Park, summit area of Haast Pass, 570 m, *Engel* 17966 (F). NELSON/WESTLAND PROV. BOUNDARY: Paparoa Range, S side of Porarari River, E of Punakaiki, 10 m, *Engel* 19146. NELSON PROV.: Paparoa Natl. Park, Bullock Creek Road, along Bullock Creek, NE of Punakaiki, ca. 25 m, *Engel* 21618 (F); Paparoa Range, N side of Fox River in vicinity of cave, NE of Punakaiki, 15 m, *Engel* 19133—c. per. (F); Little Wanganui, W coast, ca. 15 m, *Child* H414 (F); Able Tasman Natl. Park, Porters Rock Track, ca. 915 m, *Child* H4693 (F). MARLBOROUGH PROV.: Kaiuma, Pelorus Sound, NEN of Havelock, ca. 30 m, *Child* H4461 (F). NORTH ISLAND. Without specific loc., "inter Colenso 1095," as *Lepidozia radiata*. KAPITI IS.: *Wilkinson*—c.  $\delta$  (CHR). WELLINGTON PROV.: Wellington, Eastbourne, *Butler* H96 (CHR); Wilton Bush, Mackenzie Burn to Boundry, *Mason* 36711 as *L. lindenberghii*—c. per. (CHR); Wairongomai River, *Zotov* 7231—c. per. (CHR); Tararua Mts., Ruamahanga Valley, *Zotov* 9273—c. sporo. (CHR); Ohau-iti River, *Zotov* 7261 (CHR); upper Tiritea River, *Zotov* 6873—c. sporo. (CHR); Mt. Marima, 185 m, *Zotov* 6943—c. sporo. +  $\delta$  (CHR); Tongariro Natl. Park, N side of Lake Rotopounamu, S of western side of Lake Taupo, 750 m, *Engel* 22420 (F). GISBORNE PROV.: Urewera Natl. Park, Waikareiti Track between track entrance and Lake Ruapani, N of eastern extremity of Lake Waikaremoana, 650–920 m, *Engel* 20577 (F). TARANAKI PROV.: Mt. Messenger, S of Ahititi, 185 m, *Whitehouse* 29875 (F);

Pukeiti Bush, near New Plymouth, *Hatcher* 351 (F); Waihou Bay and Raukokore River, Bay of Plenty, *O'Malley & Sainsbury* (CHR). SOUTH AUCKLAND PROV.: Whirinaki Forest Park, Waterfall Loop track, near Whirinaki River, SSW of Minginui, *Engel* 20687 (F); Roto-a-kui Bush, E of Taupo, ca. 670–760 m, *Allison* H3048—c. per. +  $\delta$ , H3246—c. sporo. (CHR); Run 95, Kaingaroa S. F. Plantation, Rotorua Region, H3050—c. per. +  $\delta$  (CHR); Mangaiti Bush, near Atiamuri, S of Rotorua, ca. 460 m, *Allison* H3049 (CHR); Puaiti Bush, S of Rotorua, ca. 490 m, *Allison* H79—c. per. +  $\delta$ , H3237—c. per. (CHR); opposite 7 mile hill on Rotorua-Atiamuri Road, *Allison* H3238 (CHR); Mamaku Plateau, W of Lake Rotorua on Rt. 5, 400 m, *Engel* 20495 (F); Rotorua Region, *Allison* H3240—c. per. (F); Ngongotaha Mt., Rotorua, *Allison* H3243—c. sporo. (CHR); southern extent of Herangi Range, plateau area S of Te Whakapatiki, W of Te Kuiti township, ca. 720–750 m, *Engel* 25145 (F); Pongakawa Valley, near coast, Bay of Plenty, *Allison* H3231—c. per. (CHR); Coromandel Peninsula, Mercury Bay, *Matthews & Langridge* 160 (CHR); Coromandel, *Berggren* s.n. (CHR); Coromandel Forest Park, Mt. Moehau, below summit of "Little Moehau," ca. 800 m, *Engel* 23648 (F). NORTH AUCKLAND PROV.: Anawhata Stream, near Auckland, Moore (CHR); Hunua, near Auckland, *Moore* (CHR); NE Waitakere Ranges, Swanson University Reserve, Tram Valley Road, 95 m, *Engel* 20417 (F); Waitakere Hills, W of Auckland, *Hatcher* 162—c. per. (F); Waitakere, ca. 120 m, *Child* H2223 (F); SE of Goat Is. and between Goat Is. and Cape Rodney, N of Leigh, 30 m, *Engel* 20266 (F); Omaha, just E of causeway to Omaha Beach, 2 m, *Engel* 20352 (F); Pakiri Scenic Reserve, SSE of Mangawhai Heads, ca. 30 m, *Engel* 20298 (F); Puketi Forest, Mokau Ridge, *Braggins* (F); Waipoua Forest, *Allison* H762—c. sporo. (CHR); Waipoua Kauri Forest, *Hatcher* 311—c. per. (F); Waipoua, track to Mahuta, ca. 305 m, *Child* H2142 (F); Waima Forest, Hauturu Highpoint Track in vicinity of summit area of Hauturu Trig, off Waitotemarama Track, 650–680 m, *Engel* 22615 (F); Omahuta Forest Kauri Sanctuary, E of Mangamuka Bridge, 260 m, *Engel* 20994 (F); Kiwanis Reserve, junction of Okahu Stream and unnamed stream, ca. 5 km S of Kaitaia, N edge of Herekino Forest area, ca. 60–80 m, *Engel* 20941 (F). GREAT BARRIER IS.: *Kirk* 169 (CHR). KERMADEC IS. RAOUL: Denham Bay, *Sykes* 1201K (F).

*Telaranea lindenberghii* (Gott.) Engel & Merr. var. *mellea* Engel & Merr.

*Telaranea lindenberghii* var. *mellea* Engel & Merr., *Phytologia* 79: 252. June, 1996 [1995]. Holotype: New Zealand, South Is., Otago Prov., near Herpert, *Allison* H5674 (CHR); isotype: (F).

Plants brownish yellow to rust brown; stems slender, straight, rather wiry; branches rather distant, often long-flagelliform, the secondary branches typically few; branches terete, not complanate, the leaves transversely oriented, somewhat handlike (at least on branches) due to incurving of lobes; leaf disc 2–3(4) cells high; lobes



not infrequently with a biseriate tier of cells between the uniseriate row and extreme base, the cells of the uniseriate row  $\pm$  thick-walled, weakly constricted or sometimes with feebly protruding septa.

**DIFFERENTIATION AND VARIATION**—When viewed by transmitted light under the compound microscope, plants of var. *mellea* are often suffused with a brownish yellow to rust-brown pigment, rather like that of honey. The plant also has a distinctive aspect, differing from the typical variety by its straight, wiry stems and distant, long-flagelliform branches. The same pigment is developed in *T. ferruginea* (p. 159) and *T. blepharostoma* (p. 129) of southern South America.

**DISTRIBUTION AND ECOLOGY**—Known only from a limited number of collections, primarily from the southern portion of South Island, and from Stewart Is. Known also from a single station in North Island, near Rotorua.

**SPECIMENS SEEN**—NEW ZEALAND. STEWART ISLAND: Kirk 600 as *Lepidozia lindenberghii* (CHR). SOUTH ISLAND. OTAGO PROV.: Conical Hill, *Rowlings s.n.* as *Lepidozia hepaticola* (CHR); Akatore, coastal S of Dunedin, Allison H5781—c. per. (CHR); same loc. Child 995—c. per. (F); Swampy Hill, Dunedin, ca. 610 m, Child H5218 (F); saddle W of road to Mt. Cargill, N of Dunedin, 500 m, Engel 17545 (F). NELSON: Stony Creek, E of Westport, ca. 150 m, Child H3556 (F). NORTH ISLAND: SOUTH AUCKLAND PROV.: Edge of Urewera Country: Run 95, beyond Rotorua, Allison H3241—c. per. +  $\sigma$  (CHR).

*Telaranea pallescens* (Grolle) Engel & Merr., comb. nov.

*Kurzia pallescens* Grolle, Rev. Bryol. Lichénol. 32: 177. 1963 (1964). *Microlepidozia quadriseta* fo. *pallescens* (Grolle) Schust., Nova Hedwigia 15: 456. 1968. Holotype: New Zealand, North Is., NW Ruahines, Otupae Station, 1948, Druce 8223 (*non vidi*).

*Kurzia quadriseta* Grolle, Rev. Bryol. et Lichénol. 32: 175. pl. 2. 1963 (1964) *non Lepidozia quadriseta* Steph., Spec. Hep. 3: 582. 1909 ( $\equiv$  *Telaranea quadriseta* (Steph.) Engel & Merr.). *Microlepidozia quadriseta* (Grolle) Schust., Nova Hedwigia 15: 456. 1968. Holotype: Tasmania, Williamsford, near Mt. Read, 1 Jan. 1900, Weymouth 5755 as *Lepidozia longiscypha* (M., *non vidi*); isotype: (G!).

Plants with the aspect of *T. lindenberghii*, prostrate and densely interwoven, rarely subcaespitose, pale whitish green or at times pure green, nitid when dry; shoots to 6 mm wide including branches. Branching irregularly 1-pinnate to  $\pm$

regularly 1–2(3)-pinnate, the branches dorsally ascending to suberect, the tips sporadically becoming flagelliform, typically with *Frullania*-type branches on one side of the main axis and *Microlepidozia*-type on the other; branch half-leaf of *Frullania*-type branches (1)2–3-lobed nearly to the base, the first branch underleaf 2–3-lobed, inserted on the lateral side of branch base or the juncture of main shoot and branch, aligned with underleaves of branch. Ventral-intercalary branches occasional; lateral-intercalary branches not seen. Stem cortical cells moderately thick-walled, in 12–16 rows, the medullary cells 15–20, somewhat smaller, thin-walled. Leaves stiffly and widely spreading, transversely inserted, symmetrically (3)4–6-lobed, 280–700  $\mu$ m wide (between tips of lobes)  $\times$  260–350  $\mu$ m long, the lobes widely divergent; branch leaves 4-lobed, subcontiguous, feebly succubously oriented. Lobes uniseriate to base, inserted on a triangular base composed of 2–3(4) disc cells, the uniseriate portion 5–6(7) cells long, the cells firm and rather thick-walled, gradually smaller distally, the cells 2–4.7:1, gradually shorter distally; cuticle smooth. Disc 10–12 cells broad at base, 2–4(5) cells high (including base of lobes). Cells of disc differentiated in size and shape from those of the lobes, compact, short-rectangular to subquadrate, 16–24  $\times$  (16)24–28(40)  $\mu$ m; cuticle smooth. Oil-bodies (Schuster, 1980, fig. 2: 2) (1)2–3 in cells of disc, 3–5 per cell in uniseriate row of lobe, weakly to distinctly botryoidal. Underleaves 4–6-lobed, often with 1 or more lobes abbreviated, terminating in a slime papilla, the disc 2–3 cells high.

Dioecious. Androeceia on inconspicuous, short, determinate, tightly spicate, ventral-intercalary branches from main shoot or terminal on rather short to long primary or (more often) secondary terminal branches; bracts concave, the disc especially so, 2–3-lobed to ca. 0.5, the lobes 2 or more cells wide at base, apiculate to short acuminate, terminating in a uniseriate row of several cells; dorsal margin of disc slightly dilated, with a few crenulations and slime papillae; antheridia 1 per bract, the stalk uniseriate. Gynoeceia on abbreviated ventral-intercalary branches from main axis; bracts of innermost series much larger than leaves, erect and ensheathing the perianth, the bracts concave, narrowly ovate; apices with 2–4 narrow lobes that terminate in a single cell or a uniseriate row of 2–3 cells, the lobes composed of  $\pm$  regularly rectangular cells, the apical end of the marginal cells sometimes feebly diverging, the margins at times with a partially or wholly later-

ally free cell, the lobe margins thus finely and sparingly crenulate-spinose dentate; lamina composed of  $\pm$  regularly short rectangular cells, the margin bordered by cells of variable shape, most long and narrow, a few only slightly longer than wide, the apical or free end of marginal cells at times divergent and forming a short projection or an apically oriented tooth, the margin irregularly and sparingly crenate-denticulate, the teeth rarely composed of more than 1 cell; bracteole similar in size and form. Perianth large, fusiform, hyaline,  $\pm$  terete below, bluntly trigonous only in the distal portion, the mouth strongly contracted and pluri-plicate, dentate-ciliate, the teeth free for varying lengths (at times ca. 0.5 of cell free), at times consisting of a uniseriate row of 2 cells; perianth unistratose to base.

Seta with 8 rows of large epidermal cells surrounding an inner core of numerous, leptodermous, smaller cells. Capsule ellipsoid-cylindric,  $985\text{--}1200 \times 490\text{--}515\text{ }\mu\text{m}$ , the wall largely 3-stratose,  $32\text{--}36\text{ }\mu\text{m}$  thick (locally 4-stratose and  $35\text{--}38\text{ }\mu\text{m}$  thick); outer layer with somewhat irregular 2-phase development, the primary cells with walls remaining colorless, the secondary walls with strong, brown, sinuous-nodular thickenings; innermost layer with cells  $\pm$  irregular in shape, with semiannular bands remote, well developed and almost always complete.

Spores  $12\text{--}14\text{ }\mu\text{m}$ , exine rather thin, honey-colored, with close vermiculate to granular-vermiculate ridges, which are often furcate but do not delimit areolae. Elaters feebly twisted,  $7.2\text{--}9.5\text{ }\mu\text{m}$  wide, bispiral, the spirals  $2.8\text{--}3\text{ }\mu\text{m}$  wide.

**DIFFERENTIATION AND VARIATION**—*Telaranea pallescens* is a rather uncommon plant, and it is most likely to be mistaken for *T. lindenbergii*, a common species in New Zealand. The two species are remarkably similar in appearance, due to their  $\pm$  wiry, bristly appearance, regularly pinnate branching and pale whitish green color. The leaves are transversely inserted and deeply 4–6-lobed, the lobes uniseriate to the base and inserted on 2 disc cells, with a disc 2–4 cells high. Differences include the presence of *Microlepidozia*-type branches and asymmetrically lobed underleaves in *T. pallescens*. The most conspicuous difference, however, may be in the basal tier of cells of the leaf disc, which in *T. lindenbergii* are thin-walled and longitudinally elongated ( $17\text{--}24\text{ }\mu\text{m}$  wide  $\times$   $40\text{--}60\text{ }\mu\text{m}$  long, Fig. 26: 2, 3) vs. small, compact and subquadrate in *T. pallescens* (ca.  $24\text{--}28\text{ }\mu\text{m}$  wide and long, Schuster, 1980, fig. 2: 9–

11). *Telaranea trilobata* differs from *T. pallescens* in the mostly 3-lobed leaves, and less strongly differentiated cells of the leaf disc.

**DISTRIBUTION AND ECOLOGY**—Known from New Zealand and Tasmania. In New Zealand it occurs sporadically, over a broad ecological amplitude (often in humid sites), from the southern part of South Island to the northern extremity of North Island. It occurs in forests of several different types on both South and North Islands. For example, on South Island the species grows in seepage areas (with *T. remotifolia*) among cliffs and boulders in a *Nothofagus menziesii* forest (Haast Pass area), on the floor of open boggy areas in a rather open *Leptospermum* scrub forest in a serpentine area (Red Hills), as well as in humid niches with the moss, *Distichophyllum kraussei*, in forest dominated by *Phyllocladus alpinus*, *Nothofagus solandrii*, *Leptospermum scoparium*, *Olearia lacunosa* and *Weinmannia racemosa* (Paparoa Range). It is present in several different types of lowland bogs, and is found, for example, in *Sphagnum-Hypolaena-Dacrydium* bogs with *Kurzia helophila*, *Megalembidium insulanum* and *Riccardia* sp. (Omoeroa River, Schuster 67–246), in pakihis along the west coast of South Island, as well as on wet soil among sedges and *Gleichenia* in an ecotonal area between a *Typha* swamp and a *Leptospermum* swamp (south of Cape Reinga). On North Island, it grows, for example, over soil on stream banks just above water level in old *Kunzea* forest with *Agathis* and *Phyllocladus trichomanoides* (Waitakere Ranges) and on well-shaded, bryophyte-covered stream banks, again not far above water level, in kauri forest with *Weinmannia silvicola* (Waipoua Forest). The Aongatete River plant (Kaimai Range) occurred at 425 m on soil over bedrock deep in a pocket-like drainage channel at the river margin where it occasionally may be inundated. The river is at the bottom of a narrow ravine with a dense overhang of *Blechnum* and *Freyinetia baueriana* in a mixed *Dacrydium cupressinum* and *Beilschmedia tawa* forest with a *Cyathea* understory. The Mt. Moehau plants were found at ca. 800 m growing intermingled in *Sphagnum* on the bank of a very moist seepage area in a mosaic of *Sphagnum* bog and small communities of shrub heath, including *Dracophyllum recurvum*, *Lepidothamnus laxifolius*, *Coprosma foetidissima*, *Oreobolus pectinatus*, *Corokia*, and occasional stunted *Weinmannia silvicola* and stunted *Dacrydium cupressinum*.

The species extends into the subalpine and alpine zones and is present in a variety of humid

sites, including the sides of rills and watercourses, soil on tussock bases and protected shaded niches under shrub cover. In the Arthur's Pass area it is found in a mosaic of subalpine scrub and alpine vegetation at the sides of tussock plants that grow at the edges of pools and, interestingly, *T. pallescens* may form large masses semisubmerged in the pools. In the alpine vegetation of Gertrude Valley (South Island) it occurs on protected ledges in seepage areas of cliffs.

SELECTED SPECIMENS SEEN—NEW ZEALAND. SOUTH ISLAND. SOUTHLAND PROV.: Fiordland Natl. Park, plateau and slopes below Mt. Burns, E. of Borland Saddle, S of South Branch of Borland Burn, W of Monowai, 1225–1320 m, *Engel 18572* (F); *ibid.*, head of Gertrude Valley, on track to Gertrude Saddle, NE of Homer Tunnel, 1940–1970 m, *Engel 21984*. OTAGO PROV.: Fiordland, N of McKerrow River, Martin's Bay, near sea level, *Hatcher 805* (F); Maungatua, W of Mosgiel, ca. 760 m, *Child 4120* (F). WESTLAND PROV.: Ca. 3 km. along Cascade Rd, just W of Jackson River, SW of confluence of Jackson and Arawata Rivers, 75 m, *Engel 24761* (F); bog N of Omoroa River, S of town of Franz Josef, toward Weheka Hills, *Schuster 67-246*—c. ♂ (F); 10 km S of Greymouth, ca. 150 m, *Child H4945* (F); Paparoa Range, ridge immediately N of Sewell Peak, 890 m, *Engel 19032*—c. ♂ + sporo. (F); Mt. Aspiring Natl. Park, Cross Creek, 1 km N of Haast Pass, 510 m, *Engel 21877* (F). WESTLAND/CANTERBURY PROV. BOUNDARY: Arthur's Pass Natl. Park, Dobson Nature Walk, summit area of Arthur's Pass, 920 m, *Engel 22029* (F); *ibid.*, Arthur's Pass, near Temple Basin Ski Area, *Engel 6500B*—c. per. (F). NELSON PROV.: Paparoa Range, N flank of Mt. Euclid, ca. 1–1.5 km E of Morgan Tarn, 915–1000 m, *Fife 6482* as *Kurzia quadriloba* (F). MARLBOROUGH NEAR BOUNDARY WITH NELSON PROV.: Mt. Richmond Forest Park, Red Hills, track to Maitland Hut, NE of St. Arnaud, ca. 700–920 m, *Engel 21471*—c. ♂ (F). NORTH ISLAND. TARANAKI PROV.: Pukeiti Bush, near New Plymouth, *Hatcher 226* (F). SOUTH AUCKLAND PROV.: Kaimai Range, Aongatete River, upstream from intersection of North-South Track river, 425 m, *Engel 23623* (F); Coromandel State Forest Park, ridge between Webb Creek Track and Billy Goat Track, 510–540 m, *Engel 22347* (F); *ibid.*, Mt Moehau, below summit of "Little Moehau," ca. 800 m, *Engel 23657* (F). NORTH AUCKLAND PROV.: NE Waitakere Ranges, Swanson University Reserve, Tram Valley Road, 95 m, *Engel 20487* (F); McElroys Bush Reserve, western side of Mahurangi Harbour on Cowan Bay Road, 95 m, *Engel 20382* (F); Waipoua Forest, Waikohatu Stream at Waikohatu Kauri Bridge, 290 m, *Engel 22640* (F); Omahuta Forest Kauri Sanctuary, E of Mangamuka Bridge, 260 m, *Engel 21013* (F); track to Te Werahi Beach, directly S of Cape Reinga, ca. 10 m, *Engel 20882B* (F).

*Telaranea trilobata* (Schust.) Engel & Merr., comb. nov.

*Kurzia quadrisetata* var. *trilobata* Schust., J. Hattori. Bot. Lab. 48: 363. f. 3. 1980. Holotype: New Zealand, North Is., Tongariro Natl. Park, Soda Springs, head of Mangatepopo Stream, near saddle between Mts. Ngauruhoe and Tongariro, ca. 4500 ft., *Schuster 5110a* (F).

Plants light green to grass green, with whitish stems, in densely interwoven mats or caespitose and erect, nitid when dry; shoots to 5 mm wide (including branches). Branching irregularly and rather sparingly 1-pinnate, with branches of the *Frullania*-type on one side, *Microlepidozia*-type on the other, the branches suberect to ascending; branch half-leaf of *Frullania*-type branch undivided to 2-lobed nearly to base, the first branch underleaf undivided to 2–3-lobed, inserted on the ventral-lateral side of branch base or the juncture of main shoot and branch and aligned with underleaves of branch; first appendage (ventral half-leaf) of *Microlepidozia*-type branch bilobed or undivided. Ventral-intercalary branches occasional, leafy or geotropic and stoloniform; lateral-intercalary branches occasional to rather freely produced. Stem with cortical cells moderately thick-walled, in 9–12 rows, larger than the medullary cells, which are thin-walled, in 6–7 to 12–14 rows. Leaves strongly spreading, approximate, transversely inserted, symmetrically 3(4)-lobed, 350–475  $\mu\text{m}$  (500–550  $\mu\text{m}$  wide in 4-lobed leaves)  $\times$  350–450  $\mu\text{m}$  long, the lobes divergent; branch leaves subcontiguous, weakly succubously oriented, mostly 3-lobed. Lobes ciliiform, uniseriate to the base, inserted on a triangular base composed of 2–4 cells, sporadically with an additional biseriate tier above the base, the uniseriate portion 4–5 cells long, the lobe cells elongated (2–3:1), gradually shorter distally, rather thick-walled; cuticle smooth or finely striate papillose. Disc 6–8 cells broad at insertion, 2(3) cells high, including basal cells of lobes. Cells of disc not much differentiated from lobe cells, oblong to rectangular, 22–30  $\mu\text{m}$  wide  $\times$  48–64(72)  $\mu\text{m}$  long; cuticle smooth or finely striate papillose. Underleaves 3(4)-lobed, the lobes mostly 4 cells long, uniseriate or 2-seriate in basal tier, formed of elongated cells as on leaves, the middle lobe often abbreviated, terminating in a slime papilla; disc 6–8 cells wide, 1–2 cells high, the cells small and  $\pm$  isodiametric.

Dioecious. Androeceia not seen. Gynoeceia (only juvenile known) on short lateral-intercalary branches.

DIFFERENTIATION AND VARIATION—*Telaranea*

*trilobata* most closely resembles *T. pallescens*, differing chiefly in the predominantly 3-lobed leaves and less sharply differentiated disc cells. The plants are regularly and suboppositely branched, with *Microlepidozia*-type branches on one side of the shoot and *Frullania*-type on the other. The underleaves in *T. trilobata* are dissimilarly 3–4-lobed, with 1–2 lobes abbreviated and ending in a slime papilla, and like the leaves, have a distinct basal tier of cells at the base of the disc. The cortical cells of the stem are in 9–12 rows, with 6–7 to 12–14 rows of medullary cells.

**DISTRIBUTION AND ECOLOGY**—New Zealand, where known from only a few collections, all in humid microniches. On Stewart Island the species was found near sea level in a mosaic of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium*-*Dracophyllum* heath to 1–2 m tall and dense communities of *Gleichenia dicarpa* and *Empodisma*. At this site the species occurred on the floor under very dense *Gleichenia* cover adjacent to a water channel. In the southern sector of the South Island the species occurred at 680 m on a protected rock face at the margin of a waterfall within a *Nothofagus* forest (Southland Prov., Fiordland Natl. Park, above South Branch of Borland Burn, Engel 18735). In Mt. Aspiring Natl. Park the species occurred at 430–480 m on vertical, dripping, cliff faces under *Blechnum* cover in a rich forest dominated by *Nothofagus menziesii* (Otago Prov, Blue Valley Track, above Blue River just N of confluence with Makaroa River, Engel 21906). In Tongariro Natl. Park (North Island) it occurs over soil on the lip of a stream bank within a forest dominated by *Nothofagus solandri* var. *cliffortioides* (Blyth Track, ca. 0.5 km from Ohakune Mt. Road, ca. 1230 m, Engel 21312). The type was growing at 1370 m on moist volcanic soil in rocky areas along a stream, in a subalpine open area, associated with *Temnoma quadrifidum* and *Triandrophyllum subtrifidum*.

**SPECIMENS SEEN**—NEW ZEALAND. STEWART ISLAND: Rakiura Natl. Park, Fresh Water Swamp, track to Mason's Bay, ca. 1 km W of Freshwater Hut, 5 m, Engel 24394—c. ♂ (F). SOUTH ISLAND. SOUTH-LAND PROV.: Fiordland Natl. Park, 11.3 km. by road WNW of Borland Lodge, above South Branch of Borland Burn, W of Monowai, 680 m, Engel 18735 (F). OTAGO PROV.: Mt. Aspiring Natl. Park, Blue Valley Track, above Blue River just N of confluence with Makaroa River. 430–480 m, Engel 21906 (F). NORTH ISLAND. WELLINGTON PROV.: Tongariro Natl. Park, Blyth Track, along small stream ca. 0.5 km from Ohakune Mt. Road, ca. 1230 m, Engel 21312 (F); *ibid.*, Tar-

anaki Falls Track, E of Whakapapa Village, 1240 m, Engel 22458 (F).

*Telaranea fragilifolia* (Schust.) Engel & Merr., comb. nov.

*Kurzia fragilifolia* Schust., J. Hattori Bot. Lab. 48: 364, f. 4. 1980. Holotype: New Zealand, Little Barrier Is., summit track to Mt. Hauturu, SE of summit of Mt. Herekohu, 1700–1900 ft., Schuster 57896 (F).

Plants delicate, loosely creeping to suberect, pale green, nitid; shoots to 560  $\mu$ m wide, with leaves. Branching irregularly and remotely branched, with *Frullania*- and *Microlepidozia*-type branches and lateral-intercalary branches produced; shoots occasionally becoming microphyllous, flagelliform; lateral-intercalary branches at times present nearly to the exclusion of other branch types; ventral-intercalary stolons or flagella rarely present; half-leaf of *Frullania*-type branch undivided or bilobed, the first branch underleaf undivided, inserted on ventral side of branch at base; ventral half-leaf of *Microlepidozia*-branch undivided. Stems slender and delicate, the cortical cells in 8–9 rows, faintly striolate, thin-walled, much larger than the medullary cells, which are in 6–13 rows. Main shoots and branches with 2–3 cortical cells intervening between successive leaves on either side, the leaves on prolonged, slender axes more distant, to 9 cells apart. Leaves remote, rather widely spreading, the insertion transverse, asymmetrically to  $\pm$  symmetrically 3-lobed almost to the base, the lobe bases (basal tier) biseriate, connate for ca. 0.5 or somewhat less, or the basal cells completely united, with the tier above partly united, forming a disc 1.5 cells high, occasionally with an additional biseriate tier at base of lobes; branch leaves bifid. Lobe tips caducous, at times only the basal cells of the lobes remaining, the lobes subequal to unequal, the dorsalmost lobe then somewhat shorter; lobes gradually tapering from base to apex,  $\pm$  straight, biseriate at the base (at times with an additional biseriate tier), the intact lobes with a uniseriate row of 4–6 cells; cells of basal tier 24–31  $\mu$ m wide  $\times$  48–60 up to 86–95  $\mu$ m long, the basal cell of uniseriate row 28–34  $\times$  72–84  $\mu$ m, the next cell shorter and narrower; terminal cell (in intact lobes) not distinctly shorter than the penultimate cell; lobe cells rather firm-walled, the transverse septa not projecting, the lobe straight-sided or at times weakly constricted at the septa; cuticle faintly to distinctly striolate. Underleaves

trifid, with 1–2 lobes abbreviated, consisting of a uniseriate row of 3–4 cells arising from a geminate base, terminating in a slime papilla.

Dioecious. Androecia not seen. Gynoecial branches (type) very short, all ventral-intercalary in origin.

**DIFFERENTIATION**—This species is notable for its highly fragile, caducous leaf lobes. Species of *Telaranea* with fragmenting, caducous lobes are widely separated taxonomically and geographically. They include the regional *T. perfragilis* and *T. tuberifera* (sect. *Ceraceae*), *T. mamillosa* (sect. *Cancellatae*) of New Guinea and Borneo, *T. europaea* (sect. *Telaranea*) of western Europe, and *T. diacantha* (sect. *Tenuifoliae*) of tropical America.

*Telaranea tasmanica* also commonly produces lateral- as well as ventral-intercalary branches, but differs from *T. fragilifolia* in the nonfragmenting lobes and smooth cuticle. The abbreviated disc (to 1.5 cells high) sometimes present in leaves of *T. fragilifolia* is reminiscent of the eastern North American *T. longifolia* (p. 163; compare Schuster, 1980, fig. 4: 6, *T. fragilifolia*, and Schuster & Blomquist, 1955, figs. 10, 11, as *T. nematodes*, see also Fig. 50: 3, 4).

The underleaves of *T. fragilifolia*, *T. pallescens* and *T. trilobata*, *T. blepharostoma* of southern South America (Fig. 38: 1, 3, 4), and *T. kogiana* (Grolle, 1966, fig. 3f–g) of New Caledonia and New Guinea are asymmetrically lobed, with one or more lobes abbreviated (Schuster, 1980, fig. 2, 7), as in many *Kurzia* species (see Schuster, 1969, fig. 92: 11, *K. sylvatica*). *Telaranea quinquespina* has asymmetrically bilobed underleaves with one lobe abbreviated, the other resembling the lobes of the leaves (Fig. 34: 1, 3), as do the extra-territorial *T. anomala* and *T. monocera* (sect. *Tenuifoliae*). *Telaranea herzogii* (Fig. 35: 2, 3) and *T. tasmanica* (Fig. 32: 10–14) differ in having symmetrically bilobed, caliper-like underleaves.

Schuster (1980) reported the absence of lateral-intercalary branching in *T. fragilifolia*, but in our material (Clarkson 19) lateral-intercalary branches are abundantly produced, to the almost complete exclusion of other branch types (occasional ventral-intercalary, but only 2 terminal, *Frullania*-type branches seen). In the Tasmanian plants (Jarman 99/2), only lateral-intercalary branches were observed, arising from the axil of nearly every leaf on the main axis.

**DISTRIBUTION AND ECOLOGY**—The species is known only from three stations in New Zealand

and one in Tasmania. The type (Little Barrier Is.) reportedly occurred with material of *Lembidium longifolium* Schust. on shaded, permanently moist rock walls, in transition from Kauri Forest to Tawa-Tawhere Forest. The plant from Cascade Road, Westland, occurred over soil in a protected pocket on a large vertical roadside bank at the margin of a mature *Nothofagus menziesii* forest at 45 m. The banks are bryophyte-covered (dominated by *Isotachis* sp.) with *Fuchsia excorticata* at the base of the bank. The plant from Hauraki Plains, North Island, New Zealand, occurred in ground cover with *Goebelobryum unguiculatum* and *Riccardia crassa* under *Sporodanthus ferrugineus* (Restionaceae)-dominated canopy. Other associates were *Empodisma minus* (Restionaceae) and *Leptospermum scoparium* (Myrtaceae) (see de Lange et al., 1999). The Tasmanian collection occurred with *T. herzogii* in a *Eucalyptus obliqua* wet sclerophyll forest at 130 m.

**SPECIMENS SEEN**—NEW ZEALAND. SOUTH ISLAND. WESTLAND PROV.: Ca. 10 km. along Cascade Rd. just W of Jackson River, SW of confluence of Jackson and Arawata Rivers, 45 m, Engel 24775 (F). NORTH ISLAND: Hauraki Plains, Kopuatai Peat Dome, 5 m, Clarkson 19 (F). TASMANIA. Manuka Road, W of Tahune Bridge, 130 m, Jarman 99/2 (HO).

*Telaranea tetradactyla* (Hook. f. & Tayl.) Hodgs.

*Jungermannia tetradactyla* Hook. f. & Tayl., London J. Bot. 3: 286. 1844 (3: 286 [sic] in errore pro 386). *Lepidozia tetradactyla* (Hook. f. & Tayl.) G. L. & N., Syn. Hep. 213. 1845. *Mastigophora tetradactyla* (Hook. f. & Tayl.) Trev., Mem. Ist. Lomb. Sci. Lett. III. 4: 416. 1877. *Neolepidozia tetradactyla* (Hook. f. & Tayl.) Fulf. & J. Tayl., Brittonia 11: 84. 1959. *Telaranea tetradactyla* (Hook. f. & Tayl.) Hodgs., Rec. Domin. Mus. 4: 106. 1962. Lectotype (nov.): Auckland Is., Nov. 1840, on *Jungermannia coalita*, Hooker (FH!); isolectotypes: (BM! [2 seen]).

*Telaranea longii* J. A. Paton, J. Bryol. 17: 289. fig. 1. 1992, syn. nov. Holotype: Scotland, Argyll, near Dunoon, foot of Glen Massan, Younger Botanic Garden, 40 m, Long 14231 (E!); isotypes: (E!, Herb. Paton; NY!).

Plants delicate, flexuous yet firm, procumbent, in compact, soft, silky, felt-like mats, normally silvery green to pure green; plants small, to ca. 5 mm wide, including branches. Branching somewhat irregularly 1(2)-pinnate, the branches of the *Frullania* type, typically of somewhat unequal length, complanate, the branch leaves incubously inserted and shingled; branch half-leaf bifid, usually obliquely inserted, the lobes diverging; first

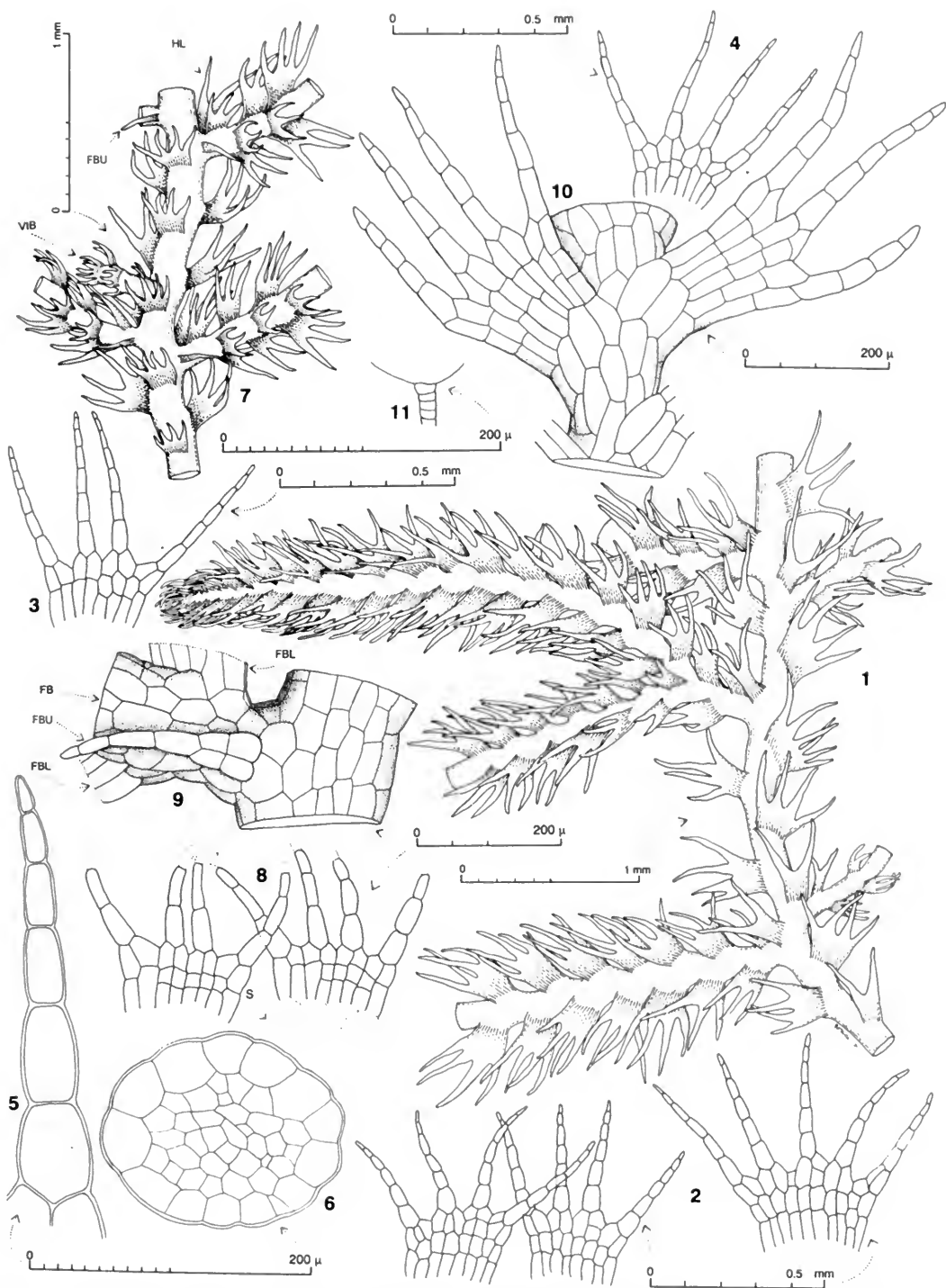
branch underleaf undivided and ciliiform, inserted on ventral side of branch at juncture of branch and main axis. Ventral-intercalary branches occasional, leafy, sometimes becoming leading shoots. Stems with cortical cells distinctly differentiated, thin walled, in 12–13 rows; cortical cells in section much larger than the numerous (ca. 18–36) medullary cells, the medullary cell walls thin. Rhizoids often copiously produced from cells of underleaf disc. Leaves on main shoot obliquely spreading, contiguous to loosely imbricate on main stems and closely imbricate on the branches, plane to moderately convex (due to broad, slight incurving of lobes), the leaves (of main axis) with insertion weakly to distinctly incubous, the branch leaves moderately to distinctly incubously inserted and oriented; leaves 220–320 (when lobes parallel) to 390–540 (when lobes divergent)  $\mu\text{m}$  wide  $\times$  490–630  $\mu\text{m}$  long, symmetric to weakly asymmetric, 4(6)-lobed to 0.6–0.75, the lobes  $\pm$  parallel to, more often, divergent, longer than disc height. Lobes ciliiform, uniseriate throughout and inserted on a triangular base composed of 2–3 disc cells or, often, with a base of (2)3–4 laterally juxtaposed cells and 1(2) additional biseriate tiers between the base and uniseriate row, the uniseriate portion (5)6(7) cells long, with cells  $\pm$  thin-walled, often weakly to moderately constricted at the septa, the basal cell of the uniseriate portion variable: 29–54  $\mu\text{m}$  wide  $\times$  67–98  $\mu\text{m}$  long (1.7–2.5:1), the next cell narrower and a little shorter, 23–43  $\mu\text{m}$  wide  $\times$  54–86  $\mu\text{m}$  long (1.8–2.7:1), the terminal cell a little smaller than the penultimate cell, rounded at the tip; cuticle smooth. Disc  $\pm$  symmetrically short cuneate, (2)3–4 cells high (from median sinus base to leaf base) including paired cells at bases of lobes, 8 cells wide in 4-lobed leaves, 12 cells wide in 6-lobed leaves; margins entire,  $\pm$  straight. Cells of disc thin-walled but firm,  $\pm$  equal in thickness to those of lobe cells, trigones lacking, the largest cells (in median sector of disc) 28–41  $\mu\text{m}$  wide  $\times$  48–64  $\mu\text{m}$  long; basal tier of disc cells often longitudinally elongate; cuticle smooth. Underleaves much smaller than leaves, strongly spreading, distant, plane to slightly incurved, 4-lobed to ca. 0.8, the lobes somewhat divergent, ciliiform, the uniseriate portion formed of 3–4 somewhat elongated

cells, terminating in a slime papilla; disc abbreviated, 2 cells high, 8 cells wide; margins entire. Rhizoid initial cells small, subquadrate, formed from some distal cells of underleaf disc.

Plants dioecious. Androecia either terminal or intercalary on short to moderately long primary or secondary *Frullania*-type branches or on short abbreviated, ventral-intercalary, spicate branches, bracts closely imbricate, dorsally assurgent, deeply concave-subcucullate, 2-lobed to ca. 0.5–0.6, the lobes acuminate to subcaudate, terminating in a uniseriate row of 4–5 somewhat elongated, thin-walled cells, the terminal cell rounded at the summit; dorsal margin of lamina somewhat dilated and incurved, crenulate and with a few slime papillae or with a 1- to several-celled, sharp tooth; bracts monandrous; antheridial stalk short, 5 cells high, uniseriate; bracteolar antheridia absent. Gynoecia strongly dorsally assurgent; bracts small for perianth size, those of innermost series closely ensheathing the perianth, concave, short ovoid, shallowly (3)4-lobed, the 2 median lobes normally larger, the median lobes subcaudate, terminating in a uniseriate cilium of 3–4 elongated cells, with a terminal slime papilla, the lateral processes shorter, the ciliiform process consisting of a single cell or a uniseriate row of 2 cells; lamina composed of  $\pm$  regularly subrectangular cells, the margins curved, with a few crenations and blunt teeth each formed by the protruding apical end of a marginal cell which is free for varying lengths, a single cell at times entirely laterally free, rarely with a tooth consisting of a uniseriate row of 2 cells, the margins thus crenate-dentate; bracteoles of innermost series similar in form and size to bracts. Perianth long emergent, terete in basal sector, obscurely trigonous and basically 3-plicate above, the perianth narrowing toward the contracted mouth; mouth fringed with 12 caudate lobes, the lobes each with a base composed of 3–5 laterally juxtaposed, moderately elongate cells and often a lateral, single-celled spinose tooth, the lobes each terminating in a cilium composed of a uniseriate row of (2)3–5 elongate, thin-walled cells, the basal 1–2 cells 11–14  $\mu\text{m}$  wide  $\times$  42–76  $\mu\text{m}$  long, (4.1–6.3:1).

Sporophyte unknown.

FIG. 27. *Telaranea tetradactyla* (Hook. f. & Tayl.) Hodg. 1. Sector of main shoot with several terminal branches, dorsal view. 2. Four- and 5-lobed leaves. 3, 4. Leaves. 5. Leaf lobe. 6. Stem, cross section. 7. Sector of main shoot (hl = half-leaf; fbu = first branch underleaf; vib = ventral-intercalary branch), ventral view. 8. Underleaves; stem



cells (= s) stippled in at right. 9. Sector of main shoot, ventral view, showing base of *Frullania*-type branch (= FB) and first branch underleaf (= fbu) (fbl = bases of first branch leaves). 10. Leaf pair of primary branch, dorsal view. 11. Antheridium. (Figs. 1, 2, 5–10 from type of *T. tetradactyla* [FH]; 3, 4 from Engel 17967, New Zealand, South Is., Otago/Westland Prov. Boundary, summit of Haast Pass, 570 m, Engel 17967; 11 from Child 991, New Zealand, South Is., Otago Prov., Akatore, 20 mi. SW of Dunedin.)



**DIFFERENTIATION AND VARIATION**—This name has previously been loosely applied to the common, widespread, and weedy plant here recognized as *T. lindenberghii* (p. 80). *Telaranea tetradactyla* s. str. has a more restricted distribution and is best characterized by the lax, incubously shingled stem and branch leaves (Fig. 27: 1, giving the plants a soft, silky aspect. The leaf disc is typically 3 (and often 4) cells high, vs. 2 (rarely 3) cells high in *T. lindenberghii*. Plants of this species are rarely encountered with perianths, and in our experience, sporophytes are unknown. This is in sharp contrast to *T. lindenberghii*, which characteristically bears perianths (and often sporophytes), as well as androecia.

Both *T. tetradactyla* and *T. lindenberghii* have the perianth mouth long ciliate (Fig. 26: 7, 9); however, in *T. tetradactyla* and *T. lindenberghii* var. *complanata*, the cells of the uniseriate cilia are thin walled and relatively short, at most 90  $\mu\text{m}$  long (Fig. 26: 10), vs. thick walled and 96–130  $\mu\text{m}$  long in *T. l.* var. *lindenberghii* (Fig. 26: 8).

A distinctive expression of *T. tetradactyla* occurs in the far south, growing in compact, silky mats, which when dry have a somewhat glasslike appearance, and shrunken leaves, reminiscent of *T. remotifolia* (p. 73). Hodgson (1956, p. 605) referred to a form *subplumulosa*, characterized by “longer, smoother, silky looking plants, mainly from the south, with a discus of at least 4 cells high, and each segment based on 2 cells,” which seems to coincide with this expression of *T. tetradactyla*. Hodgson does not formally describe this taxon, and we have not seen any of the relevant specimens cited, mostly from Stewart Is.

*Telaranea longii* is known from two localities in Great Britain, in Scotland (Argyll) and in Surrey, in both cases associated with botanic gardens, “almost certainly introduced with imported horticultural plants but country of origin unknown” (Paton, 2000, p. 59). Only ♀ plants are known. At the type locality, the plant grows on shaded logs and on moist peaty soil “on a woodland slope near the old fernery.” According to Long (pers. com., cited by Paton, 1992, p. 294) the plant was originally found on the wall of the old fernery but does not grow there now. The type agrees in almost all respects with *T. tetradactyla* (compare Paton, 1992, fig. 1; 2000, fig. 11 with Fig. 26: 9–10, 12 and Fig. 27). *Telaranea tetradactyla* is said to differ by having “almost transversely inserted lateral leaves” and “shoots always terete.” This description applies to *T. lindenberghii*, which is common and widely distrib-

uted in New Zealand, but not to *T. tetradactyla*, which has incubously inserted leaves and distinctly complanate branches.

Schuster (1963, p. 255) referred to the capsule-wall cross section in *T. tetradactyla* as being “in perfect agreement with *Telaranea* s. str.,” which we take to be a reference to *T. lindenberghii*, since that species is common and weedy, and typically produces sporophytes in abundance.

“*Telaranea trilobata*” (Schuster, Beih. Nova Hedwigia 118: 220. f. 70. 2000, *nom. inval. sin. descr. lat.*) was based on a specimen from New Zealand (Doubtful Sound, Schuster 52883). According to Schuster (p. 220), this plant is very close to *T. tetradactyla*. We have not seen the specimen.

**NOMENCLATURE**—Examination of the relevant specimens in Thomas Taylor’s herbarium (FH) and comparison with the protologue reveal that *Jungermannia tetradactyla* included two disparate elements: (1) an Auckland Is. plant, collected in November, 1840; and (2) a specimen from New Zealand, collected by Hooker in 1843, both mounted on the same sheet. The details of the gametophyte are derived from the Auckland Is. collection, as is clear from the description of the shoots as “foliis distichis patentibus laxiusculis,” and the comparison with *T. centipes*, a species with strongly incubously, almost horizontally oriented leaves. The protologue includes details of the perianth and androecia, which “occur on New Zealand specimens” (Hooker & Taylor, 1844, p. 386). The New Zealand element (2) bears abundant perianths and included sporophytes, whereas the Auckland Is. plants are barren. The New Zealand plants, moreover, are typical *Telaranea lindenberghii*, which has terete shoots and transversely inserted and oriented leaves. We therefore have no hesitation in designating element (1), the plant from Auckland Is., as lectotype of *J. tetradactyla*.

**DISTRIBUTION AND ECOLOGY**—*Telaranea tetradactyla*, as here delimited, is restricted in New Zealand to the southern sector of South Island (with only two stations on North Island, at 930–1160 m in Urewera Natl. Park), and to Auckland, Campbell, Snare, Solander, and Antipodes Is., and to Stewart Is. (fide Hodgson, 1956, p. 605). Introduced in Britain, as *T. longii*.

In New Zealand the species occurs in shaded, damp, protected niches in lower- to middle-elevation forests as well as in subalpine sites (for example, it occurs on rock, deep in protected niches between boulders at 1010–1170 m in a subalpine stream valley with *Chionochloa*, *Hebe*,



*Dracophyllum*, etc., near Mt. Burns). *Telaranea tetradactyla* is not an "abundant species" as stated by Schuster (2000, p. 216).

*Telaranea tetradactyla* has been previously understood to be an amphipacific species, with the broadest reported range of any of our *Telaranea* species: Auckland Is., New Zealand, Kermadec Is., Falkland Is. (see Engel, 1990), southern South America, Juan Fernández, Falkland Is. (Fulford, 1963a, 1966; Solari, 1987; Schuster, 2000), Fiji (Hürlimann, 1985; Miller et al., 1983), and Lord Howe Is. (Miller et al., 1983). At least some of the records of the species from the Americas are based on misidentifications of *T. plumulosa* (see Engel, 1978, p. 109). Records from Juan Fernández are probably misdeterminations of *T. fernandeziensis* (see p. 155).

Fulford (1963a, p. 77) stated that *T. tetradactyla* is "widespread in southeastern Australia [and] Tasmania . . .," and made a similar statement with regard to Australia (Fulford, 1966). Scott & Bradshaw (1986) reported the species for Victoria and South Australia, and Ratkovsky (1987) listed the species for Tasmania. We have not seen specimens of this species from either Tasmania or Australia.

SELECTED SPECIMENS SEEN—NEW ZEALAND. Without specific loc., *Petrie s.n.*, syntype of *Lepidozia hepaticola* (G). CAMPBELL ISLAND: South East Harbour, *Meurk* (F); Dent Is., ca. 100 m, *Meurk* (WELT). AUCKLAND IS.: Ranui Cove, *Fineran 1942* (CHR); No. 2 Camp, *Turbott s.n.* (CHR); NW corner of Waterfall Inlet, *Dawbin* (4 coll.) (CHR); Ewing Is., *Fineran 1347* as *T. corticola* (CHR); *ibid.*, *Black* (WELT). SNARES IS.: *Horning SA299* (CHR); Mutton Bird Creek, *Horning SA72* (CHR, F); *ibid.*, *Fineran 12pp* as *Telaranea dispar* (CHR). SOLANDER ISLAND: SE peninsula, W side, 100 m, *Johnson* as *T. gottscheana* (CHR); SW Bay, 80 m, *Johnson* as *T. gottscheana* (CHR). BIG SOLANDER ISLAND: Northeast Bay, *Wilson* as *T. gottscheana* (CHR). MUTTON-BIRD ISLANDS. LONG ISLAND: Murder's Cove, *Fineran 585* as *T. corticola* (CHR). SOUTH ISLAND. SOUTHLAND PROV.: Bluff Hill, *Allison H5162* (CHR); Open Bay Islands, *Burrows* as *Telaranea dispar* (CHR); Fiordland Natl. Park, SW of Mt. Burns, S of South Branch of Borland Burn, W of Monowai, 1010–1170 m, *Engel 18671* (F); *ibid.*, Mackinnon Pass, ca. 915 m, *Morice et al.* (CHR); *ibid.*, Moraine Creek Track, area N of Moraine Creek, W of Hollyford River, 400–530 m, *Engel 23245A* (F). OTAGO PROV.: Akatore, 20 mi. SW of Dunedin, 15 m, *Child 991*—c. per. (F); Orakanui Home, Waitati, N of Dunedin, ca. 90 m, *Child H324* (F); Frasers Gully, Dunedin, *Child 282* as *T. gottscheana*, *H283* (F); Town Belt, Dunedin, *Allison H3226* (CHR); same loc., *Child 1408* (F); Ross Creek, Dunedin, ca. 185 m, *Child H2353*—c. per. (F); Mt. Cargill, N of Dunedin, *Child 781* (F); Orakanui Home, Waitati, N of Dunedin,

ca. 90 m, *Child 321* (F); Morrison's Creek, N of Dunedin, 330 m, *Engel 17690* (F); *ibid.*, Leith Valley, Dunedin, *Allison H6803* (CHR); Allan's Beach, Otago Peninsula, *Allison H6846* (CHR); Bethune's Gully, Dunedin, *Allison H6520* (CHR). OTAGO/WESTLAND PROV. BOUNDARY: Mt. Aspiring Natl. Park, summit of Haast Pass, 570 m, *Engel 17967* (F). WESTLAND PROV.: Mt. Aspiring Natl. Park, Roaring Billy Nature area, along Haast River on road between Haast and Haast Pass, 70 m, *Engel 21859* (F). CANTERBURY PROV.: Rockwood, 610 m, *Beckett 449*, syntype of *Lepidozia hepaticola* (G). NORTH ISLAND. NEAR GISBORNE/SOUTH AUCKLAND PROV. BOUNDARY: Urewera Natl. Park, crest trail from highway 38 towards Whakataka summit, N of northern extremity of Lake Waikaremoana, 930–1030 m, *Engel 20626* (F); *ibid.*, track to Whakataka Hut from Lake Waikaremoana, N of western extremity of Lake Waikaremoana, 1160 m, *Engel 23287* (F). ANTIPODES ISLAND: Stack Bay, *Taylor 64* as *T. plumulosa* (AK 227343). SCOTLAND: Argyll, Benmore Arboretum, foot of Glen Massan, v.-c. 98, 30 m, *Long 14231*—c. young per. (F).

*Telaranea quadriseta* (Steph.) Engel & Merr., comb. nov.

*Lepidozia quadriseta* Steph., Spec. Hep. 3: 582. 1909. Type: Australia, New South Wales, East Ballina, *Watts 433* (G!).

*Lepidozia quadricilia* Steph., Spec. Hep. 6: 338. 1922, syn. nov. *Telaranea quadricilia* (Steph.) Engel & Merr., Novon 9: 344. 1999. Type: Australia, New South Wales, Clarence, *Verreaux* (com. Becherelle, Herb. Mus. Paris)—c. per. (G!).

Plants resembling *T. lindenberghii*, delicate, soft, flexuous, prostrate, pale; plants small, to 2.5 mm wide, including branches. Branching rather regularly 1–2-pinnate, the branches terete, rather closely spaced, often at right angles to main axis and subopposite, often  $\pm$  equal in length or the branching subplumose, the branches sporadically becoming flagelliform; branch half-leaf bifid; first branch underleaf undivided and ciliiform, inserted on ventral side of branch at juncture of branch and main axis. Ventral-intercalary branches occasional, forming leading, leafy shoots. Stems with cortical cells distinctly differentiated, moderately thickened, in 13 rows; cortical cells in section much larger than the numerous (ca. 42), distinctly thick-walled medullary cells. Rhizoids often copiously produced from cells of underleaf disc. Leaves rather stiff, obliquely spreading, contiguous on main stems and imbricate on the branches,  $\pm$  plane, moderately to distinctly incubous; leaves 540–600  $\mu$ m wide (between tips of lobes)  $\times$  350–440  $\mu$ m long,  $\pm$  symmetrically 4-lobed to 0.8, the lobes widely divergent, much longer than disc height. Branch leaves 4-lobed at

least initially, weakly incubous, the insertion extending dorsally almost to the midline of the branch. Lobes  $\pm$  straight, ciliiform, distinctly tapering, uniseriate to the base, inserted on a base composed of 2 short disc cells (rarely with an additional biseriate tier between base and uniseriate row), the uniseriate portion 6–8(9) cells long, the cell walls moderately thickened and firm, thickened in the corners and moderately to distinctly constricted at the septa, the basal cell of the uniseriate portion 29–35  $\mu\text{m}$  wide  $\times$  53–62  $\mu\text{m}$  long (1.6–2:1), the next cell narrower, 22–30  $\mu\text{m}$  wide  $\times$  54–70  $\mu\text{m}$  long (1.8–3.2:1), the terminal cell a little shorter than the penultimate cell, evenly tapered to the tip; cuticle finely but distinctly scabrous, roughened by minute,  $\pm$  evenly spaced, sharp prickles. Disc short-cuneate, 2 cells high (including paired cells at bases of lobes, sometimes with 1 or both basal cells of the dorsal lobe directly inserted on the stem), 8 cells wide; margins entire, straight. Underleaves much smaller than leaves, 4-lobed nearly to base, the lobes ciliiform, the uniseriate portion formed of 2(3) short to somewhat elongated, often bulging cells, the lobes terminating in a slime papilla; disc abbreviated, 2 cells high, 8 cells wide; margins entire. Rhizoid initial cells small, subquadrate, formed from some or all cells of underleaf disc. Branch underleaves 2–3-lobed, rather large and at times approaching the branch leaves in size. Cells of disc (basal tier) somewhat thinner-walled than lobe cells, trigones lacking, 20–26  $\mu\text{m}$  wide  $\times$  41–50  $\mu\text{m}$  long; cuticle smooth.

Plants dioecious. Androecia on short to moderately long primary *Frullania*-type branches with up to 4 pairs of normal vegetative leaves, subspicate; bracts loosely imbricate, dorsally assurgent, moderately concave, 2-lobed to ca. 0.6, the lobes subcaudate, abruptly narrowing from a base of 3–4 laterally juxtaposed cells to a uniseriate row of 4–5 moderately elongated cells, the terminal cell tapering to the summit, the lobe cells papillose like the leaves; dorsal margin of lamina slightly dilated, with a small tooth; bracts monandrous; antheridial stalk short, uniseriate; bracteolar antheridia absent. Gynoecia feebly dorsally assurgent, scarcely swollen at base; bracts of innermost series closely ensheathing the perianth, concave, elliptic, irregularly divided to ca. 0.5; lobes unequal in size, caudate, terminating in a uniseriate cilium of 7–8 elongated, thick-walled cells that resemble those of the leaf lobes, without a terminal slime papilla; bracteole of innermost series similar in form to bracts, but slightly smaller. Peri-

anth  $\pm$  terete in basal sector, obscurely trigonous above; mouth with ca. 10 caudate lobes, the lobes each with a base composed of 2–4 laterally juxtaposed, elongate cells, the lobes each terminating in a uniseriate row of 7–8 elongate, thick-walled cells, the basal cell 26–36  $\mu\text{m}$  wide  $\times$  139–173  $\mu\text{m}$  long (4.7–6:1), the septa weakly projecting; lateral cells of lobe base often with their distal end protruding to form a small tooth, or prolonged into one or more slender accessory cilia that are much narrower than the lobes and ca. 0.5 their length.

Sporophyte not seen.

**DIFFERENTIATION AND VARIATION**—This species is similar to *T. lindenberghii* but is distinguished by the incubously inserted stem leaves (Fig. 28: 1), the longer leaf lobes with often distinctly constricted septa, and the scabrous cuticle (Fig. 28: 3). As in *T. lindenberghii*, the leaf disc is only 2 cells high, consisting of a single tier of cells, plus the basal tier of the lobes. The uniseriate row of the lobes of the  $\varnothing$  bracts is much longer, 7–8 cells long and without a terminal slime papilla in *T. quadriseta* vs. only 2–4 cells in *T. lindenberghii*, with a terminal slime papilla.

For comparison of *T. quadriseta* with *T. granulata*, another species with a scabrous cuticle, see under that species.

Stephani's illustration (Icones, *Lepidozia*, 106) depicts a leaf with a disc 2 cells high and lobes with a uniseriate row 7–9 cells long. A young perianth and a  $\varnothing$  bract and bracteole are also illustrated.

**DISTRIBUTION AND ECOLOGY**—Known only from the types of *L. quadriseta* and *L. quadricilia*, and from a few collections from Queensland. At the Paluma site (NE of Townsville, 18° 59' S, 146° 13' E), the species occurs over rotten logs in a montane notophyll (*Cardwellia*) rain forest. The plant from Browns Creek (26° 32' S, 152° 56' E) was collected at 40 m on bare wood of a rotting log in a wet sclerophyll forest. Stephani (1922) described *T. quadricilia* as caespitose, growing in tufts on bark. The label of the type of *T. quadriseta* bears the notation, "Swamp, Heath."

**NOMENCLATURE**—*Lepidozia quadricilia* Steph. (1922) was transferred to *Telaranea* by Engel and Merrill (1999), however *Lepidozia quadriseta* Steph. (1909) proves to be an older name for this species. Grolle (1963, p. 175) listed *L. quadriseta* Steph. as a synonym of *T. tetradactyla*. Grolle's *Kurzia quadriseta* (1963), also a *Telaranea*, is treated here as *T. pallescens*, based on *Kurzia*

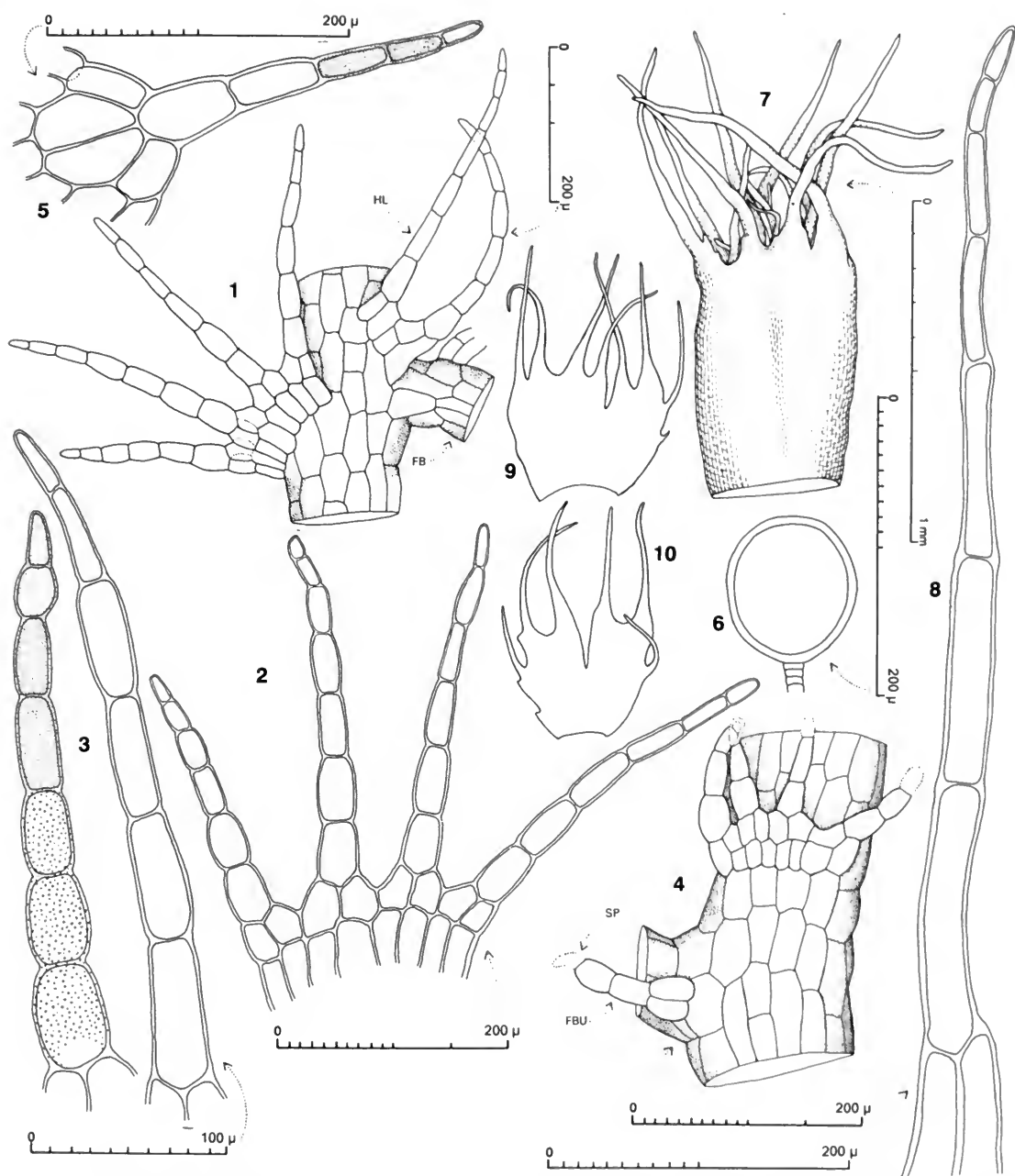


FIG. 28. *Telaranea quadriseta* (Steph.) Engel & Merr. 1. Leaf, *in situ*, with base of *Frullania*-type branch (= FB) and half-leaf (= HL); dorsal view. 2. Leaf (cuticular detail not shown). 3. Leaf lobes, cuticular detail shown for lobe at left. 4. Sector of main shoot showing underleaf and base of terminal branch (FBU = first branch underleaf; sp = slime papilla). 5. Lobe of ♂ bract, roughened cuticular shown in part. 6. Antheridium. 7. Distal portion of perianth. 8. Lobe of perianth mouth. 9, 10. Innermost ♀ bract and bracteole, respectively (after Stephani Icones, *Lepidozia* no. 106). (All from type of *Lepidozia quadricilia*.)

*pallidescens* Grolle, a name he published simultaneously.

NOTE—East Ballina, the type locality, is located at 28° 52' S, 153° 34' E. The type locality of *L. quadricilia*, "Clarence," most likely refers to the Clarence River region (ca. 29° 34' S, 152° 43' E) in north-eastern New South Wales (David Meagher, Surry Hills, VIC, Australia, *in lit.*).

SPECIMENS SEEN—AUSTRALIA. QUEENSLAND: H Track, Paluma, NE of Townsville, *Meagher 01064*—c. ♂ (F); Browns Creek, Dam road, W of Paluma, *Meagher 1128*—c. young ♀ (F); Birthday Creek, 3.5 km W of Paluma, *Leaver & Fagerberg s.n.*—c. ♂ (F); Yandina, 40 m, *Windolf 655B* as *T. ?dispar* (MELU).

### *Telaranea* sect. *Telaranea*

*Kurzia* subg. *Nanolepidozia* Schust., J. Hattori Bot. Lab. 48: 353. 1980. Type: *Lepidozia bisetula* Steph.

### *Telaranea martinii* (Hodgs.) Schust.

*Lepidozia martinii* Hodgs., Trans. Roy. Soc. New Zealand 83: 602. pl. 1, f. 11. 1956 ("martini"). *Telaranea martinii* (Hodgs.) Schust., J. Hattori Bot. Lab. 26: 256. 1963. Holotype: New Zealand, North Is., road to Dawson Falls, Mt. Egmont, 2000–3000 ft., Jan., 1955, *Hodgson 10220* (MPN!—c. ♂ + sporo.).

Plants delicate, flexuous yet firm, loosely procumbent, pale green, nitid; plants small, the main shoots (595)600–840  $\mu\text{m}$  wide. Branching sparingly and irregularly 1-pinnate, the branches of the *Frullania* type, rarely flagelliform; branch half-leaf undivided and subulate to  $\pm$  narrow-linear, very rarely bilobed, usually obliquely inserted; first branch underleaf at base of branch,  $\pm$  symmetrically or somewhat asymmetrically bilobed, typically consisting of a slender, divergent lobe with a uniseriate row of 3 rather elongate cells, the tip cell lacking a slime papilla, and a shorter, often  $\pm$  appressed lobe aligned with the branch and consisting of (1)2 rather short cells, the tip cell with a slime papilla. Ventral-intercalary branches occasional, leafy or flagelliform. Stems with cortical cells distinctly differentiated, thin walled, in 9 rows of cells much larger than those of the medulla; medullary cells thin-walled, consisting of an outer row of 6(7) cells and, within, a core of 3 cells that are smaller than those of the outer ring. Rhizoids sparsely developed, from either tier of underleaf disc cells. Leaves on main shoot widely spreading, contiguous to feebly imbricate both on main stem and branches, plane or nearly so, the insertion distinctly incubous both

on main stems and branches; leaves 175–525  $\mu\text{m}$  wide  $\times$  330–455  $\mu\text{m}$  long,  $\pm$  symmetric to weakly asymmetric (the ventral lobe sometimes weaker), 3-lobed to 0.5–0.7 (exceptionally with some 4-lobed leaves, 2-lobed on branches and weaker sectors of main shoot), the lobes divergent, longer than disc height. Lobes narrowly attenuate to ciliiform, consisting of a uniseriate row of (2)3–4(5) cells inserted on a triangular base composed of 2–3(4) laterally juxtaposed cells, often with 1(2) additional biseriate tiers between lobe base and uniseriate row in 1 or more lobes (particularly the dorsal and middle lobes), the cells of uniseriate portion thin-walled, not or weakly constricted at the septa and somewhat thickened in the corners, the basal cell of the uniseriate portion 28–32  $\mu\text{m}$  wide  $\times$  62–84  $\mu\text{m}$  long (2.4–2.8: 1), the next cell narrower and shorter, 18–22  $\mu\text{m}$  wide  $\times$  50–66  $\mu\text{m}$  long (2.7–3.3:1), the terminal cell about the same length as the penultimate cell or, often, somewhat shorter, rounded at the tip; cuticle of lobe tips finely roughened to indistinctly striate-papillose or smooth. Disc  $\pm$  symmetrically short cuneate to subrectangular, 2–4(5) cells high (from dorsal sinus base, including paired cells at bases of lobes), 6–7 (exceptionally 10) cells wide; margins entire, straight to somewhat incurved. Cells of disc thin-walled but firm, trigones minute or lacking, the largest cells 24–36(42)  $\mu\text{m}$  wide  $\times$  (30) 42–52  $\mu\text{m}$  long; basal tier of disc cells often somewhat longitudinally elongate; cuticle smooth. Oil-bodies pale, smokey grey, coarsely granular, the spherules only slightly protruding beyond membrane, the median disc cells with ca. 6, irregular in shape, narrowly to broadly elliptic to subcrescentic, at times appearing pinched, 6.3–6.8  $\times$  9.7–12.3  $\mu\text{m}$ , a few ca. 7.2  $\times$  16.4  $\mu\text{m}$ . Underleaves much smaller than leaves, widely spreading to squarrose, distant, plane, 3(4)-lobed (bilobed on weaker sectors of main shoot), the lobes often widely divergent, ciliiform, the uniseriate portion formed of 2(3) slightly elongated cells, terminating in a slime papilla, the underleaves sometimes weakly asymmetric, with one lobe longer and lacking a slime papilla; disc abbreviated, 2 cells high; margins entire. Asexual reproduction lacking.

Plants monoecious. Androecia on short, abbreviated, ventral-intercalary, spicate branches from main shoot or short to long flagelliform branches which are often copiously produced toward the shoot base; bracts closely imbricate, dorsally asurgent, deeply concave, 2–3-lobed to ca. 0.5, the lobes terminating in a uniseriate row of 2–3 cells,

the terminal cell tapering to a rounded summit; dorsal margin of lamina not dilated, entire or with a tooth toward base; bracts monandrous; antheridial stalk short, 4–5 cells high, uniseriate; bracteolar antheridia absent. Gynoecia few to profusely produced, on reduced ventral-intercalary branches from main axis or short ventral-intercalary, flagelliform branches which are often copiously produced, the mature gynoecium (usually only 1 per plant) not or only feebly dorsally asurgent, scarcely swollen and with markedly long rhizoids at base; bracts rather large for perianth size, those of innermost series closely ensheathing the perianth, concave to  $\pm$  canaliculate, broad ovate, 2–4-lobulate, the armature narrowly acute to short acuminate, terminating in 2 laterally juxtaposed cells or, more often, a single cell or a uniseriate row of at most 2(3) somewhat elongated cells, often with a terminal slime papilla; lamina composed of  $\pm$  regularly subrectangular cells, the margins curved, subentire or sparingly crenate by the divergent apical or free end of marginal cells; bracteoles of innermost series similar in form and size to bracts, or slightly smaller. Perianth long emergent, fusiform to long and narrowly subclavate, terete in basal sector, obscurely trigonous above, the perianth narrowing toward the contracted mouth; mouth crenate-denticulate by the variably free tips of the thin-walled marginal cells, at times with 1 or a few processes with a complete cell laterally free and its supporting cell free by ca. 0.5.

Seta with 8 rows of outer cells, surrounding an inner core of 12 much smaller cells. Capsule long elliptic, 23–26  $\mu\text{m}$  thick, of 3 layers, the outer layer equivalent to the combined thickness of the two inner layers; outer layer of cells (surface view) in  $\pm$  tiers, thin-walled, short-rectangular, with 2-phase development, the longitudinal walls with moderately thickened continuous sheets of pigmented material and rather weakly developed nodule-like thickenings (lending a sinuous appearance to the longitudinal walls) alternating with walls that are devoid of thickenings, the transverse walls also devoid of thickenings; intermediate layer about equal in thickness to innermost layer; innermost layer of cells somewhat irregularly narrowly rectangular, the radial walls with thin but continuous sheets of wall material, the radial walls mostly with nodular thickenings and short, spinelike extensions onto the exposed tangential wall, only exceptionally with complete semiannular bands.

Spores 11–12.5  $\mu\text{m}$ , exine red brown, with a

network of low but sharply defined vermiculate markings which coalesce to delimit areolae. Elaters  $\pm$  rigid to feebly sinuous, 8.6–9.6  $\mu\text{m}$  wide, only slightly tapering toward tips, bispiral to tips, the spirals 2.9–3.8  $\mu\text{m}$  wide.

**DIFFERENTIATION AND VARIATION**—We have placed this species in sect. *Telaranea* despite superficial resemblances to *T. tetradactyla* (s. str., see p. 91). Similarities include the soft, silky appearance of the plants, and the incubously shingled leaves on both the main axis and branches. *Telaranea martinii* differs in the uniformly 3-fid stem leaves (Fig. 29: 1–4, 6), compared to 4(6)-lobed in *T. tetradactyla* (Fig. 27: 1–4). Moreover, the branch half-leaves of *T. martinii* are undivided (Fig. 29: 1), and the first branch underleaves  $\pm$  asymmetrically bifid (Fig. 29: 6, 10). The reverse is true of *T. tetradactyla*, where the half-leaf is 2(4)-lobed (Fig. 27: 1), and the first branch underleaf undivided and ciliiform (Fig. 27: 7). The stems of *T. martinii* are more slender, with only 9 outer cells plus a medulla of 6(7) outer cells and a central strand of 3 much smaller cells (Fig. 29: 8). The stem of *T. tetradactyla* has 13 cortical cells plus numerous (ca. 36) small medullary cells (Fig. 27: 6). The perianth mouth is crenate-denticulate in *T. martinii* (Fig. 30: 1, 4, 5) vs. laciniate-ciliate in *T. tetradactyla* (Fig. 26: 9, 10).

A single collection cited below (*Engel 24402*) had some shoots with 4-lobed leaves. On these shoots the branch half-leaf was bilobed. In all other respects, the plants were typical *T. martinii*, and were autoecious.

This species is resolved as the basal species in sect. *Telaranea* (see Figs. 77, 78). Characteristics shared with other members of the section include consistently 3-lobed stem leaves, undivided half-leaves (Fig. 29: 1), and asymmetrically bifid first branch underleaves, with one lobe resembling a leaf lobe and the other shorter and ending in a slime papilla, thus resembling a normal underleaf lobe (Fig. 29: 6). *Telaranea martinii* is also monoecious (Fig. 30: 1); the other monoecious species of the genus are found almost exclusively in sect. *Tenuifoliae* and in sect. *Telaranea* (e.g., *T. longifolia* and *T. chaetophylla*, the type of the genus).

The reproductive biology of *T. martinii* is unusual. As is usual in the Lepidoziaceae, gametangia are produced on short, abbreviated ventral-intercalary branches. In this species, however, adjacent to a  $\pm$  mature gynoecial branch, additional stoloniform branches arise (Fig. 30: 1) which, in turn, may branch repeatedly and bear gynoecia.

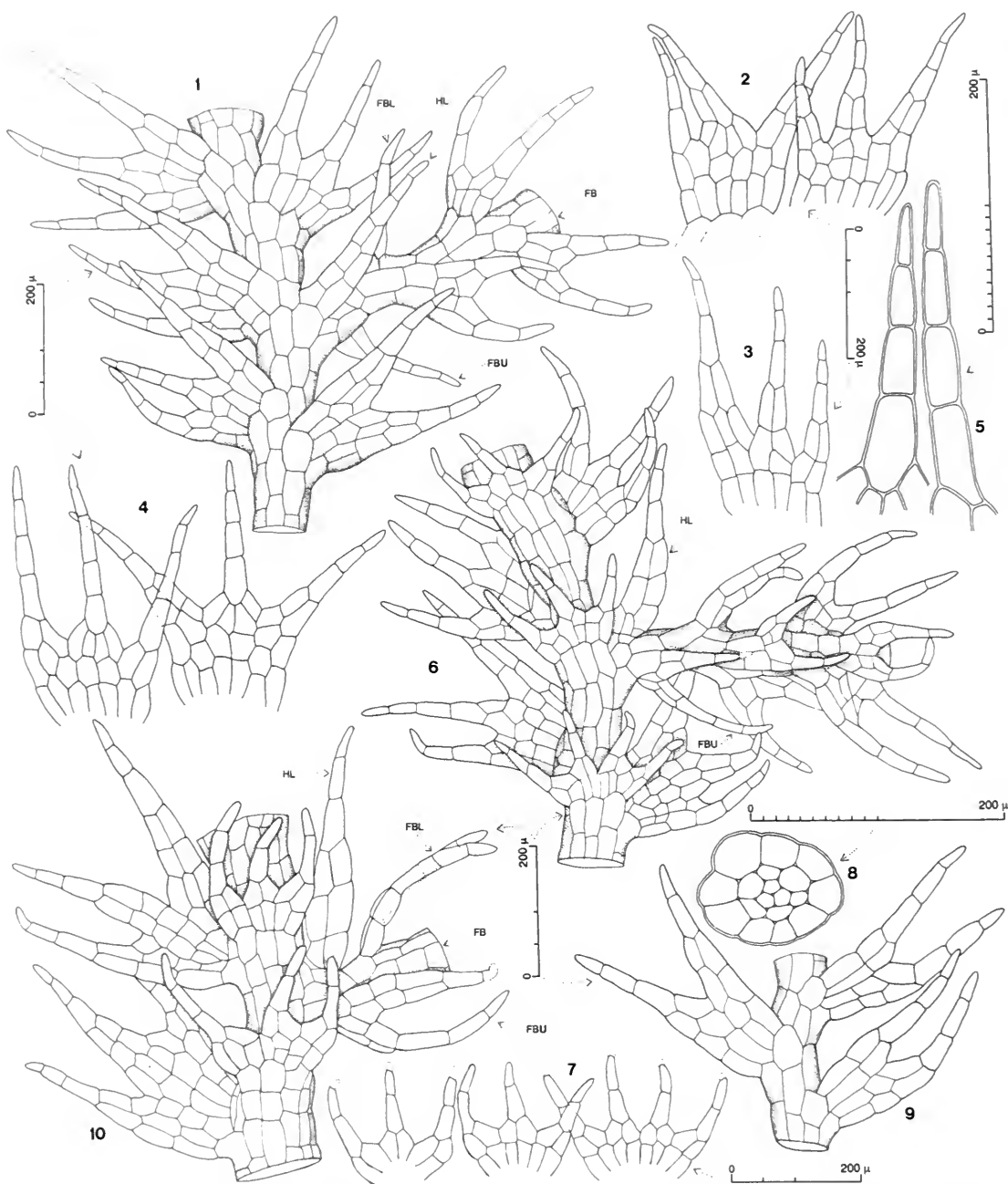


FIG. 29. *Telaranea martinii* (Hodgs.) Schust. 1. Sector of main shoot showing base of *Frullania*-type branch, dorsal view (= FB) (hl = half-leaf; fbu = first branch underleaf; fbl = first branch leaf, note 1 of the 2 lobes not in view; note also 2-lobed leaf on main shoot at right base). 2–4. Leaves. 5. Leaf lobes. 6. Sector of main shoot of somewhat weaker phase showing base of *Frullania*-type branch, ventral view (= FB) (fbu = first branch underleaf; fbl = first branch leaf; hl = half-leaf). 7. Underleaves. 8. Stem, cross section. 9. Portion of *Frullania*-type branch showing incubous insertion of the bilobed leaves. 10. Sector of main shoot showing base of *Frullania*-type branch, ventral view (= FB) (fbu = first branch underleaf; fbl = first branch leaf; hl = half-leaf). (All from type.)

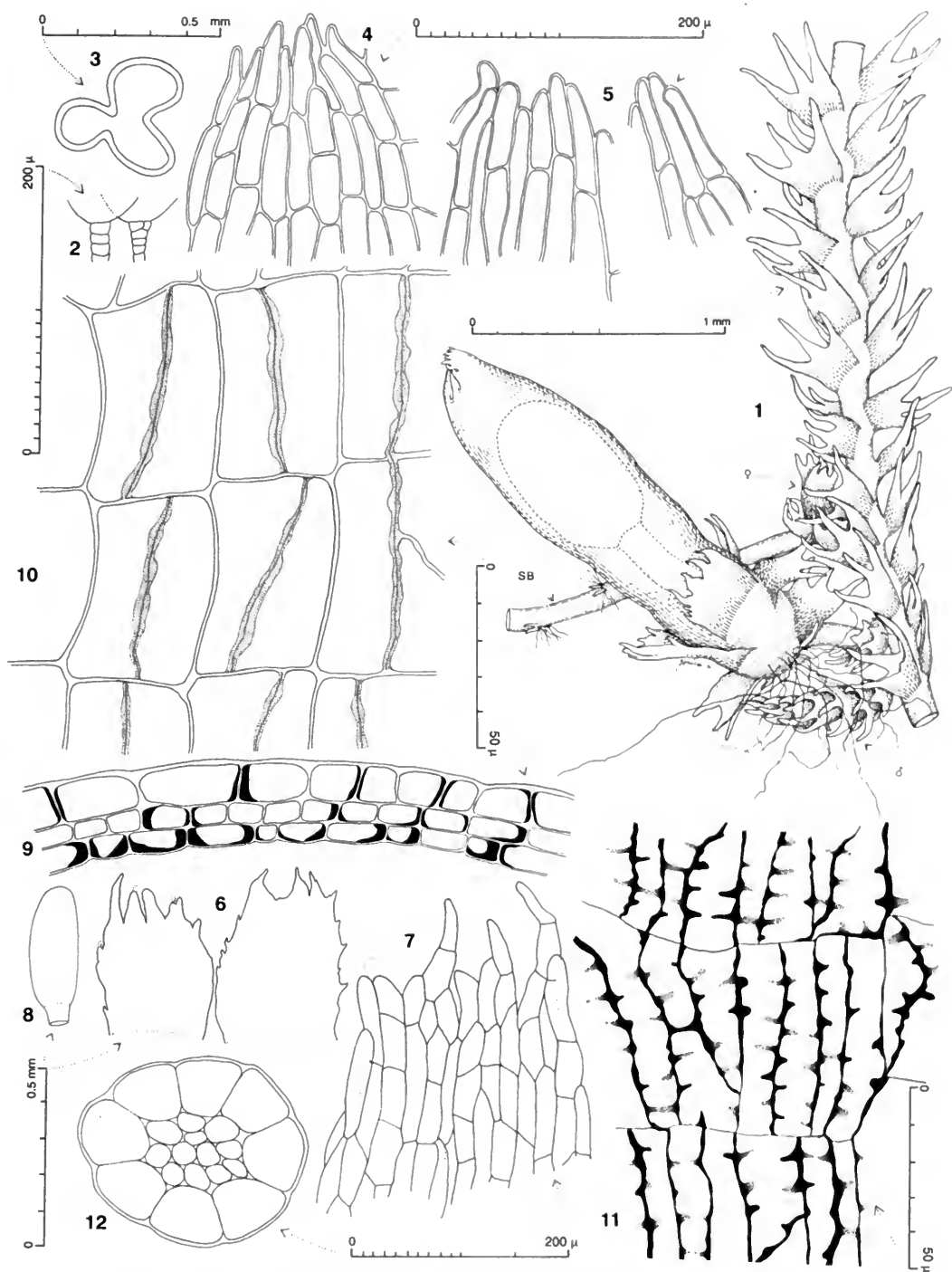


FIG. 30. *Telaranea martinii* (Hodgs.) Schust. 1. Plant showing monoecious condition (♂ = androecium; ♀ = unfertilized gynoecium; sb = stoloniform branch), dorsal view. 2. Antheridium. 3. Perianth, cross section through distal sector. 4–5. Portion of perianth mouth. 6. Innermost ♀ bracts. 7. Distal sector of ♀ bract. 8. Capsule profile. 9. Capsule wall, cross section. 10. Capsule wall, outer layer. 11. Capsule wall, inner layer. 12. Seta, cross section. (Figs. 1, 3, 5–7, 9–12 from Child 2009, New Zealand, South Is., Otago Prov., Paradise, Dart Valley; 2, 4, 8 from type of *Lepidozia martinii*.)

These additional gynoecia remain unfertilized and consist of a tight cluster of bracts. Hodgson (1956, p. 603) may have observed this phenomenon, commenting that "a short branch with imbricate, more or less appressed leaves springs like an innovation from just below the perianth. It does not appear to be a ♂ branch."

Also associated with the gynoeceal branches are 1–2 short or  $\pm$  elongate androeceal branches. Androeceal branches also may occur elsewhere on the main axis. On any given plant the number of ♀ branches is far in excess of the number of ♂ branches, and the strategy appears to be that of multiple production of gynoecia to increase the opportunity for fertilization. Curiously, in no case have we seen more than 1 perianth per plant.

**DISTRIBUTION AND ECOLOGY**—Widespread but sporadic on Stewart Island and both South and North Islands, New Zealand. On Stewart Island (track to Mason's Bay) the species was found near sea level on sandy soil under a ledge of a small bank at the track margin in a mosaic of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium*-*Dracophyllum* heath (to 1–2 m tall) and dense communities of *Gleichenia dicarpa* and *Empodisma*. The species in general occurs at lower elevations on the South Island. At Cascade Road (45 m, Westland) it occurred under the lip of projecting rock on a large vertical roadside bryophyte-covered bank at the margin of a mature *Nothofagus menziesii* forest. It is also found on vertical banks (e.g., at the forest edge near the margin of Lake Kaniere) as well as on roadside banks. It is also present over limestone outcrops and cliffs in a mixed broadleaf forest (25 m at Bullock Creek). In the Rotoiti-Rotorua lake area the species forms solid yellow-green mats in sheltered niches of stream banks in forests dominated by *Nothofagus menziesii*. It is also on silty banks in the Dart Valley (ca. 365 m, a somewhat higher elevation for the species on South Island). The species also occurs on roadside banks on North Island, but at higher elevations (610–915 m, type). The species reportedly occurs (Hodgson, 1956) in shady pockets on roadside cuttings, on earth in mixed forests, and on tree fern stems (Stewart Island).

**SPECIMENS SEEN**—NEW ZEALAND. STEWART ISLAND: Rakiura Natl. Park, Fresh Water Swamp, track to Mason's Bay, ca. 1 km W of Freshwater Hut, 5 m, *Engel* 24402—c. ♂ + ♀ (F). SOUTH ISLAND. OTA-GO PROV: Paradise, *Child* H2009—c. sporo. + ♂ (F). WESTLAND PROV.: Ca. 10 km. along Cascade Rd, just W of Jackson River, SW of confluence of Jackson

and Arawata Rivers, 45 m, *Engel* 24773 (F); Lake Kaniere Scenic Reserve, Lake Kaniere, 125 m, *Engel* 24903 (F). NELSON PROV: Paparoa Natl. Park, Bullock Creek Road, along Bullock Creek, NE of Punakaiki, ca. 25 m, *Engel* 21587 (F); Nelson Lakes Natl. Park, off Lakehead Track, near juncture with southern end of Loop Track, NE end of Lake Rotoiti, SSE of St. Arnaud, 630 m, *Engel* 22728 (F); *ibid.*, NE margin of Lake Rotorua, W of St. Arnaud, 520 m, *Engel* 21507 (F). NORTH ISLAND. NORTH AUCKLAND PROV.: Waipoua Forest, *Allison* H5923 (CHR).

### *Telaranea nivicola* Schust.

*Telaranea nivicola* Schust., Nova Hedwigia 15: 460. pl. 52. 1968. Holotype: New Zealand, South Island, above Sealy Lakes, Sealy Range, Mt. Cook Natl. Park, ca. 5,500 ft., *Schuster* 67-491b (F).

Plants very delicate (leaf cells collapsing in drying), lax, light or clear green, whitish with age, rather nitid to glistening; shoots 670–800  $\mu$ m wide with leaves. Branching rather common, irregular, of the *Frullania* type, some branches and shoot apices becoming microphyllous and flagelliform; branch half-leaf often dorsally assurgent, undivided, biseriate at base; first branch underleaf on ventral-lateral side of branch somewhat above its base, often strongly asymmetric, one segment leaf-lobe-like and 4–5 cells long, the other consisting of a single elongated cell with several small rhizoid initial cells at its base, ending in a slime papilla, or aborted. Ventral-intercalary branches at least as common as terminal branches. Stems rather succulent in appearance, with 9–10 rows of large, delicate, leptodermous, cortical cells (being ca. 3.5–4 $\times$  the radial diam. of medullary cells); medulla with (14–)18–24 rows of small, thin-walled cells. Leaves distant, transverse to feebly incubous, (230–)365–415  $\mu$ m long, asymmetric, with the ventral lobe of 3-fid leaves smaller, (2)–3-fid on leading stems, (the basal cell pairs connate for up to 0.5 their length, forming a vestigial disc 4–6 cells broad). Lobes acuminate, strongly tapered, broadly incurved, consisting of a basal pair of distinctly elongate cells and a uniseriate row of 3–4 cells (rarely biseriate for an additional tier above base), the dorsal lobe(s) usually somewhat longer, the ventral lobe of 3-fid leaves at times uniseriate to base. Cells large, turgid and barrel-shaped, the paired basal cells approaching 0.5 the length of lobe, ca. 38–40  $\times$  85–120  $\mu$ m to 50–55  $\times$  150–180  $\mu$ m; first cell of uniseriate segment 26–40  $\times$  66–86  $\mu$ m to ca. 36–55  $\times$  95–125  $\mu$ m, the terminal 1–2 cell(s) much shorter and strongly tapering to a rounded tip; cells thin-walled but firm, the transverse septa



constricted; cuticle smooth. Oil-bodies (*vide* Schuster, 1968), colorless,  $\pm$  homogeneous but not strongly glistening, fusiform to ellipsoidal to crescentic-fusiform, (4)5–9(10) per cell (except in small 1–2 distal cells), mostly  $1.5\text{--}2 \times 3\text{--}6 \mu\text{m}$  to  $2.2 \times 2.8\text{--}3.5 \mu\text{m}$  up to  $1.5\text{--}1.8(2) \times 6.5\text{--}8 \mu\text{m}$ . Underleaves small and inconspicuous, 3–4-fid; lobes usually 1–2-celled, terminating in a slime papilla, the basal cells of lobes distinctly elongated (to 3:1), inserted on a pair of laterally juxtaposed cells or with secondary divisions resulting in a disc-like tier of small, quadrate, rhizoid initials. Asexual reproduction lacking.

Androecia not seen. Gynoecia (see Schuster, 1968, fig. 52: 1, ♀ bracts).

**DIFFERENTIATION AND VARIATION**—A distinctive species, very similar to *T. pseudozoopsis* (Herz.) Fulf. of southern South America, the Falkland Is., and Juan Fernandez (Schuster, 1968, pl. 53). Both have leaf lobes of somewhat turgid cells, constricted at the septa, with marked and progressive reduction in cell size from lobe base to apex. Both species have 2- to 3-fid stem leaves. However, *T. pseudozoopsis* has a distinct disc formed of a single cell tier of slightly elongated cells, smaller than the basal lobe cells. It also has a cortex of immense inflated cells, and the underleaves are apparently always 2-lobed, vs. 3–4-lobed in *T. nivicola*.

This species resembles a small version of *T. remotifolia*, in its rather flaccid, sinuous, loosely matted stems, and the leaves shrunken and inconspicuous when dry. The plants have a iridescent, glasslike appearance when dry.

*Telaranea nivicola* is easily distinguished from *T. herzogii* by the succulent aspect of the shoots, and the short, turgid, strongly tapering leaf lobes. In addition, *T. nivicola* is a plant of the alpine snow tussock zone, whereas *T. herzogii* is a low-to middle-elevation species. In common with most species of sect. *Telaranea*, the first branch underleaf is asymmetrically lobed, with one lobe large, mimicking the leaf lobes in size and form, and the other resembling a normal underleaf lobe.

**DISTRIBUTION AND ECOLOGY**—Known only from a few, widely scattered sites on South and North Island, New Zealand. The type occurred amidst *Phyllohallia nivicola*, *Isotachis lyallii*, *Austrolophozia paradoxa*, *Allisonia cockaynii* and *Chiloscyphus cuspidatus* on dead snow tussock culms. The plant also occurs in the subalpine tussock zone at ca. 1435 m on Mt. Brewster and was removed from mats of *Allisonia cockaynii*, with in-

termingled *T. quadriseta*, *Phyllohallia nivicola*, *Jungermannia rufiflora*, *Diplophyllum domesticum*, *Metzgeria furcata* and *Isotachis lyallii*, etc. Also known from two stations in the Ruahine Mts., both in the Whanahuia Range; the Schuster plant occurred in boggy areas at 1370 m on Mt. Mangahuia.

**SPECIMENS SEEN**—NEW ZEALAND. SOUTH ISLAND: WESTLAND PROV.: Mt. Aspiring Natl. Park, slope of Mt. Brewster, facing Haast River Valley, ca. 1435 m, *Schuster 67-451i* (F). NORTH ISLAND: W Ruahine Mts., Whanahuia Range, *Druce s.n.* (ex hb. Hodgson no. 13621) (CHR); same loc., 0.5–1 mi. W of Mt. Mangahuia, 1370 m, *Schuster 67-599* (F).

*Telaranea granulata* Engel & Merr., sp. nov.

Foliis profunde 3-fidis, in surculis validis transversim insertis, ramis conspicue complanatis cellulis corticalibus late expositis, amphigastriis primis ramorum simplicibus, disco foliorum 2 (1.5) cellulas alto, amphigastriis 3-fidis foliis aequantibus; cuticula minute scabrosis insignis.

Holotype: New Zealand, North Is., North Auckland Prov., Waima Forest, Hauturu High-point Track in vicinity of summit area of Hauturu Trig, off Waitotemarama Track, 650–680 m, *Engel 22594* (F).

Plants exceedingly delicate, threadlike, minutely prickly, appressed, epiphyllous on fern leaves, pale green, highly nitid; shoots minute, to 525  $\mu\text{m}$  wide with leaves. Branching distantly and somewhat irregularly 1-pinnate, the branches of *Frullania*-type, rather short, not tapering, the main axis terete, the branches dorsiventrally flattened; branch half-leaf undivided, occasionally bilobed; first branch underleaf consistently undivided, inserted on median ventral base of branch, biseriate at base, with a uniseriate row 2–3 cells long (or uniseriate throughout), terminating in a slime papilla. Ventral-intercalary branches occasional, at times becoming leading shoots. Stems slender, the cortical cells distinctly differentiated, thin-walled but firm, in 12 rows, in section somewhat larger than the medullary cells; medullary cells in 16 rows, firm-walled. Main shoots with 3–4 cortical cells intervening between successive leaves on either side, the branches with 2 (rarely 3) cells intervening between successive leaves on either side of branch. Leaves on main shoot rather distant, stiffly spreading, lending the stem a prickly aspect, the insertion weakly incubous to subtransverse, 245–310  $\mu\text{m}$  long  $\times$  390–495  $\mu\text{m}$  wide (at

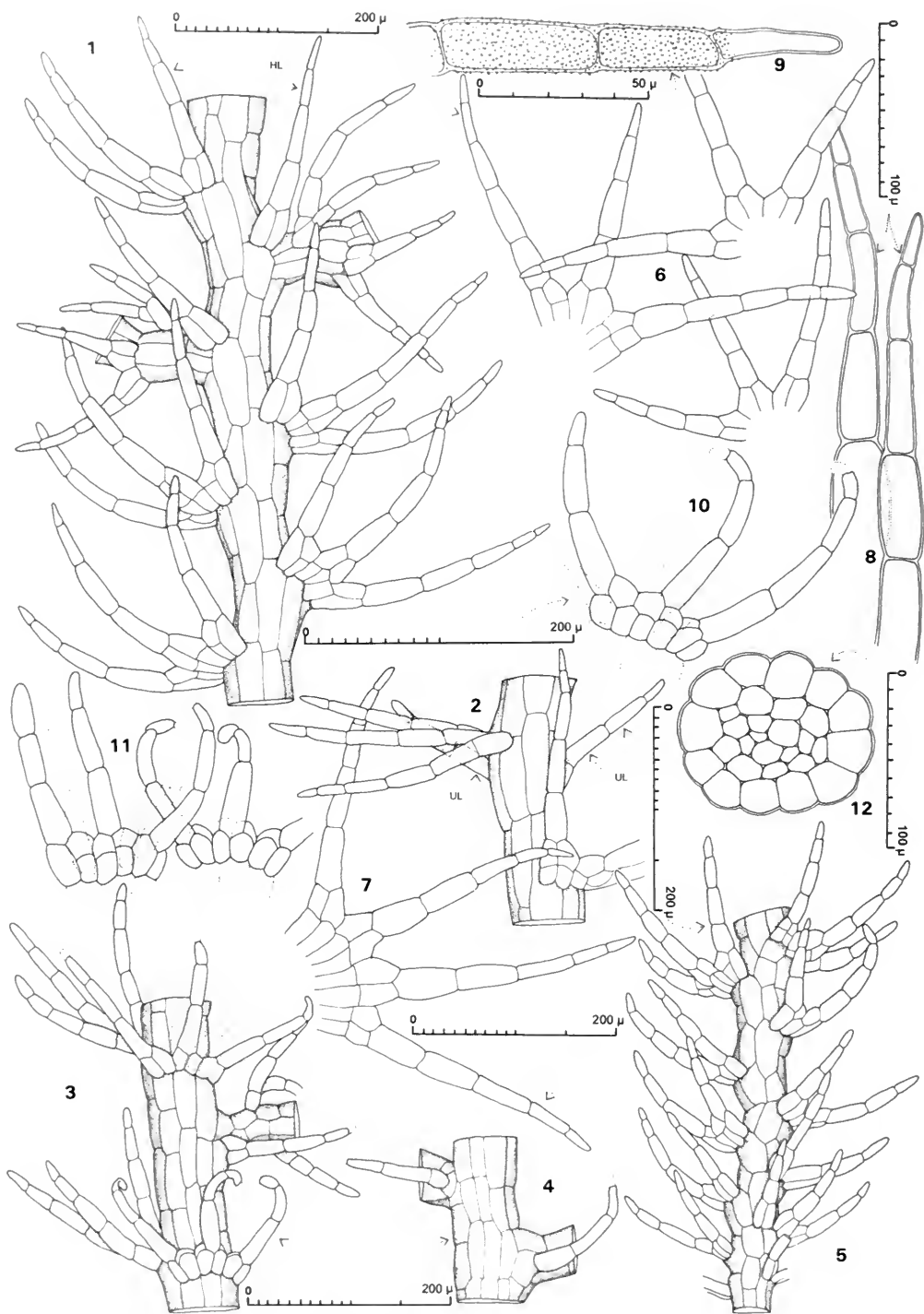


FIG. 31. *Telaranea granulata* Engel & Merr. 1. Portion of main shoot with base of *Frullania*-type branch, dorsal view; note 3 stem cortical cells between leaves, undivided half-leaf (= hl), and variation in disc of main axis leaves. 2. Portion of main shoot, dorsal view; note that portions of underleaf (= ul) are visible. 3, 4. Portions of main axis and base of *Frullania*-type branch, ventral view; note (left) first branch underleaf (= fbu) is biseriate at base or (at right) uniseriate throughout (rhizoids indicated with stipple). 5. Portion of primary branch, dorsal view. 6, 7. Three- and 4-lobed leaves of main shoot (all drawn to same scale). 8. Leaf lobes, the cuticle not shown. 9. Apical portion

tips of spreading lobes), deeply 3-lobed (4-lobed only on strongest shoots). Branch leaves 3-lobed, closely imbricate, the insertion moderately incubous, the insertion narrowly impinging on the 2 median rows of cortical cells, leaving a  $\pm$  evident median strip along the dorsal side of the branch. Lobes  $\pm$  equal in length, gradually tapering from base to apex, broadly incurved, moderately to widely divergent, from a biseriate base (at times with an additional biseriate tier), the uniseriate row 4–5 cells long; cells of basal tier 18–24  $\mu\text{m}$  wide  $\times$  26–38  $\mu\text{m}$  long, basal cell of the uniseriate row 24–30  $\times$  48–54  $\mu\text{m}$ , the next cell longer and narrower, 18–23  $\times$  50–56  $\mu\text{m}$ , the terminal cell of the lobe often appearing secondarily divided and the tip cell then distinctly shorter than the penultimate cell; lobe cells thin-walled, the transverse septa at most feebly thickened in the corners, the lobes constricted at the septa; cuticle minutely scabrous. Disc 6 cells wide (8 in 4-lobed leaves); 2 cells high (1.5 cells high, the lobe bases connate for 0.5 or as little as 0.3 their length), consisting of a single tier of cells along the insertion, plus the paired basal cells of the lobes; basal tier of disc cells often incomplete, not extending to one or both margins, the disc then 0.5 cells high at margins. Cells of disc subquadrate, 13–19  $\mu\text{m}$  wide  $\times$  24–36  $\mu\text{m}$  long; cuticle smooth. Underleaves approaching the leaves in size, symmetrically 3-lobed (4-lobed on strongest shoots), the disc consisting of the partially connate basal cell pairs of the lobes; lobes biseriate at base, with a uniseriate row of 3(4) elongate cells (the distal cell shorter and often hooked), ending in a slime papilla. Rhizoids, when present, arising from swollen cells produced by vertical division of basal cell pairs, the disc then appearing bistratose in part.

Androeceia and gynoecia not seen.

**DIFFERENTIATION AND VARIATION**—This species is unusual for its deeply divided, 3-lobed leaves (Fig. 31: 1, 3), conspicuously flattened branches, minutely scabrous cuticle (Fig. 31: 9), and large, 3-lobed underleaves, which are subequal to the leaves in size (Fig. 31: 3). The branch leaves are widely set, leaving the two dorsal rows of cortical cells broadly exposed (Fig. 31: 5), a feature that

is perhaps best developed in the type species of the genus, *T. chaetophylla* of northern South America (p. 136, Fig. 41: 2). *Telaranea lindenbergii* var. *complanata* of New Zealand has complanate-foliate branches that appear comblike, a result of the obliquely spreading, incubously oriented branch leaves. The branch leaf insertions, however, approach the midline of the branch, without leaving a conspicuous median strip. Two cells intervene between successive leaves on each side of the branch in *T. granulata* (Fig. 31: 5).

Several other Australasian species of *Telaranea* have 2–3-lobed, deeply divided leaves. In *T. herzogii*, *T. tasmanica* and similar species, however, the leaf “disc” is formed from the cells of the partially connate lobe bases, lacking a tier of disc cells along the insertion (Fig. 35: 5, 6, *T. herzogii*). In *T. granulata*, there is at least one complete tier of disc cells along the insertion, plus the basal cells of the lobes. *Telaranea trilobata* and *T. fragilifolia* have similar leaves but produce *Microlepidozia*-type branches, which are unknown in *T. granulata*. In addition, the leaf lobes of *T. fragilifolia* are caducous.

*Telaranea quadriseta* of Australia (NSW) also has leaf lobes with a minutely scabrous cuticle (Fig. 28: 3) but is not likely to be confused with *T. granulata*. Plants of *T. granulata* are more slender and distantly branched vs. regularly and suboppositely 1(2)-pinnate, with tapering to flagelliform branches in *T. quadriseta*. The leaves on the main shoot in *T. quadriseta* are incubously inserted and consistently 4-lobed (Fig. 28: 1, 2); those of *T. granulata* are subtransverse or at most only weakly incubous (Fig. 31: 1) and mostly 3-lobed, with shorter lobes (4–5 cells in the uniseriate row vs. 6–8 in *T. quadriseta*).

The underleaves of *T. granulata* are unusual in the way in which rhizoids originate. Typically, the underleaf disc is only one cell high, consisting of the paired basal cells of the lobes (Fig. 31: 3). Rhizoid initials are formed by transverse divisions of the disc cells (Fig. 31: 10), or more commonly the cells are divided vertically, the disc then appearing bistratose (Fig. 31: 3, 11).

Branch half-leaves in *T. quadriseta* are consistently bilobed (Fig. 28: 1), but in *T. granulata* they are typically undivided (Fig. 31: 1). The disc

of leaf lobe, the cuticle shown in part. 10, 11. Underleaves, the underleaf at right in fig. 11 with rhizoid initials formed but lacking rhizoids, the other underleaves with rhizoids shown in stipple (all drawn to same scale). 12. Stem of main shoot, cross section. (All from holotype.)

cells (basal tier) are smaller in *T. granulata*, 13–19 × 24–36 µm vs. 20–26 × 41–50 µm in *T. quadriseta*; the lobe cells in *T. granulata* are thin-walled (Fig. 31: 8, 9), vs. moderately thick-walled and firm, and distinctly constricted at the septa (Fig. 28: 2, 3). The stems of the latter are stouter, with 42 rows of medullary cells vs. 16 in *T. granulata* (Fig. 31: 12). Finally, *T. granulata* is epiphyllous on fern leaves, whereas *T. quadriseta* occurs on bark or rotted wood.

**DISTRIBUTION AND ECOLOGY**—Known only from Waima Forest (type), North Island, New Zealand and Three Kings Islands. The type is from a wind-pruned scrub consisting of *Coprosma grandifolia*, *Melicytus ramiflorus* and *Olearia rani* at 650–680 m. Plants occurred epiphyllous on *Hymenophyllum* sp. on a deeply shaded log with other filmy ferns. The Three Kings Islands specimen occurred on rock in a stream shaded by kanuka canopy, growing with *Distichophyllum* sp., *Balantiopsis* sp., *Riccardia* sp. and *Leiomitra* sp.

**SPECIMEN SEEN**—THREE KINGS ISLANDS: Great Island, lower Baylis Stream, Baylis Track, 60 m, *Cameron 11612b* (F).

*Telaranea tasmanica* (Steph.) Engel & Merr.

*Lepidozia tasmanica* Steph., Spec. Hep. 3: 580. 1909.  
*Telaranea tasmanica* (Steph.) Engel & Merr., Phytologia 79: 253. June, 1996 [1995]. *Paracromastigium tasmanicum* (Steph.) Schust., Nova Hedwigia Beih. 118: 382. 2000. Type: Tasmania, *Moore* (G!).

Plants exceedingly delicate, in densely interwoven tufts, with erect leafy branches arising from a prostrate, profusely branched, distantly leafy to ± leafless axis; erect leafy shoots minutely prickly, whitish green to pale grass green and nitid, to 770 µm wide with leaves. Branching common, irregular, primarily intercalary, with terminal, *Frullania*-type branches sparingly produced, confined to upright leafy shoots, at times subflagelliform; branch half-leaf undivided (rarely bilobed), setaceous, biseriate at the base; first branch underleaf at base of branch, asymmetrically bilobed, one lobe divergent and resembling a leaf lobe, biseriate at base, with a uniseriate row 4–5 cells long, the other lobe variable, with a biseriate base and 1–2 curved, cylindric cells, or resembling the other lobe but with a shorter uniseriate row, terminating in a slime papilla. *Microlepidozia*-type branching not seen. Ventral- and lateral-intercalary branches common, from prostrate axes, less commonly from lower portions of

erect shoots, leafy or stoloniform. Stems very delicate, rather stiff for plant size, the cortical cells in 6–8 rows, leptodermous, much larger than the medullary cells which are in 3 rows or in robust phases up to ca. 8 rows. Main shoots and branches with 3–4(5) cortical cells intervening between successive leaves on either side, the leaves on prostrate axes more distant, 6–8 cells apart. Leaves contiguous to weakly imbricate, rather rigid, stiffly spreading, lending the stem a prickly aspect, the insertion transverse to weakly incubous, 250–295 µm long × 220–295 µm wide (at tips of spreading lobes), 2-fid almost to the base (occasionally 3-fid in some shoots), the lobe bases (basal tier) connate for ca. 0.5 (or as little as 0.25) their length). Lobes ± equal in length (or the ventral lobe somewhat shorter), stiff, gradually tapering from base to apex, broadly incurved, moderately to widely divergent, biseriate at the base (at times with an additional biseriate tier), the uniseriate row of 4–6(7) cells; cells of basal tier 24–31 µm wide × 54–74 µm long, basal cell of the uniseriate row 25–35 × 65–83 µ, the next cell of about the same length and width; lobe cells gradually shorter and narrower distally, the terminal cell at times appearing secondarily divided and the tip cell then distinctly shorter than the penultimate cell; lobe cells rather thick-walled and firm, the transverse septa thickened in the corners but not projecting, the lobe straight-sided or at times weakly constricted at the septa; cuticle smooth or at times minutely papillose. Underleaves variable: 1) asymmetrically bilobed, one lobe with a biseriate base and a uniseriate row (3–4–)5 cells long, the other lobe shorter, biseriate at the base, with a uniseriate row of 2–3(4) cells, terminating in a slime papilla; 2) symmetrically 2- or 3-lobed, the lobes abbreviated, with a pair of basal cells, a uniseriate row of 1–2(3) lobe cells (the cells often rather short), and ending in a slime papilla; or 3) 3-lobed with one (or two) lobes abbreviated as in asymmetrically bilobed underleaves. Rhizoids sparingly produced in place of leaves and underleaves on stoloniform shoots, rare or absent on normally leafy shoots. Asexual reproduction likely by slenderly clavate tuberos swellings at the tips of stoloniform axes (or sometimes with intercalary swellings).

Androeceia not seen. Gynoeceia borne on short, stoloniform intercalary branches from lower portion of plant; bracts deeply concave, ± canaliculate distally, bilobed to 0.4 (including cilia), the lobes caudate, 6–7 cells wide at base, terminating in a cilium of 5–6 capillary cells, the terminal cell

sharply tapering to the apex, the septa thickened in the corners and projecting; lobe margins armed with 1–2(3)-celled sharp teeth, often with an opposing pair of teeth at the cilium base; disc 8–11 cells high, the disc margins armed with unicellular teeth (or marginal cells divergent at their upper ends), often terminating in a slime papilla; bracteoles 2-lobed, somewhat smaller but otherwise similar to bracts. Perianth dorsally assurgent, fusiform, strongly trigonous and deeply sulcate, tapering to the mouth, the mouth lobulate-ciliate, the cilia ca. 10 (interspersed with short few-celled teeth), flexuous, without lateral spurs, 2(3) cells wide at the base, the uniseriate portion of (3)4–5 elongate cells, the cells capillary (to 5.8:1), the septa swollen at the corners and at times weakly projecting.

Sporophyte not seen.

**DIFFERENTIATION AND VARIATION**—Distinguished from *T. herzogii* (p. 112) by the short, paired cells at the base of each lobe in both leaves and underleaves (Fig. 32: 5, 6, 9–13), the stoloniform habit of growth (Fig. 32: 1), the strongly sulcate perianth (Fig. 33: 1), and the presence of tuberous swellings on the stoloniform axes (Fig. 32: 1, 2). The leaves are bilobed, with the lobes of  $\pm$  equal length, although occasionally shoots with predominantly 3-lobed leaves (and underleaves) have been seen (Fig. 32: 4). *Telaranea herzogii* has lobes uniseriate to the base (Fig. 35: 1, 5, 6) or only sporadically one or more lobes biseriate, and the lobe cells are shorter (cells of basal tier 54–74  $\mu\text{m}$  long in *T. tasmanica* vs. (66)95–110  $\mu\text{m}$  in *T. herzogii*). The underleaves in *T. herzogii* are uniformly symmetrically 2- (rarely 3-) lobed (Fig. 35: 2–4). In *T. tasmanica* the  $\text{\text{f}}$  bracts are divided to 0.4 (Fig. 33: 2), with a disc 8–11 cells high, and the perianth cilia unbranched (Fig. 33: 6, 7). In *T. herzogii* the bracts are deeply divided, with a disc 2(3) cells high (Fig. 36: 2) and the cilia of the perianth are armed with lateral spurs (Fig. 36: 4).

Branching of the prostrate leafless axes occurs from all three merophytes in *T. tasmanica* (Fig. 32: 1). Elsewhere in the genus, lateral-intercalary branches are known in *T. fragilifolia* and *T. trilobata* (sect. *Transversae*) and *T. quinquespina* (sect. *Telaranea*). Tubers are also reported in *T. clatritexta* (subg. *Acrolepidozia*; Fig. 1: 14), *T. tuberifera* (sect. *Ceraceae*; Fig. 23: 2, 10), and *T. europaea* (sect. *Telaranea*, see Paton, 2000, fig. 9).

The growth habit of *T. tasmanica* is distinctive,

with sparingly branched, erect leafy intercalary branches arising from a tangled mass of creeping, stoloniform axes (Fig. 32: 1). In *T. quinquespina*, a similar regional species, leafy ventral- and lateral-intercalary branches originate freely from other leafy shoots, resulting in a loosely to densely interwoven, felt like mat of leafy shoots. The cells of the leaf lobes in *T. tasmanica* are broader in proportion to their length (basal cell of uniseriate row 25–35  $\times$  65–83  $\mu\text{m}$  vs. 15–25  $\times$  55–96  $\mu\text{m}$  in *T. quinquespina*). The underleaves of *T. quinquespina* are almost exclusively asymmetrically bilobed (Fig. 34: 1, 4), vs. a mixture of asymmetrically and symmetrically, 2- and 3-lobed underleaves in *T. tasmanica*, present on the same shoot. *Microlepidozia*-type branching, present in *T. quinquespina* (Fig. 34: 1, 2), has not been observed in *T. tasmanica*.

In the analysis, the half-leaf was scored as undivided; subsequently a specimen (*Jarmen 98/1*) was received in which a few symmetrically bilobed half-leaves were seen. This specimen also has more frequent *Frullania*-type branching than is usual for the species, and bears gynoeceia.

**DISTRIBUTION AND ECOLOGY**—Endemic to Tasmania. The species for the most part occurs between sea level and 430 m in riparian situations. It occurs over rock in streams or on stream banks, at times within mats of *Riccardia* spp. or *Fissidens* spp. or on soil of cliffs overlooking rivers. Also on seepage slopes with *Restio complanatus*, *R. monocephalus*, *Sprengelia incarnata* and *Hakea teretifolia*, and associated with *Goebelobryum unguiculatum*, *Campylopus introflexus*, *C. clavatus*, *Kurzia* sp., *Isotachis* sp., *Treubia tasmanica* and *Riccardia colensoi*. The sole higher-elevation station (1150 m, Lake Botsford), occurred on a lake-shore bank with *Drepanocladus fluitans*, *Fissidens apenioides* between *Carex gaudichaudiana*, *Scaevola hookeri*, *Richea scoparia*, *R. acerosa*, *Epacris gunnii*, *E. lanuginosa*, *Empodisma minus* and *Donatia novae-zelandiae*.

The report of Rodway (1916, p. 64) of *Lepidozia tasmanica* is based on misdetermined specimens of *Paracromastigum furcifolium* (Steph.) Schust. (Tasmania, Longley, Jan. 1915, leg. Rodway, HO!). Schuster (2000, p. 382) transferred this species to *Paracromastigum*, based on examination of a duplicate of this collection.

**SELECTED SPECIMENS SEEN**—TASMANIA: Cape Pillar State Reserve, Lunchtime Creek, 180 m, *Moscal 15418* as *T. herzogii* (HO); Tasman Peninsula, Long Bay Creek, 12 m, *Moscal 29675A* as *Arachniopsis herzogii*

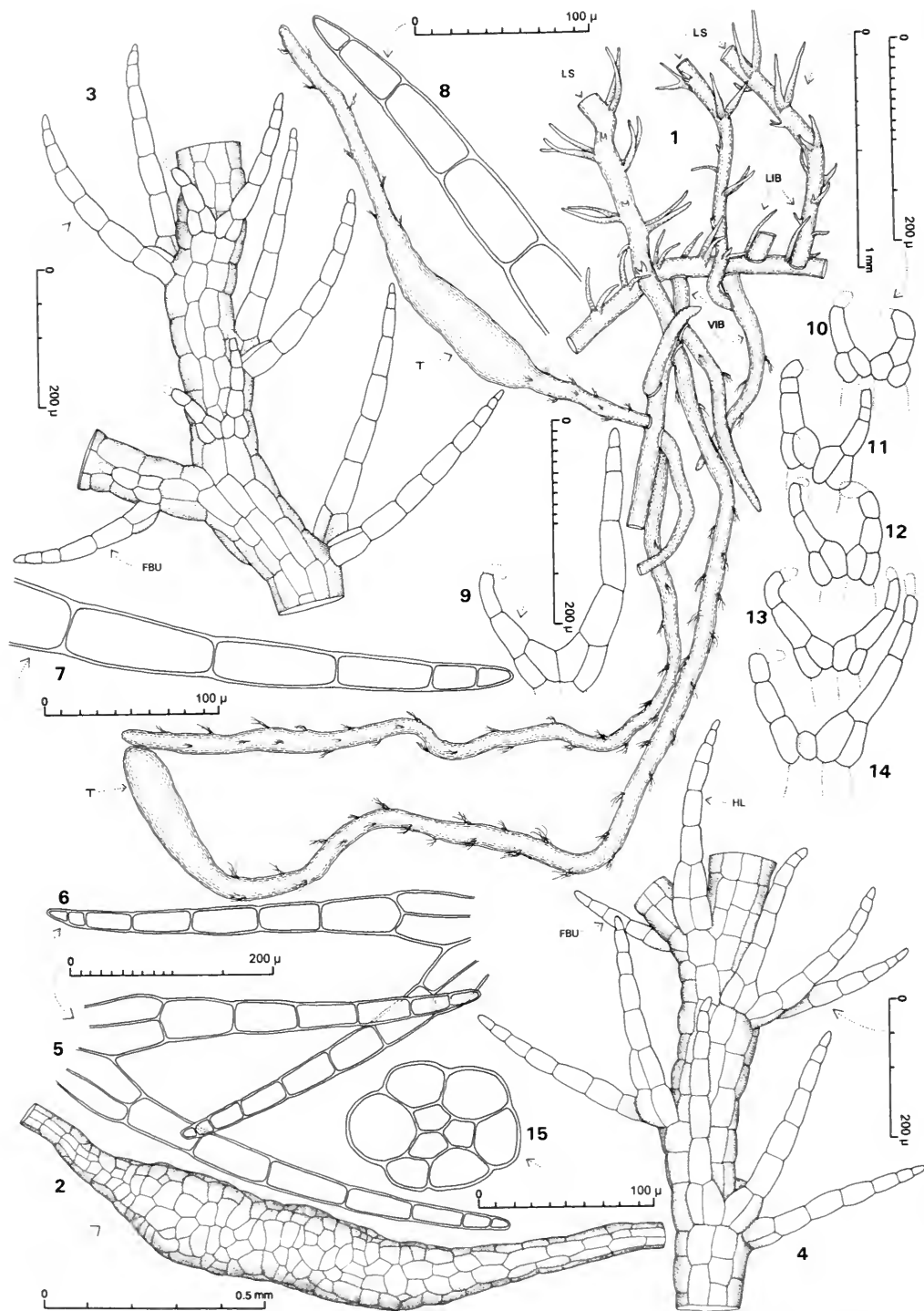


FIG. 32. *Telaranea tasmanica* (Steph.) Engel & Merr. 1. Plant showing prostrate stoloniform branches, 3 upright leafy shoots (= LS), lateral-intercalary branches (= LIB), ventral-intercalary branches (= VIB) and 2 tubers (= T). 2. Tuber drawn from portion indicated in fig. 1. 3. Portion of main shoot and base of *Frullania*-type branch (ventral view); note first branch underleaf (= fbu). 4. Portion of main shoot, dorsal view, with *Frullania*-type branch as well as 2- and 3-lobed leaves (hl = half-leaf; fbu = first branch underleaf); note leaf lobe (left side of shoot) with additional biseriolate tier. 5, 6. Leaves. 7, 8. Leaf lobes. 9-14. Underleaves (all drawn to same scale). 15. Stem, cross section. (All from type.)

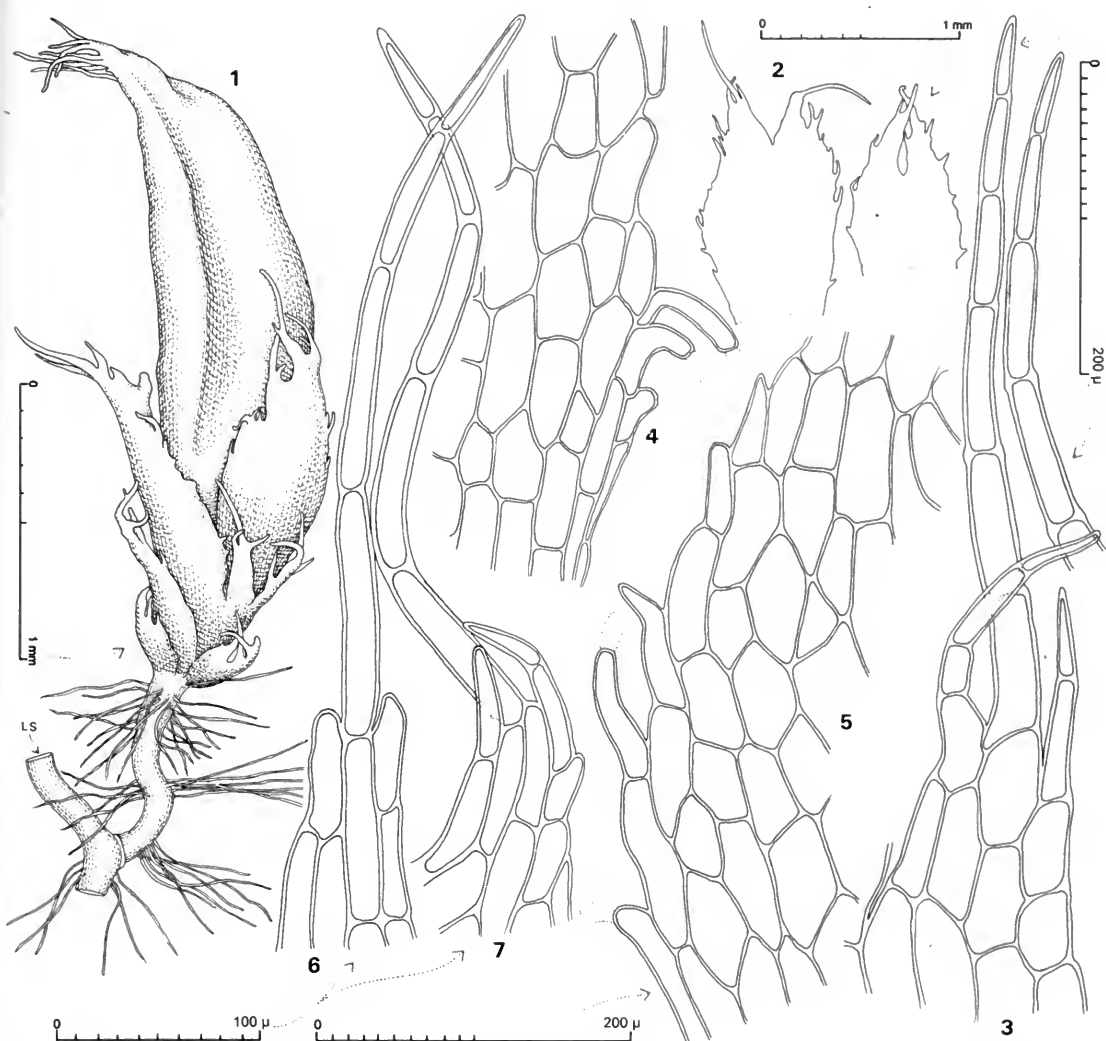


FIG. 33. *Telaranea tasmanica* (Steph.) Engel & Merr. 1. Lower portion of main, leafy shoot (= LS) with gynoeceum on short intercalary branch (dorsal aspect). 2. ♀ Bract, and to right, bracteole. 3. Lobe of innermost bract apex and to right, distal portion of a second lobe. 4, 5. Portions of the lateral margin of 2 innermost bracts. 6, 7. Lobes of perianth mouth. (All from *Jarmen 98/1*, Tasmania, Manuka Road.)

(HO); *ibid.*, Newman's Creek, Weymouth s.n. as *L. chaetophylla* (HO); Newmans Creek, "Fernleigh" property, 80 m, *Moscal 30070* as *Arachniopsis herzogii* (HO); Blackman Rivulet, 4 km W of High Yellow Bluff, 55 m, *Moscal 16977* as *T. herzogii* (HO); Maria Island Natl. Park, Four Mile Creek (headwater), 430 m, *Moscal 27092A* as *T. herzogii* (HO); Manuka Road, W of Tahune Bridge, 135 m, *Jarmen 98/1*—c. per. (HO); Ridgeway Fire Tracks, 15 Jan 1980, *Ratkowsky s.n.* (HO); Badger Hill, 7 Dec 1979, *Ratkowsky s.n.* (HO); Mt. Nelson, Pipes, 9 Dec 1979, *Ratkowsky s.n.* (HO); Snug Falls, 160 m, *Moscal 20167* as *T. herzogii* (HO); Chimney Pot Hill, Dunns Creek, 380 m, *Moscal 20009* as *T. herzogii* (HO); Gordon River, Gorge Creek, near Pine Landing, sea level, *Engel 14653* (F); Central Highlands, Lake Botsford, 0.5 km S of Lake Augusta, 1150 m, *Mos-*

*cal 24752* as *T. herzogii* (HO); nameless tributary of River Forth, 390 m, *Moscal 15207* as *T. herzogii* (HO).

***Telaranea quinquespina* (Engel & Merr.) Engel & Merr., comb. nov.**

*Kurzia quinquespina* Engel & Merr., J. Hattori Bot. Lab. 80: 217, fig. 1, 1996. Holotype: New Zealand, South Is., Buller Co., gorge of Bullock Creek, 1.2 miles E of Rte. 6, 100 ft, *Fife 4720* (F); isotype: (CHR).

Plants delicate, loosely to densely caespitose in feltlike mats (or creeping as individual strands

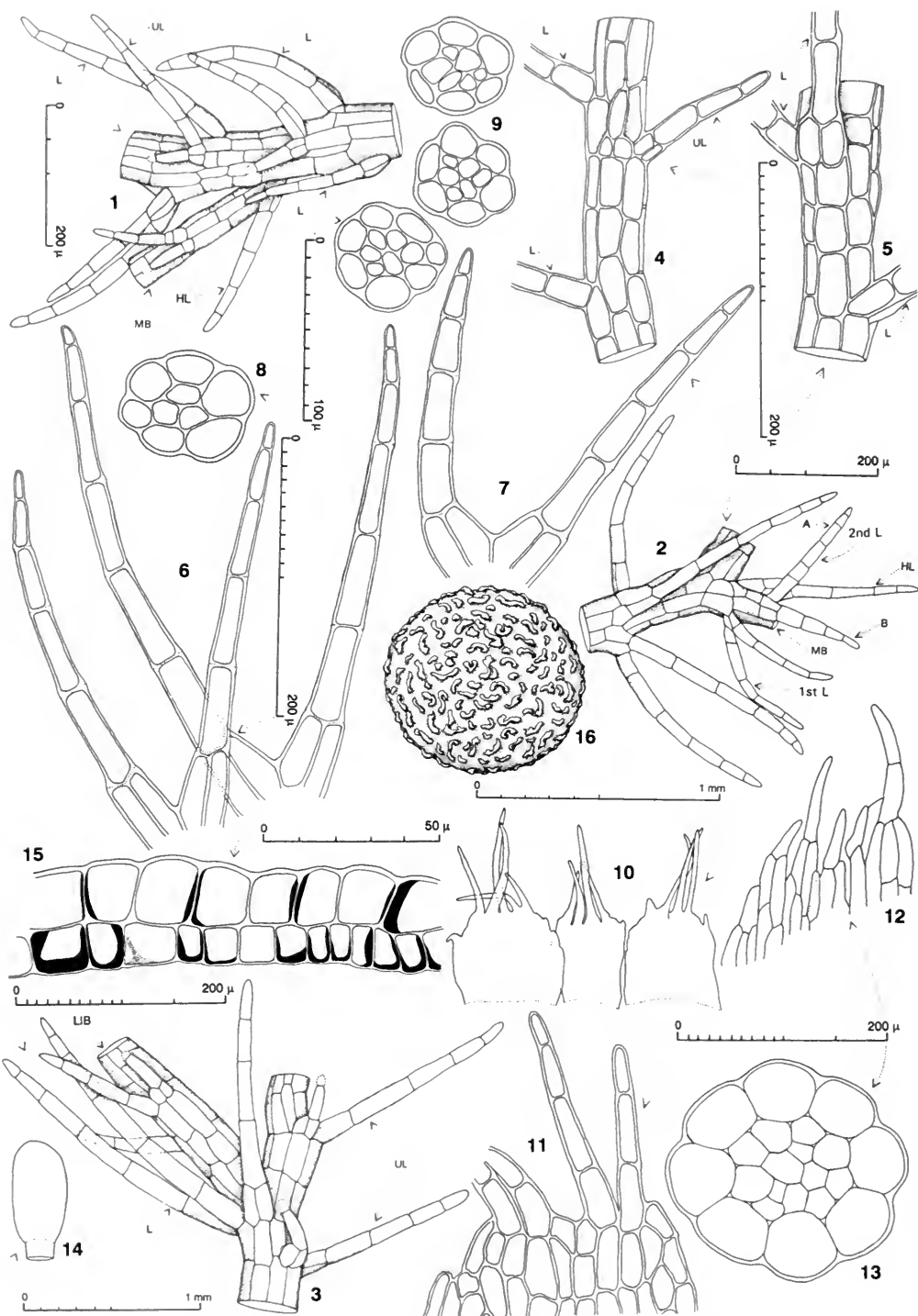


FIG. 34. *Telaranea quinquespina* (Engel & Merr.) Engel & Merr. 1. Portion of main shoot with *Microlepidozia*-type branch (= MB), ventral view (L = leaf; UL = underleaf; HL = half-leaf). 2. Portion of main shoot with *Microlepidozia*-type branch (= MB), dorsal view (1st L = first leaf; 2nd L = second leaf, with lobes A + B; HL = half-leaf on opposing side of stem). 3. Portion of main shoot with lateral-intercalary branch (= LIB) in axil of 3-lobed leaf (= L), ventral-lateral view (UL = underleaf). 4. Stem, ventral aspect (L = leaf; UL = underleaf). 5. Stem, dorsal aspect (L = leaf, at top the 2 lobes shown at arrows). 6, 7. Leaves. 8, 9. Stem, cross sections. 10. Innermost ♀ bracts and bracteole. 11. Distal sector of innermost ♀ bract. 12. Portion of perianth mouth. 13. Seta, cross section.



among other bryophytes), minutely prickly in appearance, pale green, nitid; shoots minute, to 845  $\mu\text{m}$  wide with leaves. Branching sparing to rather common, irregular, with *Frullania*- and *Microlepidozia*-type terminal branches and ventral- and lateral-intercalary branches; terminal branches with half-leaf undivided and setaceous (rarely bifid), biseriate in basal tier (occasionally with a second biseriate tier), the uniseriate row of 4–5 cells; first branch underleaf on base of branch, symmetrically bilobed, resembling a leaf but with shorter lobes, the uniseriate row 4 cells long (rarely asymmetrically bilobed and resembling the stem underleaves); ventral- and lateral-intercalary branches frequent, often becoming leading, leafy shoots; leafless geotropic ventral-intercalary and lateral-intercalary stolons frequently present. Stems straight and not zig-zag, slender, delicate and threadlike, the cortical cells in surface view large, firm-walled, short quadrate to rectangular, in cross section the cortical cells in 6(7) rows, the outer wall thicker-walled; medullary cells much smaller in diam. than the cortical cells, thin-walled, in (3)4–5 rows. Leaves contiguous to laxly imbricate, widely spreading, the insertion transverse or nearly so, 230–450  $\mu\text{m}$  long  $\times$  220–365  $\mu\text{m}$  wide (between tips of spreading lobes), 2-fid almost to the base (the basal cells connate for 0.3 to 0.5 their length), occasionally 3-lobed. Lobes  $\pm$  equal in length, stiff, subcapillary, gradually tapering from base to apex, straight to broadly curved, widely divergent, biseriate at the base (at times uniseriate to base on some shoots), with a uniseriate row of (4)5–6(7) cells; cells of basal tier (13)17–24  $\mu\text{m}$  wide  $\times$  42–62  $\mu\text{m}$  long, basal cell of uniseriate row 15–25  $\times$  55–96  $\mu\text{m}$ , the next cell of about the same length and width, the terminal cell distinctly shorter than the penultimate cell, at times appearing secondarily divided; cell walls firm, moderately thick-walled, the transverse septa of uniseriate row thickened in the corners and swollen to weakly projecting; cuticle smooth. Underleaves asymmetrically bilobed, consisting of a longer lobe that is biseriate at the base and ending in a uniseriate row of 4(5) cells, thus resembling a leaf lobe, the other lobe abbreviated, consisting of a pair of short basal cells and a  $\pm$  elongated distal cell, terminating in a slime

papilla, the underleaves occasionally 3-lobed, with middle lobe abbreviated, or sporadically with 2 abbreviated lobes; paired cells at base of the shorter lobe(s) at times transversely divided, with rhizoids produced from the resulting rhizoid initials. Asexual reproduction lacking.

Plants dioecious. Androecium on a short, determinate, lateral-intercalary branch from main shoot, loosely spicate; bracts concave, 3-lobed to ca. 0.65, the disc 1(2) cells high, the lobes 2–3 cells wide at base, slenderly tapering, terminating in a uniseriate row of up to 4 cells; antheridia 1 per bract, the stalk uniseriate. Gynoecia on short, ventral- and lateral-intercalary branches from main shoot; innermost bracts and bracteole similar, the disc subquadrate,  $\pm$  regularly (3)4(5)-lobed to 0.4 (often bisbifid, the lobes in pairs), the lobes ciliiform, uniseriate or 2 cells wide at extreme base, the uniseriate row of 3–4 cells (4 when uniseriate to base), the disc margins with several small blunt teeth. Perianth terete in basal half, tapering to the strongly plicate, shallowly lobulate-ciliate mouth, the divisions ca. 9, acuminate, 2–4 cells wide at base, ending in a single elongate, blunt-tipped cell or uniseriate row of 2 elongate cells, the margins of divisions weakly dentate by projecting ends of cells.

Seta with 8 rows of larger, firm-walled epidermal cells, surrounding an inner core of 10–12 much smaller, thin-walled cells. Capsule oblong-elliptic, the wall 28–36  $\mu\text{m}$  thick, 2(locally 3)-stratose, the outer layer subequal to the inner or slightly thicker (the inner layer thinnest in 3-stratose portions); outer layer of cells distinctly tiered,  $\pm$  regularly short-rectangular, with two-phase development, the radial longitudinal walls with rather thin, pigmented, sheetlike thickenings that are sinuate or with local, pigmented, nodular swellings (2–4 per cell), alternating with primary walls devoid of thickenings, the transverse walls without thickenings; inner layer of cells narrowly rectangular, with semiannular bands frequent, widely spaced, complete or less commonly incomplete and then extending onto the tangential wall as spinelike extensions or nodular swellings.

Spores 14.4–19.2  $\mu\text{m}$ , exine pale reddish brown, with distinct, low, rough papillae, often coalescing into short ridges that do not anastomose to form

←

14. Capsule profile. 15. Capsule wall, cross section. 16. Spore ( $\times$  1560). (Figs. 1–2, 4–6, 9, from *Engel 21201*, New Zealand, North Is., Wellington Prov., Tree Trunk Gorge, W bank of Tongariro River, E border of Tongariro Natl. Park; 3, from *Engel 21202*, same loc.; 7–8, 10–16, from isotype.)

areolae. Elaters somewhat twisted, 8.2–9.1  $\mu\text{m}$  wide, slightly tapering, bispiral to tips, the spirals 3.4  $\mu\text{m}$  wide.

**DIFFERENTIATION AND VARIATION**—*Telaranea quinquespina* resembles *T. herzogii* (p. 112), but can be readily distinguished by the biseriate tier of cells at the base of each lobe (Fig. 34: 6, 7). The leaf lobes of *T. herzogii* are typically uniseriate to the base (Fig. 35: 5, 6). In addition, the underleaves in *T. quinquespina* are asymmetrical-bilobed (Fig. 34: 1, 3), with the stronger lobe remarkably similar to (and only slightly shorter than) the lobe of a leaf (Fig. 34: 4). *Telaranea tasmanica*, like *T. quinquespina*, has lobes with a biseriate base, but as in *T. herzogii*, the underleaves are symmetrically bilobed and caliper-like, with both lobes short, terminating in a hooked slime papilla (Fig. 32: 3, 10–14, *T. tasmanica*; Fig. 35: 2, 3, *T. herzogii*). Both ventral-intercalary and lateral-intercalary branches are frequently produced in *T. quinquespina*. Terminal, *Microlepidozia*- and *Frullania*-type branches are infrequently produced, but not in regular alternation on opposite sides of the stem as, for example, in *T. quadriseta*.

This species was originally described as a *Kurzia* and assigned to *Kurzia* subg. *Nanolepidozia* Schust. (Engel & Merrill, 1996b). This subgenus is treated here as a synonym of *Telaranea* sect. *Telaranea*. The type of subg. *Nanolepidozia* is *T. bisetula* (Steph.) Engel & Merr. of New Caledonia (p. 128).

**DISTRIBUTION AND ECOLOGY**—Known from few and scattered localities on Stewart Island and South and North Islands, New Zealand. *Telaranea quinquespina* for the most part occurs loosely in damp, shaded niches on steep-sided banks, bryophyte-covered tree bases, cliff faces and stream banks in lower- to middle-elevation forests. The species appears to grow in at most moderately shaded conditions, and may even tolerate relatively open situations (Cascade ultramafic moraine). The Stewart Island as well both South Island stations are at lower elevations. On Stewart Island the species occurred near sea level in a mosaic of stagnant ponds, *Sphagnum* bog, open *Leptospermum scoparium*-*Dracophyllum* heath to 1–2 m tall and dense communities of *Gleichenia dicarpa* and *Empodisma*. At this site the species formed a loose intertwined layer below the surface litter. The type (30 m in Bullock Creek gorge), occurred on a weakly shaded limestone face with *Adiantum* and *Coprosma* sp. at the margin of a vehicular

track. The southernmost station (Cascade Road, Prov. Westland) is at 135 m in an area of ultramafic rocks and outcrops with rather open vegetation consisting mainly of *Gleichenia*, *Lycopodium*, *Juncus*, the lichen *Cladonia*, and scattered *Leptospermum*; here the species occurs terricolous on slopes with *Kurzia hippuroides*. At the northernmost station (Radar Bush, at 34° 28.5' S) the species occurs on very thin soil over rock of a bank above a stream at the bottom of a steep-sided valley within a forest of *Beilschmiedia-Vitex-Hoheria* and *Cyathea dealbata*. At the single higher-elevation forest locality (1080 m at Taranaki Falls Track), the plants occurred over soil in a shaded pocket of a bank in a steep-sided canyon through forest of *Nothofagus solandri* var. *cliffortioides*, *Griselinia littoralis*, *Pseudopanax colensoi* and *Podocarpus hallii*.

**SPECIMENS SEEN**—NEW ZEALAND. STEWART ISLAND: Rakiura Natl. Park, Fresh Water Swamp, track to Mason's Bay, c. 1 km W of Freshwater Hut, 5 m, *Engel* 24436 (F). SOUTH ISLAND, WESTLAND PROV.: Cascade Road, Cascade ultramafic moraine, W of Martyr Saddle, SSW of Jackson Bay, 135 m, *Engel* 23003—c. ♂ (F). NORTH ISLAND. WELLINGTON PROV.: Tongariro Natl. Park, Taranaki Falls Track, E of Whakapapa Village, 1080 m, *Engel* 22456 (F); Tree Trunk Gorge, W bank of Tongariro River, E border of Tongariro Natl. Park, boundary of Kaimanawa State Forest Park, ca. 700 m, *Engel* 21201, 21202 (F). GISBORNE PROV.: Near Lake Waikaremoana, *Sainsbury* 194a as *Telaranea herzogii* (CHR). SOUTH AUCKLAND PROV.: Near Atiamuri, S of Rotorua, *Allison* H3001 as *Telaranea herzogii* (CHR); Kaimai Range, network of tracks at the end of Wrights Rd. off the Katikati-Tauranga highway, Swimming Holes Track, 60 m, *Engel* 23527 (F); Coromandel State Forest Park, ridge between Webb Creek Track and Billy Goat Track, 510–540 m, *Engel* 22348 (F); *ibid.*, summit of Table Mt., 835 m, *Engel* 22379 (F). NORTH AUCKLAND PROV.: Radar Bush, WSW of Cape Reinga, S of Mt. Te Pahi, ca. 100 m, *Engel* 20832 (F).

*Telaranea* sect. *Tenuifoliae* (Schust.) Engel & Merr., comb. nov.

*Arachniopsis* sect. *Tenuifoliae* Schust., Beih. Nova Hedwigia 118: 461. 2000. Type: *Arachniopsis tenuifolia* Schust.

*Arachniopsis* Spruce, On *Cephalozia* 84. 1882, syn. nov. Lectotype (*fide* Schuster, 1965): *Arachniopsis coactilis* Spruce.

*Arachniopsis* subg. *Amphidactylopsis* Schust., Nova Hedwigia 10: 25. 1965. Type: *Arachniopsis monocera* Schust. & Grolle, *nom. inval.*

*Telaranea herzogii* (Hodgs.) Hodgs.

*Lepidozia herzogii* Hodgs., Trans. Roy. Soc. New

Zealand 83: 618. 1956, *nom. nov. pro Lepidozia bisetula* Herz. in Hodgs., Trans. & Proc. Roy. Soc. New Zealand 68: 44. pl. 5, d-f. 1938, *non L. bisetula* Steph., Spec. Hep. 6: 323. 1922. *Telaranea herzogii* (Hodgs.) Hodgs., Rec. Domin. Mus. 4: 106. 1962. *Arachniopsis herzogii* (Hodgs.) Hodgs., Tuatara 12: 6. 1964. Type: New Zealand, North Is., Russell, Bay of Islands, *Lindauer 281* (CHR!). *Telaranea exigua* Schust., Nova Hedwigia 15: 457. 1968. Holotype: New Zealand, North Is., Mt. Egmont, along Stratford Mt. Road, E side of mountain, ca. 2000 ft., *Schuster 48916b* (*non vide*).

Plants exceedingly delicate, minutely prickly in appearance, creeping to ascending, whitish green and nitid; shoots minute, to 630  $\mu\text{m}$  wide with leaves. Branching sparing to very common, irregular, not becoming flagelliform; branch half-leaf stiffly dorsally assurgent, undivided, setaceous; first branch underleaf at base of branch, strongly asymmetrically bilobed, consisting of a divergent lobe, (2)3–4 cells long, and a  $\pm$  appressed, curved lobe aligned with the branch, resembling an underleaf lobe and consisting of a short basal cell and a  $\pm$  elongated distal cell, the lobe terminating in a slime papilla, a rhizoid commonly originating from the basal cell. Ventral-intercalary branches occasional to predominant, long and leafy. Stems very delicate, rather stiff for plant size, the cortical cells in 6–9 rows, leptodermous, much larger than the delicate, leptodermous medullary cells which are in 3(4) to 6–11(18) rows. Main shoots with 3–4 cortical cells intervening between successive leaves on either side, the branches with 2–3 cells intervening between successive leaves on either side of branch. Leaves rather rigid, contiguous to weakly imbricate (strongly imbricate on branches), widely spreading to subsquarrose, the insertion transverse to weakly succubous, (245)300–450(490)  $\mu\text{m}$  long  $\times$  245–420  $\mu\text{m}$  wide (at tips of spreading lobes), 2–3-fid almost to the base (the basal cells connate for 0.1–0.4 their length), the ventral lobe somewhat shorter. Lobes stiff, gradually tapering from base to apex, straight to broadly incurved, moderately to strongly divergent, on branches disposed in  $\pm$  regular ranks, uniseriate throughout (sporadically one or more lobes biseriate at extreme base), gradually tapering, the lobes (4)5–6(7) cells long,  $\pm$  equal in length, or in 3-lobed leaves the ventral lobe perceptibly shorter; basal cells 18–26  $\mu\text{m}$  wide  $\times$  (66)95–120  $\mu\text{m}$  long, the next cell 14–20  $\times$  56–98  $\mu\text{m}$ ; lobe cells gradually shorter and narrower distally, the terminal cell usually much shorter than the penultimate cell; cell walls thin but firm to moderately thick-walled, the transverse septa

thickened in the corners and not or feebly swollen and projecting; cuticle smooth. Oil-bodies (*vide* Schuster, 1968), rather large and conspicuous, grayish, granular, the surface nearly or quite smooth; basal cells of lobes with ca. 6 oil-bodies, irregularly ellipsoidal to fusiform or ovoid, ca. 5–6  $\times$  8–9  $\mu\text{m}$  to 6–7  $\times$  10–12  $\mu\text{m}$ ; upper cells with oil-bodies progressively smaller (ca. 5 to 5  $\times$  8  $\mu\text{m}$  or smaller). Underleaves small and inconspicuous, 2 (rarely 3)-lobed, “caliper-like,” the lobes parallel to somewhat divergent, 2–3 cells long (rarely 1 cell), terminating in a hooked slime papilla, the base formed of two basally connate, curved cells forming a “U”-shaped disc, the distal cell(s) elongated; individual rhizoids originating from the base or apex (rarely both) of the basal lobe cells, or the basal cells subdivided into 6–8 small, quadrate, rhizoid initials, with a rhizoid emerging from each. Asexual reproduction lacking.

Plants apparently dioecious. Androeceia not seen. Gynoeceia bracts delicate, deeply dissected, 2–3-lobed, the lobes 2–4 cells wide at base, terminating in a uniseriate row of 5–6 elongated, tapering cells, each lobe armed with paired uniseriate cilia inserted at apex of the basal tier of lobe cells, the cilia 2–4-celled, often ending in a slime papilla; disc of 2(3) tiers of longitudinally elongate cells, the margins of disc entire or with a blunt tooth on one or both sides at base of the lateral lobes; bracteoles 2-lobed, otherwise similar to bracts. Perianth rather short, terete in basal half, bluntly trigonous above, somewhat contracted at the mouth, the mouth shallowly lobulate-ciliate, the cilia ca. 6–10 (interspersed with smaller 1–2-celled teeth), several cells wide at the extreme base, ending in a stiffly divergent uniseriate process of 4–9 elongate cells, the cilia often armed with few-celled lateral spurs or a single lateral spur inserted at the septa.

Seta with 8 rows of outer cells, surrounding an inner core of 4–10 much smaller, very delicate cells. Capsule 345  $\mu\text{m}$  long, 190  $\mu\text{m}$  wide, rather short- to long-elliptic, the wall 16–18  $\mu\text{m}$  thick, uniformly 2-stratose, the outer layer subequal to the inner, or slightly thicker; outer layer of cells  $\pm$  regularly short-rectangular, with two-phase development, the longitudinal walls with nodule-like thickenings (4–6 per cell) alternating with primary walls devoid of thickenings (or rarely with local, pigmented, nodular swellings), the transverse walls without thickenings; innermost layer of cells somewhat irregularly narrowly rectangular, the radial walls with continuous sheets of wall

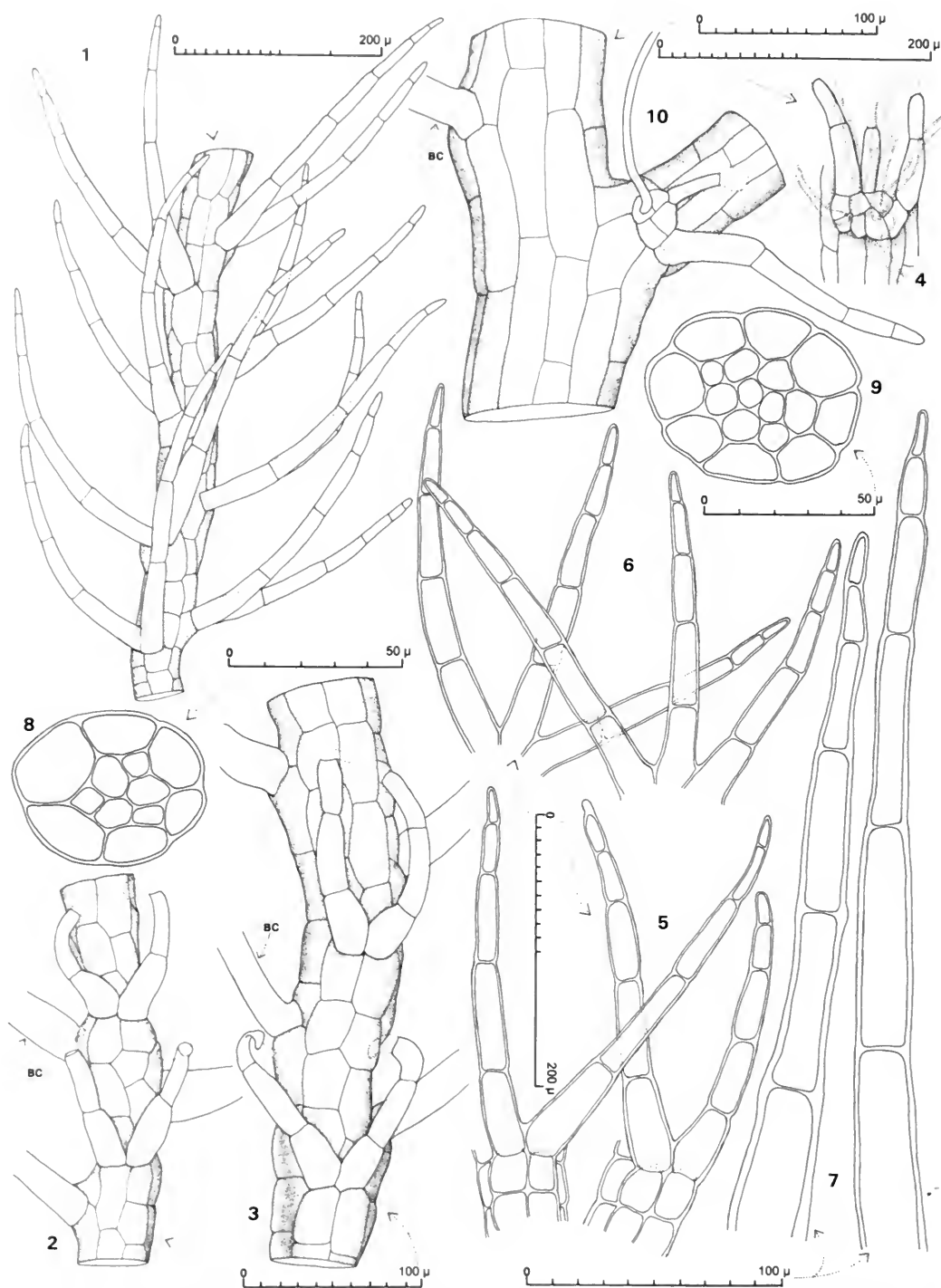


FIG. 35. *Telaranea herzogii* (Hodgs.) Hodgs. 1. Portion of main shoot, dorsal view. 2, 3. Portions of two different main shoots, each showing 2 underleaves and the basal cells of ventral lobes of 3 leaves (= bc), ventral view. 4. Three-lobed underleaf; note rhizoids (stippled outline). 5, 6. Two- and three-lobed leaves. 7. Leaf lobes. 8, 9. Stem, cross sections (note 6+6 and 8+9 anatomy). 10. Terminal branch base and first branch underleaf (ventral view); note rhizoid position and rhizoid initial cells (bc = basal cell of ventral lobe of leaf). (Figs. 1-3, 5, 7, 8 from type of *T. herzogii*; 4, 6, 9 from Engel 19239, New Zealand, South Is., Nelson Prov., Paparoa Range, upper slopes of N side).

material, the radial walls mostly with nodular thickenings and short spinelike extensions onto the exposed tangential wall, only exceptionally with complete semiannular bands.

Spores 7.5–8.8 to 10.6–12  $\mu\text{m}$  in diam., exine yellow-brown, rather thin-walled, areolate, with a low, close network of ridges coalescing to delimit areolae. Elaters rather straight, 6.5–7.5 to 9.6–11  $\mu\text{m}$  wide, only slightly tapering and bispiral to tips, the spirals 2.9–3.4  $\mu\text{m}$  wide.

**DIFFERENTIATION AND VARIATION**—The delicate, densely interwoven, prickly and highly nitid shoots of *T. herzogii* lend this species a distinctive appearance. The leaf lobes are uniseriate throughout (or sporadically biseriate at the base), and the basal cells are barely united, forming a “disc” of considerably less than one cell high (Fig. 35: 5, 6). The leaf lobes of *T. inaequalis* are rather flexuous, show essentially no taper, and are unequal in length (Fig. 37: 4), the longest up to 9 cells long, and the lobe cells are of roughly equal length throughout. The leaves of *T. herzogii* are also  $\pm$  asymmetric, but the lobes are stiffly spreading and distinctly tapering, usually 5-, rarely 6-cells long (Fig. 35: 1, 5–7), the cells progressively narrower and shorter from base to apex (Fig. 35: 7). The first branch underleaves of *T. inaequalis* are equally bilobed like the other stem underleaves (Fig. 37: 3), vs. asymmetrically bilobed in *T. herzogii* (Fig. 35: 10).

*Telaranea exigua* Schust. is described as having predominately 3-lobed leaves. In robust plants of *T. herzogii* the number of leaf lobes varies from 2 to 3 on the same plant. Weaker shoots tend to have more slender stems, with fewer rows of cortical and medullary cells. Herzog's (1938) description and illustration of *T. bisetula* ( $\equiv$  *T. herzogii*) is of a plant with bilobed leaves; Hodgson (1956) also described the leaves as bifid. Examination of the type reveals that, indeed, the leaves are apparently all bifid (Fig. 35: 5), and the stem cross-section has 6 rows of cortical cells, surrounding a medulla of 6 cell rows (Fig. 35: 8). Schuster (1968, p. 457) assigned to “*T. herzogii* s. lat.” a New Zealand plant with uniformly bifid lateral leaves; the plant illustrated as *T. herzogii* in Schuster (1969, fig. 88: 4–6), however, is *T. inaequalis*. Schuster (2000, p. 230) referred plants

with 6 rows of cortical cells and 3(4) rows of medullary cells to “var. *nana*.”

Plants of *T. herzogii* resemble those of *T. quinquespina*, but the latter can be readily distinguished by the combination of *Microlepidozia*-type branching, slender thread-like stems, firm walled cortical cells (Fig. 34: 8, 9), a biseriate tier of cells at the base of each leaf lobe (Fig. 34: 6, 7), and asymmetrically bilobed underleaves (Fig. 34: 1), the stronger lobe similar to (and only slightly shorter than) the lobe of a leaf (Fig. 34: 4). The first branch underleaf of *T. quinquespina* is also unusual in being symmetrically bilobed and resembling a leaf; in *T. herzogii* it is asymmetrically bilobed, with one lobe much shorter and ending in a slime papilla. *Telaranea quinquespina* has frequent, leafless, geotropic ventral-intercalary and lateral-intercalary stolons.

Herzog (1938) compared *T. herzogii* (as *L. bisetula*) with *Arachniopsis*. Hodgson (1964, p. 6) transferred *T. herzogii* to *Arachniopsis*, citing the “complete absence of a basal discus in the leaf.” In our treatment, the genus *Arachniopsis* is combined with *Telaranea*. As in other *Arachniopsis* species (sect. *Tenuifoliae*), the leaf lobes are typically uniseriate to the base (see Discussion of Phylogenetic Relationships, p. 240).

In the field, juvenile phases of *Temnoma paucisetigerum* have distant leaves consisting of 2–3 ciliiform lobes and a low disc, and could be confused with *T. herzogii*.

“*Telaranea herzogii* var. *nana*” (Schuster, 2000, p. 230, fig. 77: 4–9; 79, published without a Latin description) is a synonym of *T. herzogii*. The variety was based on a specimen from Stewart Is. (Schuster 60670).

**DISTRIBUTION AND ECOLOGY**—A species of New Zealand, Tasmania and Australia (Victoria). In New Zealand the species is found rather commonly on loamy, moist, shaded soil. It occurs for the most part in lower to middle elevation moist or swampy forests where on soil in protected pockets or shaded hollows associated with, for example, *Telaranea elegans*, *T. tetradactyla*, *T. tetrapila*, *Saccogynidium* sp., *Acromastigum colensoanum* and *Bazzania nitida*. It may occur over soil of the forest floor deep in humid recesses formed by rock ledges (e.g., Lake Marion, Engel 23169) or it may form a loosely creeping, pure,

←  
of Tiropahi or Four Mile River; 10, from Engel 17968, New Zealand, South Is., Otago/Westland Prov. Boundary, Mt. Aspiring Natl. Park, summit area of Haast Pass.)

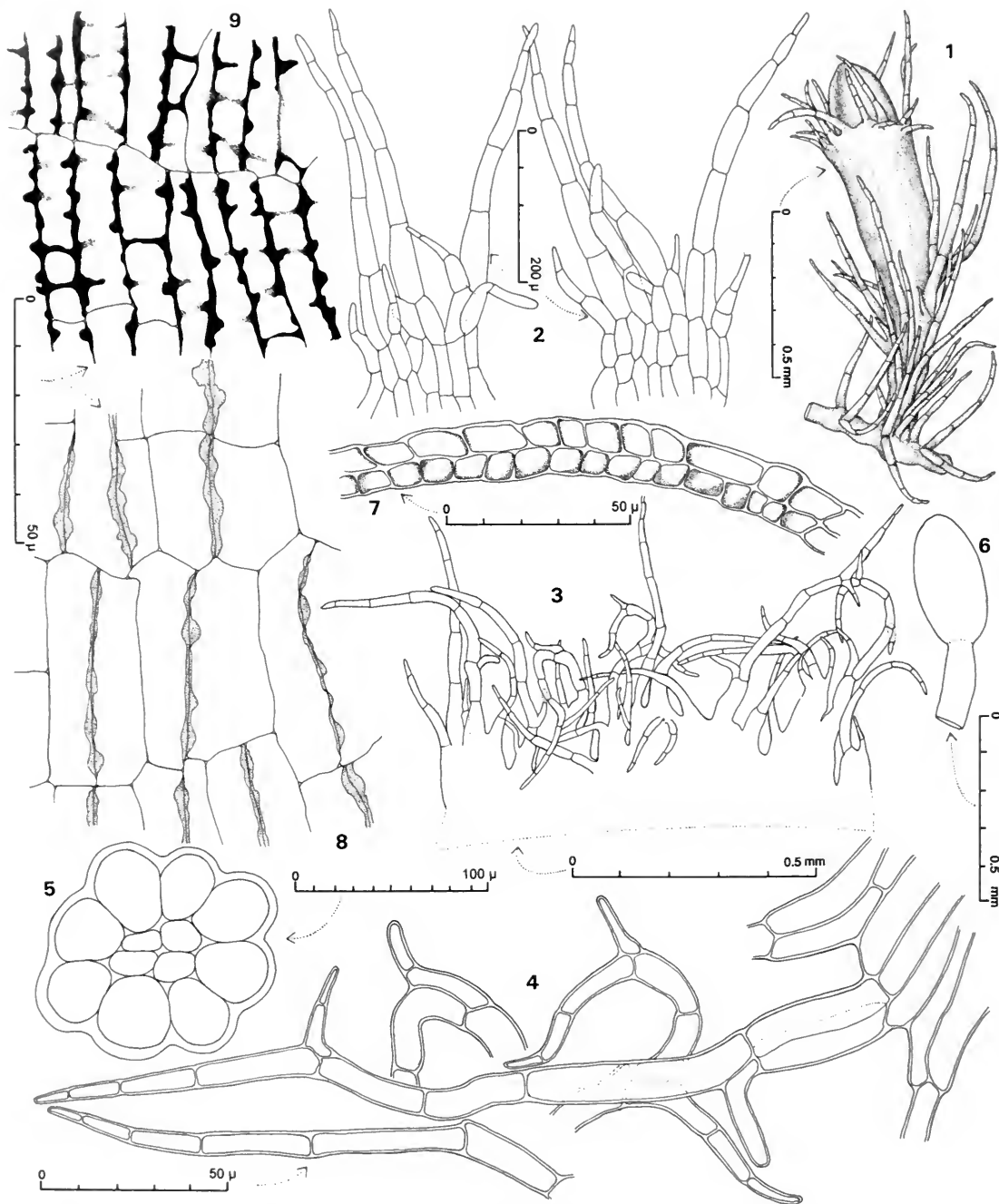


FIG. 36. *Telaranea herzogii* (Hodgs.) Hodgs. 1. Gynoeceum with mature sporophyte. 2. Innermost ♀ bracts. 3. Perianth mouth. 4. Cilia of perianth mouth. 5. Seta, cross section. 6. Capsule profile. 7. Capsule wall, cross section. 8. Capsule wall, outer layer. 9. Capsule wall, inner layer. (All from *Allison 3171*, New Zealand, North Is., South Auckland Prov., near Atiamuri, S of Rotorua.)

feltlike covering over soil deep in pockets at tree bases (e.g., Hauturu Highpoint Track, *Engel* 22599). It is rather frequent in humid sites such as steep-sided stream banks and occurs loosely over soil in protected niches; in particularly humid sites it may be epiphyllous on filmy ferns such as *Trichomanes elongata*. Also in moist, dense, tree-fern gullies, where *T. herzogii* may be terricolous or on tree-fern caudexes (of *Cyathea dealbata* or *Dicksonia squarrosa*). It also may be encountered rather commonly in cushions of *Leucobryum*. It is much less frequent at higher elevations, as in the Temple Basin Ski area (Arthur's Pass, Westland/Canterbury Prov. Boundary).

In Tasmania it is apparently confined to the eastern half of the state. At the Mt. Clark site the species occurred at 380 m over soil between rock plates with *Mitellochloa bryoides*, *Fissidens pungens*, *Racomitrium convolutaceum*, *Temnoma pulchellum*, *Chiloscyphus* sp. and *Heteroscyphus triacanthus* under *Eucalyptus regnans*, *Acacia ricceana* and *Correa lawrenciana*. The Jarmen plant from west of the Tahune Bridge occurred at 130 m on soil in *Eucalyptus obliqua* wet sclerophyll forest. At Ben Lomond it occurs in boggy situations at 870 m with sparse *Sphagnum cristatum* spread over riparian skeletal soils with a discontinuous scrub of *Leptospermum lanigerum*, *Calistemon viriflorus* and *Richea gunnii*.

SELECTED SPECIMENS SEEN—NEW ZEALAND. STEWART ISLAND: Rakiura Natl. Park, Port Pegasus, ca. 100–200 m, *Engel* 24183 (F); *ibid.*, Fern Gully Track, 20–30 m, *Engel* 24076 (F). SOUTH ISLAND: SOUTHLAND PROV.: Bluff Hill, *Allison* H5160 (CHR); Fiordland Natl. Park, S end of Lake Marion, W of Hollyford River, 695 m, *Engel* 23169 (F); *ibid.*, Moraine Creek Track, area N of Moraine Creek, W of Hollyford River, 610 m, *Engel* 23224 (F). OTAGO PROV.: Purakanui Falls, Catlins, NE of Maclellan, ca. 150 m, *Child* H1973 (F); Fiordland, N of McKerrow River, Martin's Bay, *Hatcher* 971 (F). OTAGO/WESTLAND PROV. BOUNDARY: Mt. Aspiring Natl. Park, summit area of Haast Pass, 570 m, *Engel* 17968 (F). WESTLAND PROV.: Cascade Road, just W of Jackson River, ca. 8–12 km SW of confluence of Jackson and Arawata Rivers, 25–90 m, *Engel* 22989 (F); Mt. Aspiring Natl. Park, Cross Creek, 1.1 km N of Haast Pass, 540 m, *Engel* 21882 (F); Westland Natl. Park, terminal moraine of Fox Glacier, on S side of Fox River, *Engel* 6644A (F); Lake Kaniere Scenic Reserve, Lake Kaniere Rd, 125 m, *Engel* 24875; near Hercules Creek on Route 6 in Mt. Hercules Scenic Reserve, *Engel* 6564B. WESTLAND/CANTERBURY PROV. BOUNDARY: Arthur's Pass Natl. Park, Arthur's Pass, near Temple Basin Ski area, *Engel* 6486B (F). NELSON/WESTLAND PROV. BOUNDARY: Paparoa Range, S side of Porarari River, up river from gorge and ca. 500 m WSW of ford on inland track to Bullock Creek, 10–20 m, *Engel* 19185

(F). NELSON PROV.: Paparoa Range, upper slopes of N side of Tiropahi or Four Mile River between sea and Route 6, S of Charleston, 130–170 m, *Engel* 19239 (F); Nelson Lakes Natl. Park, off Lakehead Track, near juncture with southern end of Loop Track, NE end of Lake Rotoiti, 630 m, *Engel* 22738 (F); Big Bush State Forest 48, Donald Creek, 480–600 m, *Macmillan* 77/108, 77/138 (CHR). NORTH ISLAND. WELLINGTON PROV.: Tongariro Natl. Park, Mangawhero River near juncture of Rimu Track and Forest Walk, just NE of Ohakune, 625 m, *Engel* 22720 (F). SOUTH AUCKLAND PROV.: Roto-a-kui Bush, E of Taupo, ca. 760 m, *Allison* H3054—c. per. (CHR); near Atiamuri, S of Rotorua, *Allison* H3171—c. sporo. (CHR); 10 mile on Atiamuri-Rotorua road, *Allison* H67—c. per. (CHR); between Lake Rotoehu and the coast, Bay of Plenty, *Allison* H3174 (CHR); Herangi Range, Whareorino Forest, tributary of Awakino River, W of Leitchs Road, SW of Te Kuiti township, 285 m, *Engel* 23925 (F); Kaimai Range, network of tracks at the end of Wrights Rd. off the Kaitikati-Tauranga highway, Swimming Holes Track, 60 m, *Engel* 23526 (F); Kaimai-Mamaku Forest Park, Mt. Te Aroha, S facing slope, 880–890 m, *Engel* 23848 (F); Coromandel Peninsula, *Mathews* 52pp (CHR); Coromandel State Forest Park, Kauraranga River, just SE of suspended footbridge, 150 m, *Engel* 22294 (F); *ibid.*, summit of Table Mt., 835 m, *Engel* 22375—c. per. (F); *ibid.*, Mt. Moehau, just below summit "Little Moehau," ca. 840 m, *Engel* 23725 (F). NORTH AUCKLAND PROV.: NE Waitakere Ranges, Swanson University Reserve, Tram Valley Road, 95 m, *Engel* 20462 (F); Waitakere Hills, W of Auckland, *Hatcher* 175 (F); Pohuehue Scenic Reserve, N of Auckland on State Highway 1, ca. 25 m, *Engel* 21161 (F); Waipoua Forest, *Allison* H759—c. per., H3176—c. ♂ (CHR); *ibid.*, *Hatcher* 487 (F); Waipoua Forest, Waikohatu Stream at Waikohatu Kauri Bridge, 290 m, *Engel* 22674 (F); Waimea Forest, Hauturu Highpoint Track in vicinity of summit area of Hauturu Trig, off Waitotemarama Track, 650–680 m, *Engel* 22599 (F); Omahuta Forest Kauri Sanctuary, E of Mangamuka Bridge, 260 m, *Engel* 20999 (F); Soda Springs, on Mangamuka River, Maungataniwha Range, ESE of Kaitia on State Highway 1, ca. 60 m, *Engel* 20800 (F); Radar Bush, WSW of Cape Reinga, S of Mt. Te Pahi, ca. 100 m, *Engel* 20834 (F). TASMANIA: Tasman Peninsula, Wellard Rivulet, *Weymouth* 808 as *L. chaetophylla* (HO); Mt. Clark, 6 km NW of Port Arthur, 380 m, *Moscal* 11205 (HO); Mt. Wellington Plateau, *Rodway* as *L. chaetophylla* (HO); Manuka Road, W of Tahune Bridge, 130 m, *Jarman* 98/2 (HO); Ben Lomond, corner of Memory Road and Telopea Road, 2.5 km SE of Ben Nevis, 870 m, *Moscal* 13279A (HO). AUSTRALIA. VICTORIA: Great Dividing Range, Maroonah Highway just NE of Fernshaw and NE of Healesville, *Engel* 16818 (F).

*Telaranea inaequalis* Schust. ex Engel & Merr., sp. nov.

*Telaranea inaequalis* Schust., Beih. Nova Hedwigia 118: 225, f. 76, 2000, nom. nud. (sin descr. lat.). Holotype: Tasmania, Gordon River, Sir John Falls, just up river from Butler Island, sea level, *Engel* 14685B (F); isotype: (HO).



*A. T. herzogii* bene distincta foliis omnino inaequaliter bilobatis, lobis 7–9 cellulas longis flexuosis atque latitudine non decrescentibus, et amphigastriis primis ramorum symmetricis aequaliterque bilobatis.

Plants exceedingly delicate, loosely creeping, the leaf lobes minutely threadlike in appearance, whitish green and nitid; shoots minute, to 1.1 mm  $\mu\text{m}$  wide with leaves. Branching occasional, irregular, of the *Frullania* type; branch half-leaf undivided, leaf-lobe-like; first branch underleaf similar to normal stem underleaves, symmetrically bilobed, the lobes 2–3 cells long, terminating in a slime papilla, inserted on ventral-lateral side of branch just above the base. Flagelliform and stoloniform branches apparently lacking, or rare. Ventral-intercalary branches common, long and leafy. Stems delicate, straight and wiry, rather slender for plant size, the cortical cells in surface view and cross section moderately and evenly thick-walled, in 6 rows (the dorsal larger than the ventral rows); medullary cells in 3(5) rows, smaller, moderately and evenly thick-walled. Main shoots with 2 cortical cells intervening between successive leaves on either side. Rhizoids very thick-walled, from underleaf cells. Leaves distant, widely and laxly spreading, the insertion transverse to at times weakly succubous, consistently bifid essentially to the base (the basal cells scarcely connate), the longer lobes 505–735  $\mu\text{m}$  long, the ventral lobes shorter. Lobes threadlike, not or scarcely tapering, moderately to strongly divergent, flexuous, not disposed in regular ranks, uniseriate throughout, unequal in length: the dorsal (7)8–9 cells long, the ventral 7–8 cells long (not including secondarily divided cells at lobe tips); lobe cells subequal in length except at the tip, the basal cells 22–28  $\mu\text{m}$  wide  $\times$  90–120  $\mu\text{m}$  long, the next cell 18–24  $\mu\text{m}$  wide  $\times$  78–108(120)  $\mu\text{m}$  long, the terminal cell minute, ca. 0.25 the length of the penultimate cell, occasionally with repeated cell divisions at the lobe apex resulting in 3–5 short cells, the tip at times becoming detached; cell walls  $\pm$  thick-walled, the transverse septa thickened in the corners and feebly swollen and projecting, especially in basal half of lobe, the septa in distal portion of lobe at times weakly constricted; cuticle smooth. Underleaves small and inconspicuous, bifid, the lobes parallel to

somewhat connivent, 2–3 cells long, terminating in a slime papilla, the “disc” formed of the two partially connate lobe cells. Asexual reproduction absent.

Plants dioecious. Androecia on abbreviated, tiny, inconspicuous, ventral-intercalary, spicate branches; bracts closely imbricate, the entire bract deeply concave, bilobed, each lobe terminating in a single cell, or, more often, a uniseriate row of 2 thick-walled cells, the tip cell particularly thick walled; lamina cells nontiered, irregular in shape and arrangement, the lamina margins crenulate; antheridia 1 per bract, large for bract size, the stalk short, 4 cells high, uniseriate; bracteolar antheridia absent. Gynoecia not seen.

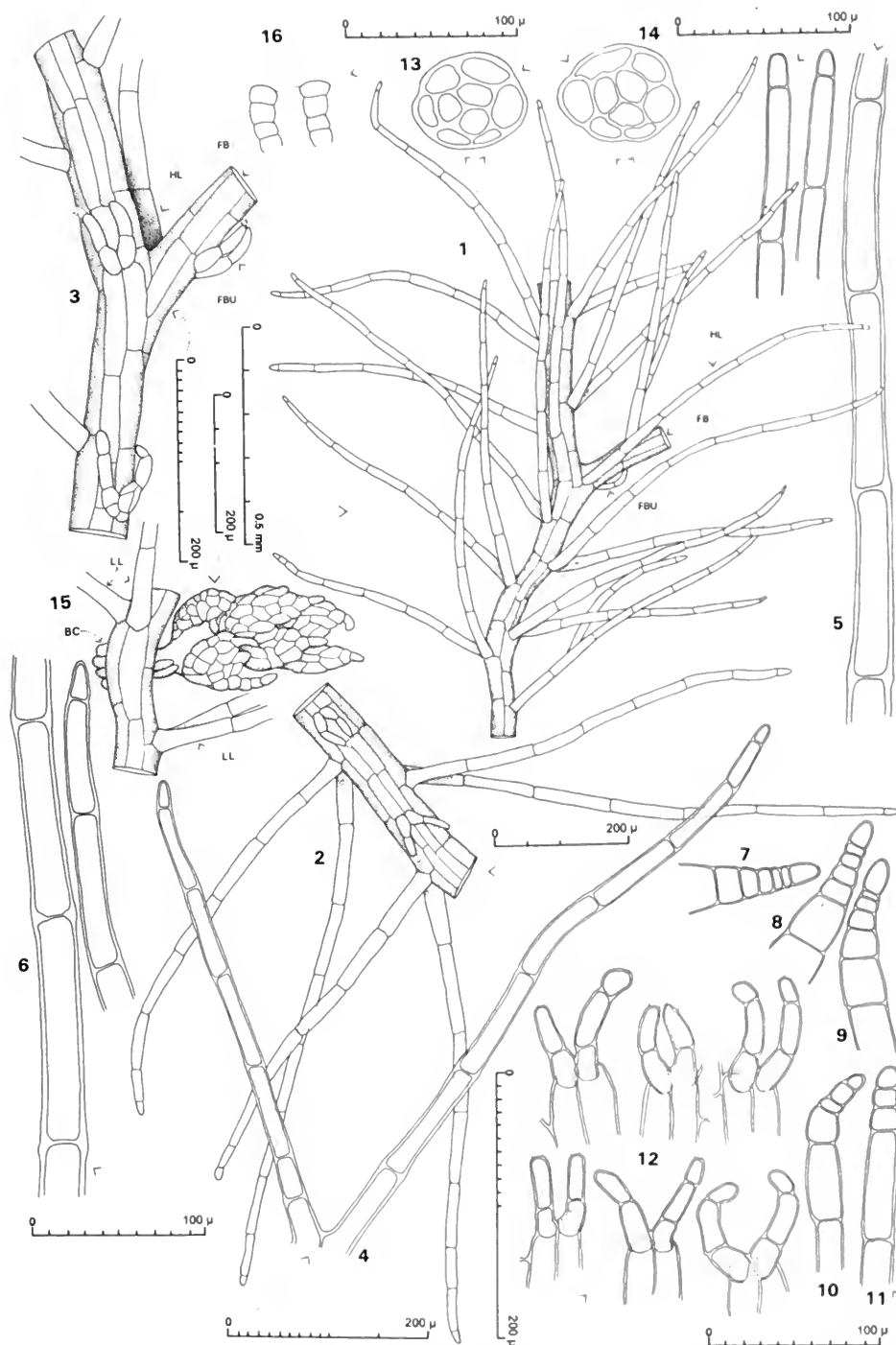
**NOMENCLATURE**—This name has appeared several times in Schuster’s publications, but has not been validly published (Schuster, 1984, p. 773; 2000, p. 225). Schuster (2000, fig. 76 legend) refers to *Schuster 60650* as the type, but without locality data or indication of where the specimen is conserved. The species is illustrated in Schuster (1969, p. 33, fig. 88: 4–6) as *T. herzogii*.

**DIFFERENTIATION AND VARIATION**—*Telaranea inaequalis* is immediately distinct from *T. herzogii* by the consistently unequally bilobed leaves, the flexuous, nontapering lobes 6–9 cells long (Fig. 37: 4) and the equally and symmetrically bilobed first branch underleaf (Fig. 37: 3). See under *T. herzogii* (p. 112) for additional comments.

Significantly, *T. inaequalis* is remarkably similar gametophytically to *T. diacantha* of the Neotropics (Fig. 46), and *T. major* Herz., a species with a broad distribution ranging from Sri Lanka to the Philippines, and Malaysia to New Hebrides. The resemblances include a slender, wirelike appearance of the plants; elongated, nontapering leaf lobes that are often caducous at the tips; the minute, button-like terminal cell of the lobes; and a similar arrangement of stem cortical cells. In addition, all three species appear to be dioecious (cf. Herzog, 1950; p. 145, *T. diacantha*). It differs from both species chiefly in the abundant production of terminal, *Frullania*-type branches (Fig. 37: 1, 3). The rarity of terminal branching in some species of sect. *Tenuifoliae* (particularly in those

FIG. 37. *Telaranea inaequalis* Schust. ex Engel & Merr. 1. Dorsal aspect of sector of main shoot with *Frullania*-type branch (= FB; hl = half-leaf; fbu = first branch underleaf). 2. Portion of leading shoot, ventral view. 3. Portion of main shoot with *Frullania*-type branch (= FB), ventral view (FBU = first branch underleaf; hl = half-leaf; only





the ventral lobes of leaves are shown); note the underleaf at base of figure has 2- and 3-celled lobes and has rhizoid initials formed but rhizoids are lacking. 4. Leaf: note unequal leaf lobes (ventral lobe at left). 5, 6. Leaf lobes (both basal and distal portions included). 7-11. Distal portions of leaf lobes showing subdivision of cells. 12. Underleaves. 13, 14. Stem, cross sections (ventral cortical cells at arrows). 15. Portion of shoot with androecium, oblique-dorsal view (LL = leaf lobe; bc = large cells of collar of the ventral-intercalary androecial branch). 16. Antheridial stalks. (Figs. 1-6, 12-14 from *Engel 14685B*, Tasmania, Gordon River, Sir John Falls; 7-11, 15, 16 from *Jarmen 87/5*, Tasmania, Mt. Sprent.)

species with predominately monocurrous leaves) is probably associated with extreme reduction of the shoot (p. 143, 178).

Occasionally, the minute, button-like terminal lobe cell becomes detached. The tips of the lobes are repeatedly subdivided, resulting in a row of 4–5 short cells (Fig. 37: 7–11), which has been observed to disarticulate and detach as a unit. A similar subdivision of the lobe apex occurs in *T. coactilis*, accompanied by proliferation of rhizoids from the lobe tip (Fig. 44: 3–10).

**DISTRIBUTION AND ECOLOGY**—A rare species known only from New Zealand and Tasmania. In Tasmania, the species is known from only two stations in the southwest. The type was collected at sea level along the Gordon River, where it occurred on thick soil over a vertical cliff face opposite a waterfall (Sir John Falls). The Jarmen specimen occurred in a buttongrass moorland at 600 m on Mt. Sprent. In New Zealand the species is known from only two stations, both at or near sea level.

**SPECIMENS SEEN**—TASMANIA: Mt. Sprent, 600 m, *Jarman 87/5*—c. ♂ (HO). NEW ZEALAND: Stewart Is., Pegasus Cr., 0.5–1 mi above mouth, 9 Jan. 1962, *Schuster 59848* (F). *Schuster* (2000, p. 229, fig. 76 legend) cites a specimen from New Zealand, Fiordland, Bowen Falls, *Schuster 55546*, as well as *Schuster 48601d* and *60650*, locality not given.

## Discussion of Extra-Australasian Species

The Conspectus of *Telaranea* (Table 3, p. 253) lists 98 species, 62 of which are extra-Australasian. The following section is a review of the extra-territorial species of *Telaranea*, with synonymy, references to previously published descriptions and illustrations, notes on nomenclature, typification and geographical distribution, considerable new data and interpretation based on the present study, and suggested systematic disposition. Many species are described in detail and illustrated for the first time. We have personally examined either type or authentic material of most of these species. A handful of species are listed which have not been seen but which are almost certainly *Telaranea* species, based on the descriptions or illustrations, e.g., *Stephani's Icones*.

A comprehensive key to the genus is not possible given the limited state of knowledge of many species, particularly those of the Old World tropics. However, we devoted considerable attention to the *Telaranea* species of south temperate South America, an area of obvious phytogeographical interest in relation to temperate Australasia. The following key is included here to facilitate comparisons with the Australasian representatives of the genus.

### Key to the *Telaranea* Species of Temperate South America

1. Leaf disc 3 or more cells high ..... 2
2. Leaves very shallowly lobed, the lobes rudimentary, 2–3 cells long including base; disc 9–13 cells high, 8 cells wide throughout ..... *T. oligophylla* (p. 174)
2. Leaves lobed to 0.4 or more, the lobes not rudimentary; disc 3–9 cells high, broader distally ..... 3
3. Leaf lobes subcapillary (no biseriate tiers), the uniseriate row 5–6 cells long; shoot and branches recurved to circinate at the tips. Antheridial stalk biseriate ..... *T. plumulosa* (p. 180)
3. Leaf lobes with one or more biseriate tiers, the uniseriate row shorter; shoots and branches not circinate at tips. Antheridial stalk (where known) uniseriate ..... 4
4. Leaf disc  $\pm$  parallel-sided, with divergent lobes; disc cells thin-walled, in orderly rows and tiers. Autoecious ..... *T. autoica* (p. 124)
4. Leaf disc cuneately or palmately lobed; disc cells thick-walled,  $\pm$  irregularly arranged. Dioecious (where known) ..... 5
5. Leaves palmately 3–4-lobed to 0.75; disc (3)4 cells high; plants brownish yellow to rust brown; underleaves unequally lobed, with 1 or more lobes shorter; cuticle striolate; *Acromastigum*-type branching common ..... *T. ferruginea* (p. 159)
5. Leaves cuneately 4-lobed to 0.4; disc 6–9 cells high, plants green or whitish;

underleaves equally lobed; cuticle glaucous or smooth; *Acromastigum*-type branching unknown . . . . . 6

6. Plants glaucous and water repellent; disc cells thick-walled and firm; first branch underleaf typically undivided . . . . . *T. seriaticulata* (p. 190)

6. Plants not glaucous; disc cells thin-walled; first branch underleaf bilobed. Tubers at tips of stoloniform branches . . . . . *T. disticha* (p. 149)

1. Leaf disc 0.5 to 1.5 cells high . . . . . 7

7. Disc (at least locally) 1.5 cells high, with a partial or complete tier of cells along the insertion . . . . . 8

8. Disc with complete basal tier of narrow, elongate cells along the insertion; shoots nearly isophyllous, the underleaves almost indistinguishable from the leaves . . . . . 9

9. Leaves 4–5(6)-lobed; disc squarrose, the lobes  $\pm$  abruptly flexed at the attachment to the disc and suberect; lobe cells misarticulated, with unilaterally projecting septa; cuticle smooth; *Acromastigum*-type branches unknown . . . *T. fernandeziensis* (p. 155)

9. Leaves 3–4-lobed; disc and lobes obliquely spreading in one plane, the lobes stiffly spreading; lobe cells aligned, the septa not unilaterally projecting; cuticle striolate; *Acromastigum*-type branches common . . . . . *T. blepharostoma* (p. 129)

8. Disc with a basal tier of cells confined to median portion of insertion; shoots anisophyllous . . . . . 10

10. Stem cortical cells turgid, transparent; leaf insertion transverse to weakly succubous; disc areolation somewhat irregular, with additional intercalated cells in the median basal portion, the walls often oblique and not strictly transverse or longitudinal; lobes constricted at the septa; underleaves equally 3-lobed . . . . . *T. pellucida* (p. 179)

10. Stem cortical cells not turgid and transparent; leaf insertion incubous; disc bordered by a single elongate cell, 1.5 cells high in the median portion, with a uniform basal tier of cells along the insertion; lobes with septa thickened in the corners but not bulging; underleaves unequally 4-lobed, with 1 or more lobes shorter . . . . . *T. marginata* (p. 166)

7. Disc 0.5 cells high, consisting of the united paired basal cells of the lobes . . . . . 11

11. Stem cortical cells turgid, inflated, transparent, the medullary strand clearly visible; lobe cells turgid, the lobes constricted at the septa; basal cell of uniseriate row large, oblong, equal to half the lobe length . . . . . *T. pseudozoopsis* (p. 184)

11. Stem cortical cells not inflated and transparent; lobe cells with septa thickened and  $\pm$  projecting; basal cell of the uniseriate row about equal to the next cell . . . . . 12

12. Leaves 2–3(4)-lobed, laterally inserted, the 2 median rows of cortical cells broadly exposed; lobes abbreviated, straight, not twisted, the uniseriate row 3(4) cells long . . . . . *T. breviseta* (p. 131)

12. Leaves (3)4–5-lobed, transversely inserted, the insertion dorsally reaching the stem midline; lobes setaceous, often appearing sinuous or twisted, variously spreading and oriented, the uniseriate row 3–5(6) cells long . . . . . *T. setosa* (p. 192)

*Telaranea anomala* Schust. ex Engel & Merr., sp. nov.

DISTRIBUTION—Venezuela.

*Arachniopsis anomala* Schust., Beih. Nova Hedwigia 118: 466. f. 196. 2000, nom. inval. sin. descr. lat. Holotype: Venezuela, Estado Bolívar, Meseta de Jaua, Steyermark 98001 (NY).

Folii 2–3-fidis, lobis distincte angustatis 5–6 cellulis longis, amphigastriis asymmetricis (longiore lobo foliorum, altero amphigastriorum mentiens), caule 5+4 distincta.

ILLUSTRATION—Schuster (2000, fig. 196).

This plant and *T. monocera* are referred to *Arachniopsis* subg. *Amphidactylopsis* by Schuster (2000), which is treated here as a synonym of *Telaranea* sect. *Tenuifoliae*. According to Schuster, the underleaves are asymmetrically bilobed, with one lobe setaceous and 4–5 cells long, the other small, consisting of a single cell and a terminal papilla (Schuster, 2000, fig. 196: 7–8), although in fig. 2 several underleaves appear to be monocrurous. Unequally bilobed leaves are a fea-

ture of several members of sect. *Tenuifoliae* (*T. coactilis*, *T. inaequalis*) here, apparently, expressed in the underleaves. Asymmetric underleaves also occur in *T. quinquespina* and *T. monocera* (p. 168), although in the latter the underleaves are more variable (Piippo, 1985). Judging from Schuster's illustrations of *T. anomala* (Schuster, 2000), leaf insertion is variable, but appears succubous in figs. 196: 3–5.

Schuster (2000, p. 466) referred this species to *Arachniopsis* because it lacks terminal branching. On the other hand, he places "*Arachniopsis borinquena*" (Schuster, 2000, p. 457) and *T. tenuifolia* (ibid., p. 461) in *Arachniopsis* even though *Frullania*-type terminal branches are present.

### *Telaranea apiahyna* (Steph.) Fulf.

*Lepidozia apiahyna* Steph., Spec. Hep. 3: 572. 1909.  
*Telaranea apiahyna* (Steph.) Fulf., Brittonia 15: 71. 1963 (Jan. issue); Schust., J. Hattori Bot. Lab. 26: 227. 1963 (29 Aug.). Type: Brazil, Apiahy, Puig-gari 653—c. immature per. (G!).

*Lepidozia digitisquama* Herz., Broteria 6: 17. f. 1. 1937. Type: Brazil, Sao Paulo, Alto da Serra, 4 Jul 1922, Gehrt.

*Telaranea quadrida* Schust., Phytologia 39: 241. 1978, syn. nov. Holotype: Venezuela, Estado Tachira, Paramo de Tama, Mirador, Schuster & Ruiz-Teran 76-1974 (F).

#### DESCRIPTION—Fulford (1963a).

ILLUSTRATIONS—Taylor (1961, figs. 1–7); Fulford (1963a, figs. 151–155; 1966, figs. 151–155); Herzog (1937, fig. 1, *L. digitisquama*); Schuster (2000, fig. 74, *T. quadrida*). Stephani, Icones, *Lepidozia* 39.

DISTRIBUTION—Costa Rica (Cartago); Southern Brazil (Apiahy, Sao Paulo); Peru (Prov. San Martin); Venezuela (Estado Bolivar, Chimantá Massif, Fulford, 1966), Mirador, subalpine. Schuster (2000, p. 222, key) distinguishes between *T. apiahyna* ("s.e. Brazil; low montane") and *T. quadrida* ("Venez.; páramo"), but on p. 211, *T. apiahyna* is "Venez.-Brazil." Fulford (1966) cited additional Brazilian localities.

Plants (when well developed) with a delicately feathery aspect, soft and flexuous, regularly to rather irregularly 2(3)-pinnate, with a somewhat straggly appearance, the branches terminal, *Frullania*-type, leafy or flagelliform; branch half-leaf 2–3-lobed; first branch underleaf inserted on ventral side of branch base, asymmetrically 2–3-lobed (rarely symmetrically bilobed), with one leaf lobe-like, the other lobe(s) consisting of a un-

iseriate row of 2(3) cylindric cells, hooked at the tip and ending in a slime papilla. Ventral-intercalary branches present, leafy. Stems stout for plant size, the cortical cells in 12–16 rows, the medullary cells often only moderately smaller, with moderately thickened walls, in 32–42 rows. Main shoots with as many as 11(13) cortical cells intervening between successive leaves on either side, the primary branches with 3–4 cells intervening between successive leaves on either side of branch. Leaves of main shoot distant, spreading to suberect, transversely inserted, 4–6(8)-lobed, variable, with a rudimentary disc consisting of the united basal cells of the lobes or at times with a partial or complete additional tier of cells along the insertion; leaves on primary branches 3–4-lobed. Leaf lobes  $\pm$  equal in length, broadly incurved, distinctly tapering, typically with 2 (or at times 3–4) basal cells), 1–2 biseriate tiers, and a uniseriate row of 4–7 cells; cells of basal tier 23–26  $\mu$ m wide  $\times$  42–54(62)  $\mu$ m long, the basal cell of uniseriate row 25–32  $\mu$ m wide  $\times$  54–66  $\mu$ m, the terminal cell, shorter than the penultimate cell, tapering to a rather sharp point (occasionally rounded at the tip); lobe cells rather firm-walled, with septa strongly thickened in the corners and not or a little projecting; cuticle smooth. Underleaves of main shoot 4-lobed, the lobes with a geminate base and a uniseriate row of 2–4(5)  $\pm$  elongate cylindric cells, the distal cell often hooked at the tip, ending in a slime papilla, the cells of the basal tier becoming subdivided into two tiers of small rhizoid initials, with rhizoids emanating from both tiers.

Dioecious. Androecia loosely subspicate, on terminal, *Frullania*-type branches;  $\delta$  bracts 3-lobed, the lobes biseriate at base, or more commonly at least the median lobe 3–4 cells wide at base. Gynoecia terminal on the main shoot, typically subtended by a pair of accessory gynoecia on short terminal, *Frullania*-type or ventral-intercalary branches; gynoecia also on ventral-intercalary branches along the shoot, often with several cycles of normal leaves and underleaves;  $\eta$  bracts 4-lobed to ca. 0.6 or more, typically basally connate with each other and with the bracteole, the connate portion up to 3 cells high; lobes 4 cells wide at the base, unequally (2)3-fid, the divisions often forked, with accessory forked cilia on the margins and in the sinuses between the lobes, the disc 4–5 cells high. Perianth inflated when young, narrowly cylindric at maturity, not narrowing toward mouth, shallowly to moderately sulcate above, mouth wide, with three broad, cil-

iate lobes, the segments forked and spurred, the ultimate divisions with a uniseriate row up to 9 cells long, the cells elongate, the septa thickened in the corners but not projecting.

Seta seen only in collapsed state. Capsule elliptic,  $805 \times 420 \mu$ , wall 3-stratose (locally 4-stratose),  $24\text{--}30 \mu$  thick, the outer layer about equal to the inner two in thickness; outer layer of cells in distinct tiers, with two-phase development, the resulting cells rectangular, the longitudinal walls with slightly thickened continuous sheets of pigmented material and nodular to short spinelike thickenings, alternating with walls devoid of thickenings, the transverse walls also without thickenings; inner layer of cells narrowly elongate, the longitudinal walls mostly without thickenings, with semiannular bands common, unevenly pigmented, occasionally incomplete, and then spinelike.

Spores  $10.6\text{--}12 \mu$  in longest diameter, light brown, reticulate-areolate, with polyhedral areoles bordered by narrow ridges, the areoles  $1\text{--}1.9 \mu$  in diameter. Elaters rather rigid,  $(9.6)11\text{--}12.5 \mu$  in largest diameter, blunt at one end, the other end slenderly attenuate, bispiral to the tips, the spirals  $3.4\text{--}3.8 \mu$  wide.

When well developed, *T. apiahyna* differs from other neotropical species of sect. *Telaranea* in having (3)4–6(8)-lobed leaves and 4-lobed underleaves. The stems are rather stout, with 12–16 rows of cortical cells and 32–42 rows of often only moderately smaller medullary cells. Robust plants are more regularly bipinnately branched (Taylor, 1961; Schuster, 2000). The branches are terete rather than conspicuously flattened as in *T. chaetophylla* and (to a lesser extent) *T. nematodes*.

The basal cells of the lobes are  $\pm$  elongated (Herzog, 1937, fig. 1b; Taylor, 1961, fig. 4; Schuster, 2000, fig. 74). An unusual feature of *T. apiahyna* is for one or more lobes to be more than 2 cells wide at the base. Often there are several biseriate tiers of cells above the base. The uniseriate row is up to 7 cells long, but is shorter in lobes with additional biseriate tiers.

Schuster's discussion and illustration of *T. quadrifida* (Schuster, 2000, p. 225, fig. 74) gives a much different impression of the species than the protologue (Schuster, 1978), where the leaves and underleaves are described as 3–4-lobed. The illustration, drawn from the type, shows 4–6-lobed leaves and 4-lobed underleaves. Schuster (2000) keys *T. apiahyna* under subg. *Neolepidozia*

(p. 211) and under subg. *Telaranea* (p. 222); his understanding of *T. apiahyna* appears to be based on Fulford (1963a, 1966).

The conspicuous, cruciform female inflorescence, formed by the terminal gynoecium and subtending paired gynoecia at the tip of the main shoot, is a startling departure from the usual condition in *Telaranea*, and indeed in Lepidoziineae as a whole. Taylor (1961) studied the type of *T. apiahyna*, and described the female inflorescence as terminal on a main axis (Taylor, 1961, fig. 1, 2). This has been confirmed by our own examination of the type, and by Taylor's microslide of serial longitudinal sections of the shoot apex, which accompanied the specimens received from G. Typically, just beneath the terminal gynoecium is an opposing pair of short, terminal, *Frullania*-type branches that also bear conspicuous gynoecia at the tip. These accessory gynoecial branches are sometimes intercalary in origin, but the branch included in Taylor's series is plainly terminal. The base of this branch is partly visible at lower left in the photomicrograph published by Taylor (fig. 1). The lateral branches associated with the terminal gynoecium are occasionally sterile and leafy. Terminal gynoecia with mature sporophytes are also present in the Costa Rican collection (Engel 8444), and in the Ule collection from Brazil, cited below.

Abundant additional gynoecia with young, inflated perianths are produced on ventral-intercalary branches along the stem. These branches are unusual in often having several cycles of normal leaves and underleaves. In the Peruvian specimen (Frahm et al. 1566) most shoots are male, with numerous androecia on short terminal, *Frullania*-type branches; a few shoots were female, producing young gynoecia on ventral-intercalary branches, but no terminal gynoecia were observed.

The ♀ bracts of *T. apiahyna* are 4-lobed, highly dissected and "antlered" (Taylor, 1961; compare Taylor's fig. 3 with Schuster, 2000, fig. 74: 3, *T. quadrifida*, and Stephani's Icones 39). Schuster's illustration (fig. 74: 3) shows both bracts and bracteole united at the base (fig. 74: 4), which we have also observed in the original material of *T. apiahyna*.

The underleaf disc normally consists of a single tier of cells, which may appear two cells high when the disc cells becomes subdivided into rhizoid initials (Herzog, 1937, fig. 1c; Fulford, 1963, fig. 154). According to Herzog (1937), *L. digitisquama*, to *T. apiahyna* "zunächst verwandt,"

differs only by the less well-developed underleaves, quadrifid, but with shorter lobes.

*Telaranea apiahyna* resembles a large *T. nematodes*, but differs in having terete branches, stouter stems with up to 11 stem cortical cells between leaves (vs. 4–5 in *T. nematodes*), 2–3-fid half-leaves, stem leaves with up to 6(8) lobes (3–4-seriate at the base, often with one or more biseriate tiers), and larger, often 4-lobed underleaves.

The specimen in the Mitten Herbarium (NY) labelled “S. Brazil, Wier,” determined as *T. apiahyna* by Fulford (see Fulford, 1966) shows the typical flattened branches of *T. chaetophylla* (Fig. 42: 2), with widely set, laterally inserted branch leaves, and a prominent 2-cell-wide dorsal median strip of quadrate cortical cells.

SPECIMENS SEEN—COSTA RICA: Cartago, NW of Cerro La Asunción, 3130 m., *Engel 8444*—c. sporo. (F). BRAZIL: Apiahy, *Puiggari 692*—c. sporo. + ♂, 792—c. per. (G); Santa Catarina, Juli 84, *Ule 353*—c. sporo. (G). PERU: Dept. San Martin, SW of Moyabamba, 915 m, edge of hot sulphur spring, *Frahm et al. 1566* as *T. nematodes*—c. ♂ + per. (Bryo. Neotropica Exsicc. 100) (E, F).

*Telaranea aubertii* (Jovet-Ast) Engel & Merr., comb. nov.

*Lepidozia aubertii* Jovet-Ast, *Candollea* 11: 35. f. 2. 1947. Type: New Caledonia, *Franc 13*.

ILLUSTRATION—Jovet-Ast (1947, fig. 2).

DISTRIBUTION—New Caledonia, New Hebrides (Jovet-Ast, 1951).

*Lepidozia aubertii* was based on material determined by Stephani as *Lepidozia “wallichii,”* an unpublished name, but as pointed out by Jovet-Ast (1947), it is clearly not *T. wallichiana*, nor can it be conspecific with *T. papulosa*, as suggested by Kitagawa (1973, p. 267), as we understand that species.

The branch leaves of *T. aubertii* are 2–3-lobed and arcuate (Jovet-Ast, 1947, fig. a, c, f, g). The leaf lobes are short, with a 2-celled base and 1, 2, or rarely 3 superposed cells. The disc of the stem leaves is 3 cells high, with cells to 25  $\mu\text{m}$  wide. Hürlimann (1985) lists *L. aubertii* as a synonym of *L. heterotexta*. The branch habit and branch leaves in Jovet-Ast’s drawing are arcuate, like those of *T. heterotexta*, but the characteristic disc areolation of that species is not evident in Jovet-Ast’s figures. The species is assigned to sect. *Cancellatae*.

*Telaranea autoica* Engel & Merr., sp. nov.

*T. tuberifera* primo adpectu simile, sed autoica, nitida, et lobis foliorum non caducis statim distincta.

Holotype: Juan Fernández, Más a Tierra, on the ridge leading to Cerro Damajuana, ca. 500 m, on branches, *G. Kunkel H290*—c. per. + ♂, as *Lepidozia disticha* (S).

DISTRIBUTION—Endemic to Juan Fernández.

Plants soft, flexuous, prostrate, highly nitid when dry, pale green. Branching loosely and irregularly pinnate, occasionally 2-pinnate, the branches of the *Frullania* type, leafy, less often stoloniform or flagelliform; branch half-leaf bifid, linear; first branch underleaf symmetrically or somewhat asymmetrically bifid, on base of branch. Ventral intercalary branches occasional, both leafy and stoloniform. Cortical cells thin walled, in 14 rows, in section much larger than the numerous (ca. 21) thin-walled medullary cells. Leaves on main shoot rigid, the leaves obliquely spreading, loosely imbricate, plane, nearly horizontally oriented, the insertion strongly incubous; leaves subsymmetric, longer than broad, 4-lobed to ca. 0.5, the lobes  $\pm$  parallel with disc margins or weakly divergent, about equal to the disc. Lobes slenderly acuminate, 2(3) cells wide at base, often with an additional biseriate tier, terminating in a uniseriate row of 3–4(5) cells, straight-sided or only weakly projecting at the septa, the cells of uniseriate portion firm-walled, somewhat thickened in the corners, the walls not bulging, 2–3:1, the paired basal cells about equal in length to the basal cell of the uniseriate row, the terminal cell rounded at the tip. Disc  $\pm$  straight-sided or weakly cuneate, 4–6 cells high from median sinus to leaf base, the ventral margin somewhat shorter, 8 cells wide at base, 8–10 cells wide in distal portion; margins entire, the ventral  $\pm$  straight, the dorsal somewhat curved. Cells of disc in regular longitudinal rows, thin-walled, trigones minute or absent; median disc cells large, short rectangular to somewhat elongated, (28)32–42  $\mu\text{m}$  wide, 36–50  $\mu\text{m}$  long, the 2 cell rows along the dorsal margin somewhat smaller; cuticle smooth. Underleaves conspicuous, to 1.5 $\times$  the width of the stem, erect spreading, 4-lobed to 0.5 or a little less, the lobes divergent, ciliiform, biseriate at base, with a uniseriate row of 3–4 elongated cells (or occasionally one or more lobes shorter), terminating in a slime papilla; disc cu-

neate, 2–3 cells high. Asexual reproduction by slender tubers at the tips of stoloniform branches.

Autoecious. Androecia on short *Frullania*-type branches or on short spicate ventral-intercalary branches, either solitary or in the same underleaf axil as a gynoeceal branch, or seemingly arising from the base of the gynoeceal branch itself; bracts in up to 7 pairs, bilobed, the disc 3–4 cells high, with a prominent dorsal tooth and a small tooth ventrally, the lobes acuminate, 3–4 cells wide at base, with a uniseriate row of 2–3 cells; antheridia solitary, stalk uniseriate. Gynoecea produced in abundance, often in a series of budlike ventral-intercalary branches along the leading shoot or on repeatedly branched mixed gametangial axes toward the base of the shoot; bracts very small for perianth size, the innermost bracts ovate, concave, 4-dentate-lobulate, the lobules 2–4 cells wide at base, ending in a single cell or with a 2-celled uniseriate row, the disc margins with a few small teeth. Perianth fusiform with a fleshy base,  $\pm$  terete in basal half, the distal portion shallowly plicate, narrowing toward the mouth, the mouth shortly and irregularly denticulate, formed by the projecting and partially free marginal cells. Sporophyte not seen.

This species is conspicuously autoecious, with gametangia of both sexes produced in abundance. The close association of androecia and gynoecea in a compound inflorescence is highly unusual, and found elsewhere only in *T. martinii* of New Zealand (p. 98). The aspect of the plant is distinctive among southern South American species, somewhat suggestive of a small *T. tuberifera* (p. 67). The plants are not glaucous, however, and the lobe tips are not caducous. Tubers are also reported for a number of other *Telaranea* species (e.g., *T. clatritexta*, *T. europaea*, *T. tasmanica*). See also comments under *T. rectangularis*.

The foregoing description is based on the type. A second collection, gathered by Skottsberg in 1917 at Cumberland Bay (S), is similar to *T. autoica* in most respects, having  $\pm$  parallel-sided leaves with disc cells in orderly rows and tiers, but differs in having predominantly 3-lobed leaves with the lobes somewhat constricted at the septa. The gynoecea arise in series on a ventral-intercalary branch and the initial  $\text{f}$  bracts are ovate and shallowly lobulate as in the type; no androecia were seen.

SPECIMEN SEEN—Juan Fernández, Más a Tierra, Cum-

berland Bay, Cave No. 2, 1917, Skoutsberg—c. young  $\text{f}$ , as *L. disticha* (S).

### *Telaranea bicruris* (Steph.) Howe

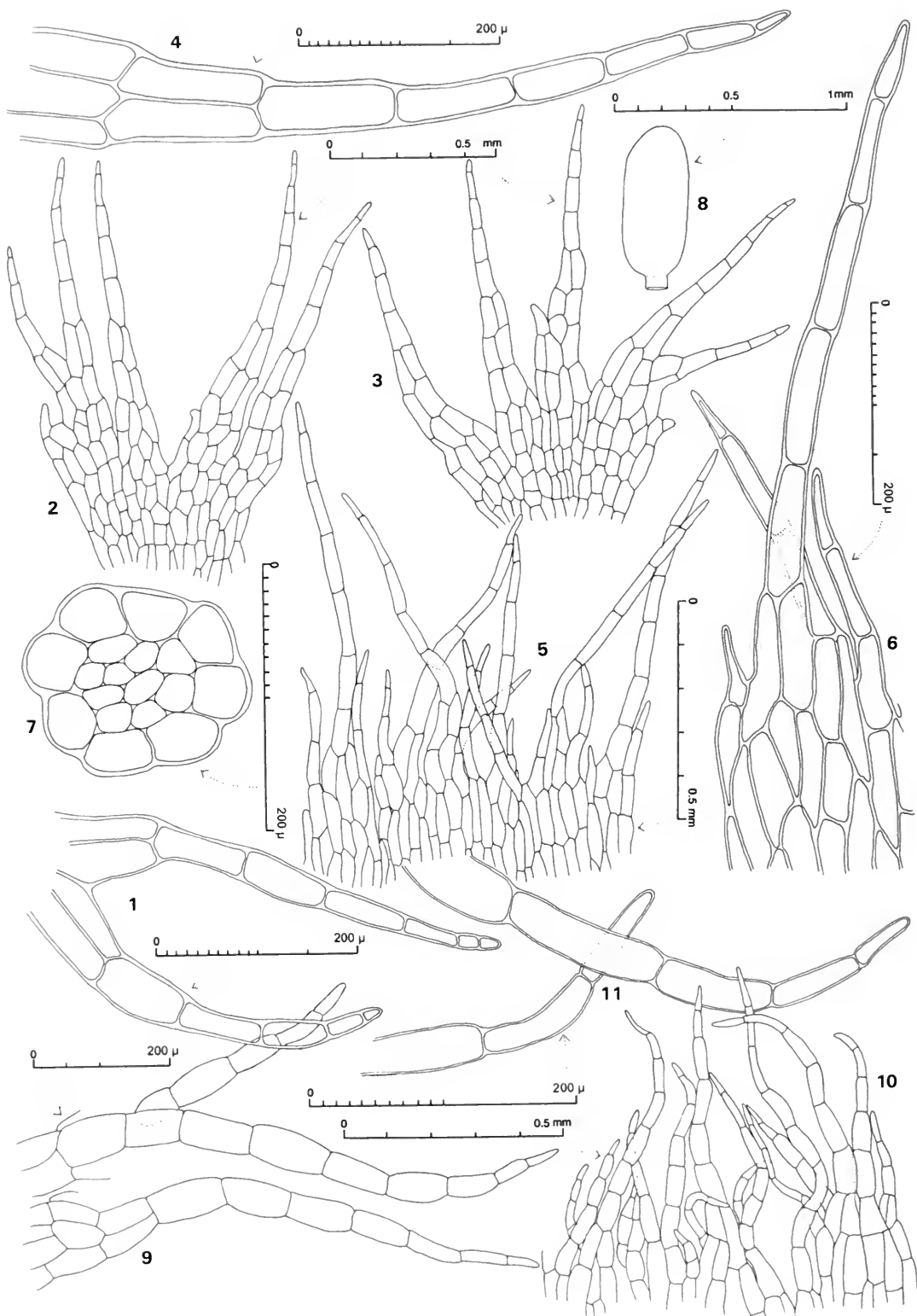
*Lepidozia bicruris* Steph., Hedwigia 24: 166. tab. 3. (April) 1885. *Telaranea bicruris* (Steph.) Howe, Bull. Torrey Bot. Club. 29: 287. 1902. Lectotype (nov.); Brazil, Sao Francisco, Ule 1—c. sporo. (G!); isolectotype (possible): NY!.

DESCRIPTION—Stephani (1909, as *L. sejuncta*).

ILLUSTRATIONS—Stephani (1885, pl. 3); Icones (*Lepidozia* 32, as *L. sejuncta*); Fig. 38: 1–8.

DISTRIBUTION—Brazil. Known chiefly from Ule's collections, presumably from Sao Francisco do Sul, Santa Catarina (one of the specimens in Stephani's herbarium is labeled "Ins. Sao Francisco"). Ule lived in Santa Catarina and collected from 1883 to 1891. The plants treated by Vianna (1974) from Rio Grande do Sul (Gramado, Guafaba) as *T. sejuncta* var. *brevisetata* are tentatively assigned to *T. bicruris*. The specimen from Goiás, cited below, differs from typical *T. bicruris* in the shorter basal cells of the lobes and somewhat constricted septa, but otherwise seems referable to this species. Reported from South Africa by Sim (1926), but the specimen in PRE (Table Mt., Woodhead Tunnel Gorge, Bews 8522, det. Sim as *T. bicruris*) is *Paracromastigium succulentum* (Sim) Engel & Merr. (Engel & Merrill, 2001).

Plants with a minutely prickly in appearance, prostrate, in thin mats adhering to substrate, with interwoven, much-branched,  $\pm$  leafless runners giving rise to other leafless axes and less often, erect leafy shoots. Branching somewhat irregular, at times becoming flagelliform or geotropic. Half-leaf bilobed or undivided. First branch underleaf asymmetrically bilobed, with one lobe resembling a leaf lobe, the other an underleaf lobe. Ventral-intercalary branches common, from leafless axes, remaining leafless or becoming leafy, or geotropic and "rooting" in the substrate. Stems slender, the cortical cells distinctly differentiated, in 8–9 rows, thin-walled but firm; medullary cells much smaller, thicker walled, in 14–15 rows; branches terete. Leafy shoots with 4–5 cortical cells intervening between successive leaves on either side (or more in lower portions of the shoot); terminal branches with 3 cells intervening between successive leaves on either side of branch. Leaves stiffly spreading, the insertion transverse to weakly succubous, 390–515  $\mu\text{m}$  long  $\times$  295–370  $\mu\text{m}$  wide (between tips of spreading lobes), (2)3–4-lobed





almost to the base, the basal cells united to about 0.2 their length, the branch leaves bilobed, the lobes mostly uniseriate to the base; lobes widely divergent, rather short, distinctly tapering, broadly incurved, from a geminate base or (often) the dorsal lobe uniseriate to the base, the basal cells about the same length as the lobe cell above, the uniseriate portion of lobe 4–5(6) cells long; cells of basal tier each 24–30  $\mu\text{m}$  wide  $\times$  90–103  $\mu\text{m}$  long (when lobe base uniseriate 42  $\mu\text{m}$  wide), the basal cell of uniseriate row of lobe 31–37  $\times$  86–109  $\mu\text{m}$ , the next cell of about equal length, the terminal cell small, ovoid, and much shorter than the penultimate cell; lobe cell walls with septa thickened in the corners and straight or somewhat projecting; cuticle smooth. Underleaves symmetrically 2–4-lobed, each lobe with a pair of small basal cells, and a uniseriate row of 1–2 narrowly cylindric cells, the tip cell ending in a slime papilla, at times unequally lobed, with 1 or more lobes resembling those of the leaves, the others shorter and underleaf lobe-like.

Diocious. Androecia abundant on short ventral-intercalary branches or on terminal *Frullania*-type branches, occasionally intercalary on a leafy shoot,  $\delta$  bracts in up to 8 pairs, strongly secund and dorsally assurgent;  $\delta$  bracts monandrous, 3-lobed, asymmetric, one lobe often with an additional biseriate tier, the dorsal lobe smaller and spur-like; antheridial stalk uniseriate. Gynoecea on short, leafless ventral-intercalary branches from leafy shoots; bracts of innermost series 4-lobed, the disc 3–4 cells high, occasionally with a marginal tooth, the lobes (3)4(5) cells wide at base, caudate, with up to 3 biseriate tiers above the base, terminating in a uniseriate row of 5–6 cells, occasionally with an accessory lacinium or unicellular tooth toward the base. Perianth fusiform, subterete below, trigonous and tri-plicate above the middle, the mouth weakly contracted and with 12 long cilia + accessory cilia about half as long, the longer cilia ending in a uniseriate row of 5–7 elongate cells. Calyptra about half the length of the perianth, with archegonia confined to the extreme base.

Seta with 8 rows of outer cells surrounding an

inner core of 10–11 much smaller cells. Capsule long elliptic to linear, the wall 20–23  $\mu\text{m}$  thick, 2-stratose; outer layer of cells elongate-rectangular, with two-phase development, the longitudinal walls with continuous sheets of pigmented material and nodule-like thickenings (the walls appearing sinuous), alternating with walls devoid of thickenings, the transverse walls also without thickenings; inner layer of cells narrowly rectangular, the longitudinal walls with semiannular bands common, rather narrow, often incomplete, the longitudinal walls also with nodular and spur-like thickenings.

Spores 14.4–16.8  $\mu\text{m}$  in longest diam., reddish-brown, the surface reticulate-areolate. Elaters long and rather straight, 8.6–9.6  $\mu\text{m}$  wide, only slightly tapering and bispiral to tips, the spirals 2.9–3.8  $\mu\text{m}$  wide.

**NOMENCLATURE**—Publication date of *Lepidozia bicruris* Steph., Hedwigia 1885 (Apr fide TL2 5: 891). Publication date of *Lepidozia chaetophylla* Spruce 1885 (Nov. in original; TL2 5: 819). Stephani (1909) listed *L. bicruris* as a synonym of *L. sejuncta*, but his description clearly applies to the former (lobes biseriate at base, etc.). Stephani apparently later abandoned *L. bicruris* in favor of *L. sejuncta*. The Icones illustration of *L. sejuncta* (*Lepidozia* 32), leg. Ule, is copied from the original plate of *L. bicruris* (Stephani, 1885, pl. 3). Specimens in Stephani's herbarium are labeled *L. sejuncta* "olim *Lepidozia bicruris*."

Selection of a lectotype is complicated by the fact that among the apparent syntypes in Stephani's herbarium, two elements are present, one corticolous, the other on soil. The protologue mentions both substrates ("in solo argilloso vel in cortice ad pedem arborum repens"), but the details apply to the terricolous plant. In particular, Stephani (1885, p. 167) described the leaves as almost without exception bilobed, and emphasized the undivided half-leaf and the "zahlreichen blattlosen Flagellen der Ventralseite" and branches becoming flagelliform and rooting at the tips as characteristic of the species. The corticolous plants have 3–4-lobed leaves and bifid half-

←

FIG. 38. *Telaranea bicruris* (Steph.) Howe (1–8) and *Telaranea nematodes* (Gott. ex Aust.) Howe (9–11). 1. Leaf. 2, 3. Innermost  $\varnothing$  bracts. 4. Portion of median lobe of  $\varnothing$  bract. 5, 6. Portions of perianth mouth. 7. Seta, cross section. 8. Capsule profile. 9. Two lobes of innermost  $\varnothing$  bract. 10. Portion of perianth mouth. 11. Distal portions of two perianth lobes. (Figs. 1–8 from type of *Telaranea bicruris*; 9–11 from type of *Telaranea nematodes* Gott. ex Aust.)

leaves, and leafless, stoloniform ventral branches are essentially lacking, even though one of these bears a red "Typus" label, and is labeled "Ule original." The lectotype selected (*Ule 1*) is one of the terricolous collections that, moreover, has abundant perianths, "Rami feminei numerosi, saepe seriatim dispositi," in accordance with the protologue. Our description and plate are based on the NY specimen (herb. Mitten, "ex Herbario auctoris"), which is terricolous and agrees with the lectotype.

COMMENTS—The habit of growth of *T. bicruris* is characterized by extensive production of leafless ventral-intercalary branches and flagelliform branches rooting at the tips. The paired basal cells of the lobes are narrowly elongate, equaling or slightly exceeding the basal cell of the uniseriate row in length. *Telaranea chaetophylla* differs chiefly in its complanate branches with widely set leaves and a broadly exposed strip of dorsal cortical cells. The innermost ♀ bracts of *T. bicruris* are palmately 4-lobed, with a disc 3–4 cells high, the lobes caudate, with as many as 3 biseriate tiers above the base (Fig. 38: 2, 3). In *T. chaetophylla* the disc is only 2–3 cells high, the lobe base composed of 2–4 turgid cells, only occasionally with an additional biseriate tier. The seta in *T. bicruris* is 8+10–11 (Fig. 38: 7), compared with 8+6 in *T. chaetophylla*, and 8+17 in *T. nematodes*.

This species usually has been described as dioecious (Stephani, 1885; Pearson, 1886; Howe, 1902), although in the NY material, male and female plants are closely intertwined. Clearly, the specimen is not the one examined by Howe, since he says he was unable to find antheridia in specimens received from Stephani. We observed androecia in abundance on some shoots, without a hint of gynoeceia, whereas those with perianths and sporophytes appear purely female and do not bear male branches even in older portions of the plant.

SPECIMENS SEEN—BRAZIL: In fossis Sao Francisco, Juli 84, *Ule 5*—c. per. (G); Goiás, 20 km N of Alto do Paraíso, Irwin, Harley & Smith 32135 as *Arachniopsis diacantha* (F). Corticolous element at G: without specific locality, "Ules Original," *Ule 2*—c. per. (G); Sao Francisco, ad lignum putridum, Aug 84, *Ule 31*—c. sporo. (G); leg. 1884, *Ule s.n.*—c. sporo. (G).

*Telaranea bisetula* (Steph.) E. Campb.

*Lepidozia bisetula* Steph., Spec. Hep. 6: 323. 1922 non *L. bisetula* Herz. (= *T. herzogii* Hodgs. 1956, New Zealand). *Kurzia bisetula* (Steph.) Grolle, Rev. Bryol. Lichénol. 32: 170. 1964 (1963). *Telar-*

*anea bisetula* (Steph.) E. Campb., J. Roy. Soc. New Zealand 1: 26. 1971. Type: New Caledonia, *Franc 143* (G!).

DESCRIPTION—Grolle (1964).

ILLUSTRATIONS—Schuster (1980), fig. 5: 12–181. Stephani, Icones, *Lepidozia* 205.

DISTRIBUTION—New Caledonia, Fiji Is. (Campbell, 1971; Miller, 1986).

NOMENCLATURE—Herzog (1938) published a *Lepidozia bisetula*, which Hodgson (1956) re-named *L. herzogii* (p. 112). Grolle (1964) listed *L. leratae* Par. ex Steph. (1922) as a synonym of *Kurzia bisetula*. A near homonym, *L. leratii* Steph. (1922), also from New Caledonia, is transferred to *Telaranea* (p. 162).

COMMENTS—*Telaranea bisetula* strongly resembles *T. tasmanica* (p. 106) in having deeply bilobed leaves, lacking a disc, with the lobes biseriate at the base. In *T. tasmanica*, however, *Microlepidozia*-type branches are not produced. The dimensions of the basal lobe cells in *T. bisetula* are  $35 \times 120 \mu\text{m}$  (Grolle, 1964), vs.  $24\text{--}31 \times 54\text{--}74 \mu\text{m}$  in *T. tasmanica*.

This species has been previously assigned to *Kurzia*, primarily because of the presence of *Microlepidozia*-type branching. Grolle (1964) observed that this species might constitute a distinct genus, but rejected this course as "inflationary." Schuster (1980) assigned *K. bisetula* to a new subgenus, *Kurzia* subg. *Nanolepidozia* Schust., characterized by diffuse branching (lacking the regular alternation between *Frullania*-type and *Microlepidozia*-type branches), presence of a hyaloderm, minute underleaves, and leaves lacking a distinct lamina (lobe bases 2-celled and united for ca. 0.2–0.32 their length), and bistratose capsule wall. Engel and Merrill (1996b) added another species, *K. quinquespina* (*T. quinquespina*, p. 109). The two species differ primarily in the form of the underleaves (symmetrically bilobed in *T. bisetula* vs. asymmetrically bilobed in *T. quinquespina*). However, one strongly asymmetric underleaf was observed in the type of *T. bisetula*: one lobe consisting only of the small paired basal cells (no cylindrical cell), and the other lobe leaf-like, consisting of the paired cells + a uniseriate row of 4 cells. The two differ also in the presence of lateral-intercalary branching in *T. quinquespina*. *Kurzia* subg. *Nanolepidozia* is treated here as a synonym of *Telaranea* sect. *Telaranea*.

The underleaves of *T. bisetula* are typically inconspicuous, symmetrically or subsymmetrically bilobed, each lobe consisting of the small paired

basal cells + 1–2 large, cylindrical cells. The size of the cylindrical cells may differ considerably. Occasionally one or both of the basal cells can be undivided (i.e., without a vertical division). The leaf lobes in the type have a uniseriate row of 5–6 cells, with lobe cells distinctly thickened in the corners and the septa straight and not bulging or constricted. Plants of the type are sparsely and irregularly branched, without the regular alternation of *Frullania*- and *Microlepidozia*-type branches typical of *Kurzia* species.

Stephani (1922, protologue) and Grolle (1964, p. 170) described the leaves of *T. bisetula* as bilobed. However, Schuster (1980) described them as asymmetrically trifid in this species, with the dorsal lobe conspicuously longer.

According to Schuster (1980, p. 353–354), the capsule wall of *T. bisetula* is bistratose, and the spores are “14–15  $\mu\text{m}$  in diam., bearing scattered, remote, very coarse, tumid to hemispherical, brown, unequal papillae, interspersed amidst which occur scattered, minute asperulae or papillae.”

Miller (1986, fig. 1a–h) reported *T. bisetula* from Vanuatu, Figi. The plant illustrated, however, has 2–3-lobed leaves with a disc 2 cells high.

### *Telaranea blepharostoma* (Steph.) Fulf.

*Lepidozia blepharostoma* Steph., Bih. Kongl. Svenska Vetenskapskad. Handl. 26 (III, 17): 22. 1901. *Telaranea blepharostoma* (Steph.) Herz., Rev. Bryol. Lichénol. 20: 189. 1960, *nom. inval.* *Telaranea blepharostoma* (Steph.) Fulf., Brittonia 15: 73. 1963. Type: Chile, Prov. Magallanes, Isla Desolacion, Puerto Angosto, *Dusén* 142 (G!).

DESCRIPTIONS—Stephani (1909); Fulford (1963a, 1966).

ILLUSTRATIONS—Fig. 39; Fulford (1963a, figs. 156–167; 1966, pl. 53, fig. 4). Stephani's *Icones* (*Lepidozia* 132) is not based on the type.

DISTRIBUTION—Falkland Is.; southern South America (Magellanian + Valdivian); see Engel (1978; 1990, fig. 30).

Plants in soft, resilient mats, the shoots lax and straggling, prickly in appearance, subisophyllous, brownish yellow to rust brown in older portions of the shoot. Branching distant and irregular, the branches forming a narrow angle with the stem, primarily *Frullania*-type, leafy or long flagelliform and thread-like; branch half-leaf bilobed or undivided, with up to 3 biseriate tiers; first branch underleaf symmetrically or asymmetrically bi-

lobed (one lobe like a leaf lobe, the other shorter, ending in a slime papilla), inserted on the branch base. *Acromastigium*-type branches common, the half-underleaf bilobed with one lobe abbreviated, or subulate (Fig. 39: 1) and resembling a leaf lobe, the first branch underleaf asymmetrically bilobed. Ventral intercalary branches also present, leafy or microphyllous and thread-like. Stems slender for plants size, the cortical in 9–11 rows, larger than the 11–14 thin-walled medullary cells. Leaves transversely inserted, 3–4-lobed, the disc and lobes obliquely spreading in one plane (Fig. 39: 1), widely divergent, long attenuate, biseriate at the base (at times with an additional biseriate tier), the uniseriate row 5–7 cells long, evenly tapering to a sharp-tipped terminal cell (Fig. 39: 2, 5), the septa thickened in the corners and projecting. Disc 1.5 cells high, composed of a basal tier of disc cells and the 2-celled bases of the lobes, the cells thick-walled and firm. Cuticle of leaf lobes faintly to distinctly short-striate papillose (Fig. 39: 5), of the disc smooth. Underleaves as large as the leaves, 3–4-lobed, with the middle lobe (or one of the middle lobes) shorter, with 1–3 biseriate tiers of subquadrate cells at the base (Fig. 39: 3, 4), the disc cells beneath often transversely divided, the longer lobes resembling the lobes of the leaves.

Androecia on flagelliform and threadlike terminal, *Frullania*-type branches and on short ventral-intercalary branches, rather lax, the bracts in up to 7 series, 2–3-lobed to ca. 0.7, the lobes caudate, 3–4 cells wide at the base, followed by a biseriate tier and a uniseriate row of 3–4 cells, the lobe base with 1 or more small 1–2-celled teeth, the disc 2 cells high, the dorsal margin or both margins with a small 1–2-celled tooth; antheridia 1 per bract, the stalk rather stout, uniseriate. Only young gynoeceia seen.

This is a distinctive plant, forming rather resilient, light tan to brownish mats. The leafy shoots are slender and very sparingly branched, with a characteristic prickly appearance, but often becoming rather abruptly microphyllous and exceedingly long and threadlike. The shoots are almost perfectly isophyllous, the underleaves differing from the leaves only in having one or more abbreviated lobes. *Telaranea fernandeziensis* is also subisophyllous, with transversely inserted leaves, a disc 1.5 cells high, and large, unequally lobed underleaves; *T. blepharostoma* differs, however, in the straggling habit, brownish pigmentation, 3–4-fid leaves with straight, stiffly divergent lobes, and

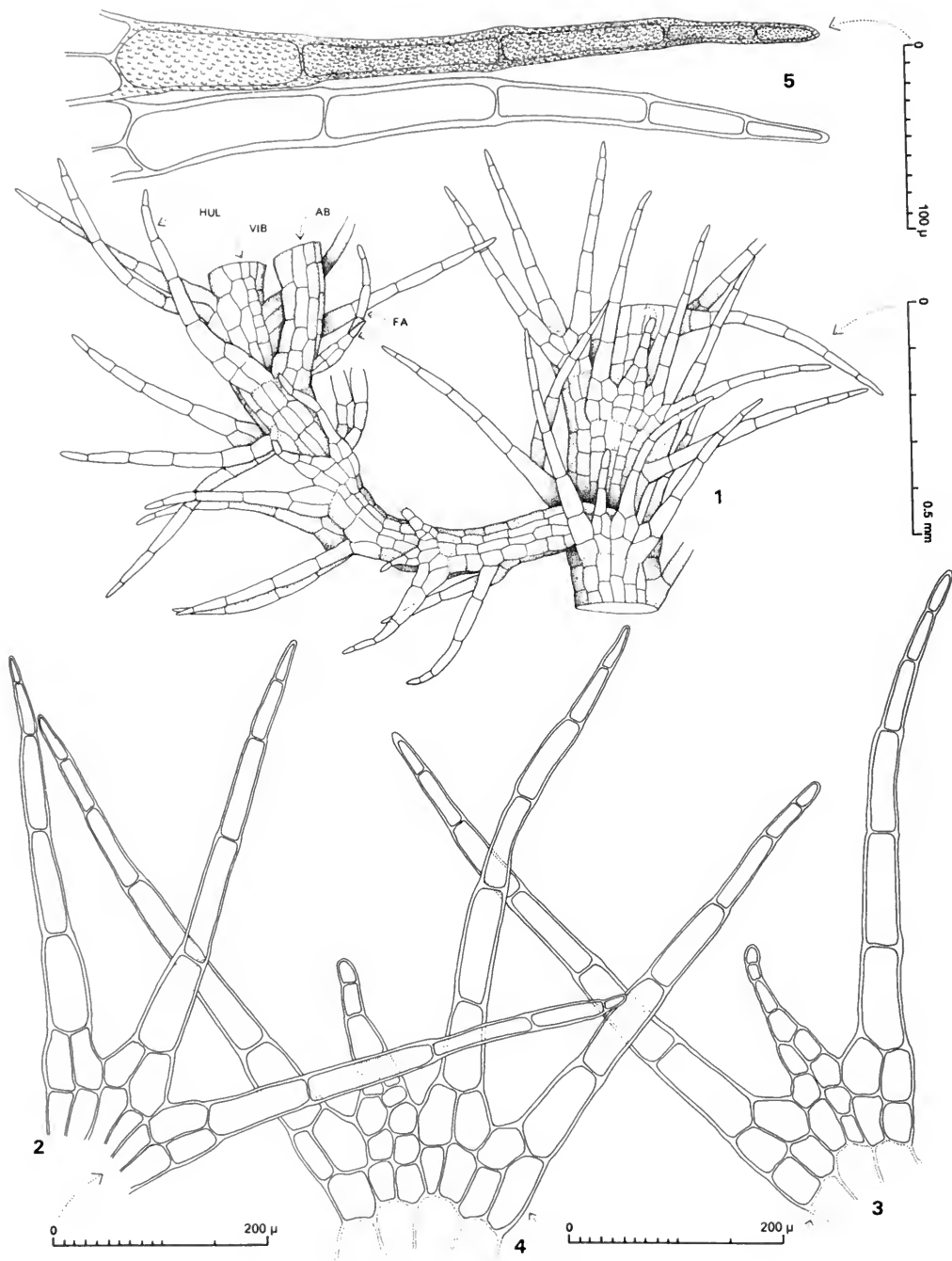


FIG. 39. *Telaranea blepharostoma* (Steph.) Fulf. 1. Portion of main shoot showing subisophylly, with ventral-intercalary branch (= VIB), and *Acromastigum*-type branch (= Ab); note half-underleaf (= hul) and first branch appendage (= fa) of the ventral-terminal branch. 2. Leaf. 3, 4. Three- and 4-lobed underleaves drawn to same scale as fig. 2; note smaller median lobes (stem cells indicated by stipple). 5. Leaf lobes, the cuticle shown on one lobe. (All from Engel 3201, Falkland Is., East Falklands, Stanley, Goat Ridge.)

striate-papillose cuticle, and there is no evidence of the characteristic off-center alignment of lobe cells of *T. fernandeziensis*. A less obvious difference is the frequent production of *Acromastigum*-type branches in *T. blepharostoma*. Fulford (1963a) describes the gynoeceia.

*Telaranea blepharostoma* is placed in sect. *Transversae*, together with other species with transversely inserted leaves, capillary lobes, low disc, and unequally lobed (*Kurzia*-like) underleaves. For a comparison of this species with *T. ferruginea*, see under that species.

**ECOLOGY**—In the Falklands the species occurs only in the Port Stanley region under *Blechnum* in a dwarf shrub heath, and on moist, sandy, sheltered, vertical, north-facing rocks along the south shore of the Murrell River. In southern South America the species has a scattered distribution, near sea level in forests of e.g., *Drimys*, *Nothofagus betuloides*, *Berberis ilicifolia* and *Pernettya* at Bahía Tuesday (Isla Desolación) or in scrubby bush consisting of *Drimys*, *Weinmannia*, and *Blechnum* at Puerto Edén. It is associated most frequently with cliff faces, especially in protected hollows or deep under overhangs or in masses of vegetation. For example, on Isla Gordon in Antártica Chilena, the species occurred in soft, felt-like mats on a sheltered, vertical, dripping cliff face near the edge of a forest of *Nothofagus* and *Drimys*. The species occurs in pure tufts or is admixed with other hepatics, such as *Blepharidophyllum clandestinum*, *Anastrophyllum semifissum*, *Frullania magellanica*, and *Lepidozia* sp. Herzog (1954, 1960) records the species from several localities in the Valdivian zone.

**SELECTED SPECIMENS SEEN**—FALKLAND IS.: East Falklands, Stanley, Goat Ridge, 185 m, *Engel* 3201 (F); *ibid.*, S shore of Murrell River, opposite Island Point, *Longton & Smith* 1027 (F). CHILE. PROV. ANTÁRTICA CHILENA: Comuna Cabo de Hornos, N side of Isla Gordon at W side of Bahía Romanche off Brazo Noroeste of the Beagle Channel, ca. 15 m, *Engel* 25448 (F); *ibid.*, Isla Grande de Tierra del Fuego, W shore of Seno Ventisqueros, ca. 200 m, *Engel* 25389 (F). PROV. MAGALLANES: E side of Bahía Borja (Península Córdova, Isla Riesco, Paso Tortuoso), *Engel* 6165—c. young ♀ (F, MSC); Bahía Tuesday (Isla Desolación), head of inner harbor, *Engel* 5646B (F, MSC); Puerto Charrúa (S side of Isla Wellington), *Engel* 4815 (F, MSC); Puerto Alert (Isla Mornington, Canal Trinidad), W side of harbor, *Engel* 4896—c. ♂ (F, MSC); Puerto Edén (Isla Wellington, Canal Messier), *Engel* 4576 (MSC); near shore at SE point of Isla Williams (Bahía Tribune, Canal Messier), *Engel* 4487 (F, MSC).

*Telaranea breviseta* (Herz.) Engel & Merr., comb. nov.

*Lepidozia sejuncta* var. *breviseta* Herz. in Skottsberg, Nat. Hist. Juan Fernández, Bot. 2: 723. 1942. *Lepidozia breviseta* (Herz.) S. Arnell, Results Norw. Sci. Exped. Tristan da Cunha 1937–38, 42: 14. 1958. *Telaranea breviseta* (Herz.) S. Arnell, Results Norw. Sci. Exped. Tristan da Cunha 1937–38, 42: 14. 1958, *nom. inval.* (Art. 34.2). *Telaranea sejuncta* var. *breviseta* (Herz.) Fulf., Brittonia 15: 71. 1963. Type: Juan Fernández Is., Más Afuera, Quebrada del Mono, 370 m, *Skottsberg* 142 p.p.

**ILLUSTRATIONS**—Fulford (1966, fig. 52: 1k).

**DISTRIBUTION**—Juan Fernández, Chile (Valdivian). Reported from Tristan da Cunha by Arnell (1958), to our knowledge the only report of a *Telaranea* from this remote Atlantic island.

Plants minute and delicately threadlike, with irregularly branched microphyllous axes giving rise sparingly to leafy shoots and branches, the leafy axes minutely prickly in appearance. Terminal, *Frullania*-type branches occasional; half-leaf undivided or bilobed; first branch underleaf undivided or asymmetrically bilobed, with one lobe resembling a leaf lobe, the other an underleaf lobe. Ventral-intercalary branches common, remaining microphyllous or becoming leading leafy shoots. Both terminal and intercalary branches increasing in diameter at the tips and forming long, slender fleshy tubers, the tuber cells thin-walled, transparent and parenchymatous. Stems slender, the cortical cells distinctly differentiated, in 9 rows, thin-walled and transparent; medullary cells much smaller, in 16–17 rows. Leafy shoots with 3–4 cortical cells intervening between successive leaves on either side. Leaves inconspicuous, small in proportion to the shoot, 2–3(4)-lobed, ± transversely inserted, the basal cells of the lobes minute and inconspicuous, united for most of their length, forming a disc 1 cell high, the leaves wide-set and almost lateral in position, the 2 median rows of cortical cells ± completely exposed. Lobes widely and stiffly divergent, very short, tapering, from a geminate base, the uniseriate portion of lobe 3(4) cells long; cells of basal tier minute, ± isodiametric, 14–18 µm wide × 12–20 µm long, the basal cell of uniseriate row of lobe 14–19 µm wide × 48–60 µm long, the next cell much shorter, 10–14 µm wide, (18)22–36 µm long, the terminal cell often appearing secondarily divided; lobe cells firm-walled, the septa thickened in the corners, straight or slightly constricted; cuticle smooth. Underleaves small, 3(4)-lobed

on leafy shoots, each lobe with a pair of small basal cells and 1–2 elongate cylindric cells, ending in a slime papilla.

Dioecious. Androecia at the tips of long leafy shoots and terminal branches, compactly spicate, wider than sterile portion of shoot; ♂ bracts in 3–5 pairs, secund and dorsally assurgent; ♂ bracts monandrous, 4-lobed, asymmetric, the lobes erect, 1–2 cells wide at the base, the uniseriate row of 3–4 firm-walled cells, the disc 4 cells high dorsally, 2 cells high ventrally, with small, sharp 1–2-celled teeth between the lobe bases, the dorsal margin of the disc (as well as the dorsal lobe) sharply inflexed, forming a narrow pocket; antheridia 1 per bract, the stalk uniseriate. Gynoecia on abbreviated ventral-intercalary branches; bracts 3-lobed, divided to a little more than half their length, the lobes 3–4 cells wide at base, with a uniseriate row of 2–4 cells, the lobe cells elongate, firm-walled, with constricted septa; disc 3–4 cells high, with shorter, 1–2-celled cilia between the bases of the lobes, ending in a slime papilla. Perianth cylindric, shallowly plicate in the upper half, ciliate at the mouth, the cilia ca. 10, interspersed with shorter 1–2-celled blunt cilia, the longer cilia 2–3 cells wide at the base, with a uniseriate row 3–4 cells long, the cells  $\pm$  cylindric but each successive cell narrower than the last, the tip cell thick-walled and slender and blunt at the tip, the septa constricted in the basal portion of the cilium, thickened above and not or weakly projecting.

Seta not seen. Capsule valves 2-stratose, 22–23  $\mu\text{m}$  thick, the outer layer somewhat thicker than the inner; outer layer of cells  $\pm$  uniform, rectangular, with two-phase development, the longitudinal walls with continuous sheetlike pigmented thickenings and nodule-like to short spinelike projections, alternating with walls devoid of thickenings, the transverse walls also without thickenings; inner layer of cells very narrowly rectangular,  $\pm$  uniformly scalariform, the longitudinal walls with thin continuous sheets of wall material, the semiannular bands broad and closely spaced (only sporadically incomplete).

Spores 12–14.4  $\mu\text{m}$  in largest diam., light orange-brown, reticulate-areolate, precociously germinating, many spores bicellular, to 17.3  $\mu\text{m}$  in

largest diam., others 3–4-celled, the spore wall ruptured. Elaters somewhat sinuous, 7.2–8.6  $\mu\text{m}$  wide, moderately tapering and bispiral to tips, the spirals 2.4–3.4  $\mu\text{m}$  wide.

Herzog (1942) described this plant as a variety of *T. sejuncta*, smaller in stature, with larger cortical cells, with leaf lobes shorter and straighter. The comparison with *T. sejuncta* is not particularly instructive in view of the checkered history of the application of this name (see p. 187). Fulford (1963a, p. 71), provided a description of var. *breviseta* based on the type and later (1966, fig. 52: 1k) published a drawing of a portion of a leafy shoot. According to Fulford, the leaves and underleaves are very small and delicate, “a condition which one might expect to find on branches of depauperate plants. However, these plants do not appear to be depauperate.” Our concept of *T. breviseta* is based on several collections from the Valdivian region, which are reasonably consistent with what little is known of this species. In our material, the leaves are indeed disproportionately small, but both androecia and gynoecia with sporophytes are present.

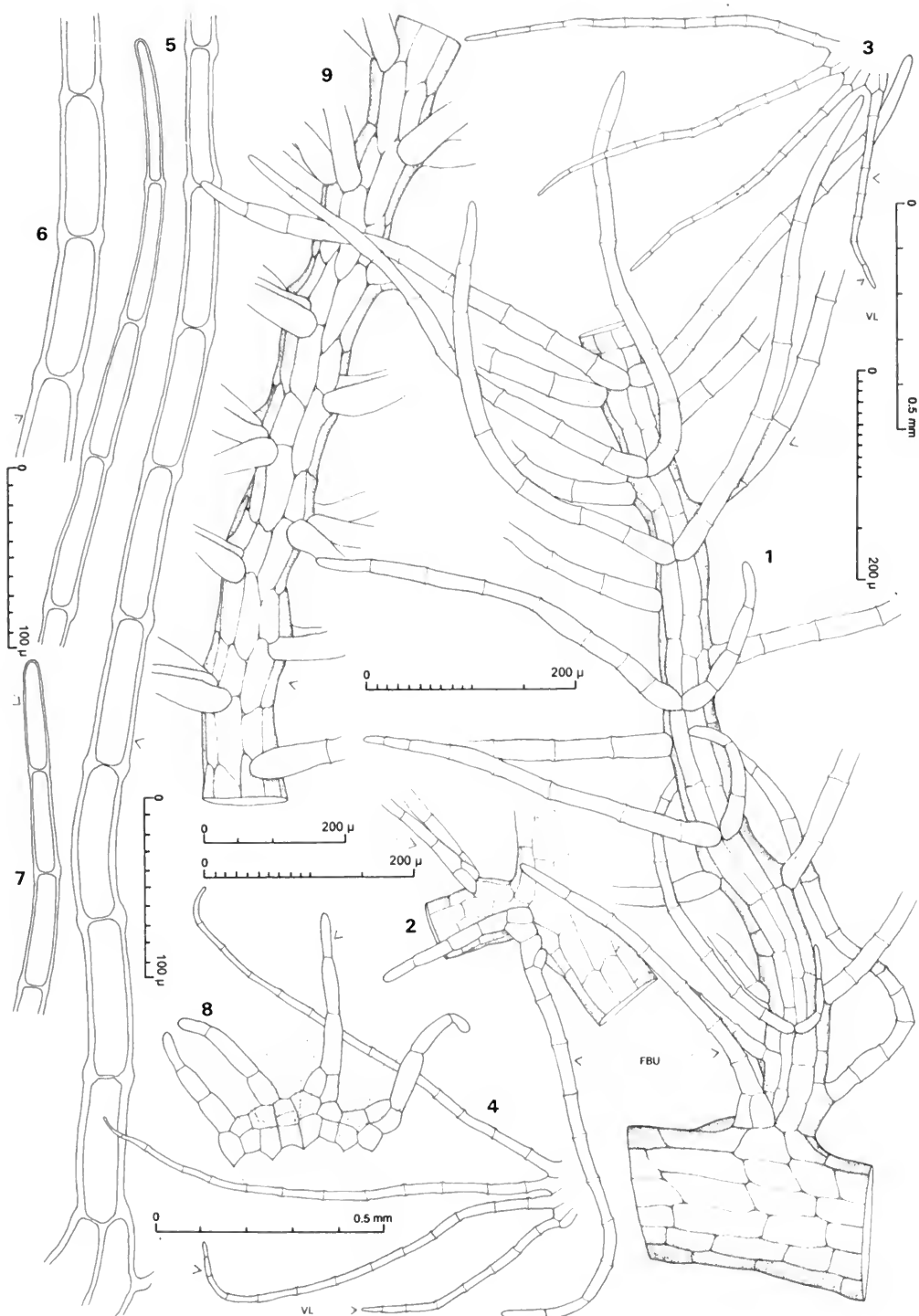
ECOLOGY—Known only from the Valdivian zone of southern South America, and Juan Fernández. In southern South America the species occurs over soil on the forest floor in forests of, for example, *Nothofagus nitida*, *Weinmannia*, *Myrceugenella* and *Chusquea* in the Lechagua area, Isla Chiloé, and ranges from sea level to 360 m.

SPECIMENS SEEN—CHILE. PROV. CHILOE: Isla Chiloé, Aguas Buenas area, 4.7 km E along Aguas Buenas road from Ancud-Quemchi road, ca. 100 m, Engel 12217—c. ♂ (F); ibid., Lechagua area, 5 km by road W of Ancud, near sea level, Engel 11695—c. ♂ (F). PROV. OSORNO near Prov. Valdivia boundary: Anticura, near Salto del Indio, 19 km by road E of Termas de Puyehue along international highway, 300 m, Engel 11653 (F). PROV. VALDIVIA: Near Río Futa in vicinity of Futa, 10.5 km by road S of junction of highway T-60 and T-65, 10 m, Engel 11028—c. per. (F). PROV. MALLECO: Cordillera Nahuelbuta, along trail from western entrance of Parque Nacional Contulmo, 7 km by road E of Contulmo, 330–360 m, Engel 12492—c. sporo. + ♂ (F).

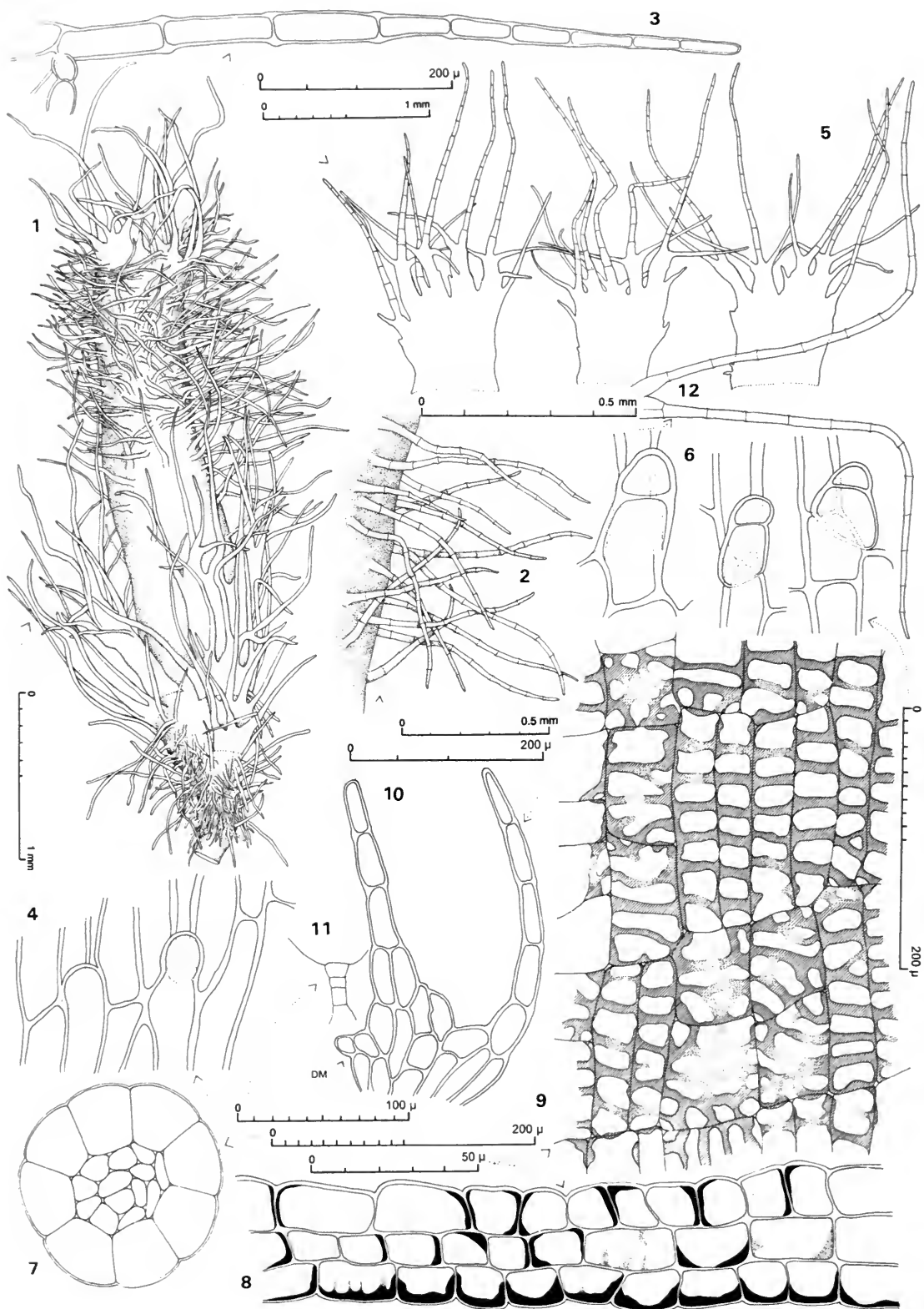
*Telaranea chaetocarpa* (Pears.) Grolle

*Lepidozia chaetocarpa* Pears., J. Linn. Soc., Bot. 46:

FIG. 40. *Telaranea chaetocarpa* (Pears.) Grolle 1. Portion of main axis with primary branch (ventral view) showing undivided first branch underleaf (= fbv), asymmetrically and symmetrically lobed branch underleaves and side-by-side alignment of branch cortical cells. 2. Portion of main axis and base of primary branch showing asym-



metrically bilobed first branch underleaf (= fbu). 3, 4. Leaves of main shoot (vl = ventral lobe). 5. Leaf lobe of 10 cells, the apex to immediate left. 6. Basal portion of leaf lobe. 7. Distal portion of leaf lobe. 8. Underleaf of main shoot, stem cells and rhizoids shown in stipple. 9. Sector of primary branch showing alignment of stem cortical cells, dorsal view; leaf bases included to show insertion. (All from *Hürlimann* 2786, New Caledonia, Koghi Mts, S flank of Moné summit.)





27. pl. 2: f. 35–51. 1922. *Telaranea chaetocarpa* (Pears.) Grolle, J. Hattori Bot. Lab. 29: 282. 1966. Type: New Caledonia, Mont. Koghi, 3000 ft, *Compton* 740.

ILLUSTRATIONS—Grolle (1966, fig. 1i–k); Figs. 40, 41.

DISTRIBUTION—Endemic to New Caledonia.

Plants with a delicately feathery aspect, the primary branches secund and plumose when dry, stiffly dorsally assurgent when moist, highly nitid when dry, pale yellowish green in herb; the shoots to 350  $\mu\text{m}$  wide with leaves. Branching primarily of *Frullania* type, densely and regularly 1(2)-pinate, the branches of roughly equal length, normally with only one leaf intervening between branches on either side, the main axis strongly anisophyllous, the branches subisophyllous; branch half-leaf bilobed; first branch underleaf undivided and ciliiform, inserted on ventral side of branch base, leaf lobelike, consisting of a pair of short basal cells and a uniseriate row of 8–13 cells, less often asymmetrically bilobed, one lobe shorter, with a uniseriate row of 2–3 short cylindrical cells, ending in a slime papilla. Ventral-intercalary branches present, long and leafy. Stems stout for plant size, the cortical cells distinctly differentiated, in 12 rows (8 dorsal + 4 smaller ventral rows), with moderately thickened walls; cortical cells in section larger than the numerous (21–23), firm-walled medullary cells. Main shoots with (3)4 cortical cells intervening between successive leaves on either side, the branches with 2 cells intervening between successive leaves on either side of branch, the cortical cells of branches conspicuously aligned side-by-side. Leaves of main shoot stiffly spreading, transversely inserted, 700–980  $\mu\text{m}$  long  $\times$  980–1200  $\mu\text{m}$  wide (between tips of spreading lobes), 3–4-fid almost to the base, the paired basal cells united to 0.3–0.5 their length (at times with one or more lobes uniseriate to base). Branch leaves 2–3-lobed, the lobes a little longer than those of the stem, uniseriate throughout or sporadically with a paired basal tier, barely connivent at the extreme base (as

little as 0.15 their length). Leaf lobes ciliiform, rigid to somewhat flexuous,  $\pm$  equal in length (the ventral lobe often somewhat shorter), stiffly spreading and bristle-like, gradually tapering, moderately to widely divergent, with a basal tier of short paired barrel-shaped cells, the uniseriate row (10)13–15 cells long; cells of basal tier 22–28  $\mu\text{m}$  wide  $\times$  49–64  $\mu\text{m}$  long, the basal cell of uniseriate row 24–30  $\times$  70–80  $\mu\text{m}$ , the next cell of about equal length and width, the apical cell narrowly lanceolate, not much different in length from the penultimate cell, the walls strongly thickened at the apex, forming a knoblike tip; lobe cells thick-walled, subcapillary, with septa strongly thickened in the corners and distinctly swollen and projecting; cuticle smooth. Underleaves of main shoot small and inconspicuous, 3–4-lobed, the lobes with a uniseriate row of 3 cells, ending in a slime papilla, the disc 2 cells high (including paired basal cells of lobes), the cells of the basal tier becoming subdivided into two tiers of small rhizoid initials, with rhizoids emanating from both tiers. Underleaves of primary branches variable, typically similar in size and form to the branch leaves, symmetrically 2–3-lobed, the lobes uniseriate throughout or less often with a biseriate base, or the underleaves asymmetrically bilobed, the longer resembling a leaf lobe, 8–10(11) cells long, the other shorter, 3 cells long, ending in a slime papilla. Underleaves of secondary branches tending to be small, bilobed and caliper-like. Asexual reproduction lacking.

Androecia long spicate, on determinate ventral-intercalary branches or terminal on primary, *Frullania*-type branches, rarely intercalary on rather long primary, terminal branches;  $\delta$  bracts in up to 7 pairs, symmetrically to somewhat asymmetrically bifid, the disc to 4–6 cells wide, 2–4 cells high, the dorsal margin with a few-celled tooth, the lobes with a uniseriate row of 3–5 thick-walled cells, monandrous, antheridial stalk short, 3 cells long, uniseriate. Gynoecia on very short leafless ventral-intercalary branches from main shoot;  $\eta$  bracts in 4 series, 5-lobed, divided to ca. 0.7, the lobes with an opposing pair of basal cilia,

←

FIG. 41. *Telaranea chaetocarpa* (Pears.) Grolle 1. Mature gynoecium (old sporophyte not shown). 2. Portion of perianth surface showing cilia. 3. Cilium of perianth mouth. 4. Portions of perianth surface showing prorate condition. 5. Innermost  $\eta$  bracts and, in middle, bracteole. 6. Three portions of abaxial face of innermost  $\eta$  bract disc showing prorate condition. 7. Seta, cross section. 8. Capsule wall, cross section. 9. Capsule wall, inner layer. 10.  $\delta$  Bract (dm = dorsal margin). 11. Antheridial stalk. 12. Half-leaf of terminal branch. (All from *Hürlimann* 2786, New Caledonia, Koghi Mts, S flank of Moné summit.)

often as long as the lobe itself, the segments uniseriate throughout, up to 15 cells long, the disc 3–4 cells high, 16–18 cells wide, the abaxial surface with scattered, few-celled teeth (prorate). Perianth narrowly cylindric, not narrowing toward mouth, terete in basal half, becoming bluntly trigonous above, the plicae rounded, with rather deep, broad intervening sulci; mouth wide, ciliate, with ca. 15 cilia, each with a basal tier of 2–3 cells (occasionally with a blunt lateral spur) and a uniseriate row of 8–12 elongate cells, identical in appearance to the lobes of the leaves, the septa strongly thickened in the corners, swollen and projecting; perianth surface hispid, armed throughout with long, stiffly-spreading cilia like those of the perianth mouth and short prorate projections from the upper ends of cells, the cilia unbranched or at times with 1–2 short, few-celled spurs at the base; perianth unistratose, the cells elongate rectangular, thick-walled.

Seta with 8 rows of outer cells surrounding an inner core of 13 much smaller cells. Capsule wall 3-stratose (locally 4-stratose), 40–42  $\mu\text{m}$  thick (46–48  $\mu\text{m}$  when 4-stratose), the layers of about equal thickness; outer layer of cells with two-phase development, the resulting cells rectangular, 3–4:1, the longitudinal walls with moderately thickened continuous sheets of pigmented material and nodular to spinelike thickenings (the walls appearing sinuous), alternating with walls devoid of thickenings, the transverse walls also without thickenings; inner layer of cells somewhat irregularly narrowly rectangular, the longitudinal walls with rather thick continuous sheets of wall material, with well-developed, regularly spaced with rather wide, closely spaced, complete semiannular bands, the bands at times forked and anastomosing to delimit fenestrae, the cells occasionally subquadrate, and thickenings forming a fenestrate pattern.

Spores 17.3–17.8(19.2)  $\mu\text{m}$  in longest diam., dark chestnut-brown, the surface prominently reticulate, with polyhedral areoles bordered by narrow ridges, the areoles 2.4–2.9  $\mu\text{m}$  in diameter.

The perianths of this handsome plant are clothed in numerous, stiffly spreading cilia (Fig. 41: 1, 2), a unique feature in the genus, as well as in the family Lepidoziaceae (Grolle, 1966). The densely ciliate perianths are by no means the only distinctive feature of the species. The leaf lobes are exceedingly long and subcapillary, with prominent swollen and bulging septa (Fig. 40: 5, 6),

with a uniseriate row up to 15 cells in length. The branches are nearly isophyllous.

Grolle (1966, key) distinguished between this species and *T. trisetosa* of New Guinea (p. 196), both with a smooth cuticle, vs. other similar Indomalayan *Telaranea* species with a disc to 1.5 cells high (*T. neesii*, *T. lawesii*, etc.), which are punctate or distinctly papillose. Pearson (1922) described the cuticle as striolate.

The leaves of *T. trisetosa* are also transversely inserted and 3–4-lobed nearly to the base, with stiff, ciliiform leaf lobes up to 10–11 cells long (Fig. 58: 3). However, in that species the lobe cells are only weakly projecting, and the terminal cell is abbreviated and much smaller than the penultimate cell (Fig. 58: 3, 4; Grolle, 1966, fig. 1g, h). In *T. chaetocarpa* the tip cell and the penultimate cell are narrowly elongate and  $\pm$  similar in length.

This species is the type of *Telaranea* subg. *Chaetozia* (Grolle, 1966). *Telaranea trisetosa* was originally included in the subgenus, but later excluded (Grolle, 1968), since the perianth of this species is smooth (Grolle, 1968). Subgenus *Chaetozia* was subsequently placed in synonymy of subg. *Telaranea* by Schuster (1973).

Pearson (1922) describes the cilia on the perianth as simple or bicurvous, but in the material examined the cilia are unbranched (Fig. 41: 2). He described the type as “pallide-brunneis,” whereas in our material the plants are a pale straw yellow in color. The type was growing on the upper surface of a fallen log.

SPECIMEN SEEN—NEW CALEDONIA: Koghi Mts., S flank of Moné summit, on dead trunk in montane forest, ca. 750 m, *Hürlimann* 2786 (F, comm. Hürlimann).

### *Telaranea chaetophylla* (Spruce) Schiffn.

*Lepidozia chaetophylla* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 365. 1885. *Telaranea chaetophylla* (Spruce) Schiffn. in Engl. & Prantl, Nat. Pflanzenfam. 1 (3): 103. 1893. Lectotype (nov.): Venezuela, silva Amazonica, Rio Negro, Hep. Spruceanae Amaz. et Andin. (BM!—c. sporo. +  $\delta$ ); isolectotype (possible): “in sylvis Venezuela australis, juxta San Carlos del Rio Negro, supra truncos emortuos,” 1853, *Spruce* (BM!—c. per. +  $\delta$ ).

DESCRIPTION—Spruce (1885).

ILLUSTRATIONS—Figs. 42, 43.

DISTRIBUTION—Colombia, Venezuela and Peru (confirmed). An additional specimen of this species is at NY, labeled in Mitten’s hand, “S. Brazil,

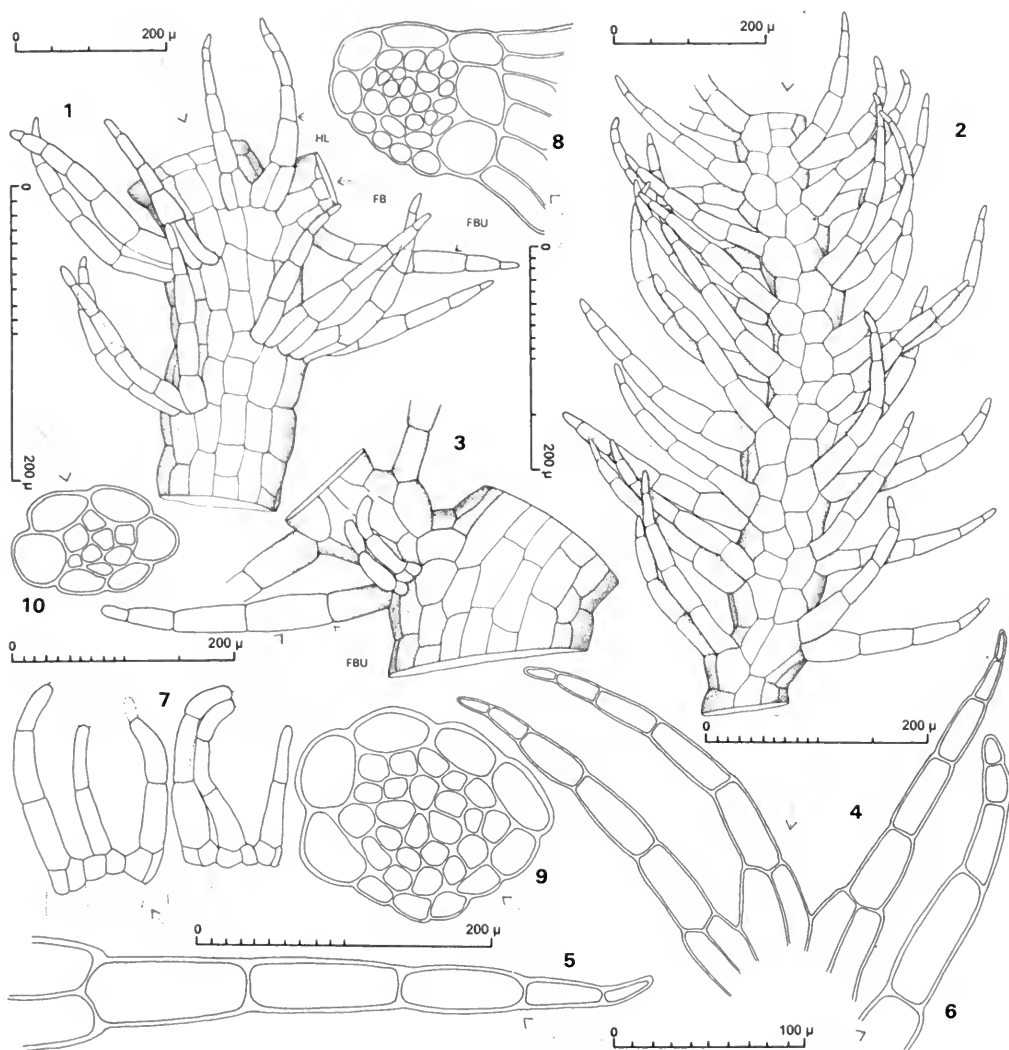


FIG. 42. *Telaranea chaetophylla* (Spruce) Schiffn. 1. Portion of main shoot with base of *Frullania*-type branch, dorsal view; note, at left, 3 stem cortical cells between leaves; note also 4 lobed leaf at right, half-leaf (= hl), and first branch underleaf (= fbu). 2. Portion of primary branch, dorsal view. 3. Main axis and base of *Frullania*-type branch, ventral view; note first branch underleaf (= fbu). 4. Leaf of main shoot. 5, 6. Portions of leaf lobes, stem cells shown in stipple. 7. Underleaves of main shoot. 8. Stem of main shoot, cross section, and leaf base. 9. Stem of main shoot, cross section. 10. Stem of primary branch, cross section. (Figs. 1–9 from isoelectotype of *T. chaetophylla*; 10, from lectotype of *T. chaetophylla*.)

Wier" (see comments under *T. apiahyna*). Reports of the species from elsewhere require confirmation. Reported for Tasmania by Weymouth (1903) and Rodway (1916) as *Lepidozia chaetophylla*; Rodway's specimens from Mt. Wellington (HO) are *T. herzogii*, the Weymouth plants from Tasman Peninsula (HO) are *T. tasmanica*. A specimen from New Zealand, leg. Cunningham (Herb. Pearson, BM), labeled *Lepidozia chaetophylla* var. *tenuis*, is *T. lindenbergii*.

Plants minutely prickly in appearance, prostrate, pale green in herb.; shoots minute, to 575 μm wide with leaves. Branching of *Frullania* type very common, rather regularly bipinnate, the ultimate branches rather short, very rarely becoming flagelliform, the main axis terete, the branches dorsiventrally flattened; branch half-leaf undivided or bifid; first branch underleaf asymmetrically bilobed or, occasionally, asymmetrically 3-lobed at base of branch. Ventral-intercalary branches oc-



casional, subflagelliform. Stems rather stout for plant size, the cortical cells distinctly differentiated, in 10 rows (6 dorsal + 4 smaller ventral rows), with moderately thickened walls; cortical cells in section much larger than the numerous (22–26), firm-walled medullary cells; branches dorsiventrally flattened in section, with 6 rows of cortical cells and 8 medullary cells. Main shoots with 3 cortical cells intervening between successive leaves on either side, the branches with 2 cells intervening between successive leaves on either side of branch. Leaves of main shoot rather rigid, approximate, stiffly spreading, the insertion transverse or nearly so, 345–390  $\mu\text{m}$  long  $\times$  340–465  $\mu\text{m}$  wide (between tips of spreading lobes), 3 (rarely 4)-fid almost to the base, the basal cells of the lobes connate for about  $\frac{1}{3}$  to  $\frac{1}{2}$  their length. Branch leaves 2-lobed, distichous, complanate, oriented in an almost horizontal plane, distinctly incubous to almost longitudinally inserted, with 2 full rows of cortical cells broadly exposed and forming a prominent median strip along the dorsal side of the branch; lobes of branch leaves uniseriate to base. Leaf lobes  $\pm$  equal in length, stiffly spreading and bristle-like, gradually tapering, moderately to widely divergent, the lobe base (basal tier) barrel-shaped and noticeably contracted to the uniseriate portion of the lobe, the uniseriate row (4)5 cells long; lobe bases typically biseriate (in dorsal lobe at times uniseriate), the lobe bases in branch leaves almost all uniseriate; cells of basal tier 26–34  $\mu\text{m}$  wide  $\times$  74–84  $\mu\text{m}$  long, the basal cell of uniseriate row 29–38  $\times$  80–95  $\mu\text{m}$ , the next cell of about equal length and width, the terminal cell somewhat shorter than the penultimate cell, at times appearing secondarily divided; cell walls rather firm, with septa thickened in the corners but not projecting; cuticle smooth. Underleaves small and inconspicuous, (2)3-lobed, each lobe with a pair of small basal cells, 2–3 narrowly cylindrical lobe cells, and ending in a slime papilla, with rhizoids originating from the basal cells. Asexual reproduction lacking.

Autoecious. Androecia terminal in position on secondary *Frullania*-type branches;  $\delta$  bracts monandrous, the antheridial stalk uniseriate. Gynoecia on short ventral-intercalary branches; bracts 4-lobed, the disc 2–3 cells high, the lobes inserted on a triangular base composed of 2–4 turgid cells, uniseriate above, at times with a biseriate tier between the base and the uniseriate row, occasionally forked or with a lateral spur, or with a small unicellular accessory tooth or slime pa-

pilla at the base. Perianth slenderly fusiform-clavate from a narrowly cylindrical base, subterete below, obtusely trigonous and tri-plicate above the middle, weakly contracted and long-ciliate, with 12 long cilia + accessory cilia about half as long, ending in a uniseriate row of 7–9 elongate cells. Calyptra about half the length of the perianth, with archegonia confined to the extreme base.

Seta with 8 rows of outer cells surrounding an inner core of 6 much smaller cells. Capsule elliptic, the wall 14–16  $\mu\text{m}$  thick, 2-stratose, the outer layer slightly thicker than the inner (very rarely with a localized 3-stratose patch); outer layer of cells elongate-rectangular, 4–5:1, with two-phase development, rather thick walled, the longitudinal walls with moderately thickened continuous sheets of pigmented material and rather weakly developed nodule-like thickenings (the walls appearing sinuous), alternating with walls devoid of thickenings, the transverse walls also without thickenings; inner layer of cells somewhat irregularly narrowly rectangular, the longitudinal walls with very thin continuous sheets of wall material, with  $\pm$  irregularly spaced nodular to pale spur-like thickenings, only exceptionally with faint semiannular bands.

Spores 12–14.9  $\mu\text{m}$  in largest diam., yellow-brown, the surface areolate. Elaters rather straight, 9.1–10.1  $\mu\text{m}$  wide, only slightly tapering and bispiral to tips, the spirals 2.9–4.3  $\mu\text{m}$  wide.

**NOMENCLATURE**—This species, the nomenclatural type of the genus *Telaranea*, has usually been considered synonymous with *T. nematodes* (Pearson, 1886; Howe, 1902; Stephani, 1909; Schuster & Blomquist, 1955; Schuster, 1969) or with *T. sejuncta* (Arnell, 1963; Fulford, 1963a, 1966). Examination of original material at BM reveals that *T. chaetophylla* is distinct from both species. Like *T. nematodes*, *T. chaetophylla* is autoicous. Details of androecium, perianth, capsules, and spores are included in the protologue (Spruce, 1885). Both androecia and sporophytes are present in abundance in a specimen from the Rio Negro (Hep. Spruc. Amaz. et And.), which is here designated as the lectotype. A single fruiting plant with  $\delta$  in a packet from Pearson's herbarium (if from the same collection) provides more specific information as to locality and substrate. Also referable to *T. chaetophylla* (in mixture) is an exsiccati specimen from Mt. Campana, Peruvian Andes, labeled "forma andina." A third collection, "in fluvii Casiquiari arena inundata," Nov.

1853, Spruce, annotated "var. foliis caulinis saepius 4-partitus" and "? dioica," is another species, possibly *T. bicurris* (p. 125). According to Pearson (1886), the manuscript name *L. chaetophylla* appears on a specimen sent by Spruce to Borrer in 1852.

COMMENTS—The most distinctive features of *T. chaetophylla* are its broad, dorsiventrally flattened branches and the distichous, strongly incubous, laterally inserted branch leaves, with a prominent 2-cell-wide dorsal median strip of quadrate cortical cells (Fig. 42: 2). By contrast, the main shoots are terete, with the leaves for the most part 3-lobed (rarely 4-lobed), and  $\pm$  transversely inserted, without a median strip (Fig. 42: 1). The branches of *T. nematodes* are also somewhat flattened, but the median strip is not so broad or pronounced, since the leaf insertions impinge upon the cortical cells to either side (Fig. 53: 8). In addition, the lobes of the branch leaves are uniseriate to the base in the type of *T. chaetophylla* (Fig. 42: 2), vs. predominately biseriate in *T. nematodes* (Fig. 53: 8). The capsule wall in *T. chaetophylla* is bistratose (Fig. 43: 10), vs. 3-stratose in *T. longifolia* (Schuster & Blomquist, 1955, fig. 1), and 2–3-stratose in *T. nematodes* (Fig. 53: 9). For other comparisons between these species, see p. 164 (*T. longifolia*) and p. 173 (*T. nematodes*).

In the light microscope, the spores of *T. chaetophylla* appear delicately reticulate. Under the scanning electron microscope (Fig. 69: 1), the spore markings appear as broad ridges enclosing irregular polygonal depressions (areolae), the ridges forming a more or less closed reticulate pattern. The surfaces of both ridges and areolae are roughened with smaller granular projections.

Two temperate Australasian taxa, *T. tetradactyla* and *T. lindenberghii* var. *complanata*, have strongly complanate-foliate branches, but the branches themselves are terete (Fig. 27: 10, *T. tetradactyla*). The branch leaves are strongly incubously inserted, and the insertions extend between successive cortical cells, approaching the midline and thus lack a conspicuous median strip.

*Telaranea chaetophylla*, as understood by Schuster (2000, p. 221, 230, fig. 190: 1–12) is not

this species. It is placed, questionably, as a synonym of *T. nematodes*, but is listed separately in the key (p. 223). On the other hand, it is said to "closely approach" *A. caduciloba*, which is a true *Arachniopsis* (*Telaranea* sect. *Tenuifoliae*) and a synonym of *T. diacantha*. In the figure legend, figs. 190: 1–12 are labeled as *T. chaetophylla*, but on p. 457, figs. 190: 4–6 are cited as "*Arachniopsis borinquena*." The branch illustrated in fig. 190: 2 appears terete rather than plano-distichous as in *T. chaetophylla*; the stems of the lectotype are 10 + 20–26 (Fig. 42: 8, 9), vs. 6–7 + 6 in Schuster's plant (Schuster, 2000, fig. 190: 1). It is probable that a minor variant of *T. nematodes* is at hand.

SPECIMENS SEEN—COLOMBIA: Chocó, Mun. de Nuquí, El Amargal, SW of Arusi, alt. 30 m., *Gradstein* 8900 (Bryo. Neotropica Exsicc. 349) (F). PERU: "Andes Peruviani: M. Campana Hepaticae Spruceanae: Amazonicae et Andinae," syntype of *Lepidozia chaetophylla* (BM—c. sporo.). S. BRAZIL: Without specific loc., Wier (NY).

*Telaranea coactilis* (Spruce) Engel & Merr., comb. nov.

*Arachniopsis coactilis* Spruce, On Cephalozia: 85. 1882. Type: Brazil, Rio Uaupés, Spruce (*non vidi*); Rio Negro, San Carlos, Spruce (NY!). *Arachniopsis madagascariensis* Steph., Spec. Hep. 6: 347. 1922, *syn. nov.* Type: Madagascar, Villaume 81pp—c. per. + sporo. +  $\delta$  (G!).

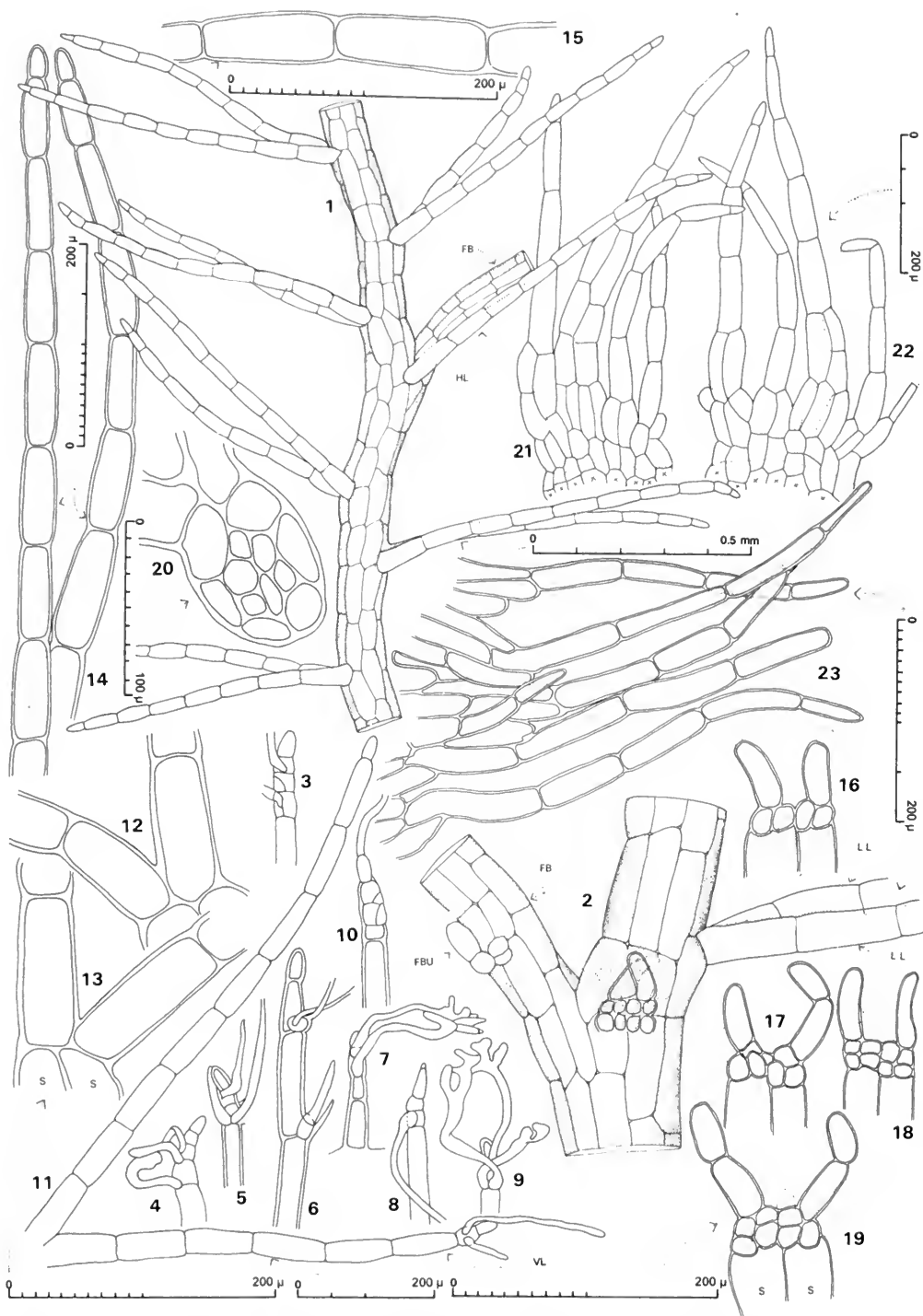
DESCRIPTIONS—Howe (1902); Fulford (1968).

ILLUSTRATIONS—Spruce (1885, pl. 13); Herzog (1950, figs. 12d, 13c); Fulford (1968, pl. 96, fig. 2a–d, g, k, *A. coactilis* type); Schuster (2000, fig. 191, *A. coactilis* type). Stephani, Icones, *Arachniopsis* 2a–d. Stephani's *Arachniopsis* 4a (*A. madagascariensis*) appears to be a species of sect. *Telaranea*, with lobe bases geminate, and is not the type. Figs. 44, 45.

DISTRIBUTION—Brazil, Guyana, Madagascar. Reported from Colombia and Venezuela (Fulford, 1968, 1972); Puerto Rico (Fulford, 1971).

The species is widely reported from Africa. Herzog (1950) described *A. coactilis* f. *africana*,

FIG. 44. *Telaranea coactilis* (Spruce) Engel & Merr. 1. Portion of main shoot with *Frullania*-type branch (= FB), dorsal view (hl = half-leaf); note the weakly succubous leaf insertions. 2. Portion of main shoot (ventral view) with *Frullania*-type branch (= FB) showing asymmetrically bilobed first branch underleaf (= fbu) with one lobe consisting of two small cells, one above the other, and a longer lobe resembling an underleaf lobe, consisting of a short basal cell + a long cylindric cell capped by a slime papilla (LL = leaf lobe). The basal cells of the main shoot underleaf have each subdivided, with each of the 8 cells giving rise to a rhizoid (shown in stipple). 3–10. Rhizoids originating



from distal cells of leaf lobes (redrawn from Fulford, 1968). 11. Leaf (vl = ventral lobe). 12, 13. Leaf bases (s = stem cell). 14. Two lobes of same leaf. 15. Portion of leaf lobe. 16–19. Underleaves (s = stem cells; note that underleaf cells have subdivided to form rhizoid initials, and that all 8 of the initial cells produce rhizoids, which are shown with stipple). 20. Stem, cross section + leaf base. 21, 22. Innermost ♀ bracts (x = stem cortical cell). 23. Perianth mouth. (All from type of *Arachniopsis coactilis*, San Carlos del Rio Negro, Spruce, NY.)

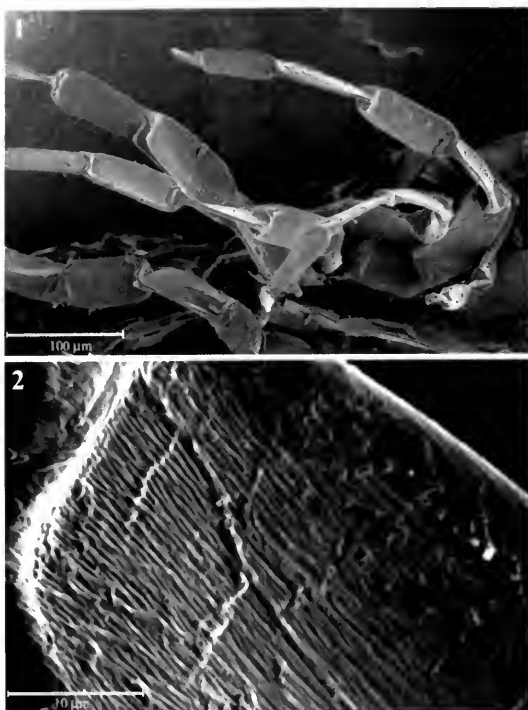


FIG. 45. *Telaranea coactilis* (Spruce) Engel & Merr. 1. SEM, portion of shoot showing showing alternating collapse of leaf lobe cells. 2. SEM, portion of leaf lobe cell showing elongated striae. (From *Arachniopsis coactilis* type.)

based on a P. W. Richards specimen from Nigeria, as only slightly different from the South American *A. coactilis*. Arnell (1956) reported *A. madagascariensis* from Annobón (W Africa), and indicated a close relationship to *A. coactilis*. Pócs (1984) treated *A. coactilis* as a variety of *A. diacantha*, and cited both as widespread in tropical Africa. Fischer (1993, fig. 4) illustrated a plant from Rwanda (as *A. diacantha*), which is similar to *T. coactilis* and has succubously inserted leaf lobes. We have seen a collection determined as *A. diacantha* from Tanzania (East Usambara Mts, Tanga Distr., Amani Forest Reserve, T. & S. Pócs 6091/1, F) which resembles *T. coactilis* but has weakly incubously inserted lobes. The plant illustrated by Arnell (1963, fig. 278a) also resembles *T. coactilis*. See comments under the distribution of *T. diacantha*.

Plants delicate, the leaf lobes minutely thread-like in appearance. Branching of terminal, *Frullania*-type occasional; branch half-leaf (Fig. 44: 1) monocurrous; first branch underleaf (Fig. 44:

2) ventral lateral in position on the branch, asymmetrically bilobed, with one lobe consisting of two small cells, one above the other, the longer lobe resembling an underleaf lobe, with a short basal cell and a long cylindric cell, ending in a slime papilla. Ventral-intercalary branches common, leafy. Stems delicate, straight and wiry, the cortical cells short-rectangular, firm-walled, in cross section in 5–6 rows (the dorsal larger than the ventral rows); medullary cells in 6 rows, smaller, moderately and evenly thick-walled. Shoots with 3–4 cortical cells intervening between successive leaves on either side. Rhizoids freely produced from cells of the underleaves and from distal cells of the leaf lobes. Leaves rather stiffly spreading, asymmetrically bilobed or monocurrous, the insertion transverse to weakly succubous. Lobes moderately divergent, uniseriate to the base, unequal in length, the dorsal lobes 8–10 cells long, the ventral lobes shorter, 7–9 cells long and often producing rhizoids from the tip (Fig. 44: 3–11). Lobe cells short rectangular (2–3.5:1), the basal cell 36–42  $\mu\text{m}$  wide  $\times$  102–120(134)  $\mu\text{m}$  long, the next cell 36–41  $\mu\text{m}$  wide  $\times$  82–90(104)  $\mu\text{m}$  long, the terminal cell small, elliptical, much shorter than the penultimate cell, the tip at times becoming detached; cell walls moderately thick-walled and firm, the transverse septa somewhat thickened in the corners and the lobes straight-sided to moderately constricted at the septa; cuticle minutely striolate. Underleaves small and inconspicuous, bifid, consisting of two partially connate basal cells (becoming subdivided as rhizoid initials), the lobes each with 1–2 curved cylindrical cell(s), terminating in a slime papilla.

Autoecious. Androecia on short ventral-intercalary branches adjacent to gynoecial branches; bracts bilobed. Gynoecia on short ventral-intercalary branches; bracts (Fig. 44: 21, 22) 4-lobed, the disc 1.5–2.5 cells high, composed of short-rectangular cells; basal cells of lobes elongate, from a biseriate base, with 1–3 additional biseriate tiers in some lobes, ending in a uniseriate row of (3)4–5 cells. Perianth mouth (Fig. 44: 23) ciliate, the cilia with a uniseriate row of 4–5 narrowly elongate cells, moderately contracted at the septa. Spores papillose-vermiculate.

The distinctions between this species and *T. diacantha* (including *A. coactilis* var. *capillacea* Spruce) have been widely misunderstood. Apart from sexuality (see p. 146), these two species differ in the size, shape, and proportions of the lobe cells, and spore surface markings. Lobe cells in



both species are moderately thick-walled and firm, but in *T. diacantha* are elongate and subcapillary, 6–10:1 and ca. 16–24  $\mu\text{m}$  in diameter, vs. 2–3.5(4):1 and ca. 36–44  $\mu\text{m}$  in *T. coactilis*. Thus, the lobes of *T. diacantha* are only 4–6 cells long, vs. 8–10 cells long in *T. coactilis*. The lobes in *T. coactilis* tend to be somewhat contracted at the transverse septa (Fig. 44: 14, 15), whereas in *T. diacantha* the lobes are straight-sided to distinctly bulging at the septa (Fig. 46: 5–7). Spores of *T. coactilis* (Fig. 72: 2–4) are papillose-vermiculate, whereas those of *T. diacantha* (Fig. 69: 2, 3) are reticulate-areolate. See the discussion under *T. sejuncta* for differences between that species and *T. coactilis*.

The insertion of the leaf lobes in *T. coactilis* is transverse to weakly succubous (Fig. 44: 1), with 3–4 stem cortical cells intervening between leaves on each side of the shoot. The leaves tend to be asymmetrically lobed, with the dorsal lobe 1–2 cells longer than the ventral (Fig. 44: 1, 11, v1). Typically, it is the shorter, ventral lobe which bears rhizoids at its tip (see Schuster, 2000, fig. 191: 5, 6, *A. coactilis* type). The lobe cells are marked by very fine longitudinal striae, seen with difficulty under the light microscope but plainly visible under the SEM (Fig. 45: 2). In dry material, the lobe cells are collapsed (Fig. 45: 1), with the cells flattened in alternate planes at 90° to one another.

*Arachniopsis coactilis* is the lectotype of the genus *Arachniopsis*, designated by Schuster (1965). *Arachniopsis* has usually been described as lacking terminal branching. However, terminal, *Frullania*-type branching was observed in the type of *T. coactilis* (Fig. 44: 1). Terminal, *Frullania*-type branching has now been reported from many species of sect. *Tenuifoliae*; it appears to be rare in some species, but in others (*T. inaequalis*) it is common. Admixed with the type of *Lepidozia quintasii* Steph. (G!, = *T. nematodes*) from the Gulf of Guinea Is. (San Thome) is an *Arachniopsis* with incubously inserted, bicurrous leaves, with *Frullania*-type branching and an unequally bilobed first branch underleaf.

The type of *A. coactilis* is autoicous (“monoica,” as described by Spruce, 1882) with the short  $\delta$  ventral-intercalary branch located immediately adjacent to the  $\varphi$ . In contrast, distinctive intercalary androecia were observed in the type of *T. sejuncta* (Fig. 57: 1; p. 189). Spruce (1885, pl. 13); redrawn by Fulford (1968, pl. 96, fig 2j) illustrated the  $\varphi$  bract of *T. coactilis*, which agrees with the  $\varphi$  bracts of the San Carlos plant (Fig.

44: 21, 22). Stephani (Icones, *Arachniopsis* 2a) also illustrated  $\varphi$  bracts and bracteole from the original material.

The type of *A. madagascariensis* has leaves uniseriate to the base. The lobe cells are ca. 2–2.5(3.3):1, thin-walled, slightly thickened in the corners and straight or somewhat constricted at the septa, the uniseriate row 6–7 cells long. The underleaves are inconspicuous, consisting of 2 small, partially connate cells + 1 cylindric cell. Plants are autoecious, with  $\delta$  and  $\varphi$  branches rather closely juxtaposed.

SPECIMENS SEEN—BRAZIL: Vicinity of first cachoeira of Igarapé Foibará off Rio Negro, Buck 2629—c. per. (F), with *Monodactylopsis monodactyla*. GUYANA: Upper Mazaruni District, Jawalla, at confluence of Kukui and Mazaruni rivers, 500 m, Gradstein 4901—c. sporo. (F).

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

*Arachniopsis pecten* var. *confervoides* Schust., Beih. Nova Hedwigia 118: 455. f. 193A. 2000. *Arachniopsis confervoides* Schust., J. Hattori Bot. Lab. 64: 245. f. 1. 1988, nom. inval. sin. descr. lat. Holotype: Brasil, Serra Curicuriari, S of mouth of Rio Curicuriari, above Rio Negro, Schuster 79-1686 (NY).

ILLUSTRATIONS—Schuster (1988, fig. 1; 2000, fig. 193A).

DISTRIBUTION—Brazil.

*Arachniopsis confervoides* has monocrurous leaves and was treated as a variety of *A. pecten* by Schuster (2000). The leaf lobes are short, (5)6(7) cells long, and the lobe cells “strongly elongated” and subcapillary, 25–26(28)  $\mu\text{m}$  wide  $\times$  135–155(175)  $\mu\text{m}$  long, and thus strikingly similar to those of *T. diacantha*. The stems are of the “simplex” type, with 4 rows of cortical cells and a single medullary cell row. A notable feature of the plant is the production of *Acromastigum*-type, terminal branches (Schuster, 1988, fig. 1: 1, 2; 2000, p. 457). Judging from the aspect of the plant, this may be a monocrurous form allied to *T. diacantha* (see comments sub *T. pecten*, p. 178).

NOMENCLATURE—Schuster (2000) provided a Latin description of this plant, as *A. pecten* var. *confervoides*, and cited two variants of the collection number of the type; 79-1686 is probably correct.

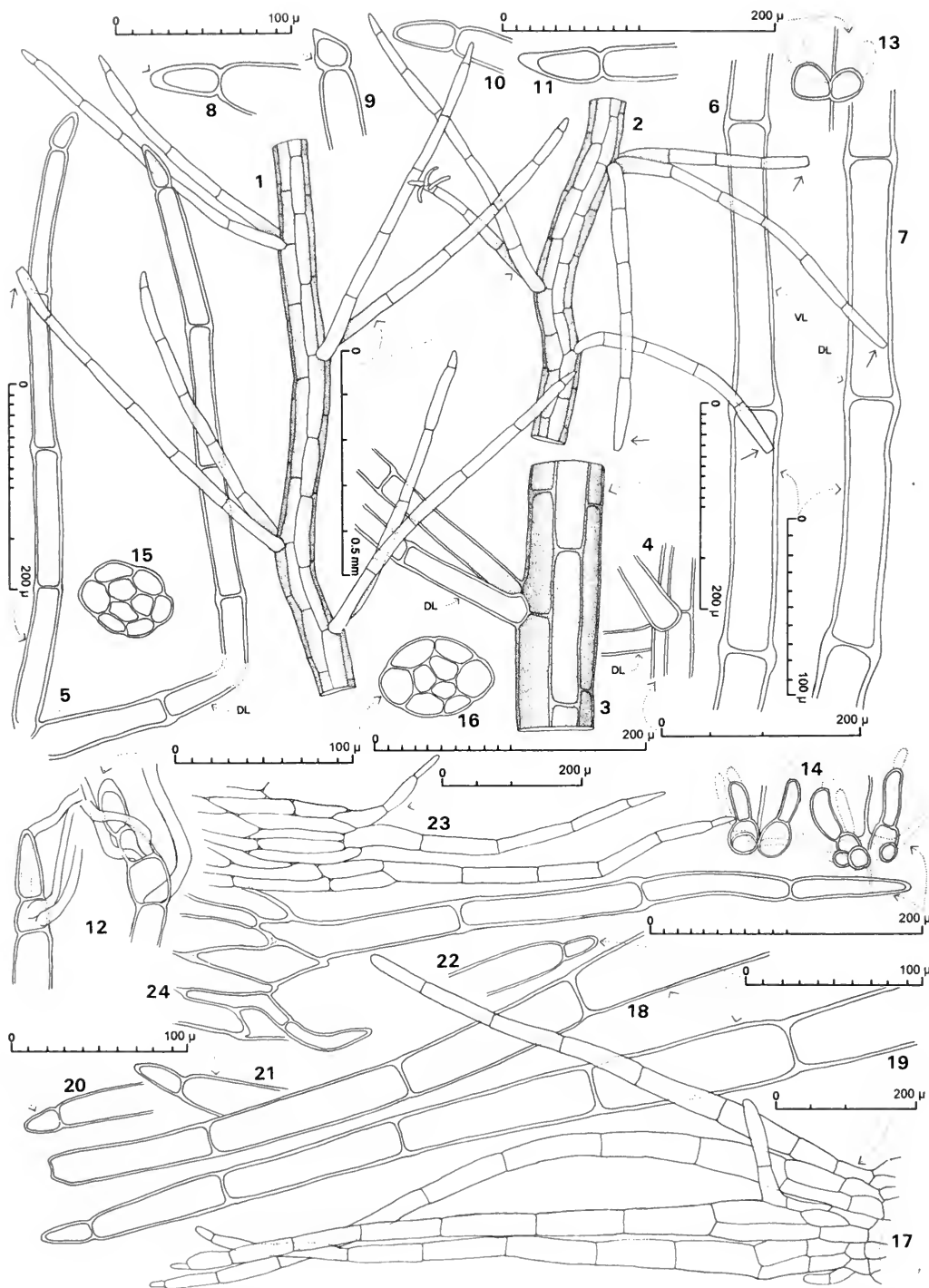


FIG. 46. *Telaranea diacantha* (Mont.) Engel & Merr. 1. Portion of shoot, dorsal view; note 4 cortical cells intervening between successive leaves on either side, and caducous leaf tip (at arrow). 2. Portion of shoot (dorsal view), with 3- and 2-lobed leaves + a monocruous leaf; note caducous leaf tips (at arrows) and rhizoids originating from tip cell of ventral lobe of bilobed leaf. 3, 4. Leaf bases, dorsal and ventral views (left and right, respectively), showing succubous insertion (dl = dorsal lobe). 5. Leaf (dl = dorsal lobe); note all septa are swollen except for immediately below the tip cell. 6, 7. Portion of ventral (= vl) and dorsal lobe (= dl) of leaf. 8-11. Distal portions

*Telaranea cuneifolia* (Steph.) Engel & Merr.,  
comb. nov.

*Lepidozia cuneifolia* Steph., Spec. Hep. 3: 618. 1909.  
*Neolepidozia cuneifolia* (Steph.) Fulf. & J. Tayl.,  
Brittonia 11: 85. 1959. Lectotype (nov.): New  
Guinea, montosis Moroka, 1300 m, 1893, Loria  
(G!).

*Lepidozia massartiana* Steph., Spec. Hep. 3: 611.  
1909, syn. nov. non *Lepidozia massartiana*  
Schiffn., Hedwigia 39: 196. 1900, nom. nud. Type:  
Moluccas Is., Amboina, Karsten; Tahiti, Nadeaud;  
New Caledonia, Etesse.

*Lepidozia augustana* Steph., Spec. Hep. 6: 320. 1922,  
syn. nov. Type: Papua New Guinea, Augusta River,  
1910, Schultze—c. per. (G!).

ILLUSTRATIONS—Piippo (1984, fig. 4: c, f, h, j,  
type of *L. cuneifolia*). Stephani, Icones, *Lepidozia*  
263; 203 (*L. augustana*); 227 (*L. massartiana*).

DISTRIBUTION—New Guinea, New Hebrides.  
See also comments under *T. wallichiana*, specifically  
with respect to the identity of *L. massartiana*.

This species was synonymized with *T. wallichiana*  
by Inoue (1979), and this synonymy was  
adopted by Piippo (1984). The catalog of New  
Guinean hepatics by Grolle and Piippo (1984)  
lists *L. cuneifolia* (and *L. augustana*) as synonyms  
of *L. wallichiana*. The chief differences are in the  
branch leaves, which in *T. cuneifolia* are asym-  
metrical, often subfalcate, with a disc as much as  
6–10 cells high. The branch leaf lobes are broad  
and typically 4 cells wide at the base (Icones),  
whereas in *T. wallichiana* the branch leaves are  
symmetrically lobed, and the lobes of both stem  
and branch leaves are biseriate at the base (Jovet-  
Ast, 1947, fig. 3: b, c). For additional comparisons  
between these species (including gynoecia) and  
the confusion surrounding the name *L. massarti-*  
*ana*, see below, under *T. wallichiana*.

*Lepidozia augustana* Steph. is placed here pri-  
marily because of the strongly asymmetrical  
branch leaves, although in the type (G!) the lobes  
are typically only 2 cells wide at the base.

SPECIMENS SEEN—NEW GUINEA: West Sepik Prov.,

8 km WNW of Frieda Base Camp, 500 m, Koponen  
35935—c. sporo. (F); ibid., Mt. Hartley, 8 km N of Frieda  
Base Camp, 1350 m, Koponen 35258, 35336 (F).  
NEW HEBRIDES: 1903, Joly, syntype of *L. cuneifolia*  
(G).

*Telaranea diacantha* (Mont.) Engel & Merr.,  
comb. nov.

*Jungermannia diacantha* Mont., Ann. Sci. Nat. Bot.  
IV. 5: 349. 1856. *Arachniopsis diacantha* (Mont.)  
Howe, Bull. Torrey Bot. Club 29: 288. 1902. Lec-  
totype (nov.): Peru, Weddell s.n. (PC!).

*Arachniopsis coactilis* var. *capillacea* Spruce, On Ce-  
phalozia: 85. 1882, syn. fide Howe (1902). Type:  
Peru, Monte Campana, Spruce (NY!).

*Arachniopsis capillacea* Steph., Spec. Hep. 6: 347.  
1922, syn. nov. Type: Brazil, Puiggari 2137—c. ♂  
(G!).

DESCRIPTIONS—Howe (1902); Fulford (1968, *A. diacantha*).

ILLUSTRATIONS—Fulford (1968, pl. 96, fig. 1,  
type of *A. coactilis* var. *capillacea*, as var. “*cap-*  
*illaris*”); Schuster (2000, fig. 190A, as *A. cadu-*  
*ciloba*). Stephani Icones, *Arachniopsis* I (*A. cap-*  
*illacea*). The plant illustrated by Schuster (2000,  
fig. 191) as *A. diacantha* is the type of *A. coac-*  
*tilis*. Fig. 46.

DISTRIBUTION—Brazil, Peru, Trinidad, Puerto  
Rico. Presumably widespread in the Neotropics,  
but previously published statements of distribu-  
tion must be re-evaluated in the light of revised  
understanding of *T. coactilis*, *T. diacantha*, and *T. se-*  
*juncta*. Reported from Bahia by Vital and Vis-  
nadi (1994), Guyana (Roraima) by Gradstein and  
Florschütz-de Waard (1989), Dominica (Schäfer-  
Verwimp, 1999), and Costa Rica (Gradstein et al.,  
1994).

Representatives of sect. *Tenuifoliae* certainly  
occur in Africa, and there are numerous referenc-  
es in the literature to the African distribution of  
*T. diacantha* and similar Neotropical taxa. How-  
ever, the African specimens we have seen resemble  
*T. coactilis* rather than *T. diacantha* as we  
know it. Descriptions and illustrations in literature  
reports also appear to refer to a *T. coactilis*-like  
plant. The question of identity is not further ex-

of leaf lobes (all at same scale). 12. Rhizoids originating from distal cells of two ventral leaf lobes. 13, 14. Underleaves (rhizoids indicated with stipple). 15, 16. Stem, cross sections (both at same scale). 17. Innermost ♀ bract. 18, 19. Lobes of ♀ bract. 20–22. Apices of ♀ bract lobes (all at same scale). 23. Portion of perianth mouth. 24. Lobe of perianth mouth, note basal spur. (Figs. 1–3, 5–12, 14–16 from type of *Arachniopsis capillacea*; 4, 13 from type of *Arachniopsis diacantha*; 17–24, from Crosby 2393, Trinidad, St. George Co., trail to Morne Bleu from summit of Arima-Blanchisseuse Rd.)

plored here. Gradstein et al. (1983, p. 141) give the African distribution of *A. diacantha* (incl. *A. coactilis*) as "East Africa from Rwanda to Cape in the West from Sierra Leone to Gabon, on Madagascar and the Mascarenes," in addition to its tropical American range, and include a map of its distribution (fig. III/14). Grolle (1969, fig. 11: 3, distribution map) characterized *A. diacantha* (incl. *A. coactilis*) as an "neotropisch-tropisch/subtropisch-afrikanischer" species. *Arachniopsis diacantha* is reported from Uganda (Pócs and Lye, 1999; Porley et al., 1999), Rwanda and Zaire (Vána et al., 1979; Fischer, 1993), Réunion (Vána et al., 1979), Mauritius (Grolle, 1995), Grand Comore Is. (Pócs, 1995), and Mahe and Silhouette Is., Seychelles (Grolle, 1978). For the disposition of 2 specimens from Seychelles determined as *A. diacantha*, leg. Onraedt, see p. 246, *Amazoopsis gracilis*. *Arachniopsis madagascariensis* is referred to *A. diacantha* by Arnell (1963), Pócs (1984) and Grolle (1995), but the type of this species is, in fact, *T. coactilis*.

Plants slender and wiry in appearance. Branching of terminal, *Frullania*-type occasionally present, the half-leaf monocrurous. Ventral-intercalary branches common, leafy. Stems slender, straight and wiry, cortical cells narrowly elongate, the exterior wall moderately thick walled, in 6 rows (reduced to 4 in monocrurous sectors); medullary cells in 3 rows, smaller but not sharply differentiated, firm-walled. Shoots with 3–4 cortical cells intervening between successive leaves on either side. Rhizoids produced from cells of the underleaves and occasionally from distal cells of the leaf lobes. Leaves rather stiff and bristle-like, 2(3)-lobed, sporadically or (in weaker shoots) wholly monocrurous, the insertion transverse to weakly succubous. Lobes moderately divergent, uniseriate to the base, 4–6 cells long, the lobe tips often caducous. Lobe cells elongate and subcapillary (6–10:1), the basal cell (16)21–24  $\mu\text{m}$  wide  $\times$  132–144(180)  $\mu\text{m}$  long, the next cell 16–19(23)  $\mu\text{m}$  wide  $\times$  120–144(156)  $\mu\text{m}$  long, the next 16–20  $\mu\text{m}$   $\times$  156–168  $\mu\text{m}$ , the terminal cell small, slenderly elliptical, much shorter than the penultimate cell; cell walls moderately thick-walled and firm, the transverse septa thickened in the corners and often distinctly bulging, the septum delimiting the tip cell constricted; cuticle finely striolate. Underleaves small and inconspicuous, bifid, consisting of two partially connate basal cells, each with 1(2) curved cylindric cell(s), terminating in a slime pa-

pill. Asexual reproduction by fragmenting leaf tips.

Dioecious. Androecia on short ventral-intercalary branches as well as intercalary in position on leading shoots, often producing two or more fertile sectors in succession; bracts bifid, the basal cells of the lobes united to about 0.5 their length, the dorsal lobe with a pair of basal cells, the other lobe uniseriate to the base. Gynoecia on short ventral-intercalary branches; bracts 4-lobed, the disc 1.5–2 cells high, the lobes biseriate at the base, with a uniseriate row of 8–9 cells, straight-sided or the septa weakly protruding or at times slightly constricted, the tip cell minute and often caducous. Bracts deeply 4-lobed, the disc 1.5 cells high, with a basal tier of short-rectangular cells; basal cells of lobes elongate, biseriate, the uniseriate row above of 8–9 cells. Perianth plicate above, tapering to the mouth; mouth ciliate, the divisions (2)3–4 cells wide at the base, at most with an additional biseriate tier, the uniseriate row above consisting of 4–6 narrowly elongate cells, the septa swollen and projecting, the distalmost septum constricted.

Spores reticulate-areolate.

TYPEIFICATION—*Jungermannia diacantha* is represented in Montagne's herbarium (PC) by two specimens. We have selected one of these as the lectotype, since it bears the name "*Jungermannia diacantha* Montg. nov. Sp." in Montagne's own hand. It appears also to be the specimen seen by Howe (1902, p. 288), which he described as "two small sterile fragments fastened to pieces of mica." The packet bears the notation "in surcula Dicrani? Peruvia. M. Weddell." The other specimen is labeled "*Jungermannia bispinosa* Mntg. var. potiss. *J. diacantha* Mntg.! Carabaya. cel. Weddell."

COMMENTS—Howe (1902) observed that the type of *Jungermannia diacantha* "agrees perfectly, so far as it goes" with that of *Arachniopsis coactilis* var. *capillacea* Spruce, and this has never been disputed in the literature. The type of the variety is illustrated in Fig. 46, as well as by Fulford (1968, pl. 96). The salient differences between this species and *T. coactilis* are discussed under that species (p. 142).

The type of *T. diacantha* (PC!) consists of only a few stems, and is sterile. The specimen from Trinidad (Crosby 2393), cited below, has abundant androecia and gynoecia, and appears to be dioecious (both *T. coactilis* and *T. sejuncta* are monoecious). Male and female shoots are closely

intertwined, but we could not demonstrate a physical connection between them. Androecia are freely produced on short ventral-intercalary branches as well as intercalary in position on leading shoots.

The type of *T. diacantha* could not be moistened for examination, since Montagne's mica slides are enclosed in a packet of transparent film which has firmly adhered to the slide. However, it was possible to make some observations. Most leaves are bilobed, but (weaker) shoots have predominantly monocrurous leaves. The insertion of the two leaf lobes is transverse to weakly succubous. The leaf lobes are uniseriate to the base and 4–5 cells long (not counting the terminal cell, which is missing in most lobes). The lobe cells are moderately thick-walled and ca. 6–10:1. Seen in the type of var. *capillacea*, the septa are thickened in the corners and conspicuously bulging (Fig. 46: 6, 7).

Schuster (2000) observed the bracts of *A. diacantha* to be 3–5 cells high. We have not seen bracts of this sort in *T. diacantha* (Crosby 2393, Fig. 46: 17) or in any of the *Arachniopsis* specimens examined, all of which have a disc 1.5–3 cells high, including the basal cells of the lobes.

The type of *A. capillacea* Steph. (G!) consists of both well-developed and weaker shoots. The stronger shoots have bilobed leaves, while the leaves of weaker shoots are predominantly monocrurous, and only sporadically bilobed. Stephani (1922) described the leaves as setiform (thus, monocrurous); the Icones illustration (*Arachniopsis* 1) shows all the leaves but one to be monocrurous. As noted elsewhere, both *T. coactilis* and *T. diacantha* have monocrurous counterparts—*T. pecten* and *T. confervoides*, respectively—which have been described as distinct species. In the size, shape and proportions of the lobe cells, *T. capillacea* Steph. more closely resembles *T. diacantha*.

The leaf lobes in the type of *A. capillacea* are 6–8 cells long. The cells are thin-walled with septa straight or a little constricted, (22)24(28)  $\mu\text{m}$  wide  $\times$  (100)114–140(156)  $\mu\text{m}$  long and range from 4.2 to 5.6(6.5):1. Underleaves consist of 2 partially connate basal cells, each with a cylindrical cell capped by a slime papilla. Stephani (1922) described the underleaves as lacking. Stephani's plant is evidently dioecious (as, apparently, is *T. diacantha*). Androecia are present, but no gynoeia were observed. According to Stephani, the plants he examined were sterile.

"*Arachniopsis cauduciloba*" (Schuster, 2000,

p. 468, fig. 190A), which is lacking a Latin description, is based on a collection from Dominica, and said to be dioecious, although only  $\delta$  plants are known. The leaf lobe cells are elongate (7–9.5:1) and "all or almost all" of the lobe tip cells are caducous. The type of *T. diacantha* also has caducous lobes; the type of var. *capillacea* has caducous lobes and proliferation of rhizoids from the lobe tip cells (Fig. 46: 2, 12).

SPECIMENS SEEN—PUERTO RICO: Distr. Caguas, Reserva Forestal Carite, at intersection of Hwys 184 and 179, ca. 900 m, Buck 16093 (F). TRINIDAD: St. George Co., trail to Morne Bleu from summit of Arima-Blanchisseuse Rd., forest, Crosby 2393—c.  $\delta$  + sporo. (DUKE).

*Telaranea disparata* Engel & Merr., sp. nov.

*Telaranea pennata* aemulans (ramis complanatis foliis ramulorum imbricatis asymmetric lobatis), caulibus foliis symmetrice cuneatis 4–6-lobatis, apicibus loborum caducis disparata.

Holotype: Australia, Queensland, Daintree Region, Noah Creek, 23 July 1991, Stone s.n. (MELU); isotype: (F).

ILLUSTRATION—Fig. 47.

DISTRIBUTION—Australia (Queensland).

Plants rather stiff and wiry, loosely prostrate and matted, pale yellowish green, highly nitid when dry; plants medium, to 6 mm wide, including branches. Branching very regularly 1-(rarely 2-) pinnate, the branches exclusively terminal, *Frullania*-type, subopposite, stiffly at right angles to stem, leafy or flagelliform and geotropic, the leafy branches determinate, short and subequal in length, comblike in appearance, complanate-foliate, the microphyllous branches initially leafy but becoming abruptly flagelliform and rooting in the substrate; branch half-leaf 2(3)-lobed; first branch underleaf ventral in position on branch base, small and inconspicuous, undivided, with 2(3) basal cell tiers and 1 (or at most 2) sequential cells, ending in a slime papilla. Ventral-intercalary branches rare, leafy. Stem cortical cells subquadrate to short rectangular in surface view, thick-walled and firm, in section in 14–15 rows, uniformly thick-walled, larger than the numerous, thick-walled medullary cells, the medullary cell walls appearing highly pitted. Leaves of main shoot somewhat distant, the insertion strongly incubous; leaves 245–345  $\mu\text{m}$  wide  $\times$  220–295  $\mu\text{m}$  long,

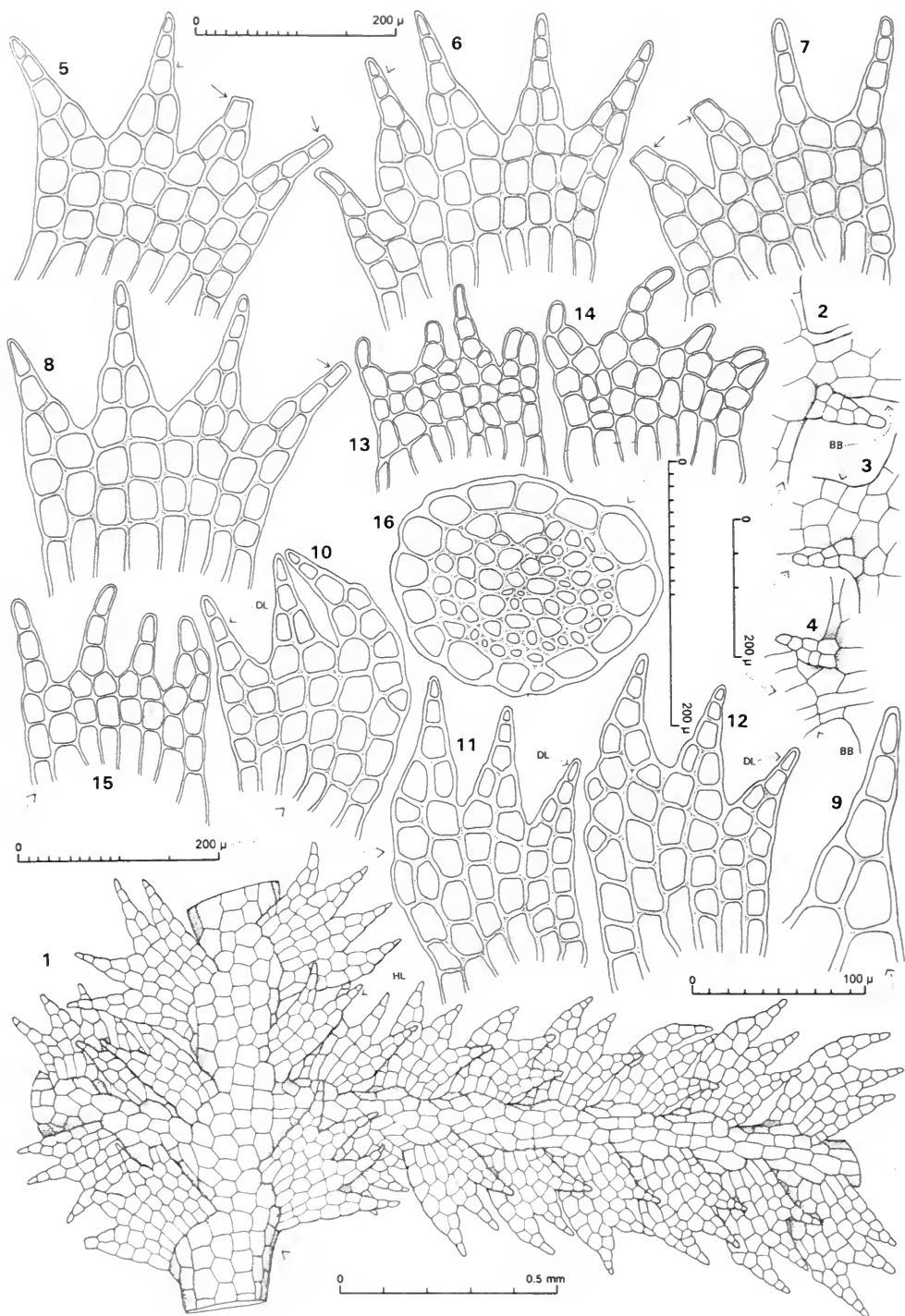


FIG. 47. *Telaranea disparata* Engel & Merr. 1. Portion of main shoot with two *Frullania*-type branches (hl = half-leaf); note the terminal branch at right has asymmetrically lobed,  $\pm$  falcate leaves and dorsal cortical cells broadly exposed. Note also the leaves of main shoot are symmetric and weakly cuneate. 2-4. Branch bases (= bb), each with an undivided first branch underleaf. 5-8. Leaves of main shoot (all drawn to same scale); note caducous lobe tips (at arrows). 9. Distal portion of leaf lobe. 10-12. Branch leaves (all drawn to same scale); note the ventral margin is strongly arched and longer than the dorsal; note also the smaller dorsal lobe (= dl). 13-15. Underleaves (all drawn to same scale); stipple indicates subdivision of cells to form rhizoid initials. 16. Stem, cross section. (All from type.)

symmetrically 4–5(6)-lobed to ca. 0.5, the lobes shorter than the disc. Branch leaves imbricate, subfalcate and arched toward the tip of the branch, strongly incubous to almost laterally inserted and leaving the two median rows of cortical cells broadly exposed, asymmetrically 3(4)-lobed, the ventral margin longer than the dorsal, the ventral lobe largest, the dorsal lobe smaller and more slender. Lobes divergent, slenderly acute to weakly acuminate, biseriate at the base, often with an additional biseriate tier, then  $\pm$  abruptly contracted to a uniseriate row of 2–3(4) cells (the lobes uniseriate for ca. 0.5 the length); lobe cells subquadrate to short rectangular, neither contracted nor projecting at the septa, the lobe tips (and occasionally the entire lobe) often caducous; cuticle of lobe tips indistinctly roughened. Disc of stem leaves weakly cuneate, 4(5) cells high, 8 cells wide throughout (10 cells wide in 5-lobed leaves); disc of branch leaves  $\pm$  asymmetric, the ventral margin curved, 5–7 cells high, the dorsal rather straight, 3–4 cells high. Cells of disc evenly thick-walled and firm, lacking trigones, in regular rows and tiers, uniformly quadrate to short rectangular, 26–32  $\mu\text{m}$  wide  $\times$  34–42  $\mu\text{m}$  long; disc cells often with a dilute, hazy appearance. Underleaves erect-spreading, equal to the stem in width or a little wider, plane, 4(6)-lobed to ca. 0.5, the lobes slender, typically biseriate at base, with a uniseriate row of up to 3 cells which is at times caducous, or the lobes consisting of 1–2 biseriate tiers, emarginate at the tip and terminating in a slime papilla; disc subrectangular, 3(4) cells high, 8 cells wide (wider in 5–6-lobed underleaves); rhizoids produced from distal cell tiers of the disc.

Androecia not seen. Only very young gynoecia seen, on short ventral-intercalary branches.

This species resembles *T. pennata* in the ribbon-like branches and shingled, asymmetrically lobed, subfalcate branch leaves (Fig. 47: 1), but in *T. disparata* the stem leaves are symmetrically, weakly cuneate (Fig. 47: 1, 5–8), whereas in *T. pennata* the stem leaves are at least moderately asymmetric (Fig. 4: 2, 3). In both species the branch leaf symmetry is of the “reversed” type, with the dorsal lobe smallest (Fig. 47: 10–12). The leaf disc is only 4(5) cells high and 8(10,12) cells wide throughout (Fig. 47: 5–8) vs. 16–19 cells wide in the distal portion and as many as 9 cells high in *T. pennata* (Fig. 4: 3). An interesting feature of *T. disparata* is the slender geotropic, flagelliform terminal branches, to the apparent exclusion of stoloniform, rooting ventral-intercalary

branches. *Telaranea disparata* is assigned to sect. *Neolepidozia*.

Scott (1985, p. 98) reports *Telaranea dispar* from Victoria and “presumably in other States,” citing a wedge-shaped disc, spreading, digitate lobes, thick-walled, “squarish” disc cells and caducous lobe tips, all of which are characteristic of *T. disparata*. The true *T. dispar* (*Jungermannia dispar* Mont. ex Tayl. & Hook. f.) is a synonym of *Kurzia hippuroides* (Engel & Merrill, 1996). In addition to *T. disparata*, other species in the MELU herbarium determined as *T. dispar* were *T. verruculosa* (2 specimens, including the type), *T. tridactylis* and *T. quadriseta*. For comparisons with *T. verruculosa*, see under that species.

SPECIMEN SEEN—AUSTRALIA. QUEENSLAND: Sullivans Track, Kennedy Creek, near Cardwell, *Stone s.n.* as *T. dispar* (F. MELU 568).

### *Telaranea disticha* (Steph.) Solari

*Lepidozia disticha* Steph., Kongl. Svenska Vetenskap-sakad. Handl. 46(9): 62. f. 24a, b. 1911. *Neolepidozia disticha* (Steph.) Fulf. & J. Tayl., Brittonia 11: 85. 1959. *Telaranea disticha* (Steph.) Solari, Bol. Soc. Argent. Bot. 25: 145. 1987. Type: Juan Fernández, Más a Tierra, 1908, *Skottsberg 117* (G!).

DESCRIPTIONS—Stephani (1922); Solari (1987).

ILLUSTRATIONS—Stephani (1911b, fig. 24a, b); Solari (1987, fig. 1: C, F, type). Stephani, *Icones, Lepidozia* 148.

DISTRIBUTION—Endemic to Juan Fernández.

Plants irregularly once-pinnate, the branches terminal, *Frullania*-type, at times becoming elongate and straggling; branch half-leaves bifid; first branch underleaf uniformly bifid, ventral-lateral in position at branch base; ventral-intercalary branches occasional, leafy or stoloniform, producing tubers at the tips (1 seen); stoloniform ventral-intercalary branchlets also frequently produced from primary terminal branches. Leaves of the main shoot asymmetrically 4-lobed, distant, the insertion nearly longitudinal in ventral  $\frac{2}{3}$ , becoming abruptly hooked at dorsal end, the line of insertion thus distinctly “J”-shaped; branch leaves  $\pm$  symmetrically 3–4-lobed, becoming 2-lobed towards the tip of branch, loosely imbricate, incubously shingled, the dorsal margin erect. Lobes of stem leaves narrowly acute, somewhat splayed and somewhat curved, 3–4 cells wide at base, with 1–3 biseriate tiers and a uniseriate row of 3–

4 short rectangular cells; branch leaf lobes more broadly acute, often with two tiers of 4 cells each, followed by successive tiers of 3 and then 2 cells, ending in a short uniseriate row of 2–3 short cells, the lobe tips often caducous. Disc of stem leaves asymmetrically cuneate, the dorsal margin subampliate, the ventral margin incurved and ventrally decurrent, the disc 6–8 cells high, 8 cells wide at base, (10)11–15 cells wide distally, the areolation somewhat irregular, the cells of unequal size: in the dorsal half smaller, often with longitudinal divisions of the dorsalmost row, resulting in a  $\pm$  distinct border of narrow cells, 22–31  $\mu\text{m}$  wide, in the median portion of the disc larger, 36–42  $\mu\text{m} \times 43$ –50  $\mu\text{m}$ , the cells at ventral base inflated, 48–60  $\mu\text{m} \times 54$ –66(78)  $\mu\text{m}$ , hexagonal to trap-ezoidal in the ventral decurrency. Underleaves 3–4-lobed, the disc 2–3 cells high, the lobes biseriate at the base, with a uniseriate row of 2 cells ending in a slime papilla.

Androecia and gynoecia not seen.

The types of *Lepidozia disticha* and *L. fernandeziensis* each contain plants of the other species, but *L. disticha* is a minor element in both. Fulford (1966) cites a Bertero collection from Juan Fernández as *T. seriatitexta*, which may be *T. disticha*. What little can be gleaned about *T. disticha* is certainly strongly suggestive of *T. seriatitexta*, but the two differ in several notable respects. The first branch underleaf in the Juan Fernández plants is consistently bilobed, vs. typically undivided in *T. seriatitexta*, and tubers were observed only in *T. disticha*. The latter is a smaller plant, the leaf cells are thinner walled vs. uniformly thick-walled and firm in *T. seriatitexta*, and there is no suggestion of a glaucous cuticle. The production of ventral-intercalary branches on terminal, *Frullania*-type branches in *T. disticha* is an unusual feature which, in our experience with *Telaranea*, is unique to this species.

*Telaranea europaea* Engel & Merr., sp. nov.

Autoicae. Plantae minute aculeatae nitidae plerumque laete viridae,  $\pm$  ordinatim 1–2-pinnatae, ramificatione terminali *Frullania*- vel *Acromastigum* typorum. Cellulae corticalis tumidae quadratae vel brevi-rectangulares. Folia erecto-patentia, insertione transversa, 3–4-fida, disco 0.5–1.5 cellulas alto, lobis ad basin biseriatis, parte uniseriata 5–7 cellulas longis. ♀ Bracteeae 4-fidae, disco 3–4 cellulas alto, lobiis caudatis laciniato-ciliatis, calcaribus lateralibus armatis, ad apicem furcatis. Perianthium teres vel leviter compressum, subclavatum, haud plicatum, ad orem laciniatum, divisionibus lobis ♀ bracteorum simulantibus. Surculi geotropi tuberiferi.

Apices lorum (aeque foliorum, bracteorum, perianthiorum) plerumque caduci.

Holotype: Ireland, W. Cork, Castletown Bearhaven, near entrance to Dunboy Castle, 8 Jun. 1968, Paton 3887—c. ♂ + sporo. (E); isotype: (F).

DESCRIPTION—Paton (2000).

ILLUSTRATIONS—Müller (1956, fig. 434: a–h); Paton (2000, fig. 9, as *T. nematodes*); Figs. 48, 49. In Paton's plate (fig. 9) the gynoecial branch with sporophyte, perianth mouth (pe. m.), male bract (♂), seta cross section (t/s. s.), spore (sp. di.), and the oil bodies in lobe tip cells were drawn from Paton 3887, the type of *T. europaea* (Paton, *in litt.*).

DISTRIBUTION—Hyperoceanic coastal regions of W. Ireland, W. Cornwall, France (Pyrenees), N. Spain (below 400 m, and first reported in Allorge, 1939), Portugal; Azores, San Miguel, Terceira, San Jorge, Fayal (*fide* Müller). Infante (2000, p. 103) provided a map of the distribution in Spain and Portugal.

Plants minutely prickly in appearance, in thin, loose mats, nitid, living plants deep emerald green to yellowish green. Branching of *Frullania*-type common, rather regularly and suboppositely 1–2-pinnate, the branches occasionally becoming flagelliform; branch half-leaf undivided or bifid; first branch underleaf asymmetrically bilobed, the longer lobe resembling a branch leaf lobe, the other an underleaf lobe. *Acromastigum*-type branches occasionally produced; ventral-intercalary branches common, leafy. Stems somewhat flexuous, rather stout for plant size, the cortical cells in surface view conspicuously quadrate to short rectangular and bulging, in section distinctly differentiated, in 11–12 rows, thin-walled but firm; medullary cells much smaller, in 22–24 rows, thin-walled. Main shoots with 4–5 cortical cells intervening between successive leaves on either side (8–10 on more rapidly growing shoots), the branches with 2–3 cells intervening cells. Leaves of main shoot rather rigid, erect spreading, slightly incurved, transversely inserted, 3–4-fid almost to the base, the lobe bases connate for 0.5–0.8 their length. Branch leaves 2-lobed, transversely inserted, the insertion extending to about half or more of the width of the cortical cells either side of the midline. Leaf lobes  $\pm$  equal in length, gradually tapering, moderately to widely divergent, at times fragmenting, occasionally with only the



basal cells of the lobes remaining, the lobe base barrel-shaped and usually distinctly contracted to the uniseriate portion of the lobe, the uniseriate row 5–7 cells long; lobe base biseriate (occasionally with an additional biseriate tier), the basal cells 22–29  $\mu\text{m} \times 46\text{--}60\text{ }\mu\text{m}$ , the first cell of the uniseriate row 30–36  $\mu\text{m} \times (50)60\text{--}74\text{ }\mu\text{m}$ , the terminal cell about equalling the penultimate cell in length, but lobes more typically with a short tip cell seemingly as a result of secondary division; lobe cells often rather thick-walled and firm, with septa thickened in the corners, the lobe margins straight or weakly constricted at the septa, or at times the proximal lobe cells barrel-shaped and bulging, the distal lobe cells merely with constricted septa; cuticle smooth. Leaf disc variable, consisting of the connate lobe bases (united to 0.5 their length), or with some of the basal cells locally transversely divided, or the disc consisting of a complete tier of disc cells + the paired cells at lobe bases. Oil-bodies (Paton, 2000) 4–9(12) per cell, 3–6  $\mu\text{m} \times 3\text{--}12\text{ }\mu\text{m}$ . Underleaves 3–4-lobed, each lobe with a basal pair of short, barrel-like cells, the lobes uniseriate, of 2–4 cylindric cells, the tip cell sometimes hooked, ending in a slime papilla. Underleaves of branches symmetrically bilobed or occasionally asymmetrically bilobed and resembling the first branch underleaf. Asexual reproduction by fragmenting leaf lobes and production of tubers (bulbils).

Chromosome number  $n = 9$  (Paton, 2000, citing Newton, unpubl.).

Autoecious. Androecia on primary and secondary *Frullania*-type branches, the bracts in 2–6 pairs; bracts 3(4)-lobed, the disc 2 cells high, the lobes 2–4 cells wide at base, with a uniseriate row of 5–7 cells, submoniliform basally, the lobe cells barrel-shaped and bulging,  $\pm$  straight-sided distally; antheridia solitary, stalk uniseriate. Gynoeceia on short, ventral-intercalary branches from main shoot; bracts much larger than the stem leaves, 4-lobed to about 0.5, the disc 3–4 cells high, the cells firm walled, the lobes laciniate-ciliate, caudate, 3–4 cells wide at the base and 2–3 cells wide for about half their length, armed with lateral spurs and forked at the tips, the ultimate divisions uniseriate, 4–8 cells long, the tips often caducous. Perianth terete to somewhat compressed and dorsally furrowed, subclavate, not at all plicate, the mouth lobulate-laciniate, the segments caudate, forked and spurred, resembling the lobes of the  $\text{f}$  bracts, or more slender and biseriate for up to half their length, the lobe and spur tips often caducous.

Seta with 8 rows of outer cells surrounding an inner core of 11–13 much smaller cells. Capsule wall 2-stratose and 19–23  $\mu\text{m}$  thick, at times with a localized 3-stratose patch (and then 26  $\mu\text{m}$  thick), the outer layer slightly thicker than the inner; outer layer of cells with shape irregular: sometimes elongate-rectangular, sometimes subquadrate, with two-phase development, thin walled, the longitudinal walls with moderately thickened continuous sheets of pigmented material and moderately developed nodule-like thickenings (the walls appearing sinuous), alternating with walls devoid of thickenings or sporadically with 1–2 isolated nodules, the transverse walls without thickenings; inner layer of cells somewhat irregularly narrowly rectangular, the longitudinal walls with thin continuous sheets of wall material, with semiannular bands common, often incomplete, the radial walls with nodular to spur-like thickenings rather common, irregularly and distantly spaced.

Spores 13.4–14.9(18)  $\mu\text{m}$ , reticulate-areolate (“alveolate,” Paton, 2000) with prominent ridges. Elaters  $\pm$  straight to moderately sinuous, 9.6–11  $\mu\text{m}$  in largest diameter, bispiral to the blunt tips, the spirals 3.8–4.3  $\mu\text{m}$  wide.

Previous reports of *T. nematodes* from Europe and Macaronesia belong to this species. The most instructive comparisons, however, are not between *T. europaea* and *T. nematodes* sens. str. (p. 171), but with *T. longifolia* (p. 163), which is the basis of most workers’ understanding of *T. nematodes*, and the detailed study of this eastern North American plant by Schuster and Blomquist (1955). The most striking differences are the thread-like leaf lobes, with distinctly elongate cells, typically 4:1 in *T. longifolia* (Fig. 50: 4) vs. 2:1 in *T. europaea* (Fig. 48: 8–10), with the paired basal cells parallel-sided and elongate in *T. longifolia* (Fig. 51: 2–4, 7) vs. short, barrel-shaped, and typically constricted at the septa in *T. europaea* (Fig. 48: 9, 10). The leaf lobes in *T. longifolia* are typically biseriate for 1–2 additional tiers above the partially united basal cells (Fig. 51: 3, 4), and the lobes are never fragmenting and caducous.

*Telaranea europaea* is distinguished from both *T. longifolia* and *T. nematodes* by its bulging, subquadrate stem cortical cells (Fig. 48: 1, 4), and leaves with short, barrel-shaped biseriate lobe bases and short, rather rigid, tapering lobes (Fig. 48: 1, 7; 48: 4). The geminate cells of the leaf lobe

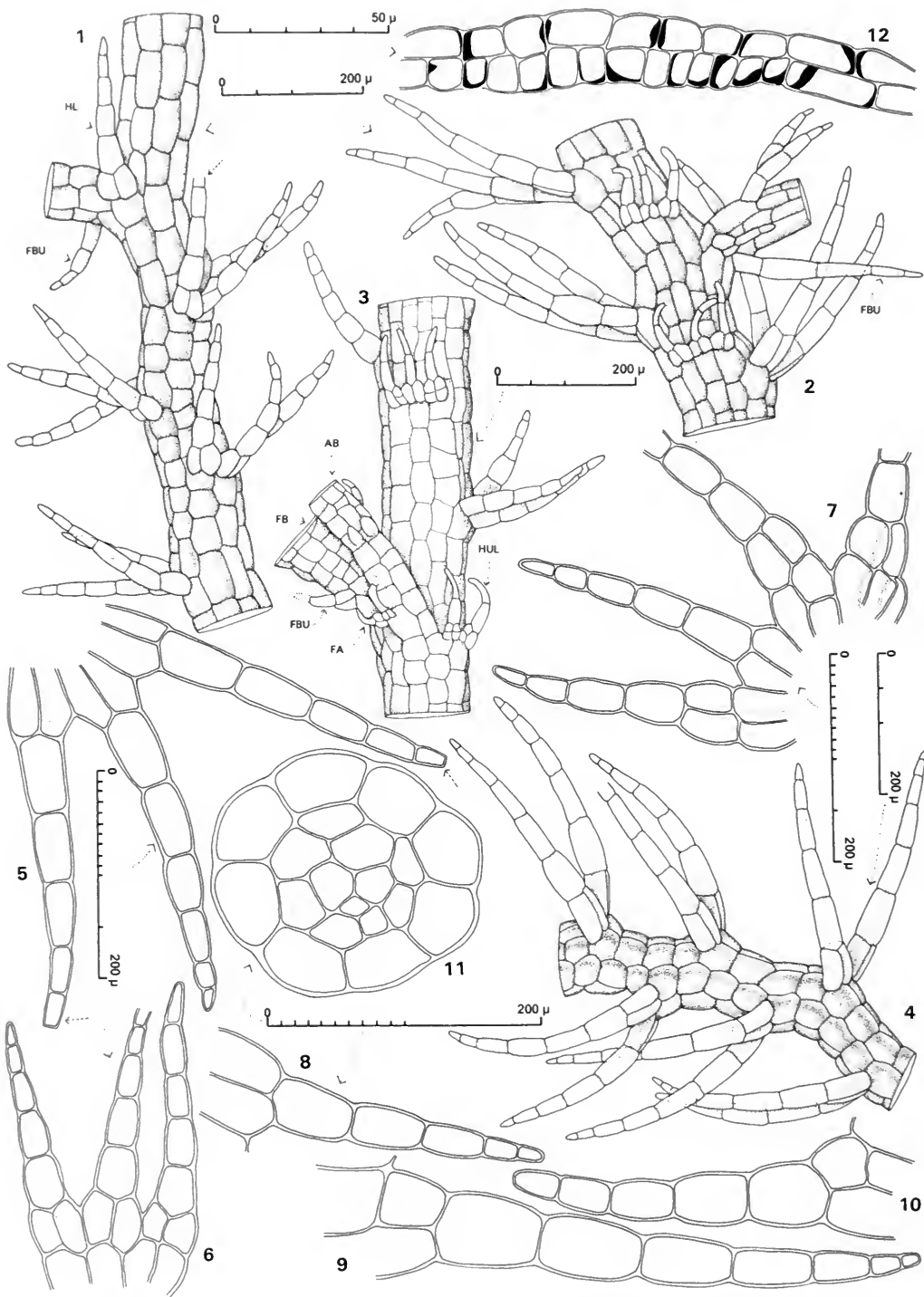


FIG. 48. *Telaranea europaea* Engel & Merr. 1. Portion of main shoot with base of *Frullania*-type branch, dorsal view (hl = half-leaf; fbu = first branch underleaf); note caducous leaf tip (at arrow). 2. Portion of main shoot with base of *Frullania*-type branch, ventral view (fbu = asymmetrically bilobed first branch underleaf). 3. Portion of main shoot with terminal branches of *Acromastigum* type (= Ab) and *Frullania* type (= Fb; fbu = one lobe of first branch underleaf, the other lobe now shown) in close proximity; note half-underleaf (= hul) and first foliar appendage (= fa) of the ventral-terminal branch. 4. Portion of primary branch, dorsal view. 5-7. Three- and 4-lobed leaves; 8. Single leaf; 9. Single leaf; 10. Single leaf; 11. Cross-section of leaf; 12. Single leaf.

base in *T. europaea* are short (2:1), and just over half the length of those of *T. nematodes*.

The ♀ bracts and perianth of *T. europaea* are strikingly distinct. Unlike *T. longifolia* and *T. nematodes*, the perianth of *T. europaea* (Fig. 49: 5) is not at all plicate and has a lacinate mouth (Fig. 49: 9). The perianth of *T. nematodes* is ciliate at the mouth, with 12 long, uniseriate cilia and a fringe of shorter accessory cilia (Fig. 38: 10). The ♀ bracts of *T. nematodes* (Fig. 38: 9) have lobes uniseriate and resembling those of the leaf. Bracts of *T. europaea* (Fig. 49: 6, 7) have caudate lobes, 2–3 cells wide for about half their length, forked at the tips, and armed with lateral spurs. In addition, in *T. europaea* the lobe and spur tips of both bracts and perianths are often caducous (Fig. 49: 6–10) like those of the leaves. The tip cell (when present) of both lobes and spurs is smaller and tapers to the summit (Fig. 49: 6, 7, 11, 12).

Branch leaves are transversely inserted, with the insertion extending to about half or more of the width of the cortical cells either side of the midline (Fig. 48: 4). *Telaranea nematodes* differs in having primary branch leaves incubously inserted, but the dorsal insertion of branch leaves is similar (Fig. 53: 8). Branch leaves of *T. chaetophylla* differ from both these species in being distinctly incubous to almost longitudinally inserted, and in having a prominent median strip of 2 full rows of cortical cells along the dorsal side of the branch (Fig. 42: 2).

Other distinctive features of *T. europaea* include the production of tubers (bulbils, illustrated by Paton, 2000, fig. 9, bu.), and caducous, fragmenting leaf lobes in some populations (Fig. 48: 5). In addition, *Acromastigum*-type branching was observed in Irish plants (Long 11719, 28522, 28531, and others, Fig. 48: 3). This type of branching has not been observed in either *T. longifolia* or *T. nematodes*.

ECOLOGY—Paton (2000) provided details of the ecology for the species in the British Isles and Engle (2000) for Spain. In Spain, at the Mount Jaizkibel site, plants occurred at 50 m in a humid niche within a wooded ravine; vegetation consisted of *Smilax aspera*, *Athyrium filix-femina*, *Stachys officinalis*, *Erica vagans*, *Genista hispanica*,

*Woodwardia radicans*, *Osmunda regalis*, *Blechnum spicant* and *Pteridium aquilinum*. In Spain the species is confined to coastal areas, and presence at the Río de Nueva site, ca. 3–4 km from the sea, is noteworthy. The river runs west to east in a very deep and narrow valley, with quartzite bedrock, that lies on the northern slope of the Cantabrian Range and, significantly, receives winds from the sea. At this site the species occurred at 160 m in a wooded ravine with vegetation consisting of *Alnus glutinosa*, *Fraxinus excelsior*, *Corylus avellana* and *Salix atrocinerea* together with a very rich and noteworthy fern flora (including the remarkable presence of *Culcita macrocarpa* and *Woodwardia radicans*, along with *Hymenophyllum tunbrigense* and *Vandemboschia speciosa*). The species was confined to boulders near the river on the north facing side of the valley. The boulders were bryophyte-covered (e.g., with *Jubula hutchinsiae*, *Diplophyllum albidans*, *Plagiochila bifaria*, *P. exigua*, *Saccogyna viticulosa* and *Leucobryum* sp.) on banks in moderate (but not heavy) shade and moist, permanently humid (but not in constant dripping or soaked) conditions. Fernández Ordóñez and Collado Prieto (2000) provided useful information on the Río de Nueva site.

SELECTED SPECIMENS SEEN—UNITED KINGDOM: W Cornwall, Newlyn, N of Trevelloe, SW of Paul, Paton 3883 (E). IRELAND: CO. KERRY. Garinish Is., near Sneem, 10 m, Long 28531 (E, F); Derreen near Lauragh, 15 m, Long 28522 (E); Killarney, Upper Lake, Loose Caunagh Hill, Paton 6621—c. per. (E); ibid., near Queen's Cottage, Paton 3886—c. ♂ + sporo. (E); ibid., E of Doo Lough, Muckcross Park, 20 m, Long 11721 (E); ibid., Torc Cascade, Long 11719 (DUKE). CO. GALWAY. Near chapel, Kilemore Abbey, 40–70 m, Long 13908, 29928 (E); Connemara, Kilemore, Richards 208A (E). CO. MAYO. Achill Is., Glendarary House, near Achill Sound, 25 m, Long 14340 (E); N of Killary Harbour, near Delphi, Paton 3889 (E). AZORES: S Miguel, Parc de Furnas, 210 m, Allorge (Bryophyta Azorica no. 7) (F). Island of Terceira, 1 km S of Algar do Carvão, 525 m, Crundwell 912 (E); ibid., Serra de Santa Barbara, 460 m, Crundwell 1523 (E). Island of Santa Maria, Cha de Joao Tome, 220 m, Crundwell 651 (E). SPAIN: CANTABRIA. Alfoz de Lored, Arroyo Conchuga, near Cobrecas, Heras & Infante (VIT 676/2000)—c. per. (F). GUIPUZCOA. Mount Jaizkibel, ravine at Biosnar, ca. 50 m, Engel 25211 (F); ibid., Atxaina ravine, Fuenterrabía, 75 m, Engel 25220—c. ♂

←  
note caducous lobe tips (at arrows). 8–10. Leaf lobes. 11. Seta, cross section. 12. Capsule wall, cross section. (Figs. 1, 3, 6–8, 10 from Long 11719, Ireland, Co. Kerry, Torc Cascade; 2, 4 from Allorge, Azores, S Miguel, Parc de Furnas; 5, 11, 12 from type; 9 from Engel 23518, Spain, Guipuzcoa, Mount Jaizkibel, Atxaina ravine.)

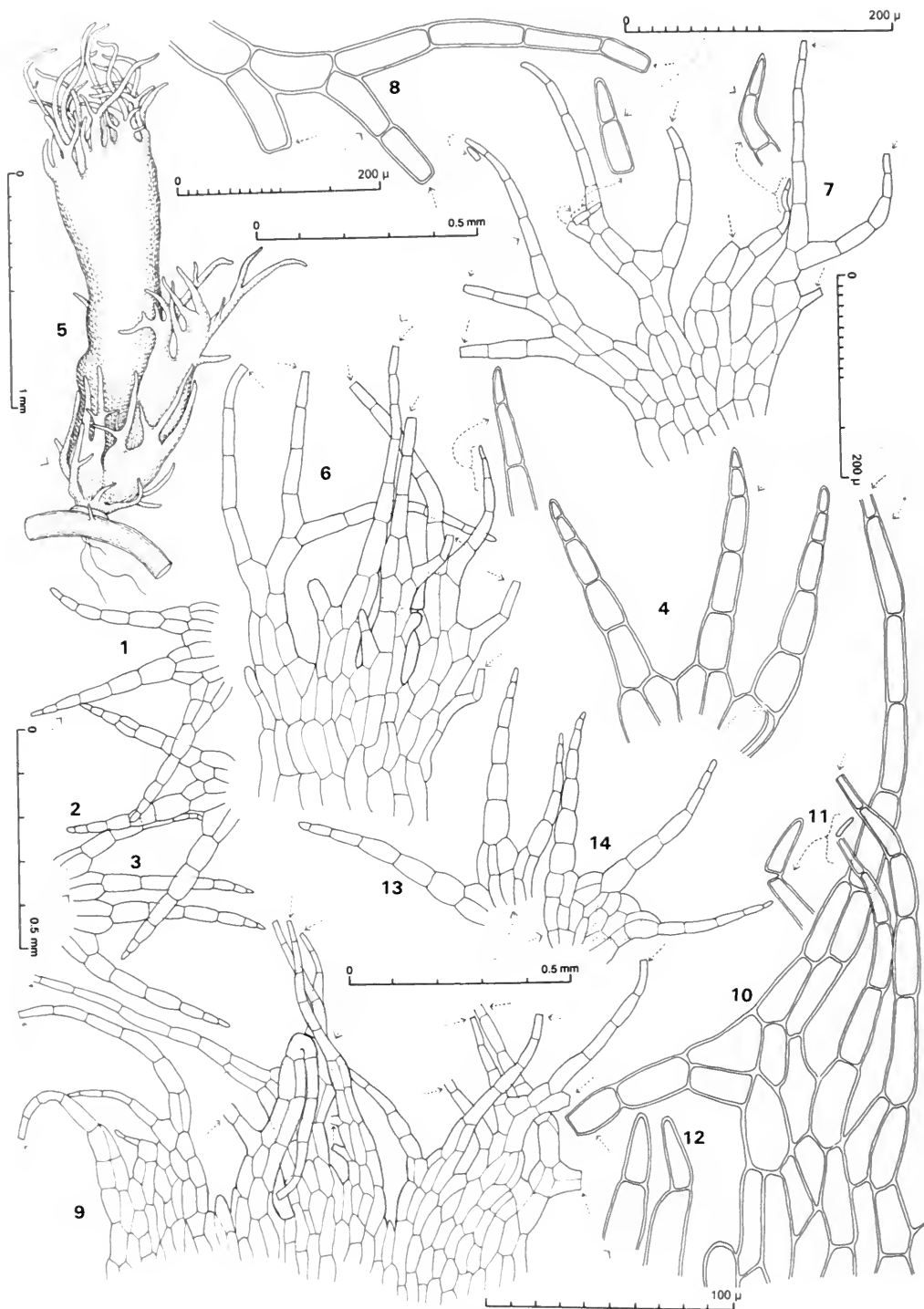


FIG. 49. *Telaranea europaea* Engel & Merr. 1–3. Three leaves from one shoot; note variation of bases. 4. Leaf. 5. Portion of shoot bearing mature gynoeceum on an abbreviated intercalary branch. 6, 7. Innermost ♀ bracts; note tips of lobes and lateral spurs are often caducous (at arrows), the distal portion of an intact lobe and 2 spurs all drawn at (same) higher magnification. 8. Lobe of ♀ bract; note lobe tip and lateral spurs have caducous tips (at arrows). 9. Portion of perianth mouth; note tips of lobes and lateral spurs are often caducous (at arrows). 10. Lobe of perianth mouth; note lobe tip and 1 of lateral spurs have caducous tips, the other spur with the tip cell partially detached. 11.

+ ♀ (F). ASTURIAS. Llanes, Nueva, Río de Nueva, 160 m, *Engel 25225*—c. per. (F).

*Telaranea fernandeziensis* (Steph.) Engel & Merr.

*Lepidozia fernandeziensis* Steph., Kongl. Svenska Vetenskapsakad. Handl. 46(9): 63. f. 24e. 1911. *Telaranea fernandeziensis* (Steph.) Engel & Merr., Novon 9: 341. 1999. Lectotype (*fide* Solari, 1987): Juan Fernández, Más a Tierra, El Yunque, 24 Aug. 1908, *Skottsberg* sub num. 18 (S!).

*Lepidozia effusiseta* Steph., Spec. Hep. 6: 325. 1922, *syn. fide* Herzog (1942). Lectotype (*nov.*): Juan Fernández, Más a Tierra, 1908, *Skottsberg 194* (G!).

ILLUSTRATIONS—Stephani, *Icones*, *Lepidozia* 134 (as *L. effusiseta*). Curiously, Stephani's *Icones* illustration of *L. effusiseta* appears to be redrawn, line for line, from his illustration of *L. fernandeziensis* (Stephani, 1911b).

DISTRIBUTION—Juan Fernández (Más a Tierra, 425–795 m); Chile (Valdivian + one station in Magellanian zone, 48° 46' S. According to Solari (1987), the collections from Chiloé Is. and Tierra del Fuego (Azopardo) cited by Stephani (1911b) contain no *T. fernandeziensis*. Stephani (1922, *L. effusiseta*) cites a Dusén collection from Isla Desolación, which we have not seen. Herzog (1954) reported the species from Puyuhuapi, west Patagonia.

Plants ± regularly (1)2-pinnate, the branches terminal, *Frullania*-type, oriented ± at right angles to the shoot, the shoots and branches essentially isophyllous, the underleaves almost indistinguishable from the leaves, pale green, at times straw yellow tinged with brown. Half-leaves symmetrically 2–3-lobed; first branch underleaf symmetrically to weakly asymmetrically 2–3-lobed, inserted on the base of the branch. Stems stout for plant size, the cortical cells thick-walled, especially the exposed wall, in 16 rows, the medullary cells 34–39, somewhat smaller than the cortical cells, thick-walled and appearing pitted. Leaves deeply 4–5(6)-lobed, the disc squarrose, the lobes divergent, inflexed and suberect, the insertion subtransverse to incubous, the insertion extending to the stem midline, with 3–4 cortical cells interven-

ing between successive leaves on each side of the shoot; branch leaves 4-lobed, with 2 cortical cells between leaves on each side of the branch. Lobes with a biseriate base and a uniseriate row 5–6 cells long, ± abruptly flexed at the base of the uniseriate row; lobe cells elongated and subcapillary, the septa thickened in the corners and moderately to strongly projecting, in profile the cells misaligned and slightly “off-center,” the adaxial side of the curving lobe “stepped” in appearance, with (often) unilaterally projecting septa, the basal cell of the uniseriate row 23–28 µm wide × 72–96 µm long, the next cell 17–23 µm wide × 73–91 µm long, the terminal cell tapering to a sharp point, thickened in the tip; cuticle smooth. Disc 2 (exceptionally 3) cells high, consisting of a tier of narrowly longitudinally elongate cells along the insertion plus the basal cells of the lobes. Underleaves 4–6-lobed, similar to the leaves but with 1–2(3) lobes (typically the median lobes) 1–2 cells shorter than the others, ending in a slime papilla, the other underleaf lobes identical to those of the leaves; branch underleaves 3–4-lobed, similar to the branch leaves, the lobes often lacking slime papillae at the tips.

Dioecious. Androecia spicate, on terminal, secondary *Frullania*-type branches and on short ventral-intercalary branches; ♂ bracts bilobed, the lobes caudate, 2–4 cells wide at base, the uniseriate row of 3–4 elongate cells, the terminal cell tapering to a sharp point, the disc 5–6 cells high, the ventral margin with a spine to 3 cells long resembling the uniseriate row of the lobes; dorsal margin slightly dilated, with a slime papilla and, distally, a 1-celled tooth; antheridial stalk uniseriate. Gynoecea infrequently produced, on short ventral-intercalary branches, the innermost ♀ bracts ovate, shallowly 5-lobulate, the lobules subcaudate, 4 cells wide at the base, with 1–2 biseriate tiers and a uniseriate row of 3 elongate cells, the tip cell tapering to a sharp point, the lobule margins occasionally with a tooth at base; lamina margins subentire or with a few blunt teeth; bracteole similar in size and form to the bracts. Perianth long cylindric, distinctly plicate in distal third, the mouth shallowly lobulate, the

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12. Distal portion of intact lateral spurs of perianth lobe (both drawn to same scale). 13, 14. ♂ Bracts. (Figs. 1–3, 13, 14 from *Engel 23518*, Spain, Guipuzcoa, Mount Jaizkibel, Atxaina ravine; 4 from *Long 11719*, Ireland, Co. Kerry, Torc Cascade; 5 from *Engel 23523*, Spain, Asturias, Llanes, Río de Nueva; 6–12 from *Heras & Infante* (VIT 676/2000), Spain, Cantabria, Arroyo Conchuga.)

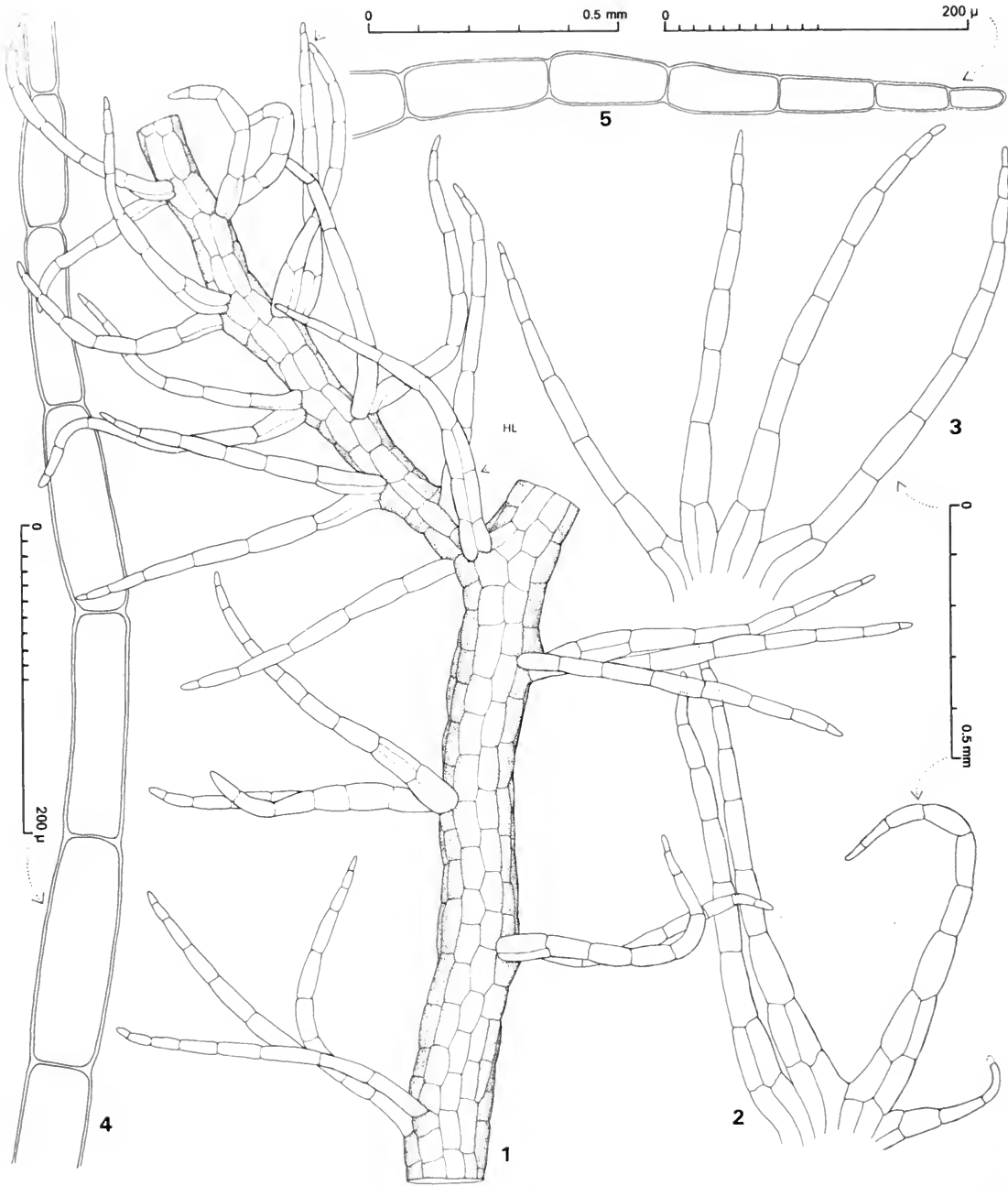


FIG. 50. *Telaranea longifolia* (Howe) Engel & Merr. 1. Portion of main shoot with *Frullania*-type branch, dorsal view (hl = half-leaf); note 3 cortical cells between branch leaves and 7–8 cortical cells between main shoot leaves. 2, 3. Leaves of main axis. 4. Portion of leaf lobe. 5. Distal portion of leaf lobe. (Fig. 1 from Schuster 28622, North Carolina, Durham Co., 3–4 miles NW of Durham, [F]; 2–5 from Anderson 23200, South Carolina, Chesterfield Co., 2.3 mi. S of Patrick, [DUKE].)

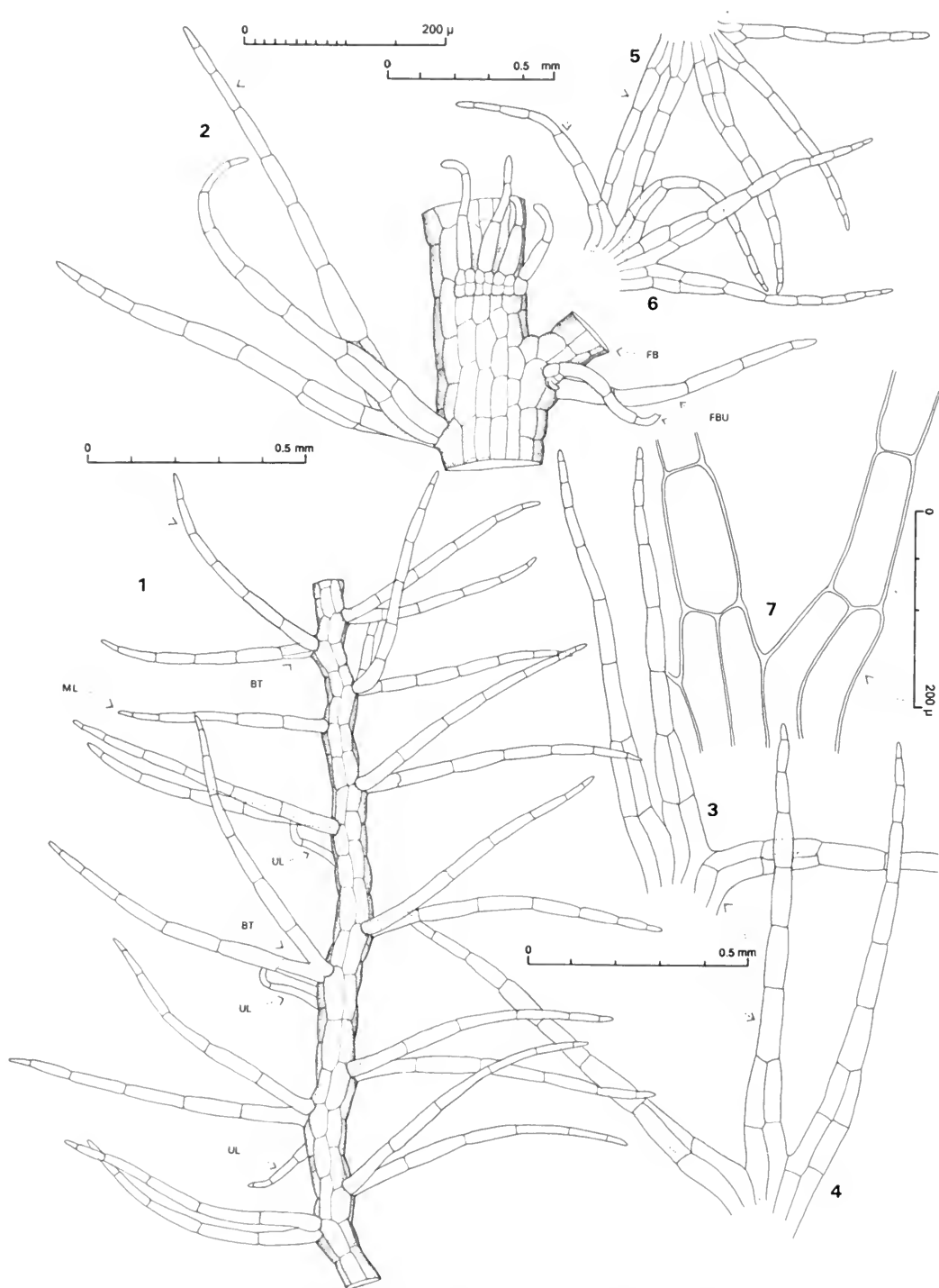


FIG. 51. *Telaranea longifolia* (Howe) Engel & Merr. 1. Portion of primary branch showing *Arachniopsis*-like aspect, dorsal view; note a few leaves have a biseriate tier at base (= bt); note also the monocurrous leaf (= ml) and the underleaf lobes (= ul). 2. Main axis with leaf (note biseriate tiers), a 4-lobed underleaf and base of *Frullania*-type branch (= Fb), ventral view; note first branch underleaf (= fbu). 3–6. Leaves of main axis; note some leaves have lobes with 2 additional biseriate tiers (figs. 4–6); note also the 5-lobed leaf (fig. 5). 7. Portion of leaf disc. (Fig. 1, from *Smith 4226*, Tennessee, Grundy Co., Savage Gulf State Nat. Area, *Smith 4226* [DUKE]; 2–7, from *Anderson 23200*, South Carolina, Chesterfield Co., 2.3 mi. S of Patrick, [DUKE].)

divisions toothed or with a  $\pm$  contorted bristle-like tip 1–2 cells in length.

**TYPIFICATION**—The packet at G labeled *L. fernandeziensis* contains two stems of *Lepidozia chordulifera* Tayl. Fulford (1966, p. 206) cited *L. fernandeziensis* as a synonym of *L. chordulifera*. Solari (1987) lectotypified *L. fernandeziensis* on the Stockholm specimen and listed the species as a synonym of *T. tetradactyla*. Fulford also stated that the description and figures of *L. fernandeziensis* were interchanged with those of *L. disticha* when, in fact, it is the Icones illustration of *L. effusiseta* (*Lepidozia* 134) that appears identical to Stephani's (1911b) illustration of *L. fernandeziensis*. Fulford (1963a, 1966) included *L. effusiseta* in the synonymy of *T. tetradactyla*.

The cells of the leaf lobes in *T. fernandeziensis* are oddly articulated: the lobes are  $\pm$  abruptly flexed at the base of the uniseriate row; the attachment of the basal cell is off-center, so that it forms a "knuckle" on the outer (abaxial) face of the disc. A similar, but more extreme expression of this character is seen in *Psiloclada clandestina* (Schuster, 1980, fig. 15: 1–4), although there it is the elongate terminal cell of the lobe that is asymmetrically attached. The lobe cells themselves are cylindrical and successively smaller in diameter, but when seen in profile are misaligned and slightly off-center, with unilaterally projecting septa. As a result, the outside (abaxial side) of the lobe is flush, but the inside (adaxial side) of the curving lobe is stepped in appearance. The lobes of *T. marginata* are similarly articulated, though not accentuated by unilaterally projecting septa. Moreover, in *T. fernandeziensis* the basal tier of cells extends the full width of the disc, whereas the disc in *T. marginata* is bordered by a single elongate cell. In *T. setosa*, the lobe cells are individually curved, and the lobes appear sinuous, or at times, even spirally twisted, moreover, the leaf disc is only 0.5 cells high.

*Telaranea fernandeziensis* resembles *T. lindenbergii* of New Zealand in having  $\pm$  transversely inserted, squarrose stem and branch leaves, with a disc 2(3) cells high, and the basal tier of cells narrowly elongate (Fig. 26: 2, 3, *T. lindenbergii*). It differs, however, in being essentially isophyllous, the underleaves 4–6-lobed and almost indistinguishable from the leaves, "foliis subaequimagna, simillima" (Stephani, 1922). The first branch underleaf of *T. fernandeziensis* is inserted on the base of the branch and symmetrically to

weakly asymmetrically 2–3-lobed, vs. undivided and ciliiform in *T. lindenbergii*.

*Telaranea fernandeziensis* resembles *T. kaindina* of New Guinea in the 4–5(6)-lobed leaves, height of the disk, and in the subisophyllous branches and asymmetrically lobed, *Kurzia*-like stem underleaves. In *T. kaindina*, however, the underleaves of the main shoot (Grolle, 1968, fig. 3: a, f), are smaller and distinctly differentiated from the stem leaves, and the first branch underleaf (Grolle, fig. 3: a) is undivided.

Weaker phases of *T. plumulosa* may be confused with this species, particularly when the leaf disc is only 3 cells high. Typically, however, *T. plumulosa* is a more robust plant than *T. fernandeziensis*, with plumose, circinate shoot and branch tips, the leaves incubously inserted, with a disc 3–5 cells high, composed of small quadrate cells. For further comparisons, see under *T. plumulosa*.

**ECOLOGY**—Rather common in the Valdivian zone and on Juan Fernández, but known from only one station in the Magellanian zone (sea level at 48° 46' S on Isla Williams, Prov. Magallanes). A plant of wet, mossy forests e.g., of *Nothofagus*, *Weinmannia*, *Laurelia*, *Drimys* and *Chusquea* (Butalcura, Isla Chiloé) or of *Drimys*, *Myrceugenia* and *Lauralia* (along the harbor at Puerto Ballena, Isla Mulchey, Prov. Chiloé). For the most part, the species occurs at sea level to 100 m, but to the north it extends to 680 m. It typically occurs on stumps and logs, particularly on the side or toward the underside of old well-rotted logs; also on bark of living trees, particularly at the base or on exposed roots. It is less often found on the forest floor in protected, shaded hollows.

**SELECTED SPECIMENS SEEN**—CHILE, PROV. MAGALLANES: Isla Williams, Bahía Tribune, Canal Messier, *Engel* 4501 (F, MSC). PROV. CHILOÉ: Isla Mulchey, Puerto Ballena, along shore of harbor, *Engel* 4185 (F, MSC); Isla Chiloé, Chadmo Central, just N of Puente San Juan along Ruta 5, 20.9 km by road N of Quellon, ca. 50 m, *Engel* 11962 (F); *ibid.*, Cerro Pirulil, S of Cucao near W coast, 50 m, *Engel* 12083 (F); *ibid.*, E of Cucao near SW end of Lago Cacao, Loncomilla (alto de la Vergen), 75 m, *Engel* 12130 (F); *ibid.*, 1.3 km by road N of junction of Ruta 5 and road to Delcahue, ca. 100 m, *Engel* 12167 (F); *ibid.*, Río Puidi, near aserradero at San Pedro, Cordillera San Pedro, 320 m, *Engel* 11870 (F); *ibid.*, Butalcura, near Río Butalcura, 11 km by road from Ruta 5, Cordillera San Pedro, 100 m, *Engel* 11819—c. ♂ (F); *ibid.*, Aguas Buenas area, 4.7 km E along Aguas Buenas road from Ancud-Quemchi road, ca. 100 m, *Engel* 12201 (F); *ibid.*, Chepu, S side of Río Chepu, near sea level, *Engel* 11738 (F); *ibid.*, Lechagua area, 5 km by road W of Ancud, near sea level, *Engel*



11725 (F). PROV. OSORNO: Agua Caliente, margin of Río Chanleufú near falls, 4 km by road from Termas de Puyehue along road to Refugio Antillanca, 400 m, *Engel 11434* (F). PROV. VALDIVIA: W slope of Cordillera Pelada, 6.2 km by road W of El Mirador on road between La Unión and Punta Hueicolla, 680 m, *Engel 12321*—c. per. + ♂ (F); Isla Teja, just W of Parque de Exposiciones Saval, Valdivia, near sea level, *Engel 10914* (F); Fundo Santa Rosa, 8 km by road N of Puente Callecalle, near sea level, *Engel 12219* (F). JUAN FERNANDEZ: Más a Tierra, western slope of Piramide Ridge, S of Portezuelo de Villagra, *Hatcher & Engel 24* (F, MSC); western slope of Piramide Ridge, trail to Portezuelo de Villagra, 425–550 m, *Hatcher & Engel 12a* (F, MSC); slopes above Portezuelo de Villagra, 550 m, *Hatcher & Engel 323*, 420 (F); Quebrada Damajuana, 400–450 m, *Skottsberg H184* (S); Centinela Ridge, 530 m, *Skottsberg 214* (S); SW side of Co. Piramide, ca. 600 m, *Skottsberg 215* (S); west-facing slope of Cordon Salpuedes, 520–610 m, *Hatcher & Engel 8a* (MSC); Salpuedes, 660 m, *Skottsberg 217* (S); ridge S of Pangal, E of Yunque, 795 m, *Skottsberg 211* (S).

*Telaranea ferruginea* Engel & Merr., sp. nov.

A *T. blepharostoma* foliis palmatim (3)4-lobatis, lobis in dimidio inferiore saepe biseriatis ad basim 3–4(5) cellulas latis, disco (2)3(4) cellulas alto recedit.

Holotype: Chile, Prov. Magallanes, Isla Desolación, Bahía Tuesday, head of inner harbor, *Engel 5649* (MSC); isotype: (F).

DISTRIBUTION—Southern Chile (southern portion of the Magellanian zone).

Plants in soft mats, the shoots lax and straggling, prickly in appearance, essentially isophyllous, amber to rust brown. Branching distant and irregular, often appearing almost dichotomous, the branches at an acute angle with the stem, with terminal branches of both *Frullania* and *Acromastigum* type, leafy or becoming long flagelliform and thread-like; branch half-leaf of *Frullania*-type branches bilobed, the first branch underleaf symmetrically or asymmetrically 3-lobed, with one lobe shorter, ending in a slime papilla; *Acromastigum*-type branches with half-underleaf symmetrically or asymmetrically bilobed with one lobe abbreviated, the first branch underleaf asymmetrically bilobed. Ventral intercalary branches also present, leafy or stoloniform. Stem cortical cells in 12 rows, firm-walled, larger than the 17–18 thin-walled medullary cells. Leaves  $\pm$  concave, loosely to locally densely imbricate, the disc spreading to subsquarrose, the lobes stiffly spreading to broadly incurved,  $\pm$  equally and rather deeply palmately (3)4-lobed to ca. 0.75, the insertion transverse to weakly incubous. Lobes

widely divergent, long attenuate, 3–4(5) cells wide at the base, the basal cells narrowly elongate, with up to 3 biseriate tiers (lobes biseriate for up to half their length), the uniseriate row 3–4 cells long, evenly tapering to a sharp-tipped terminal cell, the cells thick-walled, the septa strongly thickened in the corners but only moderately projecting. Disc (2)3 cells high, including the basal cells of the lobes, locally 4 cells high by transverse division of distal cells, the cells thick-walled and firm. Cuticle of lobes distinctly short-striate to distinctly striolate, the disc cells faintly striolate. Underleaves as large as the leaves, equally (3)4-lobed, the lobes resembling the lobes of the leaves, or with one lobe shorter, uniseriate, ending in a slime papilla, the disc 1.5 cells high, with rhizoid initials forming only at the base of the shorter lobes.

Androecia on short ventral-intercalary branches, either sessile or for a short distance leafy or stoloniform, arising from leafy branches or greatly elongate stoloniform branches both terminal and intercalary, subspicate, in up to 20 series, suberect, dorsally assurgent, concave, weakly asymmetrically 2–3-lobed to ca. 0.5, the lobes resembling the leaf lobes, caudate, 3–4 cells wide at the base, with 1–2 biseriate tiers, the uniseriate row of 3–4 cells, the disc 4–5 cells high, the disc margins entire or the dorsal margin inflexed with a prominent tooth and the ventral with 1–2 teeth; antheridia 1 per bract, the stalk uniseriate. Gynoecia (only young ♀ seen) on short ventral-intercalary branches, arising from elongate stoloniform ventral-intercalary branches.

*Telaranea ferruginea* resembles *T. blepharostoma* in the rust brown pigmentation, near isophylly, and indiscriminate production of both *Frullania*- and *Acromastigum*-type branches. It differs by the palmately (3)4-lobed leaves, the lobes 3–4(5) cells wide at the base and biseriate for as much as half their length, and disc (2)3(4) cells high. In *T. blepharostoma* the leaves are 3–4-lobed, the lobes widely divergent, uniseriate from a biseriate base, and the disc is only 1.5 cells high.

The color of *T. ferruginea* deserves mention, since *Telaranea* has been often described as lacking secondary pigments. The color is “rust brown” (6E7 in Kornerup and Wanscher, 1981), the same as in *T. blepharostoma* and in *T. lindenbergii* var. *mellea* of New Zealand. *Telaranea fernandezensis* and *T. plumulosa* are also light tan to

brownish, but are at most "brownish yellow" (5C6).

**ECOLOGY**—Known only from the type and one other collection, both from the southern portion of the Magellanian zone (Isla Desolación), on rock of cliffs in forests of *Drimys*, *Nothofagus betuloides* and *Berberis ilicifolia*. This is the only southern South American *Telaranea* so far observed on rock (except *T. seriaticincta*, which rarely occurs saxicolous).

**SPECIMEN SEEN**—CHILE. PROV. MAGALLANES: Isla Desolación, Puerto Churruca, head of Brazo Lobo, at boat portage, *Engel* 5840 (MSC).

*Telaranea fissifolia* (Steph.) Hürl.

*Lepidozia fissifolia* Steph., Spec. Hep. 3: 610. 1909. (*Lepidozia fissifolia* Steph. ex Par., Rev. Bryol. 33: 28. 1906, *nom. inval.*, Art. 32.1). *Telaranea fissifolia* (Steph.) Hürl., *Bauhinia* 8: 105. 1985. Type: New Caledonia, Mt. Koghi, June 1905, *Etesse* (G!).

**ILLUSTRATIONS**—Jovet-Ast (1947, fig. 4, type); Hürlimann (1985, fig. 2e–g). Stephani, *Icones, Lepidozia* 211.

**DISTRIBUTION**—Endemic to New Caledonia.

**COMMENTS**—The branch leaves of *T. fissifolia* (termed "aberrant" by Stephani) are bifid, planodistichous, strongly incubous, and obliquely spreading, hence the name of the species. The leaves of the main shoot (type) are 3-lobed, with a disc 2(3) cells high. Stem leaves in the specimens cited below (Hürlimann 2082, 2873) are also 3-lobed, but with a disc only 1–2 cells high, and vary from moderately to distinctly incubous. The lobes in the type specimen are biseriate at the base, sometimes with an additional biseriate tier, and the uniseriate row is 5 cells long and constricted at the septa.

As in *T. chaetophylla* (Fig. 42: 2) there is a prominent 2-cell-wide dorsal strip of short quadrate cortical cells between the almost laterally inserted branch leaves. In *T. fissifolia*, however, the branch leaves have a distinct disc, which is typically 2(3) cells high (3–4 cells high in the *Icones* illustration).

The half-leaf is undivided, or occasionally bilobed. The first branch underleaf is located on the ventral base of the branch, undivided, consisting of 1–2 tiers of basal cells, ending in a uniseriate portion of 2 narrowly cylindric cells, capped by a slime papilla. The cuticle is indistinctly punctate in the type as well in Hürlimann 2873, but in one

of the specimens seen (Hürlimann 2082) is sharply punctate.

Androecia are borne on short, *Frullania*-type branches and are unusual in being wider than the sterile portion of the branch.

**SPECIMENS SEEN**—NEW CALEDONIA: Flanc Sud Des Monts Koghi au SE du sommet Bouo, env. 650 m, Hürlimann 2082 (F); ridge in valley of haut Diahot between river and a tributary, 550 m, Hürlimann 2873—c. per. + ♂ (F).

*Telaranea fragilis* Miz.

*Telaranea fragilis* Miz., J. Hattori Bot. Lab. 40: 449. f. 1. 1976 non *T. fragilis* Engel & Merr., Novon 9: 341. f. 2. 1999 (New Zealand). Type: Philippines, Negros Is., Mt. Canlaon, 500–1700 m, Iwatsuki & Sharp 14514 (NICH).

**ILLUSTRATION**—Mizutani (1976).

**DISTRIBUTION**—Philippines.

**COMMENTS**—This is a species belonging to sect. *Telaranea*, based on the deeply divided, 2–3-lobed leaves and reduced underleaves. Mizutani (1976) compared *T. fragilis* with *T. trisetosa* (p. 196), which also has deeply divided leaves and the basal cells of the lobes biseriate or undivided and united for about half their length (l.c., fig. 1d–i). However, the leaves of *T. trisetosa* are 3–4 lobed (Fig. 58: 2, 5), vs. 2–3 lobed in *T. fragilis*, and the underleaves (fig. 11–p) are 2–4-lobed, with a disc 1 cell high, vs. 6–8 cells wide and 2 cells high in *T. trisetosa* (Fig. 58: 6).

The stem cross section illustrated by Mizutani (1976, fig. 1c) is unusual for members of sect. *Telaranea* in having ca. 10 cortical cells and only ca. 6 thin-walled medullary cells only slightly smaller in size.

*Telaranea heterotexta* (Steph.) Engel & Merr., comb. nov.

*Lepidozia heterotexta* Steph., Spec. Hep. 6: 329. 1922. Type: New Caledonia, in jugo Dogny, 1050 m, Jul 1909, *Lerat* 346, 371 (G!).

*Lepidozia theriotii* Steph., Spec. Hep. 6: 343. 1922 ("Thériotii"), *syn. fide* Hürlimann (1985). Type: New Caledonia, plateau de Dogny, 900 m, 1911, *Franc*, ex hb. Theriot (G!).

**ILLUSTRATIONS**—Stephani, *Icones, Lepidozia* 217; 252 (*L. theriotii*).

Plants closely and often suboppositely pinnate, the branches rather short and approximately equal in length, with terminal, *Frullania*-type branches

occasionally becoming flagelliform and whiplike. Half-leaf bilobed; first branch underleaf small, undivided, inserted on the base of branch, with 2 basal tiers + a single cell capped by a slime papilla. Ventral-intercalary branches common, giving rise to leafy shoots. Cortical cells of the branches (particularly those of the secondary branches) bullate. Stem leaves 4-lobed, strongly incubously inserted and ventrally decurrent. Branch leaves almost longitudinally inserted, second and "paw-like," the ventral margin broadly arcuate, the dorsal straight or incurved, the lobes short and hooked toward the apex of the shoot. Lobes biseriate at base, ending in a uniseriate row of 2–3 cells, the proximal cells subisodiametric or a little longer than wide, the tip cell somewhat longer (ca. 2:1) and tapering to narrowly rounded tip, the lobe cells bulging (type), with constricted septa. Lobe of both stem and branch leaves often caducous at base of the uniseriate row. Disc 8 cells wide throughout, 3–4 cells high along the ventral margin, but up to 5 cells high along dorsal margin due to smaller size of the cells; disc cells differentiated, with the two dorsal longitudinal rows of cells forming a  $\pm$  distinct border, the dorsal cells often quadrate, with protruding septa, the cells of the ventral half of the disc larger and longitudinally elongate. Lobes and dorsal margin of the disc papillose, the cells of the ventral portion of disc smooth. Underleaves quadrate, 4-lobed, disc 2–3 cells high, the basal tier of disc cells elongate, the lobes a single short cylindrical cell or occasionally with a uniseriate row of 2 cells. Androecia and gynoecia not seen.

The specific epithet "heterotexa" refers to the distinctive areolation of the leaf disc, in which the two dorsal longitudinal rows of disc cells form a  $\pm$  distinct border along the dorsal margin. Compared to the type of *L. heterotexa*, *L. theriotii* represents a better-developed expression of the species with strongly incubous, asymmetrical leaves and slenderly acuminate, hooked lobes (esp. the dorsal lobe), reminiscent of *T. paludicola* of New Zealand (Fig. 19: 5, 6). The type of *L. heterotexa* (Icones, *Lepidozia* 217) has  $\pm$  symmetrically quadrate stem leaves, with shorter, few-celled lobes. For further discussion, see Hürlimann (1985).

**SPECIMENS SEEN**—NEW CALEDONIA: Ravin en bas de la route vers la Mtge. des Sources en face du Pic du Casse-Cou, ca. 520 m, *Hürlimann* 2172a (G); pente de l'entanoir près de la crete de la Mtge. des Sources vers le Pic du Rocher, ca. 960 m, *Hürlimann* 2402 (G); Mé Amméri, ca. 700 m, *Guilleumin & Baumann* 9135 (G);

ravin en bas de la route vers Yaté au NE du Pic Mouirange, env. 200 m, *Hürlimann* 2312a (G); flanc Sud du Mt. Moné en bas de la crete vers le Mt. Bouo (massif des Koghis), env. 700 m, *Hürlimann* 2790 (G); Pic des Moussees au Mt. Mou, 1200 m, *Hürlimann* 5728 (G); sur la "Routa de Goman" au-deussus d'Oubatche, 450 m, *Hürlimann* 2824b (G).

### *Telaranea jowettiana* H. A. Mill.

*Telaranea jowettiana* H. A. Mill., J. Bryol. 14: 235. f. 2a–h. 1986. Holotype: Norfolk Is., SE slopes of Mt. Pitt, 250–300 m, on tree fern, *Jowett* 16 (MU!—c. per. +  $\delta$ ).

ILLUSTRATION—Miller (1986, fig. 2a–h).

DISTRIBUTION—Endemic to Norfolk Is.

Branches differentiated, flattened, the branch leaves strongly incubous, laterally inserted, with a 2-cell-wide median strip; branch half-leaf bilobed, less commonly subulate; first branch underleaf subulate, with paired basal cells and a uniseriate row 2–3 cells long, ending in a slime papilla, inserted either on ventral side of branch near its base, or on ventral-lateral side of shoot at branch base. Stem leaves are incubously inserted (Miller, 1986, figs. 2a, c) and 3-lobed (or 4-lobed on strongest shoots). Leaf lobes thin-walled, not thickened in corners, somewhat constricted at the septa. Cuticle of lobes smooth or sporadically faintly punctate, of disc smooth.

♀ Bracts only shallowly lobed, the lateral margins with small teeth and slime papillae. Perianth distinctly trigonous (3-sulcate distally with 3 broad angles), constricted to rather short-ciliate mouth (fig. 2h), the cells of the perianth and ♀ bracts projecting at upper ends, the distal perianth cells prorate.

A plicate, scabrous perianth is a feature of *T. praenitens* (Fig. 10: 9) of Australasia; in *T. jowettiana* the minute projections of the perianth cells are barely detectable. In most respects, this species resembles *T. tetradactyla*, and is therefore placed in sect. *Transversae*. A punctate cuticle is a feature of *T. quadriseta*, also in that section. Miller et al. (1983) reported *T. tetradactyla* from neighboring Lord Howe Is. Apparently, *T. jowettiana* is the only *Telaranea* species reported from Norfolk Is.

### *Telaranea kaindina* Grolle

*Telaranea kaindina* Grolle, J. Hattori Bot. Lab. 31: 9. f. 3. 1968. Type: New Guinea, Prov. Morobe, Mt. Kaindi, 2650 m, *Hewson* 467.

DESCRIPTION—Piippo (1984).

ILLUSTRATION—Grolle (1968, fig. 3).

DISTRIBUTION—Papua New Guinea (1300–2650 m); Solomon Is. (2000–2300 m).

COMMENTS—The branches of *T. kaindina* are almost radially symmetrical. The branch underleaves are 3-lobed, but otherwise similar to the branch leaves in size and form (Grolle, 1968, fig. 3a). By contrast, the underleaves of the main shoot (fig. 3f) are much smaller and strongly differentiated from the leaves, and the lobes are dissimilar, the middle pair shorter and underleaf lobe-like, and the lateral lobes longer and widely divergent.

### *Telaranea kogiana* (Steph.) Grolle

*Lepidozia kogiana* Steph., Spec. Hep. 6: 332. 1922.  
*Telaranea kogiana* (Steph.) Grolle, J. Hattori Bot. Lab. 29: 284. 1966. Type: New Caledonia, Mt. Koghis, 1.11.09, Franc, ex hb. Thériot—c. young per. (G!).

DESCRIPTIONS—Grolle (1966); Piippo (1984).

ILLUSTRATIONS—Grolle (1966, fig. 3). Stephani, Icones, *Lepidozia* 219, “*koghiana*.”

DISTRIBUTION—Papua New Guinea (400–1300 m); New Caledonia.

COMMENTS—Two specimens of this species have been seen, in addition to the type. The species is described in some detail and illustrated by Grolle (1966). The leaves of the type are 4-lobed and weakly to moderately incubously inserted. The disc is 2 cells high, consisting of a basal tier of cells along the insertion + the paired cells at the base of the lobe. The uniseriate row is 5–6 cells long, composed of firm-walled cells that are constricted at the septa. The cuticle is finely and indistinctly papillose in the type, but in the other specimens the surface of the lobe cells is distinctly roughened with fine, sharp papillae.

Plants of *T. koghiana* are regularly and suboppositely branched, and resemble *T. tetradactyla* in having both stem and branch leaves incubous, although the leaf disc is shorter, 2–3 cells high vs. 3–4 cells high in *T. tetradactyla*. In addition, the branch leaves are widely set, leaving the two rows of cortical cells along the midline of the branch prominently exposed.

SPECIMENS SEEN—PAPUA NEW GUINEA: Koitaki, Owen Stanley Range above Port Moresby, ca. 500 m, Carr 12061—c. ♂ + per. (F); West Sepik Prov., Kokomo Creek, 2.5 km NW of Frieda Base Camp, 550 m, Koponen 35729—c. young ♀ (F).

### *Telaranea lawesii* (Steph.) Grolle

*Lepidozia lawesii* Steph., Hedwigia 28: 264. 1889. *Telaranea lawesii* (Steph.) Grolle, J. Hattori Bot. Lab. 28: 53. 1965. Type: Papua New Guinea, Astrolabe Range, 1885, Lawes—c. young per. (G!).

DESCRIPTIONS—Stephani (1909); Grolle (1966); Piippo (1984).

ILLUSTRATIONS—Grolle (1966, fig. 2h–n). Stephani, Icones, *Lepidozia* 220a, b.

DISTRIBUTION—New Guinea, Solomon Is.; Philippines (Mizutani, 1976).

Grolle (1966) provided a full description and an illustration of this species, based on an isotype at M, leg. Lawes. Stephani (1889) described the leaves of this species as 4-lobed, with a disc only one cell high. The height of the disc in the type of *T. lawesii* is variable, due chiefly to the varying numbers of transverse divisions of the paired cells at the lobe bases. In general, the disc is 1.5 cells high, but in the type may be only 1 cell high at the margins (as in *T. marginata*) or locally 2 high cells high, resulting from transverse divisions of one or more of the basal cells of the lobes. Only occasional leaves have a disc 1 cell high, consisting only of the paired cells at the lobe bases, as in Stephani's Icones (*Lepidozia* 220).

Our concept of the species is based on the type. The plant cited below (Norris 62123) was identified by Piippo as *T. lawesii*, but differs in having 6–8-lobed leaves, the disc 2 cells high, including the basal tier of the lobes, and branch leaves transversely inserted and 4-lobed.

SPECIMEN SEEN—PAPUA NEW GUINEA: Morobe Prov., E part of Cromwell Mts., ca. 3 km WSW of Siwea, 1800–2100 m, Norris 62123 (F).

### *Telaranea leratii* (Steph.) Engel & Merr., comb. nov.

*Lepidozia leratii* Steph., Spec. Hep. 6: 333. 1922, non *L. leratii* Steph. ex Par., Rev. Bryol. 33: 28. 1906, nom. nud. (“*Le Ratii*,” Rev. Bryol. 37: 130. 1910, nom. nud. Lectotype (fide Hürlimann, 1985): New Caledonia, summit of Mont Mou, July 1909, Lerat, sub Paris no. 89 (G!).

*Lepidozia trifida* Steph., Spec. Hep. 6: 344. 1922, nom. illeg. (Art. 64.1), non *L. trifida* Steph. in Mildbraed, Wiss. Ergebn. Deutsch. Zentr.-Afrika Exped. 2: 120. 1911. (Rwanda). Type: New Caledonia, Mé Areinbo, Lerat, “Général Paris misit” (G!).

ILLUSTRATION—Stephani, Icones, *Lepidozia* 253 (*L. trifida*).

DISTRIBUTION—Endemic to New Caledonia.

Plants with a ragged appearance due to the caducous lobes of the leaves. Branching terminal, *Frullania*-type, the first branch underleaf undivided, inconspicuous, consisting of 1 or 2 biseriate tiers followed by a single cell. Leaves 3–4-lobed to 0.5; lobes 2 cells wide at the base with a uniseriate row of 4 cells long, the lobe cells barrel shaped and bulging and distinctly constricted at the septa; disc 4 cells high and 8 cells wide throughout (6 cells wide in 3-lobed leaves), the cells subisodiametric. Branch leaves subsymmetric, the lobes 2 cells wide at base, with a uniseriate row (2)3–4 cells long, the cells barrel-shaped and bulging, the lobes caducous like the stem leaves; disc 5 cells high. Cuticle of lobes distinctly papillose. Underleaves about as wide as the stem, the lobes inconspicuous, consisting of a single barrel-shaped cell capped by a slime papilla, the disc 3 cells high. The foregoing notes are based on the types (G!).

Grolle (1964, p. 170) stated "*Lepidozia leratii* ... ist eine *Telaranea* aus der *Neolepidozia*-Gruppe," but the transfer was not made. We have assigned this species, endemic to New Caledonia, to sect. *Cancellatae*. According to Kitagawa (1973, p. 267), this species is "closely related to and may be conspecific with" *T. papulosa*. The latter also has barrel-shaped, bulging lobe cells and distinctly constricted septa.

The type of *Lepidozia trifida*, based on a Lerat collection from New Caledonia, has mostly 3-lobed leaves, with some 4-lobed leaves present. Nearly all leaf and branch leaf lobes are caducous, with complete lobes seldom present. We are treating *L. trifida* as a 3-lobed expression of *T. leratii*. This plant should not be confused with an earlier published *Lepidozia trifida* (Stephani, 1911a), an African species transferred to *Telaranea* by Schuster (1966; see p. 195).

*Lepidozia leratae* Par. ex Steph., Spec. Hep. 6: 333. 1922., which made its debut on the same page as *L. leratii*, is *Kurzia bisetula* (Steph.) Grolle (Grolle, 1964).

***Telaranea longicaulis* (Piippo) Engel & Merr., comb. nov.**

*Kurzia longicaulis* Piippo, Acta Bot. Fenn. 131: 174. f. 2. 1985. Holotype: Papua New Guinea, East Sepik Distr., eastern ridge of Sumset (Mt. Hunstein), 4700 ft, Hoogland & Craven 11024 c. per. (CANB!).

ILLUSTRATION—Piippo (1985, fig. 2).

DISTRIBUTION—Endemic to New Guinea (1435–2100 m).

COMMENTS—The overall aspect of this plant is suggestive of the group of species formerly placed in *Kurzia* subg. *Leucolepidozia* (*T. pallescens*, *T. trilobata*), with deeply divided, transversely inserted leaves and asymmetrically lobed underleaves. As treated here, *Telaranea* sect. *Transversae* includes species of similar aspect, both with and without *Microlepidozia*-type branches.

*Telaranea longicaulis* is similar to *T. kaindina* in the transverse insertion of both stem and branch leaves, and subisophyllous branches, but differs most notably in the length of the leaf lobes (3–5 cells long vs. (8)10–12 cells long in *T. kaindina*), and in the form of the ♀ bracts. In addition, the cuticle of *T. longicaulis* is "verrucose," whereas in *T. kaindina* it is described as smooth or very finely punctate (Grolle, 1968). The specific epithet, "longicaulis," is a reference to the unusual length of the stem (to 10 cm).

The ♀ bracts of *T. longicaulis* are broadly ovate, and irregularly 4-lobed and toothed (fig. 2i, j) vs. with 4 caudate lobes, ending in a uniseriate row up to 14 cells long, with lateral lobes which are much shorter and often forked (Grolle, 1968, fig. 3i).

The stem underleaves of *T. longicaulis* are variable, ± equally 4–6-lobed, with all lobes ending in a slime papilla (fig. 2e) or of the *Kurzia*-type (asymmetrically lobed, with the lateral lobes similar to the leaf lobes and the median lobes shorter (fig. 2f). The underleaves on the larger branches resemble the leaves, but on smaller branches the underleaves are often asymmetrically 2–3-lobed (Piippo, 1985, fig. 2g).

Piippo (1985) does not discuss branching in this species, but her illustrations (fig. 2a, b) clearly show *Frullania*-type branches with the first branch underleaf 2(3)-lobed, whereas in *T. kaindina* the fbv is undivided (Grolle, 1968, fig. 3a).

***Telaranea longifolia* (Howe) Engel & Merr., comb. nov.**

*Telaranea nematodes* var. *longifolia* Howe, Bull. Torrey Club 29: 286. 1902, non *Lepidozia longifolia* Steph., Spec. Hep. 3: 606. 1909 (Amboina). Holotype: New York, Long Is., Freeport, on humus in a swampy wood, 17 Oct 1898, Howe—c. ♂ + young per. (NY!).

DESCRIPTIONS—Howe (1902); Frye & Clark

(1937–47, p. 663, fig. 1–6); Schuster & Blomquist (1955), Schuster (1969), both as *T. nematodes*.

ILLUSTRATIONS—Schuster & Blomquist (1955, fig. 1–23), Schuster (1969, figs. 89, 90), both as *T. nematodes*; Lincoln & LaGreca (2002, fig. 1); Figs. 50, 51.

DISTRIBUTION—Eastern North America (Atlantic and Gulf coast, from Mississippi to New Jersey, eastern Long Is. and Martha's Vineyard; Oklahoma, Tennessee). Insofar as is known the species does not occur outside the continental United States. Reported from Martha's Vineyard (as *T. nematodes*) by Lincoln & LaGreca (2002). Howe (1902) referred a collection from Bermuda to typical *T. nematodes*. A specimen from Franklin Co., Arkansas (*Redfearn* 28665, DUKE) is *Kurzia sylvatica*.

COMMENTS—The only North American representative of the genus, *T. longifolia* is fully described and illustrated (as *T. nematodes*) by Schuster and Blomquist (1955) and Schuster (1969). It differs from *T. chaetophylla* (p. 136) and *T. nematodes* (p. 171) chiefly in having both the branches and main shoots terete, lacking a 2-cell-wide median strip (compare Fig. 51: 1, *T. longifolia*, and Fig. 42: 2, *T. chaetophylla*). The slender, thread-like branches of *T. longifolia*, with deeply divided ciliiform-bilobed leaves and lobes frequently uniseriate to the base, are remarkably *Arachniopsis*-like in appearance (Fig. 51: 1; compare Fulford, 1963a, figs. 132, 133, type of *T. sejuncta*; Piippo, 1985, fig. 1a, b, *A. major*), quite different from those of *T. chaetophylla* and *T. nematodes*.

The leaves in *T. longifolia* are 3–4-lobed (or exceptionally 5-lobed, Fig. 51: 3–6), the leaf lobes typically biseriate for 1–2 additional tiers above the partially united basal cells (Fig. 51: 3, 4; Frye & Clark, 1937–47, fig. 2; Schuster & Blomquist, 1955, figs. 10, 11). The basal cells themselves are narrow, straight-sided, and about equal in length to the cells of the uniseriate row vs. barrel-shaped,  $\pm$  contracted to the uniseriate portion of the lobe, and lacking a second biseriate tier in *T. chaetophylla*. Occasionally the basal cells are completely united, and the tier above partly united, “the sinuses extending to within 1.3 cells of the base” (Schuster & Blomquist, p. 592). Howe (1902) gave the range of leaf lobe lengths as 5–8 cells long in the variety (*T. longifolia*), vs. 4–6 cells in typical *T. nematodes*, the lobe cells 2–4.5:1 in the former vs. 2–3:1 in the latter.

The leaves on the main shoot in *T. longifolia* are separated by as many as 6–10 cortical cells

on either side (Fig. 50: 1) vs. 3 in *T. chaetophylla* (Fig. 42: 1) and 3–5 in *T. nematodes* (Fig. 53: 1). On the branches 3–4 cells intervene between leaves in *T. longifolia* (Figs. 50: 1; 51: 1), vs. 2 in *T. chaetophylla* (Fig. 42: 2) and 2–3 in *T. nematodes* (Fig. 53: 8). Underleaves of *T. longifolia* are typically 2–3 lobed (see Schuster & Blomquist, 1955, figs. 15, 19), or exceptionally 4-lobed (Fig. 48: 2).

The perianth in *T. longifolia* (Schuster & Blomquist, 1955, fig. 17) is rather compact, trigonous and distinctly plicate above. The ♀ bracts and bracteole (ibid., figs. 20, 21) have lobes 2- or more seriate and deeply dissected for much of their length. The seta (ibid., figs. 6, 7) is stouter than in *T. chaetophylla*, with 16–24 rows of internal cells, vs. 6 internal cells in *T. chaetophylla* (Fig. 43: 8), and the capsule wall is 3-stratose (ibid., fig. 1), vs. 2-stratose in *T. chaetophylla* (Fig. 43: 10).

According to Howe (1902), the variety (*T. longifolia*) “gives the impression of being two or three times the size of the Cuban plant” (*T. nematodes*), the leaves of *T. longifolia* being as much as 0.8 (rarely 0.9) mm long, vs. 0.25–0.5 in typical *T. nematodes*.

SELECTED SPECIMENS EXAMINED—USA: Florida, Sarasota, Mar. 1878, (*Austin*), ex hb. Austin, syntype of *T. nematodes* var. *longifolia* (NY); Port Orange, *Straub s.n.* (Hepaticae Americanae no. 180), syntype of *T. nematodes* var. *longifolia* (F); Highlands Co., Highland Hammock State Park, W of Sebring, *Schuster F-101*—c. sporo. (F). Mississippi, Ocean Springs, shade of grass in pine bog, *Pennebaker 133* (DUKE). South Carolina, Chesterfield Co., 2.3 mi. S of Patrick, *Anderson 23200* (DUKE). North Carolina, Durham Co., 3–4 mi. NW of Durham, *Schuster 28622* (F). Virginia, Nansemond Co., ca. 3 mi. NE of Cypress Chapel, *Schuster 34516* (F). New Jersey, Ocean Co., Island Beach State Park, *Merrill 18180*—c. young sporo. (F); Monmouth Co., Highlands, *Haynes* (DUKE). New York, Suffolk Co., Hither Hills St. Park, near Montauk, *Schuster 22074* (DUKE). Oklahoma, Atoka Co., N end of Boehler Lake, 13 mi. E of Atoka on highway 3, 9 mi. S on 109A, *Studlar 88B*—c. per., 89B; *Studlar & McAlister B162* (hb. Studlar). Tennessee, Grundy Co., Savage Gulf State Nat. Area, wet shaded floor of hardwood swamp, *D. K. Smith 4226* (DUKE).

### *Telaranea longitudinalis* (Herz.) Schust.

*Lepidozia longitudinalis* Herz., Trans. Brit. Bryol. Soc. 1: 312. f. 29. 1950. *Acrolepidozia longitudinalis* (Herz.) Schust., J. Hattori Bot. Lab. 26: 254. 1963. *Telaranea longitudinalis* (Herz.) Schust., Hep. Anthoc. N. Amer. 2: 30. 1969. Type: Borneo, Sarawak, L. C. Dulit, under 300 m, *Richards 2548* (but see note on typification below).

DESCRIPTION—Schuster (1973).

ILLUSTRATION—Herzog (1950, fig. 29a–f).

DISTRIBUTION—Borneo.

TIPIFICATION—Mizutani (in herb., 1976, JE) suggested that the original material cited for this species and for *Cololejeunea fissilobula* (Herzog, 1950, p. 323) are transposed in Herzog (1950), and regards the specimen cited below (Richards 2047, JE) as the probable type of *L. longitudinalis*. The specimen bears the annotation “*Lepidozia longitudinalis* n. sp.” in Herzog’s hand, and contains no *Cololejeunea*. According to Schuster (1973), the specimen at Kew labeled as holotype contained only *Jackiella angustifolia*.

COMMENTS—Schuster (1963) proposed the genus *Acrolepidozia* Schust., distinguished principally by the creeping axis giving rise on one side of the stem to leafy, ascending branches, with those on the other side flagelliform. The genus was reduced to a subgenus of *Telaranea* by Schuster (1969, p. 30, footnote), emphasizing the extreme reduction of the half-leaf and first branch underleaf as distinctive for the subgenus.

The stems and branches are thick and fleshy in appearance. Branching is (often rather regularly) pinnate, and almost exclusively of the *Frullania* type, with occasional ventral-intercalary branches, usually leafy. Slender, flagelliform branches are interspersed with normally leafy branches. The half-leaf is shallowly bidentate; the first branch underleaf is undivided, with 1–2 biseriate basal tiers and a uniseriate row of 1–2 short cylindrical cells, inserted on the ventral side of the branch at its base in line with the underleaves of the branch.

The leaves of *T. longitudinalis* are dimorphic. Those of the main shoot are small and inconspicuous, subrectangular, shallowly 4-lobed, the disc 4 cells high and 8 cells broad throughout. The branch leaves are larger, narrowly trapezoidal, shallowly 3(4)-fid, widely set (the stem broadly exposed dorsally), ventrally decurved, almost longitudinally inserted and often decurrent ventrally as a wing. The disc is up to 10 cells high and up to 11 cells wide at the insertion, narrowing to 6(8) uniform rows above. The lobes are short, consisting of a single cell or a uniseriate row of 2–3 cells. Underleaves are small, 2(rarely 3)-fid and scalelike. The stem cortical cells are in 12–16 rows, firm, with thick walls (particularly apparent in surface view), much larger than the numerous, firm-walled medullary cells. The cortical cells in our material are smooth, rather than striolate (Schuster, 1973).

The aspect of *T. longitudinalis* is strikingly like that of *Lepidozia microphylla* of New Zealand; the shallowly toothed branch leaves resemble leaves of *T. oligophylla* (Fig. 54: 1–4), a South American species.

This species, together with *T. clatritexta* and *T. meridiana*, comprise the subg. *Acrolepidozia*, which is strongly supported in all the cladograms presented here (e.g., the strict consensus of all trees, Fig. 73).

SPECIMEN SEEN—SARAWAK: Slopes of Mt. Dulit, Ulu Koyan, ca. 800 m, Richards 2047 (JE), the probable type.

*Telaranea major* (Herz.) Engel & Merr., comb. nov.

*Arachniopsis major* Herz., Trans. Brit. Bryol. Soc. 1: 294, figs. 12a–c, 13a, b. 1950. Original material: Borneo, Sarawak, Dulit Ridge, ca. 1320 m, Richards 2056; Dulit Trail, ca. 800 m, Richards 2579.

DESCRIPTION—Piippo (1985).

ILLUSTRATIONS—Herzog (1950, figs. 12, 13); Miller (1985); Piippo (1985, fig. 1a–b).

DISTRIBUTION—Sri Lanka (140–1000 m, Eggers & Schäfer-Verwimp, 1987), Malaysia (Malacca, Pahang), N Borneo, New Guinea (1400–1650 m). Reported from West Irian (Grolle & Piippo, 1984), the Philippines (Mizutani, 1976, p. 448), Vanuatu, and New Hebrides (Miller, 1985).

Herzog (1950) distinguished *A. major* from *A. coactilis* by its larger size, and underleaves consisting of 2 geminate cells, each capped by a slime papilla (fig. 12b). Piippo (1985, p. 170) described the underleaves as bilobed, with lobes consisting of “two isodiametric to short rectangular, occasionally curved cells with a terminal slime papilla.”

Miller (1985) wrote, “The tips of leaf segments normally bear one, sometimes two, isodiametric cells which are easily broken off (fig. 5). It is likely that these cells function as gemmae.” Fragmenting apices of leaf lobes also occur in at least a half dozen species of the genus, including a Neotropical species of sect. *Tenuifoliae*, *T. diacantha*. Rhizoids may originate from distal leaf lobe cells (Schuster, 2000; see Fig. 44: 3–10, *T. coactilis*). Piippo (1985) described the cuticle of the leaves as smooth. Herzog (1950, fig. 13b) illustrated a ♀ bract resembling a leaf of *T. lindenbergii*, with a basal disc up to 1–2 cells high. According to Schuster (2000), the basal cells of the

leaf lobes are rigid and thick-walled, in contrast to the more delicate, thin-walled distal cells.

*Telaranea mamillosa* (Schiffn.) Engel & Merr., comb. nov.

*Lepidozia mamillosa* Schiffn., Nova Acta Acad. Caes. Leop.-Carol. 60: 254, pl. 10: 15–19, 1893. Type: New Guinea, 1875, Naumann—c. per. (G!).

DESCRIPTION—Stephani (1909).

ILLUSTRATION—Piippo (1984, fig. 4: d, g, i, k, type). Stephani, Icones, *Lepidozia* 226.

DISTRIBUTION—New Guinea, Borneo (Grolle, 1967). Grolle and Piippo (1984) listed several localities for the species in New Guinea, ranging from wet mossy forest to 2350 m to muddy hummocks in mangrove swamps near sea level.

Plants whitish gray (“albido-cinerea”), densely caespitose, profusely and irregularly branched. Branching terminal, *Frullania* type. Half-leaf ligulate, shallowly bilobed, inserted some distance above the branch. First branch underleaf undivided, irregular in form (typically with a few biseriate tiers + a short uniseriate row), median-ventral on branch base. Stem hyaloderm moderately differentiated, consisting of 12–13 rows of thin-walled cortical cells, surrounding 18–20 rows of somewhat smaller, firm-walled medullary cells. Leaves of both main shoot and branches densely imbricate, plano-distichous, the disc plane, the lobes ventrally decurved and claw-like. Branch leaves almost longitudinally inserted, leaving the 2 dorsal rows of cortical cells almost entirely exposed. Leaves of main shoot shallowly 4-lobed, the disc parallel-sided, 2–3 cells high and 8 cells wide throughout, with strongly crenate margins. Lobes with 1–2 biseriate tiers at the base and a short uniseriate row of 2(3–4) cells, the cells barrel-shaped and bulging, the uniseriate row submoniliform, distinctly constricted at the septa, the lobe tips sharply inflexed and clawlike and often caducous. Disc and lobe cells moderately thick walled and firm, with a translucent, cloudy appearance. Underleaves 3–4-lobed, the disc 2 cells high and 6–8 cells wide, the lobes consisting of a uniseriate row of 2(3) cells or merely of a single cell, the lobe cells barrel-shaped and bulging as in leaves.

Androecia on ventral-intercalary branches on main shoot and primary branches, exceedingly long spicate, equalling the leafy branches in length, with up to 10–12 pairs of bracts.

A highly unusual species, the lobe cells of the leaves and underleaves distinctly turgid and bulging. The species is named for the mamillose perianth, which is conspicuously roughened by blunt projections of the cell lumen (Schiffner, 1893, fig. 10: 19). The mamillae tend to occur in the apical ends of cells, rarely extending over the distal end-wall, a condition called prorate. A scarious perianth occurs in *T. praenitens* (p. 32, Fig. 10: 9) and (to a much lesser degree) in *T. jowettiana* (p. 161), an endemic species on Norfolk Is.

Piippo (1984) illustrated the type of *T. mamillosa*, and commented on the relationship between this species and *T. wallichiana*. According to Piippo (p. 316), the two are indistinguishable except for the perianth. In fact, *T. mamillosa* most nearly resembles *T. papulosa*, which also has submoniliform lobes with distinctly constricted septa. For further discussion, see comments under *T. papulosa* and *T. wallichiana*.

Grolle (1967) called this species a “charakterpflanze der Mangrove Malesiens,” terrestrial on sandy soil (and crabhills) in mangroves in both Borneo and New Guinea. Few hepatics are known to tolerate saline conditions (see Engel & Schuster, 1973). The flora of the muddy, tidal waters of mangroves is a very specialized one, consisting of the mangroves themselves and a few associated species (of flowering plants) rarely or never found elsewhere (Good, 1964).

SPECIMEN SEEN—PAPUA NEW GUINEA: Port Moresby Distr., Kanosia, terrestrial in mangrove swamp, near sea level, Carr 11532—c. ♂ + per. (F).

*Telaranea marginata* Engel & Merr., sp. nov.

A *T. fernandezensis* lobis sinuatis, disco margine unus tantum aliter 1.5 cellulas alto differt.

Holotype: Chile, Prov. Valdivia, near Río Futa in vicinity of Futa, 10.5 km by road S of junction of highway T-60 and T-65, 10 m, Engel 11035—c. ♀ (F).

DISTRIBUTION—Chile (Valdivian zone).

Plants wiry in appearance, pale whitish green, highly nitid when dry, loosely and irregularly 1–2 pinnate, the branches typically terete and strigose, with leaf lobes erect-appressed; branching terminal, *Frullania*-type, the branch half-leaf bifid; first branch underleaf symmetrically bilobed, with both lobes resembling leaf lobes, or asym-



metrically bilobed, with one lobe shorter, resembling an underleaf lobe and terminating in a slime papilla. Ventral-intercalary branches rather common, leafy and becoming leading shoots. Stem cortical cells in section with the exposed walls moderately thickened, in 10–11 rows, larger than the 12 firm-walled medullary cells. Leaves symmetrically 4–5-lobed, the insertion incubous, extending dorsally to the midline of the stem; branch leaves 3-lobed. Leaf lobes divergent, the uniseriate row 4–5 cells long, the cells firm walled, the septa thickened in the corners but not bulging, the lobe straight-sided along the outer (abaxial) side, the inside of the curving lobe “stepped” in appearance; leaves basal cell of the uniseriate row 22–30  $\mu\text{m}$  wide  $\times$  55–76  $\mu\text{m}$  long, the next cell similar in length but narrow, 14–23  $\mu\text{m}$  wide  $\times$  55–78  $\mu\text{m}$  long, the terminal cell typically appearing secondarily divided; cuticle of lobe cells smooth. Disc 2 (1.5) cells high in median portion, the basal cells of the lobes connate for about 0.5 their length, the cells along the disc margins typically not transversely divided (disc 1 cell high at the margins); cuticle of disk smooth or finely striolate. Underleaves 4-lobed, notably smaller than the leaves, unequally lobed, with one or more (or all 4) lobes short, with a terminal slime papilla, the longer lobes with a uniseriate row of 3–4 cells, without a slime papilla; disc margins 1 cell high as in the leaves, 2 cells high in median portion, typically only the disc cells beneath the short lobes becoming subdivided into rhizoid initials.

Androecia not seen. Gynoecia (only young ♀ seen) on short ventral-intercalary branches; bracts 4–5-lobed to ca. 0.5, the lobes subcaudate, 3–4 cells wide at the base, with a uniseriate row of 2–5 cells, the lobe cells with projecting septa, the terminal cell tapering to a sharp point. Perianth with lobes similar to those of the bracts, ending in a uniseriate row of 4–5 rather thick-walled cells with projecting septa.

When well-developed, *Telaranea marginata* is immediately recognizable by the compact, terete branches, the leaf lobes short and not spreading but parallel and stiffly erect. The unique areolation of the leaf disc is present in all the specimens seen: the disc is bordered by a single longitudinally elongate cell, but is 1.5 cells high in the median portion, with a basal tier of cells along the insertion plus the paired cells at the base of the lobes. The same pattern is expressed in the underleaves, where the subdivision of disc cells to

form rhizoid initials is largely confined to the median portion of the disc and the marginal cell remains undivided. By contrast, in *T. fernandeziensis* the disc is 2 cells high at the margins, the basal tier of cells extending across the full width of the disc.

The leaf lobes of *T. marginata* show the same offset alignment of the leaf lobe cells as in *T. fernandeziensis*, but without the strongly (and often unilaterally) projecting septa of that species. *Telaranea fernandeziensis* is a more robust plant,  $\pm$  regularly bipinnately branched and essentially isophyllous, the leaves 4–6-lobed, the disc squarrose, with longer, spreading subcapillary lobes which abruptly inflexed at the base of the uniseriate row. In *T. setosa* the leaf disc is only 0.5 cells high and the lobes appear sinuous as a result of the curvature of the individual lobe cells. An interesting feature of *T. marginata* is that the stem medullary cells are approximatedly equal in number to the cortical cells.

The perianth mouth of *T. marginata* is lobate, with subcaudate lobes 3–4 cells wide at the base, with a uniseriate row of 4–5 cells vs. shallowly lobulate in *T. fernandeziensis*, the divisions toothed or with a  $\pm$  contorted bristle-like tip 1–2 cells in length.

**ECOLOGY**—Known only in the Valdivian zone from Isla Chiloé north to Cordillera Nahuelbuta. A plant of forests from sea level to 440 m, occurring on tree bark (*Nothofagus*, *Drimys*), on decorticated, decayed wood or, less often, over rich humus.

**SELECTED SPECIMENS SEEN**—CHILE. PROV. CHILOE: Isla Chiloé, Cocauque area, across Estero Yaldad from village of Yaldad, sea level, *Engel 11997B* (F); *ibid.*, Cerro Pirulil, S of Cucao near west coast, 50 m, *Engel 12061* (F). PROV. OSORNO: Agua Caliente, near falls, along Río Chanleufú, 4 km from Termas de Puyehue along road to Refugio Antillanca, 400 m, *Engel 11464* (F). PROV. VALDIVIA: Valdivia, Isla Teja, just W of Parque de Exposiciones Saval, near sea level, *Engel 10915* (F); Cerro Tralcan, W of western end of Lago Riñihue, 440 m, *Engel 10951*—c. ♂ (F); Fundo Santa Rosa, 8 km by road N of Puente Callecalle, near sea level, *Engel 10863*—c. ♂ (F). PROV. MALLECO: Cordillera Nahuelbuta, trail from western entrance of Parque Nacional Contulmo, 7 km by road E of Contulmo, 330–360 m, *Engel 12541* (F). PROV. ARAUCO: Western foothills of Cordillera Nahuelbuta, S of Cerro Lanalhue, SW of Lago Lanalhue, Fundo Tranquivora, 200 m, *Engel 12576*—c. young per. (F).

*Telaranea melanesica* H. A. Mill.

*Telaranea melanesica* H. A. Mill., J. Bryol. 14: 237. f. 1f–g; 3a–f; 4:a–c. 1986. Holotype: Pacific Is.,

Vanuatu, Erromango, Mt. Fedmoghum, ca. 630 m, Miller 15157 (MU!—c. sporo.).

ILLUSTRATION—Miller (1986, figs. 1f–g; 3a–f; 4a–c).

DISTRIBUTION—Endemic to Fiji Is.

Seta with 8 rows of outer cells surrounding an inner core of 18 much smaller cells. Capsule elliptic (Miller, 1986, fig. 3c) to elliptic-ovate, the wall 29–30  $\mu\text{m}$  thick, 3-stratose, the layers of about equal thickness; outer layer of cells elongate-rectangular, 3–4:1, with two-phase development, the longitudinal walls with thin continuous sheets of pigmented material with sporadic, weakly developed swellings (the walls weakly sinuous), alternating with delicate walls completely devoid of pigment or thickenings, the transverse walls also without thickenings; inner layer of cells in tiers, rather regularly narrowly rectangular, the longitudinal walls with thin continuous sheets of wall material, with complete, rather wide semianular bands.

Spores 13.0–15.4  $\mu\text{m}$  in largest diam., pale yellowish brown, the surface conspicuously areolate. Elaters rather straight, 9.6–10.6  $\mu\text{m}$  wide, somewhat tapering and bispiral to tips, the spirals 3.8  $\mu\text{m}$  wide.

This species is similar to *T. quadriseta* (p. 95), a rare Australian species, which differs in the terete branches, with only moderately incubous, imbricate branch leaves, the insertion extending dorsally almost to the midline of the branch. The leaf lobes of *T. quadriseta* are more distinctly tapering and less constricted at the septa, with firmer walls.

*Telaranea melanesica* is a regularly once-pinnate plant with strongly complanate branches, the branches rather closely spaced, often subopposite, and oriented at  $\pm$  right angles to the shoot. The half-leaf in *T. melanesica* is undivided or bilobed and the first branch underleaf monocurous, with a biseriate base, inserted on the ventral side of the branch near its base. Leaves of the main shoot are distinctly incubous and (3)4-lobed, with a disc 2 cells high. The uniseriate portion of the lobes is 6–7 cells long, from a biseriate base, thin-walled and distinctly constricted at the septa. The branch leaves are strongly incubous and widely set, with a prominent two-cell-wide median strip dorsally. The cuticle of the lobes is finely punctate.

Miller (1986) compared *T. melanesica* with *T. neesii* but the two are not likely to be confused.

The latter has repeatedly, dichotomously branched and flabellate lateral branches, 6-lobed stem leaves, and coarsely papillose cuticle.

### *Telaranea microstipulata* Schust.

*Telaranea microstipulata* Schust., Phytologia 39: 241. 1978. Holotype: Venezuela, Estado Tachira, Paramo de Tama, Schuster & Ruiz-Teran 76-1904 (F).

ILLUSTRATION—Schuster (2000, fig. 75).

DISTRIBUTION—Venezuela.

The status of this species has been somewhat clarified by the recently published illustration in Schuster (2000, fig. 75). Branching is described as nearly always ventral-intercalary, but with terminal, *Frullania*-type branches also present. Schuster (fig. 75: 9, 10) illustrates the  $\varnothing$  bracts of *T. microstipulata*, which are essentially bifid; cells of the disc are not shown, but judging from the outlines the bracts have a relatively high disc. This species is assigned to sect. *Tenuifoliae*.

### *Telaranea monocera* Mitt. ex Engel & Merr., sp. nov.

*Arachniopsis monocera* Mitt. ex Schust. & Grolle, Nova Hedwigia 10: 25. 1965, nom. inval. (Art. 42.1). Type: Malaysia, Malacca, Mt. Ophir, Griffith (BM); isotype: JE (fide Piippo, 1985).

Folii 2-fidis vel in partim simplicibus, amphigastriis symmetrice vel asymmetrico 2-fidis vel simplicibus, caule 5+2, rhizoideis septatis notabilis.

DESCRIPTION—Piippo (1985).

ILLUSTRATIONS—Piippo (1985, fig. 1c–g); Schuster (2000, figs. 194, 195).

DISTRIBUTION—Malaysia, Malacca; Sumatra; Papua New Guinea (1550 m); Solomon Is. (2300 m) (cf. Piippo, 1985). Miller (1985) erroneously listed the type locality (Mt. Ophir) as in India.

NOMENCLATURE—The species is the type of *Arachniopsis* subg. *Amphidactylopsis* Schust., but has not been validly published, since the subgenus and species were given a single description (Schuster, 1965). Combined descriptions of infrageneric taxa and species are not sanctioned in the Code (Art. 42.1). Schuster (2000) described another species in the subgenus as *A. anomala* (see p. 121). We are including *Amphidactylopsis* in *Telaranea* sect. *Tenuifoliae*. “*Arachniopsis amphidactylopsis*” (Schuster, 2000, p. 446) is a *lapsus*, probably a reference to *T. monocera*.

Schuster (1965, p. 34, key) described *A. mon-*

*ocera* as as “isophyllous and triseriate or nearly so,” with both leaves and underleaves usually undivided. According to Piippo (1985, p. 170), however, the leaves of the species are monocrurous on lower or poorly-developed portions of shoots but otherwise 2-lobed, the lobes 3–4(6) cells long, with the apical cell acute and about 0.5 the length of the cell beneath. Piippo describes the underleaves as always 2-lobed but “characteristically variable,” either symmetrical, with both lobes 2-celled, or with one lobe longer, and similar in appearance to a leaf lobe. In such asymmetric underleaves (Schuster, 2000, fig. 194: 4) the shorter lobe consists of a single cell plus a slime papilla, and an elongate, septate rhizoid appears to originate from the basal cell. Asymmetrical lobing is seen in the underleaves of *T. anomala* (Schuster, 2000, fig. 196: 7–8), *T. quinquespina* (Fig. 34: 1, 4), and *T. tasmanica* (Fig. 32: 3, 9). Moreover, the first branch underleaf of many species of sect. *Telaranea* (e.g., *T. remotifolia*, *T. herzogii*) is asymmetrically bilobed. The ♀ bract of *T. monocera* is 3–4-lobed, the lobes armed with lateral teeth, and a disc 2 cells high (Piippo, 1985, fig. 1g). Schuster (1965) described the stem anatomy as 5+2.

#### *Telaranea murphyae* J. A. Paton

*Telaranea murphyae* J. A. Paton, Trans. Brit. Bryol. Soc. 4: 776, fig. 1. 1965. Holotype: England, Cornwall, Isles of Scilly, Tresco, Paton—c. ♂ (E!); iso-type: (E!, Herb. Paton).

DESCRIPTION—Paton (2000).

ILLUSTRATIONS—Paton (1965, fig. 1; 1992, fig. 2; 2000, fig. 10).

DISTRIBUTION—Isles of Scilly (Tresco), Dorset (Branksome Dene Chine, Poole, Woods; see Paton, 2000, p. 57). Male plants only are known.

The following comments are based on the type. Plants are irregularly branched and straggling, with very long,  $\pm$  indeterminate *Frullania*-type branches that typically retain their branchlike appearance (e.g., the leaves remain 3-lobed). The stems appear rather fleshy, with cortical cells subisodiametric to short rectangular and rather turgid. The half-leaves associated with *Frullania*-type branches are bifid and straplike, occasionally with a disc 4 cells high; the first branch underleaf is subulate, often with 2 biseriate tiers.

Leaves of the main shoots are 4-lobed, and distinctly incubously inserted, with a disc 3 cells high, including the basal cells of the lobes. Disc

cells are 26–34  $\mu\text{m}$  wide, subrectangular and rather turgid in appearance (Paton, 1965, fig. 1d). The lobes are 2(3) cells wide at the base, often with an additional biseriate tier, and a uniseriate row 4–5 cells long, and are moderately constricted at the septa.

Androecia are intercalary in position on elongate, leafy, ventral-intercalary branches (or exceptionally on *Frullania*-type branches), and are notably broader than sterile portions of the branch, with up to 7 pairs of large, cupulate bracts.

We cannot match this plant with any Australasian species, nor does it resemble any Neotropical or African species known to us. The differences between *T. murphyae* and *T. longii* are discussed by Paton (1992); according to Paton (p. 295) “both species are associated with gardens and may have been imported accidentally from unknown countries of origin.” It has also been suggested (Grolle and Long, 2000) that these may represent males and females of a single species. The latter, however, described from Argyll and reported from Surrey, is *T. tetradactyla* (p. 91), a New Zealand species. *Telaranea murphyae* differs chiefly in the areolation of the leaves, the disc cells subrectangular, turgid and bulging. In position and appearance, the androecia of *T. murphyae* are highly distinctive.

SPECIMEN SEEN—ENGLAND: Isles of Scilly, Tresco, N slope of Abbey Hill, v.-c. 1, 15 m, Long & Paton 12026—c. ♂ (F).

#### *Telaranea neesii* (Lindenb.) Fulf.

*Lepidozia neesii* Lindenb. in G. L. & N., Syn. Hep. 212. 1845. *Telaranea neesii* (Lindenb.) Fulf., Brittonia 15: 80. 1963. Type: Java, Blume (see Grolle, 1966, p. 288).

*Jungermannia capillaris* B. javanica Nees, Enumeratio Plant. Crypt. Javae . . . 1: 13. 1830. *Lepidozia javanica* (Nees) Mont. in Hombron & Jacquinet, Voyage au Pole Sud . . . 1: 246. 1845. *Mastigophora javanica* (Nees) Trev., Mem. Ist. Lomb. Sci. Lett. III. 4: 416. 1877. Type: Java.

*Telaranea iriomotensis* Yam. & Miz. in Yamaguchi, Misc. Bryol. Lichen. 9: 161. f. 1. 1983, syn. nov. Type: Japan, Ryukyus, Okinawa Pref., Iriomote Is. Urauchi River, ca. 200 m, Yamaguchi ty-3331.

DESCRIPTIONS—Stephani (1909); Grolle (1966) and Piippo (1985); Yamaguchi (1983).

ILLUSTRATIONS—Lindenberg and Gottsche (1846, tab. 12); Fulford (1963a, figs. 168–169, type); Grolle (1966, fig. 4); Del Rosario (1977, fig. 84); Yamaguchi (1983, fig. 1, as *T. iriomotensis*; Fig. 52).

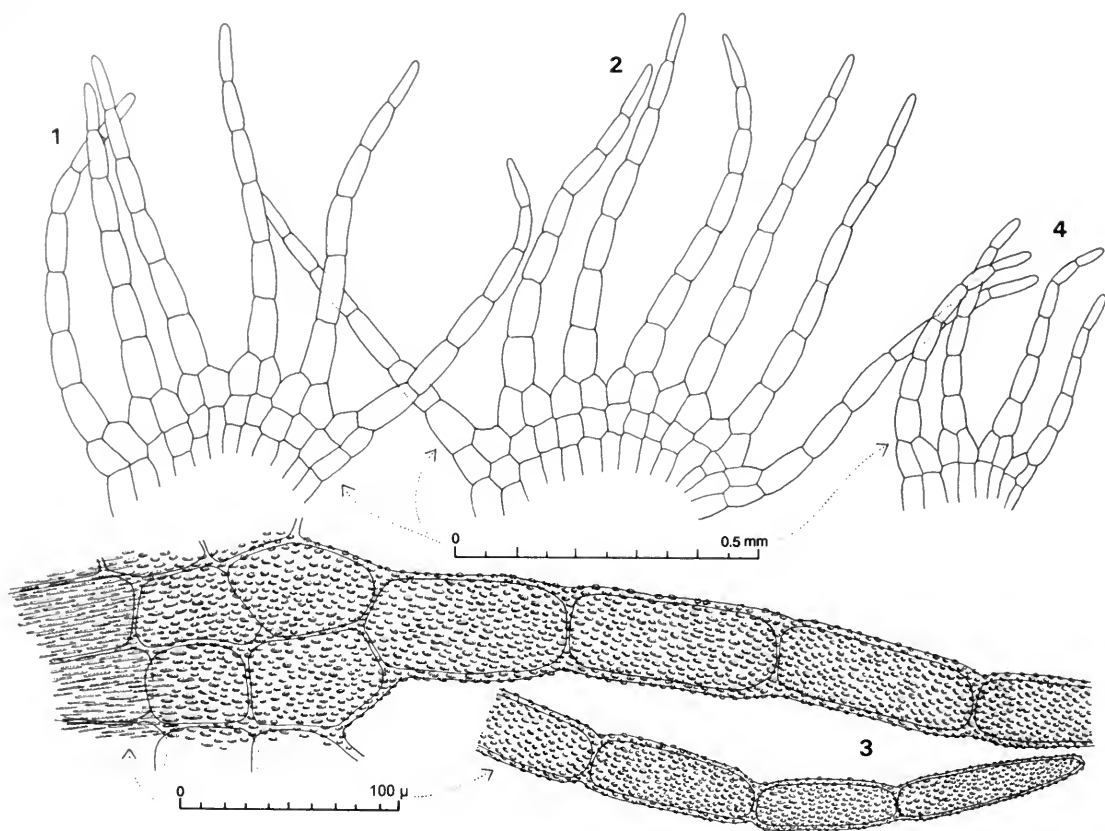


FIG. 52. *Telaranea neesii* (Lindenb.) Fulf. 1, 2. Leaves of main shoot. 3. Portion of leaf of main shoot including disc and lobe (the distal portion of lobe shown below); note cuticular striae of basal cell of disc, but the remainder of disc and lobe with a papillose cuticle; note also the elongate terminal cell of the uniseriate row. 4. Branch leaf. (All from 14 April 1894, *Schiffner*, Java, Prov. Preanger, Mt. Pangerango [F].)

**DISTRIBUTION**—Grolle (1966) gave the range as Sumatra (1000–2000 m), Java (1500–1920 m), Borneo (500–1000 m), Halmahera (600 m) and Papua New Guinea (1500–2300 m). Reported from the Philippine Is. by Mizutani (1976) and Del Rosario (1977). With the inclusion of *T. iriomotensis* the range of the species is extended to the Ryukyu Is. See Engel (1978) for notes on erroneous reports of the species for southern South America.

**NOMENCLATURE**—According to Grolle (1966, p. 289, on the authority of Stafleu), the name *Lepidozia neesii* in G. L. & N. presumably predates *L. javanica* (Nees) Mont.

**COMMENTS**—The habit of *T. neesii* is unusual in the differentiation of the main shoot and branches. In well-developed plants the main axis is stout and rather wiry, and branching is fundamentally pinnate, the primary branches oriented at right angles to the shoot. The branches them-

selves are repeatedly, almost dichotomously branched and flabellate, soft and complanate, and falcate. The leaves of the main shoot are typically 6-lobed (occasionally 7-lobed) and weakly asymmetric,  $\pm$  transversely inserted to weakly incubous for much of their length, becoming abruptly short-decurrent in the ventral third. The lobes are stiffly erect and appressed to the stem, often giving the main axis the aspect of a *Psiloclada*. Branch leaves, on the other hand, are distinctly incubous and complanate, with second lobes (Fig. 52: 4). Underleaves are somewhat smaller than the leaves, but commonly 6-lobed. The branches are subsophyllous (Grolle, 1966, fig. 4a).

The cuticle of the leaf lobes is coarsely papillose (Fig. 52: 3), the papillae rounded to somewhat elongate; the basal tier of disc cells (and stem cortical cells) is finely, closely striolate (Fig. 52: 3). The uniseriate portion of the leaf lobes is 5–7 cells long, moderately constricted at the sep-

ta, the cells firm-walled,  $\pm$  cylindrical, to 3.5:1, the terminal cell about equal to the penultimate cell in length and broadly rounded at the apex (Fig. 52: 3). In stem leaves (Fig. 52: 1, 2) the disc is 3 cells high in the dorsal portion, 2 cells high (1.5 cells high) in the ventral portion, the cells quadrate; in branch leaves (Fig. 52: 4) the disc is 2 cells high and distinctly cuneate, with the basal tier of cells narrowly elongate.

Branching is primarily *Frullania*-type throughout, but ventral-intercalary branches are also produced from the main axis, becoming leading shoots. The half-leaves of the branches are 2-fid and positioned midway in the dichotomy between stem and branch. The first branch underleaves are 2(3)-fid. The cilia of the ♀ bracts and perianth mouth are unilaterally armed with short spurs (Fulford, 1963a, figs. 168, 169; Grolle, 1966, fig. 4g-i, k).

*Telaranea iriomotensis*, described from Ryukyu Is., Japan, was scored independently of *T. neesii* in our cladistic analysis (Table 2 and cladograms), based on the original description and illustration of the species (Yamaguchi, 1983). The author compared *T. iriomotensis* to *T. neesii* and *T. kogiana*. Material of this plant has since become available, which we now think is best referred to *T. neesii*. The Ryukyu plants are described as densely bi- or tripinnately branched, which is somewhat misleading. The leading shoots appear to be almost horizontal, with the primary branches erect and oriented at right angles to the shoot, the fronds almost dichotomously branched and flabellate. The coarsely papillose cuticle (Yamaguchi, 1983, fig. e) is developed on the lobes, with the basal tier of disc cells distinctly striolate.

**SPECIMENS SEEN**—JAVA: Prov. Batavia, Mt. Pantjar, 28 Dec. 1893, *Schiffner* (F); Prov. Preanger, Mt. Pangrango, above Tjibodas, 1610 m, 14 Apr. 1894, *Schiffner*—c. ♂ (F); *ibid.*, above Tjiburum, 1910 m, 2 May 1894, *Schiffner*—c. per. (F). SUMATRA: Res. Sum. Westk., in m. Singalang, 2000 m, *Schiffner*—c. per. (Hep. Sel. Crit. 319) (F). MALAYA: Prov. Pahang, Cameron Highlands, Gunong Jasar, 1525 m, *Inoue* (Bryo. Sel. Exsicc. 24) (F). JAPAN: Ryukyu Is., Iriomote Is., Okinawa-ken, N of Mt. Goza, 330 m, *Yamaguchi & Matsumoto* (Bryophytes of Asia no. 100, as *T. iriomotensis*) (F).

*Telaranea nematodes* (Gott. ex Aust.) Howe

*Cephalozia nematodes* Gott. ex Aust., Bull. Torrey Bot. Club 6: 302. 1879. *Lepidozia nematodes* (Gott. ex Aust.) Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 366. 1885. *Blepharostoma nematodes*

(Gott. ex Aust.) Underw., Bull. Torrey Bot. Club 23: 383. 1896. *Telaranea nematodes* (Gott. ex Aust.) Howe, Bull. Torrey Bot. Club 29: 284. 1902. Lectotype (*vide* Grolle, 1975): Cuba, Wright (MANCH); isoelectotypes (NY!—c. sporo. + ♂; DUKE!).

*Blepharostoma antillanum* Besch. & Spruce, Bull. Soc. Bot. France 36 (suppl.): 183. 1889 (1890). *Telaranea nematodes* var. *antillanum* (Besch. & Spruce) Howe, Bull. Torrey Bot. Club 29: 286. 1902. Type: Guadeloupe, *Le Gommier*, s.n. (not seen).

*Lepidozia quintasii* Steph., Spec. Hep. 6: 339. 1922. Type: Sao Tome Is., *Quintas* (G!).

**DESCRIPTIONS**—Stephani (1909); Howe (1902). **ILLUSTRATIONS**—Figs. 38: 9–11; 53. Stephani *Icones, Lepidozia* 9; 13 (*L. quintasii*).

**DISTRIBUTION**—West Indies (Cuba, Puerto Rico, Guadeloupe), Mexico (Veracruz), Guatemala, Honduras, Colombia (30 m). Africa (Ghana, Sierra Leone, Uganda); Gulf of Guinea Is. (San Thome). This distribution is based on actual specimens examined. The range of *T. nematodes* must be reevaluated in view of the confusion between this species and *T. bicruris*, *T. chaetophylla*, *T. europaea*, *T. longifolia*, and *T. sejuncta*. Formerly considered “an austral to tropical species, of wide distribution in oceanic regions” (Schuster, 1969, p. 36; see also Schuster, 2000, p. 230 and Gradstein et al., 2001), as reflected by the distribution map in Gradstein et al. (1983, fig. VIII/46).

In the Americas, in addition to eastern North America, *T. nematodes* is reportedly “widespread in the Caribbean region, in the tropical Andes and occurs again in the south Brazilian highlands” (Gradstein et al., 1983), and Bermuda (Howe, 1902). Schuster (1969) characterized *T. nematodes* as a Coastal Plain-outer Piedmont species in eastern North America, but this portion of the distribution pertains to *T. longifolia*.

In Africa, the species is reportedly bicentric, occurring in the Guinea-Congo rain forest basin and South-East Africa (Gradstein et al., 1983). African reports include Natal, South Africa (Pearson, 1886, as *T. chaetophylla* var. *tenuis*), Uganda (Pócs and Lye, 1999; Porley et al., 1999), Rwanda and Zaire (Vána et al., 1979; Fischer, 1993); Burundi (Vána et al., 1979); Madagascar (Grolle & Onraedt, 1974), and Réunion (Pócs, 1995). According to Grolle (1995), the report of *T. nematodes* by Arnell from Seychelles is unsubstantiated. The South African plants (Pearson, 1886) are *T. redacta* (p. 186). *Telaranea nematodes* is also reported from Ireland and Cornwall (Paton, 1976, map, as *T. sejuncta*), France, northern

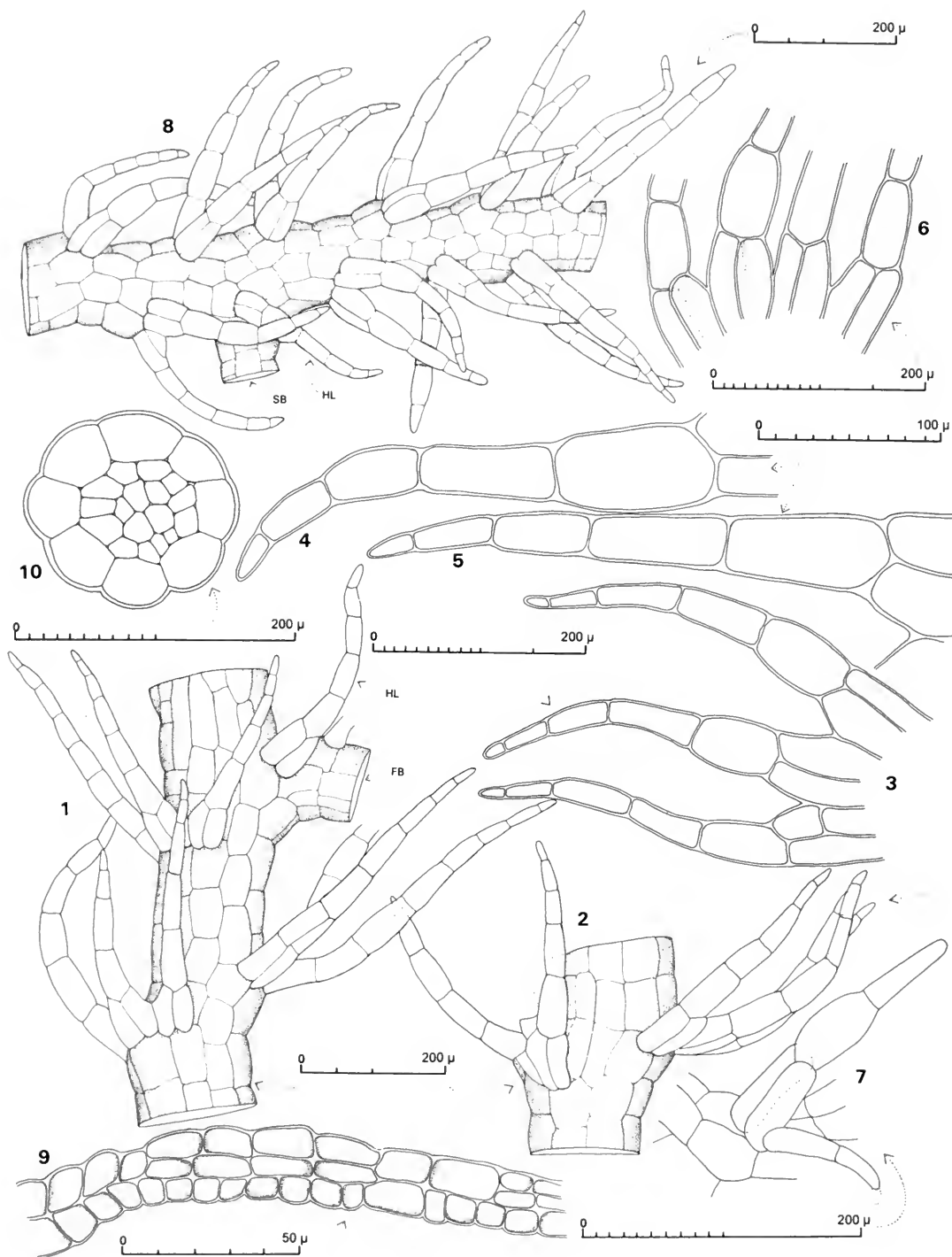


FIG. 53. *Telaranea nematodes* (Gott. ex Aust.) Howe. 1, 2. Portions of main shoot, dorsal view; at left including a half-leaf of a *Frullania*-type branch (= Fb; hl = an undivided half-leaf); at right showing a leaf pair (note 4-lobed leaf at arrow). 3. Leaf. 4, 5. Leaf lobes. 6. Base of 4-lobed leaf. 7. Base of terminal branch showing first branch underleaf, ventral view. 8. Primary branch, including base of secondary branch (= SB) and its associated half-leaf (= HL); dorsal view. 9. Capsule wall, cross section. 10. Seta, cross section. (All from type of *Telaranea nematodes*, NY.)

Spain, and the Azores. For the reports of *T. nematodes* from Europe and Macaronesia, see *T. europaea* (p. 150).

Plants soft, somewhat flexuous, prostrate, in compact mats. Branching of *Frullania*-type common, irregularly 1–2-pinnate, the branches occasionally becoming flagelliform; branch half-leaf undivided (rarely bifid); first branch underleaf asymmetrically bilobed. Ventral-intercalary branches occasional, leafy. Stems rather stout for plant size, the cortical cells in surface view short rectangular, in section distinctly differentiated, in 10–11 rows (6 dorsal + 3–4 slightly smaller ventral rows), thin-walled but firm; medullary cells much smaller, in 19–20 rows, thin-walled. Main shoots with 4–5 cortical cells intervening between successive leaves on either side, the branches with 2–3 cells intervening between successive leaves on either side of branch. Leaves of main shoot rather rigid, erect spreading, the insertion transverse or nearly so, 3–4-fid almost to the base, the lobe bases connate for about 0.5 their length. Branch leaves 2-lobed, incubously inserted, the insertion extending dorsally to about half the width of the adjacent cortical cell rows on either side of the branch, the lobes predominately biseriate at base. Leaf lobes  $\pm$  equal in length, erect spreading, gradually tapering, moderately to widely divergent, the lobe base straight or only slightly contracted to the uniseriate portion of the lobe, at times with an additional biseriate tier, the uniseriate row (4)6(7) cells long, moderately constricted at the septa; cells of the basal tier narrowly rectangular,  $24\text{--}31\text{ }\mu\text{m} \times 72\text{--}90\text{ }\mu\text{m}$ , the first cell of the uniseriate row  $31\text{--}50\text{ }\mu\text{m} \times 79\text{--}94\text{ }\mu\text{m}$ , the terminal cell about half (or in branch leaves approaching) the length of the penultimate cell; lobe cells thin-walled but firm, with septa scarcely thickened in the corners; cuticle smooth. Underleaves on main shoot 2–3-lobed, each lobe with a basal pair of rather short, barrel-like cells, 2–3 very long-cylindric lobe cells, ending in a slime papilla. Asexual reproduction lacking.

Autoecious. Androecia on primary and secondary *Frullania*-type branches. Gynoecia on short, ventral-intercalary branches from main shoot; bracts 4-lobed, the disc 2–4 cells high, the lobes (1)2–3-celled at base, at times with an additional biseriate tier, occasionally forked near the base or with a lateral spur, the uniseriate row of 7–8(10) cells. Perianth terete below or slightly flattened, trigonous and plicate in upper third, not constricted at the mouth, the mouth ciliate, with 12 longer

cilia interspersed with shorter cilia about half as long, the cilia with a 2-celled base and a uniseriate row of 5–8 elongate cells, constricted at the septa and resembling the leaf lobes.

Seta with 8 rows of outer cells and 17 rows of internal cells. Capsule 2-stratose and 17–18  $\mu\text{m}$  thick, to 3-bistratose and 19–20  $\mu\text{m}$  thick; outer layer of cells (surface view), thin-walled, moderately long rectangular, with 2-phase development, the longitudinal walls with moderately thickened continuous sheets of pigmented material and rather weakly developed nodulike thickenings (lending a sinuous appearance to the longitudinal walls) alternating with walls that are devoid of thickenings, the transverse walls also devoid of thickenings; innermost layer of cells somewhat irregularly narrowly rectangular, the radial walls with thin but continuous sheets of wall material, with semiannular bands rather common, distantly spaced, often pale and barely perceptible in median portion of outer tangential wall, the bands often complete, the radial walls with nodular and short spinelike extensions often present.

Spores 12–14.9  $\mu\text{m}$ , exine light brown, reticulate, with polyhedral areolae bordered by narrow ridges, the areoles 1–1.4  $\mu\text{m}$  in diam. Elaters  $\pm$  rigid to feebly sinuous, 8.6–9.6  $\mu\text{m}$  wide, only slightly tapering toward tips, bispiral to tips, the spirals 3.4–3.8  $\mu\text{m}$  wide.

NOMENCLATURE—Pearson (1886) considered *Cephalozia nematodes* to be a variety of *Lepidozia chaetophylla* Spruce. Pearson was followed by Howe (1902), who adopted the older name for the combined species. The two species are treated here as distinct. A number of authors placed *T. nematodes* as a synonym of *T. sejuncta*, e.g., Fulford (1963a, 1966); Schiffner & Arnell (1964); Vanden Berghen (1972, 1973), however, the type of the latter name is an *Arachniopsis* (p. 187). *Telaranea longifolia*, described by Howe as a variety of *T. nematodes*, is also a distinct species (see p. 163).

COMMENTS—The type of *Cephalozia nematodes* (isoelectotype, NY!) bears both androecia and sporophytes and is autoecious. Howe (1902), who appears to have seen original material of both species, noted the “flaccidity” of *T. nematodes* in contrast to *T. chaetophylla*, but considered this of minor importance. The basal cells of the leaf lobes are biseriate, united to about 0.5, and about the same length as the cell above (Fig. 53: 3, 6), very rarely with a second biseriate tier, vs. 1–2 additional biseriate tiers, as commonly seen in *T. lon-*

*gifolia* (Fig. 51: 3, 4, 6). The lobes are moderately constricted at the septa (Fig. 53: 4, 5), with the terminal cell in some cases only slightly shorter than the penultimate cell, or with the tip cell much shorter (Fig. 53: 3). The underleaves are 2–3-lobed, each lobe inserted on a pair of basal cells, with a uniseriate row of 2–3 narrowly cylindrical cells, capped by a slime papilla. The first branch underleaf is asymmetrically bilobed (Fig. 53: 7).

*Telaranea nematodes* and *T. chaetophylla* differ in the stoutness of the seta, with 8 rows of outer cells and 17 rows of internal cells in *T. nematodes* (Fig. 53: 10) vs. 8+6 in *T. chaetophylla* (Fig. 43: 8), and in the thickness of the capsule wall.

In branches of *T. nematodes* the dorsal rows of cortical cells are less broadly exposed than in *T. chaetophylla*; the leaf insertions extend to the middle of the adjacent cortical cell row on either side (Fig. 53: 8) rather than being laterally inserted as in *T. chaetophylla* (Fig. 42: 2). For further comparisons between *T. nematodes*, *T. chaetophylla* and *T. longifolia*, see comments under those species.

SPECIMENS SEEN—PUERTO RICO: El Yunque, *Evans 16* (DUKE). GUATEMALA: Dept. Chiquimula, Cerro Tixixi (Tishishí), 3–5 mi. N Jcotán, 500–1500 m, *Sreyermark 31629*—c. sporo. (F); Dept. Quezaltenango, W slope of Volcán de Tumil, Fuentes Georginas, ca. 2850 m, *Standley 67425* (DUKE). MEXICO. VERACRUZ: Near Pepe's Bar, Esquilon, above Naolinca, 1185 m, *Long, Garcia & De Luna 29648* (E); Xalapa, natural forest beside Jardín Botánico, 1240 m, *Long 29658* (E). HONDURAS: Dept. Morazán, Reg. Agua Amarilla, above El Zamorano, 900–1100 m, *Standley et al., H5115, H5108*—c. sporo. (F). COLOMBIA: Choco, Mun. de Nuquí, El Amargal at Pacific coast SW of Arusi, 30 m, *Gradstein 8900*—c. ♂ + young ♀ (E). AF-RICA. GHANA: Eastern Region, Atewa Hills For. Res., *Jones & Hall 1321* (E); Atewa Range FR., 795 m, *Richards & Hossain s.n.*—c. ♂ + ♀ (E). SIERRA LEONE: Lome Mts, valley NW of Biutnonwi, (Kongbundu valley), 1525 m, *Jones 1502* (E). UGANDA: Kyotera county, Masaka U 4 District, Nanuzinna swamp SW of Bugera, 1150 m, *Lye B376*—c. ♂ (E).

### *Telaranea octoloba* Del Ros.

*Telaranea octoloba* Del Ros., Philipp. J. Sci. 100: 239, f. 48–49, 1973 (1971). Type: Philippines, Mindanao, Davao, Mt. McKinley, *Edano 605* (PNH, reportedly lost).

ILLUSTRATION—Del Rosario (1973, figs. 48–49).

DISTRIBUTION—Endemic to Philippines.

Plants “irregularly pinnate to bi- or tri-pinnate,” with 8-lobed leaves, the disc 3–4 cells high, the lobes (5)6(8) cells long (Del Rosario, 1973, fig. 48). The stem cortical layer consists of 22 cells; the underleaves (fig. 49) are usually 6-lobed. The perianth mouth is ciliate, with cilia unbranched, 4–6 cells long.

The species is evidently a member of sect. *Tricholepidozia*, and may be allied to *T. pulcherrima* of New Zealand and Tasmania and *T. trichocoleoides* of Borneo and New Guinea. *Telaranea neesii* is also a possibility, and has been reported from the Philippines (Mizutani, 1976; Del Rosario, 1977). The latter two species have a coarsely papillose cuticle, but a cuticle is not mentioned in the protologue of *T. octoloba*. The distribution of *T. neesii* extends northward to the Ryukyu Is. (as *T. iriomotensis*).

### *Telaranea oligophylla* (Lehm. & Lindenb.) Engel

*Jungermannia oligophylla* Lehm. & Lindenb. in Lehmann, Nov. Minus Cogn. Stir. Pug. 6: 26, 1834. *Lepidozia oligophylla* (Lehm. & Lindenb.) G. L. & N., Syn. Hep. 201. 1845. *Mastigophora oligophylla* (Lehm. & Lindenb.) Trev., Mem. Reale Ist. Lomb. Sci. Lett. III, 4: 415. 1877. *Neolepidozia oligophylla* (Lehm. & Lindenb.) Fulf. & J. Tayl., Brittonia 11: 84. 1959. *Telaranea oligophylla* (Lehm. & Lindenb.) Engel, Bryologist 79: 514. 1976. Type: Argentina, Terr. Tierra del Fuego, Isla de los Estados, *Menzies s.n.* (G!, NY!).

DESCRIPTIONS—Stephani (1909); Fulford (1966).

ILLUSTRATIONS—Lindenberg and Gottsche (1846, tab. 1); Fulford and Taylor (1959, f. 30, 32, 34–37); Fulford (1966, pl. 46, fig. 3). Stephani, Icones (*Lepidozia* 138); Fig. 54.

DISTRIBUTION—Falkland Is. (very rare); southern South America (north to 48° 04' S in Prov. Aisén); see Engel (1978; 1990, fig. 31, map). Listed from South Georgia by Herzog (1926, p. 381); the Skottsberg collection identified as *T. oligophylla* (G!, possibly the same specimen on which the Herzog record is based) is *T. seriatitexta*; see also Fulford (1966, p. 215).

Plants slender, rigid and wire-like, distantly leafy, subisophyllous, pale yellowish green, becoming brownish tinged in older portions of the plant. Branching distantly and irregularly 1-pinnate, terminal, *Frullania* type, the branches often becoming flagelliform; half-leaf 4 cells wide throughout, shallowly bidentate or unlobed with a



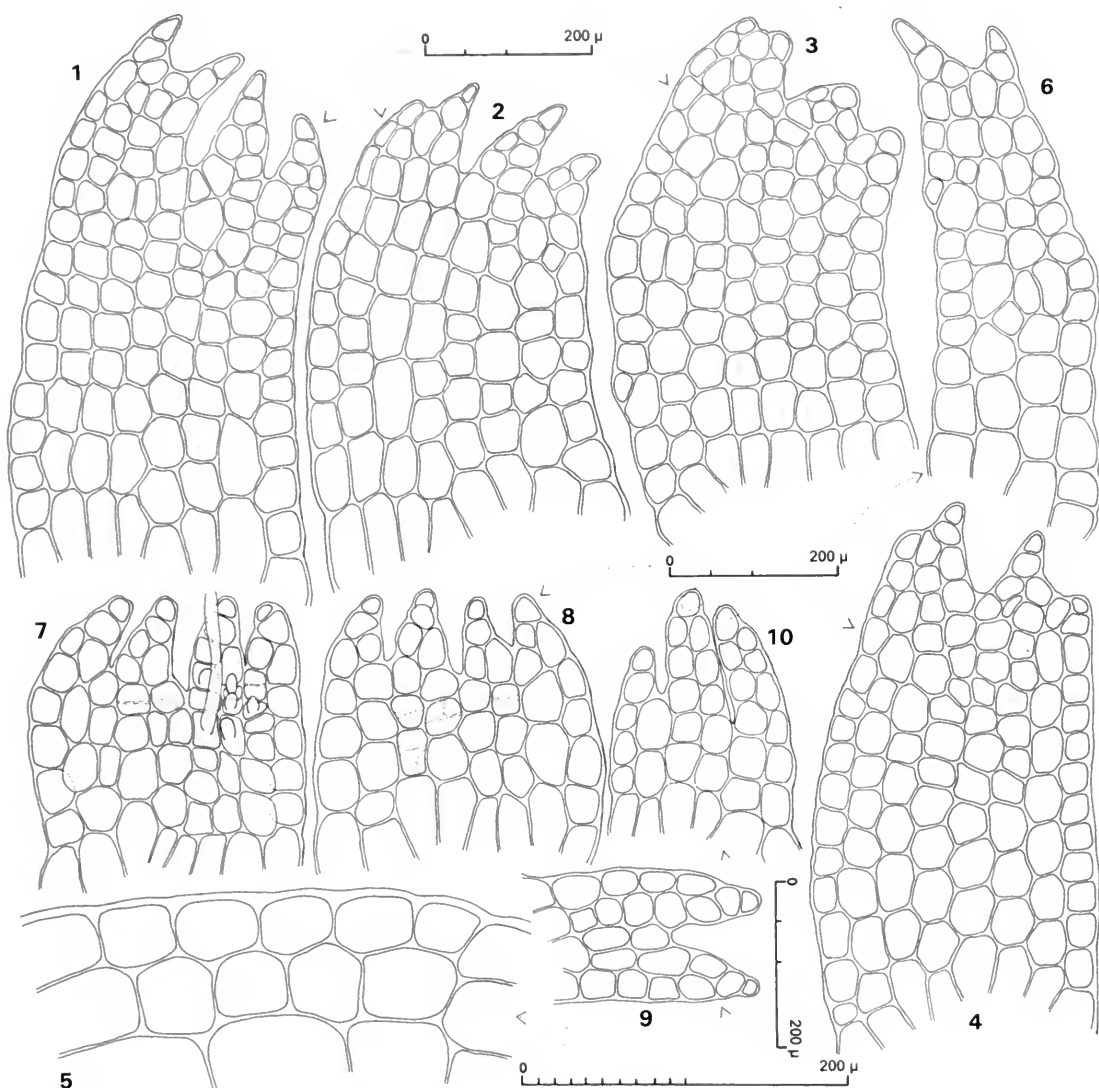


FIG. 54. *Telaranea oligophylla* (Lehm. & Lindenb.) Engel. 1-4. Leaves. 5. Portion of dorsal margin of leaf. 6. Half-leaf. 7, 8. Two underleaves, showing stages of development of rhizoids from distal cells of disc, the rhizoid initials shown with stipple. 9, 10. Two- and 3-lobed first branch underleaves. (Figs. 1, 2, 5-9 from Engel 6386B, Chile, Prov. Magallanes, W side of Bahía Nicolás; 3-4 from Engel 2214, Chile, Prov. Magallanes, Puerto Cutter.)

bluntly acute apex; first branch underleaf at base of branch, shallowly 2-3-lobed. Ventral-intercalary stoloniform branches common. Stem fleshy, appearing large in proportion to the leaves, the cortical cells subquadrate in surface view, in section in 16 rows, much larger than the ca. 65 firm-walled medullary cells, the outermost ring of medullary cells larger than the internal ones. Leaves distant (1-2 leaf widths apart), incubously inserted, the lamina subvertical, the dorsal margin lying above plane of axis, obliquely spreading,

strongly ventrally decurved when dry, the margins broadly inflexed, when moist plane to slightly concave below and with lobes sharply inflexed, weakly asymmetric, subfalcate, shallowly (3)4-lobed,  $\pm$  bisbifid, the median sinus slightly deeper, the lateral lobes often smaller than the median pair. Lobes abbreviated, the median 2(3) cells wide at the base (occasionally with a second biseriate tier) and a single terminal cell or a short uniseriate row of 2(3) cells. Disc parallel-sided, 9-13 cells high at median sinus, 8 cells wide

throughout. Cells of disc firm walled, the marginal cells with free wall thickened. Cuticle smooth or with a hazy, finely granular appearance. Underleaves similar to leaves but smaller, squarrose-spreading, shallowly 4-lobed, weakly bisbifid.

Apparently dioecious. Androecia with up to ca. 8 pairs of bracts, on short ventral-intercalary branches from main shoot; bracts cupulate, nearly erect, dorsally assurgent, bifid to ca. 0.4 or less, at times merely shallowly bidentate, the lobes broadly acute, at times with the dorsal lobe emarginate; disc to 6 cells high, the dorsal margin at times slightly dilated and with several small teeth; antheridia 2–3 per bract, the stalk biseriate. Gynoecia (only young seen) on short ventral-intercalary branches.

A highly distinctive species with an aspect like that of *Lepidozia* sect. *Microphyllae* (e.g., *L. fuegiensis*, *L. microphylla* of New Zealand). The distant, strap-shaped, subfalcate leaves are  $\pm$  bisbifid and very shallowly lobed, the lobes rudimentary and sharply inflexed and claw-like (Fig. 54: 1–4). The disc is 9–13 cells high and 8 cells wide throughout. The half-leaf (Fig. 54: 6) and first branch underleaf (Fig. 54: 9, 10) are also distinctive. The underleaves (Fig. 54: 7, 8) are smaller than the leaves, squarrose-spreading and weakly bisbifid, with rudimentary lobes. The firm-walled, turgid, rounded quadrate disc cells and the thick-walled, glistening marginal cells at the edge of the disc (Fig. 54: 5) are suggestive of the leaves of *Acromastigum* spp.

The androecia of *T. oligophylla* are unusual in having more than one antheridium per bract. The biseriate antheridial stalks of this species were not discovered until after the analysis was completed, and are an anomaly in sect. *Cancellatae*. Elsewhere in the genus, they occur in *T. meridiana* (subg. *Acrolepidozia*), in *T. centipes* and *T. perfragilis* (sect. *Ceraceae*), and in *T. pulcherrima*, *T. plumulosa* and *T. trichocoleoides* (sect. *Tricholepidozia*).

ECOLOGY—Very rare in the Falklands, admixed with other hepatics in a wet depression of a *Cortaderia* heath at 455 m on Mt. Osborne (see Engel, 1990). In southern South America it occurs at scattered sites in the Patagonian Channels north to 48°04'S in Prov. Aisén. The species grows at sea level or lower elevations in or at the edges of forests, such as of *Drimys*, *Podocarpus*, *Pilgerodendron*, and *Nothofagus betuloides* along the shore of Bahía Wide. Also occasional in the Magellanean moorland. In areas particularly rich in

bryophytes (the “bryophyte rich facies,” see Engel, 1978, p. 13), on the floor admixed with *Lepidoscyphus horizontalis* and *Megaceros* sp., or on the sides of bryophyte mounds admixed such other hepatics as *Blepharidophyllum densifolium*, *Clasmatocolea obvoluta* var. *cookiana*, *Gackstroemia* sp., *Saccogynidium* sp. and *Anastrepta*. At Caleta Olla (Antártica Chilena, sea level), the species occurred in a *Sphagnum* bog (with scattered, isolated *Empetrum*, dwarf *Nothofagus* and *Marsippospermum*) near the top of a *Sphagnum* mound, rather densely and tightly creeping among the distal parts of the *Sphagnum* shoots. The species is rather common in *Marsippospermum* mires, particularly in the southern part of its range. For example on Isla Hornos it occurred in a *Marsippospermum* mire with a mosaic of *Astelia*, *Bolax gummifera*, *Marsippospermum*, seepage areas, and shallow pools. Also on cliffs, admixed with *Acromastigum cunninghamii*, *Pleurocladopsis*, *Kurzia mollis*, and *Isotachis* sp., or in moorland, creeping among *Sphagnum* (Puerto Island).

SELECTED SPECIMENS SEEN—CHILE. PROV. ANTÁRTICA CHILENA: Comuna Cabo de Hornos, Islas Wollaston, Isla Hornos, on peninsula between Caleta San León and Punta Espolón, ca. 120 m, Engel 25869 (F); *ibid.*, Isla Hoste, Península Hardy, Bahía Orange, Caleta Misión, 25 m, Engel 25664 (F); *ibid.*, N side of Isla Gordon at W side of Bahía Romanche off Brazo Noroeste of the Beagle Channel, ca. 15 m, Engel 25459 (F); *ibid.*, Isla Grande de Tierra del Fuego, Caleta Olla off the Brazo Noroeste of the Beagle Channel, sea level, Engel 25472 (F); *ibid.*, Isla Grande de Tierra del Fuego, W shore of Seno Ventisqueros, ca. 200m, Engel 25382 (F). PROV. MAGALLANES: E side of Bahía Borja (Península Córdova, Isla Riesco, Paso Tortuoso), Engel 6157D (MSC); Bahía Tuesday, Isla Desolación, head of inner harbor, Engel 5628A (F, MSC); Puerto Cutter, N of copper mine, Engel 2214 (F); Brunswick Peninsula, W side of Bahía San Nicolás, Engel 6386B (F); E side of Isla Juan (Bahía Wide), near shore, Engel 5292—c. ♂ (F, MSC); Pta Brown, Puerto Charrúa (S side of Isla Wellington), Engel 4582B (MSC); Puerto Alert (Isla Mornington, Canal Trinidad), W side of harbor, along shore, Engel 4939A (F, MSC). PROV. AISEN: Puerto Island (Península Swett), Engel 4330 (F, MSC).

*Telaranea ophiria* (Steph.) Engel & Merr., comb. nov.

*Lepidozia ophiria* Gott. ex Steph., Spec. Hep. 3: 611. 1909. Type: Malaysia, Malacca, Mt. Ophir, *Mixon* 972c—c. per. (G!).

ILLUSTRATIONS—Mizutani, 1974, fig. 2: 1–16. Stephani, Icones, *Lepidozia* 233.

DISTRIBUTION—Malaysia (Malacca), Borneo (Mizutani, 1974); Philippines (Mizutani, 1976).

Plants small and wirelike ("gracillima tenuissima," Stephani) and markedly sparsely and irregularly branched for the genus. Branching terminal, *Frullania* type, the half-leaf bifid, the first branch underleaf on median or ventral-lateral side of the branch, undivided, with 1(2) biseriate tiers + a uniseriate row of 2 cells. Ventral-intercalary branches also present, long and leafy or long-flagelliform and whiplike. Leaves varying from slightly to distinctly incubously inserted and concave, with broadly arched-incurved lobes. Lobes biseriate at the base (sporadically with an additional biseriate tier), the uniseriate row 4–5 cells long. Lobe cells thick-walled and somewhat bulging at the septa, the basal cell of the uniseriate row often the shortest, the remaining cells subequal in length, the terminal cell tapering to a rounded summit, often exceeding the length of the penultimate cell. Disc cuneate, 3 cells high and 8 cells wide throughout. Cells of disc rather thick-walled with distinct trigones. Cuticle of leaf lobes minutely striate-papillose. Underleaves frequently asymmetrically lobed, with 1 or more lobes longer, with a uniseriate row of up to 5 cells; disc 2 cells high; lobes mostly 2(3) cells long from a biseriate base, the lobe cells thick-walled.

♀ Bract lobes caudate, 2–3 cells wide at the base, the uniseriate row up to 8 cells long, the cells thick-walled with bulging septa. Perianth plicate distally and contracted above, the mouth ± stiffly ciliate, the cilia with a uniseriate row up to 5 cells long, the cells similar to those of the bracts.

The foregoing description is based on the type. Mizutani (1974) has also discussed and illustrated this species. The species is assigned to sect. *Cancellatae*.

#### *Telaranea panchoi* Del Ros.

*Telaranea panchoi* Del Ros., Philipp. J. Sci. 100: 238. f. 43–47. 1973 (1971). Type: Philippines, Luzon, Laguna, Mt. Banahao, *Pancho 3303* (PNH, reportedly lost).

ILLUSTRATION—Del Rosario (1973, figs. 43–47).

DISTRIBUTION—Endemic to Philippines.

Similar to *T. herzogii* and *T. tasmanica*, with deeply bilobed leaves, the lobes 6–8 cells long, the lobe bases united for half their length and either uniseriate (Del Rosario, 1973, figs. 46, 47) or biseriate and the disc then "four cells across."

Underleaves are bilobed, the paired basal cells of the lobes united for about half their length (fig. 45), with a uniseriate portion 2 cells long. The stem cross section consists of 6 large cortical cells surrounding 3–4 small medullary cells (fig. 44). The cuticle is described as smooth.

#### *Telaranea papulosa* (Steph.) Engel & Merr., comb. nov.

*Lepidozia papulosa* Steph., Spec. Hep. 3: 609. 1909.  
*Neolepidozia papulosa* (Steph.) Fulf. & J. Tayl., Brittonia 11: 85. 1959. Lectotype (*fide* Kitagawa, 1973): Sumatra, near Lake Toba, *Modigliani* (G!).  
*Lepidozia gunniana* Steph. in Stephani & Watts, J. & Proc. Roy. Soc. New South Wales 48: 112. 1914, *syn. fide* Kitagawa (1973). *Neolepidozia gumiana* (Steph.) Fulf. & J. Tayl., Brittonia 11: 85. 1959. Lectotype (*fide* Kitagawa, 1973): New Hebrides, Aneityum, 1911, *Gunn 286*, ex hb. Lillie (G!).  
*Lepidozia paucidens* Steph., Sp. Hep. 6: 337. 1922, *syn. fide* Kitagawa (1973). Type: Java, *Fleischer* (G!).

ILLUSTRATIONS—Stephani, *Icones, Lepidozia* 235; 236 (*L. paucidens*); 214 (*L. gunniana*).

DISTRIBUTION—Sumatra. Reported by Kitagawa (1973) from Philippines, Thailand, Sumatra, Java, Borneo and New Hebrides, and by Hürlimann (1985) from New Caledonia, but perhaps not in the sense used here.

According to Kitagawa (1973, p. 267), *T. papulosa* is common and widespread in southeast Asia, where it has often been confused with *T. wallichiana*. Kitagawa cited the proportions of the leaf cells as 40–60 µm long and thin-walled in *T. wallichiana* vs. 30–40 µm and relatively thick-walled in *T. papulosa*, but provides no further details. Our concept of *T. papulosa* is based on the type, and is evidently somewhat narrower. Stephani's drawing of the branch leaf of *L. papulosa* shows the lobe cells as barrel-shaped and bulging, with distinctly constricted septa, which well represents the type, and is also typical of the Sumatra specimen cited below (*Meijer 6853*). Stephani (1909) described the lobes of the branch leaves as "optime papuloso-prominutis," and the leaf (disc) cells as smooth. The type of *T. papulosa* has leaves 3–4(5) cells high and has subisodiametric disc cells; the branch leaves are ± symmetric, with a disc 4–5 cells high.

Submoniliform lobe cells are a feature shared with *T. mamilliosa*. However, in our specimen the two median rows of cortical cells of the branches

are not broadly exposed, as they are in *T. mamillosa*.

SPECIMEN SEEN—SUMATRA: Mt. Sago near Pajakumbuh, ca. 1500–2000 m, Meijer 6853 (F).

*Telaranea parvifolia* (Steph.) Engel & Merr., comb. nov.

*Lepidozia parvifolia* Steph., Spec. Hep. 6: 337. 1922. *Neolepidozia parvifolia* (Steph.) Fulf. & J. Tayl., Brittonia 11: 85. 1959. Type: New Caledonia, Jugo Dogny, July 1909, Lerat (Paris no. 376)—c. per. (G!).

ILLUSTRATION—Stephani, Icones, *Lepidozia* 279.

DISTRIBUTION—New Caledonia.

Plants small and irregularly 1–2-pinnate. Branches terminal, *Frullania* type, whiplike, often flagelliform. Stem notably large and fleshy for plant size, the cortical cells markedly boxlike in surface view. Leaves strongly concave, asymmetrically 3–4-lobed, the lobes deflexed; leaf insertion not extending to the stem midline dorsally, with broadly exposed median strip 2 cells wide. Lobes very short, the ventral lobe smallest and about half the length of the other lobes, the lobes 2 cells wide at the base, with a uniseriate row 2–3 cells long; lobe cells moderately thick-walled, with slightly protruding septa. Disc 4 cells high, 6 or 8 cells wide throughout, the cells in regular rows and tiers. Cells of disc firm-walled, with distinct small trigones. Underleaves 3–4-lobed, about as wide as the stem or somewhat narrower, the disc 2 cells high, the lobes consisting of a single elongate (2:1) cell or a uniseriate row of 2 cells, each slightly longer than wide.

The foregoing description is based on the type. Stephani (Icones 279) illustrated part of a shoot with a 3-lobed leaf, the disc 6 cells wide and 5 cells high, the lobes with a uniseriate row 2 cells long; the underleaf is 3-lobed, with a disc 3 cells high, and lobes of a single cell each. Hürlimann (1985), in his treatment of the New Caledonian species, does not mention this plant. This is one of the species originally assigned to *Neolepidozia* by Fulford and Taylor (1959); it is assigned here to sect. *Cancellatae*.

*Telaranea pecten* (Spruce) Engel & Merr., comb. nov.

*Arachniopsis pecten* Spruce, On Cephalozia: 85.

1882. Type: Brazil, “ad fl. Negro et Uaupés,” Spruce.

*Arachniopsis diacantha* subsp. *borinquena* Schust., New Man. Bryol. 2: 773, 774. f. 4: 9. 1984, nom. inval. sin. descr. lat. *Arachniopsis borinquena* Schust., Beih. Nova Hedwigia 118: 457. 2000, nom. inval. sin. descr. lat.

DESCRIPTION—Fulford (1968).

ILLUSTRATIONS—Spruce (1885, pl. 13); Fulford (1968, pl. 97, fig. 3, type); Schuster (2000, fig. 193, as var. *pecten*). Stephani Icones (*Arachniopsis* 5).

DISTRIBUTION—Puerto Rico, Guyana (Roraima, Gradstein and Florschütz-de Waard, 1989), Venezuela (Fulford, 1968), Brazil (Uaupés, upper Rio Negro).

Spruce (1882, p. 85) described the stem cortical cells in *A. pecten* as “collateral,” with the leaves inserted at “the marginal junction of two consecutive cortical cells . . . on each side of the stem.” The stem of *T. pecten* consists of 4 rows of cortical cells, plus a single axial medullary cell (Spruce, 1882), illustrated by Schuster (2000, fig. 193: 5, 6). Shoots of this “simplex” type, 4+1 in section, with monocurous leaves, are sometimes observed admixed with shoots with typically bilobed leaves in members of sect. *Tenuifoliae*. The possibility that *T. pecten* (and *T. confervoides*, p. 143) may represent monocurous expressions of normally bilobed taxa cannot be ruled out. In the size, shape and proportions of the lobe cells, the former resembles *T. coactilis*, the latter *T. diacantha*.

Spruce (1882) initially described underleaves as lacking in *T. pecten*. The usual condition is for a basal pair of cells, with lobe cells lacking. In the specimen examined, rhizoids are produced in abundance from the basal cells.

Schuster (2000, fig. 193: 11, 12) illustrated ♀ bracts and perianth mouth (fig. 13) in this species. The bracts are like most species of sect. *Tenuifoliae* (e.g., *T. diacantha*) in having 3–4 ciliiform lobes and a low disc, 1–2.5 cells high.

According to Schuster (2000, p. 457) “*Arachniopsis borinquena*” is “presumably” dioecious and “perhaps identical to *A. pecten*,” but differs in producing sporadic *Frullania*-type branches. Apparently, there is no published illustration of this plant, apart from a stem cross-section with attached underleaf (Schuster, 1984, fig. 4: 9). Schuster (2000) stated that fig. 190: 4–6 is this plant, but in the legend these figures are identified as *Telaranea chaetophylla*. His fig. 5 is a plant

with 3-lobed leaves, the lobes geminate at the base.

**SPECIMEN SEEN**—BRAZIL: Along Rio Cauaburi between Rio Negro and Cachoeira do Carangueijo, *Buck* 2305 (F).

*Telaranea pellucida* Engel & Merr., sp. nov.

A *T. pseudozoopsis* foliis 3–4-lobatis, disco ex parte 2-cellulas alto, areolatione irregulari, semi-foliis saepe bilobatis distans.

**Holotype**: Chile, Prov. Valdivia, W slope of Cordillera Pelada, 3.1 km by road W of El Mirador on road between La Union and Punta Hueicolla, 840 m, *Engel* 12354 (F).

**DISTRIBUTION**—Chile (Prov. Valdivia, known only from the type).

Plants irregularly to  $\pm$  regularly 1–2 pinnate, when dry pale whitish green, highly nitid and glistening, when moist notably hyaline, the stems appearing fleshy. Branching highly variable, mostly terminal, *Frullania* type, the branches occasionally  $\pm$  indeterminate and becoming flagelliform, or abbreviated and with a terminal gynoeceium; branch half-leaf bilobed or undivided; first branch underleaf undivided or asymmetrically bilobed, with 1 short lobe of 2 cells, the other longer and to 4 cells (leaf-lobe-like), the fbv occasionally subsymmetrically bilobed, the lobes rather short, leaf-lobe-like; athecal lateral branches also observed, arising slightly below and ventral to the ventral end of the insertion of a leaf. Ventral-intercalary branches common, often seemingly arising in pairs, becoming leading leafy shoots or stoloniform. Stems with a turgid, fleshy appearance, the cortical cells in 8 rows, thin-walled, short rectangular; medullary strand distinctly visible through the almost transparent cortical cells, the medullary cells 24–25, much smaller, thin walled. Shoots typically with 5 cortical cells intervening dorsally between successive leaves on either side of shoot, branches with 4–5 cortical cells between leaves. Leaves 3–4-lobed, transversely inserted, the insertion extending nearly to the stem midline. Lobes divergent, distinctly tapering, biseriate at the base, the cells of the basal tier and the first cell of the uniseriate row bulging, with constricted septa, the uniseriate row 4–5 cells long. Cells of lobes thin-walled, the paired basal cells elliptic, 36–48  $\mu\text{m}$  wide  $\times$  66–79  $\mu\text{m}$  long; basal cell of the uniseriate row 48–62  $\mu\text{m}$  wide  $\times$  78–98  $\mu\text{m}$

long, the next cell shorter and more slender, 34–49  $\mu\text{m}$  wide  $\times$  72–90  $\mu\text{m}$  long, the terminal cell much shorter than the subapical cell, often appearing secondarily divided; cuticle smooth. Disc locally 2 cells high, the areolation somewhat irregular, with additional intercalated cells in the median basal portion of disc. Underleaves erect, 3-lobed on the main shoot, the disc 0.5 cells high, consisting of the paired, oblong basal cells of the lobes and a uniseriate row of 2–4 long-cylindric cells, the lobes typically hooked at the tips, ending in a slime papilla; rhizoid initials formed by subdivision of the basal cells of the lobes.

Androeceia not seen. Gynoeceia (only young seen) on short ventral-intercalary branches and on very short terminal, *Frullania*-type branches (see below).

*Telaranea pellucida* resembles *T. pseudozoopsis* in the pellucid and inflated cortical cells, and the medullary strand, which is distinctly visible when viewed in transmitted light, but the cortical cells of *T. pellucida* are smaller and less conspicuously bulging than those of *T. pseudozoopsis*. In addition, the leaves of *T. pellucida* are 3–4-lobed and the half-leaf is frequently bilobed. The leaves consistently have a disc 2 cells high, at least in part, unlike *T. pseudozoopsis*, in which (in all the specimens we have seen) the disc is 0.5 cells high, although Schuster (1968, fig. 53: 6) illustrates a leaf with an additional cell at the median base of the disc. The paired basal cells of the lobes in *T. pseudozoopsis* are small and relatively inconspicuous, and the basal cell of the uniseriate row is large, ovate-cylindric and as much as half the full length of the lobe. In *T. pellucida* the basal cells are elliptic and conspicuously bulging, and about equaling the basal cell of the uniseriate row in length.

The areolation of the leaf disc in *T. pellucida* is similar to that in *T. marginata*, in the sense that additional cells are present in the median portion of the disc. In *T. marginata*, however, the disc is bordered by a single longitudinally elongate cell, but 1.5 cells high in the median portion, with a uniform basal tier of cells along the insertion. The areolation of the disc in *T. pellucida* is more irregular: the cell divisions that produce the additional cells in the median portion of the disc are often not strictly transverse or longitudinal. Moreover, in *T. pellucida* the leaves do not exhibit the offset alignment of the lobe cells as in *T. marginata* (and *T. fernandeziensis*).

In the type of *T. pellucida* the lower portion of

the shoot often becomes profusely branched. These branches are ventral in position and are clearly ventral-intercalary, at least in part. These branches often occur in pairs and sometimes appear to be two ventral-intercalary branches arising side-by-side in the axil of an underleaf. Sometimes, however, it appears as if a single branch is branching so close to its origin that it is difficult to determine whether the second branch is terminal or intercalary in origin. In one case, one of two paired branches produced a terminal, *Frullania*-type branch, and all three branches produced a gynoeceium. In another case, we observed an apparently collar-less (athecal) branch immediately following a ventral-intercalary branch in sequence, but positioned slightly below and ventral to the ventral end of the insertion of a lateral leaf.

**ECOLOGY**—Known only from the type, on the side of a cushion plant in a bog of *Astelia*, *Donatia* and *Gaimardia*, with scattered patches of *Sphagnum* at 840 m on the west slope of Cordillera Pelada (Prov. Valdivia).

*Telaranea planifolia* (Steph.) Engel & Merr., comb. nov.

*Lepidozia planifolia* Steph., Spec. Hep. 3: 629. 1906. Lectotype (*vide* Hattori and Mizutani, 1958): Japan, Shikoku, Mt. Tsurugi, *Faurie* 654—c. per. (G!).

**ILLUSTRATION**—Hattori & Mizutani (1958, fig. 3: 1–15, as *Lepidozia wallichiana*). Stephani, *Icones, Lepidozia* 307.

**DISTRIBUTION**—Japan (Honshu, Shikoku, Yakushima Is.); Taiwan. According to Hattori & Mizutani (1958, map g), the species is very rare and restricted in distribution to southern Japan and Yakushima Is. The species is here reported as new to Taiwan.

Our understanding of *T. planifolia* is based on the lectotype, the Taiwan specimen (*Lai* 1092) cited below, and the description and illustration (based on *Hattori* 8041, presumably from Yakushima Is.) by Hattori and Mizutani (1958). The plants are small, irregularly pinnate, with lateral branches rather short and flattened. The stem leaves are distinctly incubously inserted and widely set, leaving the dorsal cortical cells well exposed, a feature of the branches of many *Telaranea* species, but rarely present on the main shoot. The half-leaf is bifid or (often) undivided, and the first branch underleaf undivided. The stem leaves

are ventrally decurrent, which is apparent also in Stephani's *Icones* illustration.

Kitagawa (1973, p. 267) suggested that *T. planifolia* may be conspecific with *T. papulosa*. However, the type of *T. planifolia* lacks the distinctive bulging-mamillose leaf cells and submoniliform lobes of *T. papulosa*, and is not that species. Sexuality in this species requires further study. The type has perianths (3 seen), but androecia were not seen. The Taiwan collection referred here to *T. planifolia* is autoecious, with gynoeccia on ventral-intercalary branches and androecia on terminal, *Frullania*-type branches on the same shoot. Two other autoecious species of sect. *Cancellatae* are known: *T. autoica* (Juan Fernández) and *T. trifida* (East Africa). The other monoecious species of the genus are restricted to sects. *Telaranea* and *Tenuifoliae*.

**SPECIMEN SEEN**—TAIWAN: Chitou, Nantou, *Ming-Jou Lai* 1092—c. ♂ + per. (F).

*Telaranea plumulosa* (Lehm. & Lindenb.) Fulf.

*Jungermannia plumulosa* Lehm. & Lindenb. in Lehmann, Nov. Min. Cogn. Stirp. Pug. 6: 30. 1834. *Lepidozia plumulosa* (Lehm. & Lindenb.) G. L. & N., Syn Hep. 211. 1845. *Mastigophora plumulosa* (Lehm. & Lindenb.) Trev., Mem. Ist. Lomb. Sci. Lett. III. 4: 416. 1877. *Telaranea plumulosa* (Lehm. & Lindenb.) Fulf., Brittonia 15: 77. 1963. Type: Argentina, Terr. Tierra del Fuego, Isla de los Estados, *Menzies*, ex hb. Kew (G!).

**DESCRIPTIONS**—Stephani (1909); Fulford (1963a, 1966).

**ILLUSTRATIONS**—Lindenberg and Gottsche (1846, tab. 12); Fulford (1963a, figs. 185–202; 1966, pl. 53, fig. 6); Figs. 55, 56. Stephani, *Icones, Lepidozia* 139.

**DISTRIBUTION**—Falkland Is., southern South America (Magellanian + Valdivian), and Juan Fernández, Más a Tierra (400–550 m) (see Engel, 1978, 1990). Reported from Auckland Is. and/or New Zealand by Hooker (1867), Stephani (1909), Herzog (1942), and Fulford (1963a, 1966), but not confirmed. The collection from Antipodes Is. reported by Glenny and Fife (1996) as *T. plumulosa* is *T. tetradactyla* (AK).

Plants luxuriant, plumose, shoots and branches recurved to circinate at the tips, subisophyllous, whitish green to honey-colored to brownish yellow, with a glossy sheen when dry as if highly polished. Branching rather laxly 1–2-pinnate, the branches oriented at 45° to the stem, *Frullania*-

type, the half-leaf 2–4-lobed; first branch underleaf (2)3–4-lobed (Fig. 55: 6–8), inserted on the ventral lateral side of the branch base. Ventral intercalary branches common, leafy, giving rise to new leading shoots. Stem stout, with 12–18 rows of cortical cells surrounding the smaller, more numerous medullary cells. Rhizoids from a pad of small, subquadrate cells in the distal portion of the underleaf disc, just beneath the bases of the lobes (Fig. 55: 4). The rhizoid initial cells are notably thick walled (Fig. 55: 4). Leaves subtransverse to incubous, slightly concave, symmetrically 4–6(7)-lobed (Fig. 55: 1, 2); lobes 2–3 cells wide at the base, the uniseriate row 5–6 cells long, subcapillary, long tapering to a sharply-pointed terminal cell (Fig. 55: 5), the lobe cells with septa thickened in the corners and straight to moderately projecting (Fig. 55: 5). Disc 3–5 cells high, composed of quadrate cells, often slightly asymmetric, the dorsal margin shorter than the ventral. Cuticle smooth. Underleaves leaflike, scarcely smaller than the leaves, the disc to 5 cells high, 4–6-lobed, the lobes uniseriate, some like the leaf lobes, others somewhat shorter and ending in a slime papilla (Fig. 55: 3).

Dioecious. Androecia catkin-like, circinate, with up to 15 pairs of bracts, on ventral-intercalary branches from the basal portion of the shoot; bracts 3–4-lobed to 0.5, the lobes 2–4 cells wide at the base, with a uniseriate row 3–4 cells long, the disc 4–5 cells high, the dorsal margin dilated to form a lobulus; antheridia solitary, the stalk biseriate. Gynoecia on short ventral-intercalary branches, the bracts becoming progressively less ornamented at the apex (Fig. 56: 4–7), the lower bracts lobate (Fig. 56: 4, 5), the innermost erose-dentate to crenulate (Fig. 56: 7–10); bracteoles similar in size and form to the bracts (Fig. 56: 8). Perianth mouth with cells with the apical end laterally free for varying lengths, the mouth thus crenate-dentate (Fig. 56: 1–3).

Seta with 8 rows of outer cells surrounding an inner core of 11 rows of much smaller cells (Fig. 56: 11). Capsule wall 4–5 cell layers thick, 54–60  $\mu\text{m}$  (Fig. 56: 12), the thickenings pale brown, the outer layer not significantly thicker than the intermediate layers (Fig. 56: 12).

This is among the largest of the southern Southern American species of *Telaranea*. As the name suggests, the subsophyllous plants (Fig. 55, compare 1, 2 with 3, 4) have a distinctive plumose aspect, the shoots and branches recurved to circinate at the tips. The leaves are 4–6(7)-lobed,

with a disc 3–5 cells high, composed of quadrate cells (Fig. 55: 1, 2). The underleaves are scarcely smaller than the leaves, 4–6-lobed, with a disc to 5 cells high (Fig. 55: 3, 4).

The type of *T. plumulosa* represents a well-developed expression of the species, as described above. Small phases may resemble robust *T. fernandeziensis*, which is often bipinnate and has deeply 4–5(6)-lobed leaves. The latter, however, has a leaf disc only 2(3) cells high, with a single tier of narrowly elongate cells along the insertion. Moreover, *T. fernandeziensis* has off-center leaf lobe cells and a squarrose leaf disc, with the lobes abruptly inflexed and suberect. In *T. plumulosa* the disc and lobes form a broadly and evenly concave continuum. See also comments in Engel (1990).

Fulford (1963a, p. 80), described the genus *Telaranea* as “probably the most clearly defined reduction series among the leafy Hepaticae,” and *T. plumulosa* as the most primitive condition in that series (i.e., *Telaranea* in the more restricted sense of Müller and Fulford; see Introduction, p. 3). *Telaranea plumulosa* is the sister taxon of the Old World species, *T. pulcherrima* and *T. trichocoleoides*. Among other features shared with *T. pulcherrima* are a capsule wall 4–5 cells in thickness, and biseriate antheridial stalks.

ECOLOGY—This species is very common in the Falkland Islands, and is characteristic of stream banks, particularly under *Gunnera*, *Blechnum magellanicum*, or *Empetrum* cover, and in crevices of outcrops in dwarf shrub heaths. It is also common on soil, frequently on stream banks in *Cortaderia* heaths. In southern South America it is rather common in mossy forests throughout much of the range of *Nothofagus*, and is present in a variety of niches: on rotted logs, particularly where some soil and other bryophytes have accumulated; on the forest floor, admixed, at times, with *Schistochila lamellata*, *Saccogynidium* and *Anastrepta bifida*, or, particularly in the Magellanian zone, creeping over or mixed with *Megaceros endivaefolius*; over soil in rock crevices, particularly under the shelter of rock overhangs; on stream banks, sometimes not far above water level, as well as submerged in pools; and in mats of pendent vegetation. It is present at or near sea level in the Magellanian zone, in, for example, a mossy forest of *Nothofagus betuloides*, *N. pumilio*, *Drimys*, and *Berberis ilicifolia* (Puerto Churruca, Isla Desolación). On Isla Bayly (in Antártica Chilena), it formed pure, pendant, loose masses or tight, knoblike small masses on a dripping

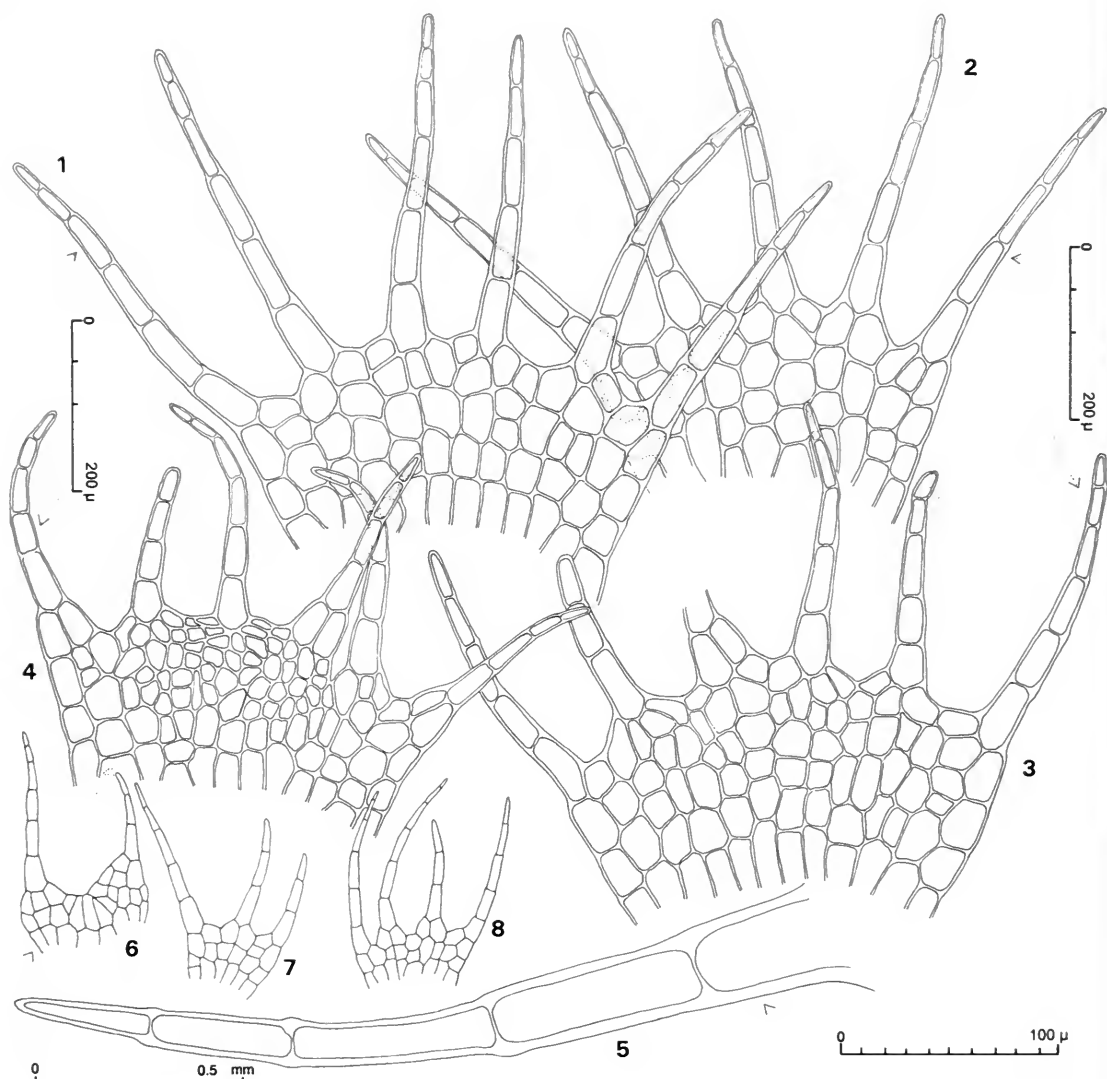


FIG. 55. *Telaranea plumulosa* (Lehm. & Lindenb.) Fulf. 1, 2. Leaves. 3, 4. Underleaves; note the underleaf at left has a distal field of thick-walled rhizoid initial cells. 5. Portion of lobe from leaf of main axis. 6-8. Two-, three- and four-lobed first branch underleaves, all from one shoot. (All from Engel 2240A, Chile, Prov. Magallanes, Brunswick Peninsula, Puerto Cutter.)

vertical bank of bryophytes within a cavelike, moist recess formed in bedrock at the base of a steep cliff. The site is at an exposed shoreline with dripping vertical rock walls and a bryophyte-covered overhang formed by the forest margin above. The species is rather common in *Marsippospermum* mires, particularly in the southern part of its range. For example on Isla Hornos it occurred in a *Marsippospermum* mire with a mosaic of *Astelia*, *Bolax gummifera*, *Marsippospermum*, seepage areas and shallow pools. On Isla Herschel (Antártica Chilena) it curiously formed enormous sol-

id, very firm cushion on stream bank with an open mosaic of *Astelia*, *Marsippospermum* and scattered small patches of dwarf *Nothofagus betuloides*. It is able to tolerate considerable light exposure, and may be present in open stands of *Nothofagus*, or, occasionally, in the Magellanian moorland. In the Brunswick Peninsula the species occurs in the evergreen forest region (for further comments, see Engel, 1978, p. 106). In the Valdivian zone it occurs from sea level to 320 m in Prov. Chiloé, and northward between 580 and 1250 m, for example, at 855 m in a forest of *Noth-*



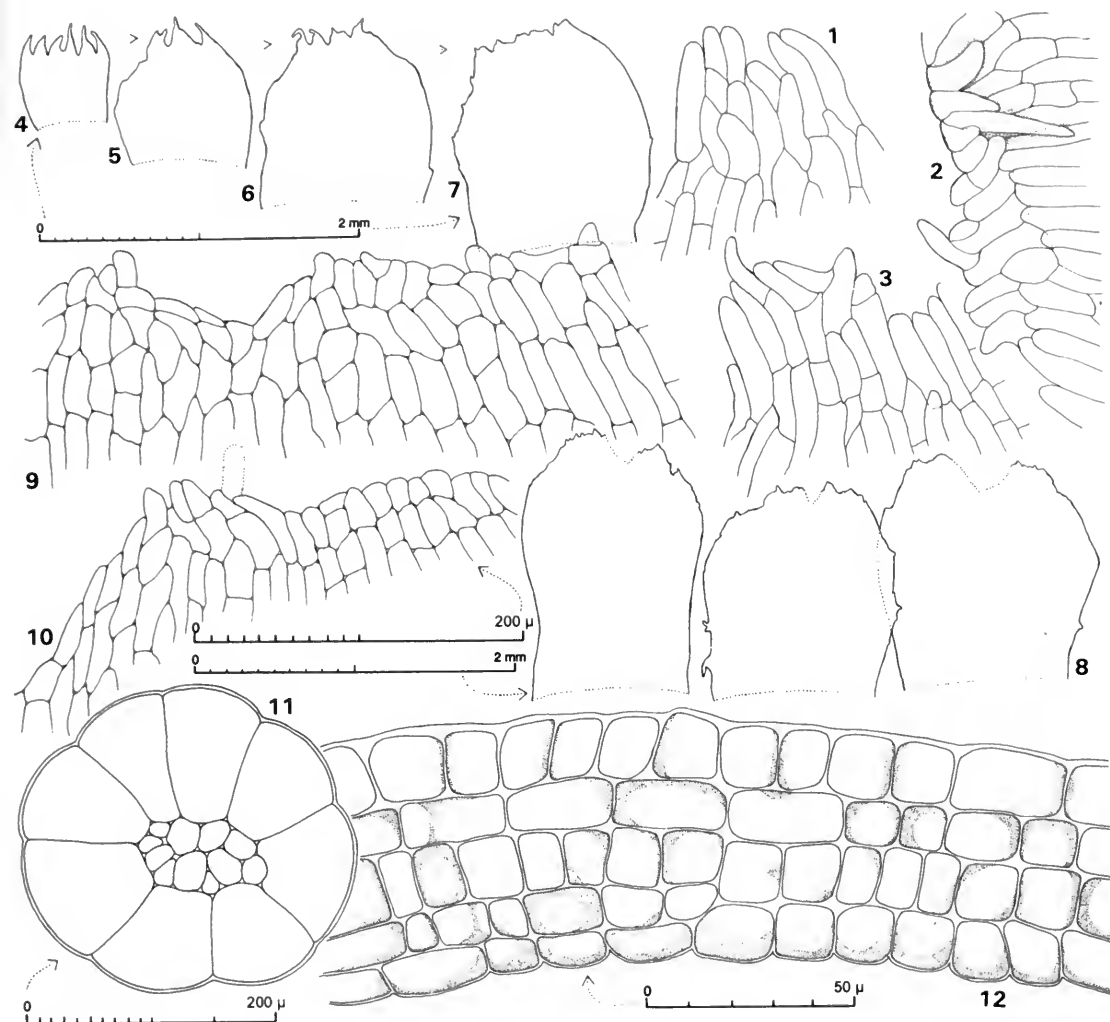


FIG. 56. *Telaranea plumulosa* (Lehm. & Lindenb.) Fulf. 1-3. Portions of perianth mouth (drawn to scale of fig. 10). 4-7. Sequential series of ♀ bracts from one gynoeceum (first series at left, innermost at right), showing reduction of lobe size. 8. ♀ Bracts and in middle, bracteole from innermost series. 9, 10. Apices of 2 different innermost ♀ bracts. 11. Seta, cross section. 12. Capsule wall, cross section. (All from *Engel* 2240A, Chile, Prov. Magallanes, Brunswick Peninsula, Puerto Cutter.)

*ofagus dombeyi*, *Drimys*, *Podocarpus*, *Laurelia*, *Saxegothaea* and *Flotowia* (below Refugio Antilanca).

SELECTED SPECIMENS SEEN—CHILE. PROV. ANT-ARCTICA CHILENA: Comuna Cabo de Hornos, Islas Wollaston, Isla Hornos, Caleta San León, sea level, *Engel* 25879 (F); *ibid.*, Islas Wollaston, Isla Hornos, on peninsula between Caleta San León and Punta Espolón, ca. 120 m, *Engel* 25854 (F); *ibid.*, Islas Wollaston, NE side of Isla Herschel, Caleta Martial, sea level, *Engel* 25817 (F); *ibid.*, Islas Wollaston, E side of Isla Bayly at S entrance to Canal Washington, 1-2 m above sea level, *Engel* 25740 (F); *ibid.*, Isla Hoste, Península Hardy, Bahía Orange, Caleta Misión, sea level, *Engel* 25682 (F);

*ibid.*, N side of Isla Gordon at W side of Bahía Romanche off Brazo Noroeste of the Beagle Channel, ca. 15 m, *Engel* 25451C (F). PROV. TIERRA DEL FUEGO: Along NE shore of Seno D'Agostini, ± opposite Punta Final, 0-20 m, *Engel* 25281 (F). PROV. MAGALLANES: Isla Navarino, La Vuelta del Perro, ca. 16.5 km E of Puerto Williams, *Buck* 41334 (F); Bahía Queta, *Roivainen* 530 as *T. fernandezensis* (S); S shore of Bahía Pond, Isla Clarence, *Engel* 6289 (F, MSC); Brunswick Peninsula, NE side of Puerto Gallant, *Engel* 6171 (F, MSC); *ibid.*, Bahía Fortescue, *Engel* 5945—c. ♂ (F); *ibid.*, Puerto Cutter, slightly W of copper mine, *Engel* 2240A—c. sporo. (F); peninsula on N side of Fondeadero Nassau, Puerto Churruca, Isla Desolación, *Engel* 5929 (F, MSC); head of Puerto Bueno, *Engel* 5528 (F, MSC); waterfalls at head of Fiordo Peel, *Engel*

3499C—c. per. (MSC); N shore of Bahía Wide, Isla Chatham, *Engel 5301* (F, MSC); NE corner of Isla Tarleton, *Engel 5081* (MSC); head of fiord E of Mte Roberto, S side of Isla Madre de Dios, *Engel 5119* (F, MSC); Puerto Charrúa (S side of Isla Wellington), at head of inlet, *Engel 4824* (F, MSC); head of fiord W of Mte Markham, Puerto Alert (Isla Mornington, Canal Trinidad), *Engel 4968* (F, MSC). PROV. AISÉN: Landing cave near glacier on N side of Fiordo Témpano, *Engel 4363A* (MSC). PROV. CHILOÉ: Puerto Ballena (Isla Mulchey), along shore of harbor, *Engel 4203* (F, MSC); Isla Chiloé, Cordillera San Pedro, Río Puidi, near aseradero at San Pedro, 320 m, *Engel 11909* (F); *ibid.*, Aguas Buenas area, 4.7 km E along Aguas Buenas road from Ancud-Quemchi road, ca. 100 m, *Engel 12195* (F). PROV. OSORNO: Crater Casablanca, 3.4 km by road above Refugio Antillanca, 1250 m, *Engel 11495* (F); 0.5 km by road below Refugio Antillanca, 1000 m, *Engel 11500* (F); Lago Toro on road to Refugio Antillanca, 855 m, *Engel 4000A*—c. per. (F, MSC). PROV. VALDIVIA: Cordillera Pelada, summit of El Mirador, near road between La Union and Punta Hueicolla, 1000 m, *Engel 12385* (F); E slope of Cordillera Pelada, 7.1 km by road E of El Mirador on road between La Union and Punta Hueicolla, 840 m, *Engel 12445*—c. ♂ (F); SW slope of Volcán Quetrupillán, Forestal Trafún, 1160–1235 m, *Engel 11166*—c. ♂ (F). PROV. CAUTIN: Salto Palguín, Río Palguín, 6.7 km along road to termas de Palguín, 580 m, *Engel 11250* (F). JUAN FERNÁNDEZ: Más a Tierra, near base of El Yunke, 490–550 m, *Hatcher & Engel 17, 311*—c. per. (F); western slope of Piramide Ridge, S of Portezuelo de Villagra, *Hatcher & Engel 33*—c. ♂ (F).

*Telaranea pruinosa* (Herz.) Engel & Merr., comb. nov.

*Lepidozia pruinosa* Herz., *Memoranda Soc. Fauna Fl. Fenn.* 27(1950–1951): 93. f. 40. 1952. Type: Fiji, Koro, eastern slope of Maine Ridge, 300–500 m, A.C. Smith 966 (BISH).

ILLUSTRATION—Herzog (1952, fig. 40).

DISTRIBUTION—Endemic to Fiji Is.

Herzog (1952) compares this species to *T. centipes* and *T. wallichiana*, but with a lower disc, only 3 cells high (including the basal cells of the lobes), and longer leaf lobes, with a uniseriate row 6–7 cells long. The species is described as “glaucescens”; however, the low disc argues against an assignment to sect. *Ceraceae*. The species of this exclusively Australasian group have a leaf disc that is high and parallel-sided, and 5–6 or more cells high. Glauous cuticle is not confined to sect. *Ceraceae* (*T. grossiseta*, *T. seriatitexta*); sect. *Cancellatae* seems more appropriate for this species.

*Telaranea pseudozoopsis* (Herz.) Fulf.

*Lepidozia pseudozoopsis* Herz. in Skottsberg, *Nat.*

*Hist. Juan Fernández*, Bot. 2: 723. f. 5. 1942. *Telaranea pseudozoopsis* (Herz.) Fulf., *Brittonia* 15: 71. 1963. Type: Juan Fernández Is., Más a Tierra, Centinela, 530 m, *Skottsberg*.

DESCRIPTIONS—Fulford (1963a, 1966).

ILLUSTRATIONS—Herzog (1942, fig. 5); Fulford (1963a, figs. 148–150; 1966, fig. 52; 2, *T. pseudozoopsis*); Schuster (1968, fig. 53).

DISTRIBUTION—Falkland Is.; southern South America (Magellanian + Valdivian); Juan Fernández Is., Más a Tierra (400–530 m, where recorded); see Engel (1978; 1990, fig. 33). Vianna (1974) described plants Brazil (Rio Grande do Sul) as *T. sejuncta* var. *brevisetata*, which appear to be *T. bicurris* (p. 125).

Plants distantly and irregularly to  $\pm$  regularly 1–2 pinnate, when dry whitish green, highly nitid and polished with a “leafless,” *Zoopsis*-like appearance, the cortical cells and leaf lobe cells collapsed, when moist the stems appearing fleshy. Branching terminal, *Frullania* type, the branches leafy or wholly flagelliform; branch half-leaf monocrurous; first branch underleaf asymmetrically bilobed, ventral lateral in position, with one lobe short, typically with paired basal cells and 1(2) long-cylindric cell(s), terminating in a slime papilla, the other longer and resembling a leaf lobe. Ventral-intercalary branches common, both leafy and stoloniform. Stems with a turgid, fleshy appearance, the cortical cells in 6–8 rows, thin-walled,  $\pm$  isodiametric to transversely elongate hexagonal, turgid and inflated, the ventral cortical cells short rectangular and somewhat smaller; medullary strand distinctly visible through the almost transparent cortical cells, the medullary cells much smaller, thin-walled. Shoots typically with 4 cortical cells intervening dorsally between successive leaves on either side of shoot, branches with 3 cortical cells between leaves. Leaves small in proportion to stem, 2-lobed to 3-lobed on robust shoots, almost laterally inserted, the two median dorsal rows of cortical cells broadly exposed, the insertion transverse or weakly succubous, the ventral end nearest shoot apex and slightly above the dorsal. Lobes divergent, biseriate at the base, the uniseriate row of 4(5) cells long, distinctly tapering and constricted at the septa, the cells progressively shorter and more slender, ending in a narrow tip. Cells of lobes thin- to firm-walled, the paired basal cells  $\pm$  isodiametric, 24–38  $\mu\text{m}$  wide and long to 43–54  $\mu\text{m}$  wide and long; basal cell of the uniseriate row often equal to half the length

of the lobe, ovate-cylindric to cylindric, 24–41  $\mu\text{m}$  wide  $\times$  72–91  $\mu\text{m}$  long to 36–55  $\mu\text{m}$  wide  $\times$  108–149  $\mu\text{m}$  long, the next cell shorter and more slender, 14–26  $\mu\text{m}$  wide  $\times$  43–65  $\mu\text{m}$  long to 22–36  $\mu\text{m}$  wide  $\times$  84–122  $\mu\text{m}$  long, the terminal cell much shorter than the subapical cell, often appearing secondarily divided; cuticle smooth. Disc 0.5 cells high, composed of the basal cells of the lobes. Underleaves 2–3-lobed, the disc inconspicuous, consisting of the paired basal cells of the lobes, the lobes  $\pm$  erect-appressed to the stem, of 1–2 long-cylindric cells, ending in a slime papilla; rhizoid initials formed by subdivision of the basal cells of the underleaf lobes.

Dioecious. Androecia on ventral-intercalary branches and at the tips of  $\pm$  elongate *Frullania*-type branches and leading shoots, rather loosely bracteate, the bracts erect-secund, foliose, 2-lobed to 0.7, the disc 1 cell high at margins, 2–3 cells high in median portion, the lobes with a uniseriate row of 3 cells, tapering like the leaf lobes, the dorsal lobe 2–3 cells wide at base; antheridia one per bract, the stalk uniseriate. Gynoecia on short ventral-intercalary branches; bracts asymmetrical-ly 3-lobed, deeply concave at base, divided to 0.7, the lobes 4 cells wide at base, followed by a linear portion of 1–3 biseriate tiers and a uniseriate row of 3–5(7) cells, the lobe cells oblong (ca. 2:1), turgid and with constricted septae, the distal cells more slender, not bulging, tapering to the tip; disc 4–6 cells high, the margins with 1–2 turgid unicellular teeth ending in a slime papilla. Perianth ovate, deeply plicate almost to the base, ciliate at the mouth, the cilia ca. 10, 4–5 cells wide at the base, followed by a tier of 2–3 cells and a uniseriate row of 3–4 narrowly elongate, thick-walled cells, the septa thickened in the corners, not or  $\pm$  projecting.

Sporophyte not seen.

This species is aptly named. Wet or dry, *T. pseudozoopsis* has a remarkably *Zoopsis*-like appearance, polished and glistening, the leaves small and inconspicuous, the cortical cells turgid and transparent and the medullary strand thus clearly visible (Schuster, 1968, fig. 53: 1–3). The leaves are 2–3-lobed and transversely to weakly succubously inserted. The lobes are short and distinctly tapering, constricted at the septa (ibid., fig. 53: 4–6). The underleaves are 2–3-lobed (Schuster (1968, fig. 53: 1). The first branch underleaf is asymmetrically bilobed, the longer lobe resembling a leaf lobe, the shorter an underleaf lobe. The stem cross sections of *T. pseudozoopsis* illus-

trated by Schuster (1968, fig. 53: 7, 8) show a 6+10 anatomy as well as 8+13; Herzog (1942, fig. 5d) illustrates 8+17. The androecia and gynoecia are described here for the first time.

For a comparison between this species and *T. nivicola* of New Zealand see Schuster (1968, figs. 52, 53).

ECOLOGY—Rather common in the Falklands, typically in moist, shaded situations (moist rock crevices, stream banks, etc.) in dwarf shrub heaths, *Hebe* associations, and (more rarely) in *Cortaderia* heaths. It is rather common on the bases of tussock grasses in tussock associations. For details of Falkland Island phytosociology, see Engel (1990). In southern South America the species occurs primarily in forests, creeping over soil on banks or cliffs, or the upper parts of stream banks (e.g., beneath the overhang of the forest edge), and seems to “prefer” well-shaded, protected niches such as pockets of banks or under rock of cavelike overhangs. On Isla Bayly (in Antártica Chilena), it occurred 1–2 m above sea level in a dripping vertical bank of bryophytes within a cavelike, moist recess formed in bedrock at the base of a steep cliff. The site is at an exposed shoreline with dripping vertical rock walls and a bryophyte-covered overhang formed by the forest margin above. The species rarely is corticolous on branches (Engel 5078). It is present at or near sea level in the Magellanian zone in forests, e.g., of *Drimys*, *Nothofagus betuloides*, *Berberis ilicifolia* and *Pernettya* at Bahía Tuesday (Isla Desolación). The species is able to tolerate some exposure, for example, in the Brunswick Peninsula it occurred on the side of a bryophyte mound in an open area rich in bryophytes (the “bryophyte rich facies” as discussed in Engel, 1978, p. 13). In the Valdivian zone it occurs from sea level to as much as 1600 m in forests of, e.g., *Nothofagus dombeyi* and *Saxegothaea* in the Río Nauto valley (Refugio Antillanca area). This species extends to higher elevations than any other southern South American *Telaranea* species, occurring at 1450–1600 m on the southwest slope of Volcán Quetrupillán (Prov. Valdivia) in an alpine-subalpine ecotonal area consisting of scattered patches of *Nothofagus pumilio* with a stream and late-melt snow.

SELECTED SPECIMENS SEEN—FALKLAND ISLANDS: East Falklands, Mt. Usborne, The Gap, 275–290 m, Engel 2461—c.  $\delta$  + per. (MSC). CHILE. PROV. ANT-ARCTICA CHILENA: Comuna Cabo de Hornos, Islas Wollaston, E side of Isla Bayly at S entrance to Canal Washington, 1–2 m above sea level, Engel 25728 (F); ibid., Isla Hoste, Península Hardy, Bahía Orange, Caleta

Mision, sea level, *Engel* 25692 (F). PROV. MAGALANES: S shore of Bahía Pond (Isla Clarence, Strait of Magellan), *Engel* 6287 (MSC); Bahía Tuesday (Isla Desolación), head of inner harbor, *Engel* 5723A (F, MSC); Brunswick Peninsula, Puerto Cutter, slightly W of copper mine, *Engel* 2238—c. ♂ (F); Isla Tarlton, *Engel* 5078 (MSC). PROV. OSORNO: Valley of Río Nauto near road (km 10–11) to Refugio Antillanca, between Laguna El Encanto and Lago Toro, 730 m, *Engel* 4102A (MSC); along road below Refugio Antillanca, 915 m, *Engel* 3935 (F, MSC). PROV. VALDIVIA: S facing slopes of Cerro Tralcan, W of western end of Lago Rihue, 440 m, *Engel* 10950 (F); Fundo Santa Rosa, 8 km by road N of Puente Callecalle, near sea level, *Engel* 12246—c. per. + ♂ (F); SW slope of Volcán Quetrupillán, immediately SW of Laguna Los Patos, Forestal Trafún, 1450–1600 m, *Engel* 11145 (F); 2.1 km by road N of Mehuín, S of Queule, ca. 15 m, *Engel* 11408 (F).

*Telaranea rectangularis* Schust.

*Telaranea rectangularis* Schust., *Phytologia* 39: 241. 1978. Holotype: Venezuela, Estado Merida, above Río Frias, Sierra Nevada de Merida, *Schuster & Ruiz-Teran* 76-1480 (F).

ILLUSTRATION—Schuster (2000, fig. 71).

DISTRIBUTION—Venezuela.

This species was described as related to *T. capilligera* (Schuster, 1978), but judging from the recently published illustration (Schuster, 2000, fig. 71) is clearly a member of sect. *Cancellatae*. Schuster's illustration of *T. rectangularis* is somewhat suggestive of *T. autoica* of Juan Fernández, particularly in the form of the leaves and the dentition of the perianth mouth. The species is evidently dioecious, since sporophytes were present, but only females are described. If the Venezuelan plant were *T. autoica* the males could hardly be missed.

The spores are reticulate-areolate (Schuster, 2000, fig. 71: 12) and the capsule wall 2–3-stratose (loc. cit., fig. 71: 10).

*Telaranea redacta* (Steph.) Engel & Merr., comb. nov.

*Lepidozia redacta* Steph. in Mildbraed, *Wiss. Ergebn. Deutsch. Zentr.-Africa Exped.* 2: 119. 1911. Lectotype (*nov.*): Deutsch Ost Africa, Ostrand des Centr. Afr. Grabens, Wald Moor, 1900 m, Exp. Ad. fr. v. Mkb. [Duke Friedrich of Mecklenburg, leader of the expedition], 814 (G!), *sub nom.* *L. "reducta"*.

*Lepidozia chaetophylla* var. *tenuis* Pears., *Chr. Videns. Selsk. Forh.* 1886 (3): 7. 1886, *syn. nov.* Lectotype (*nov.*): South Africa, Natal, near Umpumulo, 27 June 1882, *E. Bertelsen* 132, ex hb. Kiaer (BM—c. sporo.!).

ILLUSTRATION—Pearson (1886, pl. 5, var. *tenuis*). Stephani, *Icones, Lepidozia* 14.

DISTRIBUTION—South Africa, Zambia, Rwanda, Kenya, Ghana.

This species was listed as a synonym of *T. nematodes* by Wigginton and Grolle (1996). However, the distinctive features of *T. redacta* include the crooked, “zig-zag” branches (“anfractus” in Stearn, 1966), leaf insertion varying from transverse to succubous and a tendency for divisions of one or more of the basal cells of the lobes, forming a rudimentary disc. The leaf lobes are biseriate at the base, frequently with an additional biseriate tier, and the uniseriate portion distinctly constricted at the septa, the cells with a faintly roughened cuticle. The perianth (type of var. *tenuis*) is substipitate, pale, membranous, subcylindrical, eplicate, with a few cilia at the mouth, the mouth not at all constricted.

Pearson (1886) described *Lepidozia chaetophylla* var. *tenuis*, based on a collection from Natal, South Africa, leg. Bertelsen, listing as a synonym *Cephalozia nematodes*, which he regarded as a variety of *L. chaetophylla* Spruce. Pearson's description and illustration (*ibid.*, pl. 5), however, are based on the Bertelsen plant, “Hab. On stones by the river near Umpumulo” (“in saxis ad flumen” on label). *Lepidozia "reducta"* (Stephani, 1922) is apparently only an error for *L. redacta*.

SPECIMENS SEEN—SOUTH AFRICA: Transvaal, Mariepskop, S aspect of mountain summit, vertical stone ledges along streamside in full shade, 1890 m, *Vorster* 949 (PRE). ZAMBIA (Northern Rhodesia): Near ?Luwingu, *Angus* 1936 (E). KENYA: Aberdares, above Katutu Waterfall, 3030 m, *Townsend* 75/904(c) (E). GHANA: Atewa Range, 610 m, *Richards* R6322—c. ♂ (E).

*Telaranea rosarioana* H. A. Mill.

*Telaranea rosarioana* H. A. Mill., *J. Bryol.* 14: 240. f. 4: d–m. 1986. Holotype: Fiji Is., Vanuatu, Espirito Santo Is., summit of Mt. Patliu, *Miller* 15993 (MU!).

ILLUSTRATION—Miller (1986, fig. 4: d–m).

DISTRIBUTION—Endemic to Fiji Is.

The leaves of both the main shoot and branches are bilobed and incubous (the branch leaves strongly so), and the lobe bases are biseriate and united for about half (0.5–0.7) their length, occasionally with a transverse wall in one or more of the basal cells. The branches are complanate (see Miller, 1986, fig. 4: d) and the cuticle punctate. Miller compared this species with *T. panchoi*

(p. 177), but the branches in that species are evidently not flattened and the cuticle is described as smooth. The half-leaves of *T. rosarioana* are undivided with a biseriate basal tier; the first branch underleaf is inserted on the ventral side of the branch at its base, and undivided, with a single basal cell, a narrowly cylindrical cell and a slime papilla.

### *Telaranea sejuncta* (Ångstr.) S. Arnell

*Blepharostoma sejunctum* Ångstr., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 1876 (7): 78. 1876 ("sejuncta"). *Lepidozia sejuncta* (Ångstr.) Steph., Spec. Hep. 3: 563. 1909. *Telaranea sejuncta* (Ångstr.) S. Arnell, Bot. Not. 110: 18. 1957. *Arachniopsis sejuncta* (Ångstr.) Schust., Nova Hedwigia Beih. 118: 452. 2000. Lectotype (*nov.*): Brazil, Caldas, Regnell (S!—*c. sporo.*); isoelectotype: (S!—*c. per.*).

*Cephalozia confervifolia* Gott. ex Aust., Bull. Torrey Bot. Club 6: 302. 1879, *syn. nov.* *Arachniopsis confervifolia* (Gott. ex Aust.) Howe, Bull. Torrey Bot. Club 29: 288. 1902. Isotype: Cuba (Hepaticae Cubanenses Wrightianae), Wright, (DUKE! [3]).

*Arachniopsis coactilis* var. *filifolia* Spruce, On Cephalozia: 85. 1882. *Arachniopsis diacantha* var. *filifolia* (Spruce) Pócs in Vána, Proceedings of the Third Meeting of the Bryologists from Central and East Europe, p. 114. 1984. Type: Brazil, "ad Panurê fluvii Uaupés," Spruce (*non vidi*).

ILLUSTRATIONS—Fulford (1963a, figs. 132, 133, 135, 138–41, *B. sejunctum*, type); Fulford (1966, fig. 52: 1a, d); Fulford (1968, pl. 96, fig. 2e, f, var. *filifolia* type); Schuster (2000, fig. 192, as *A. confervifolia*); Fig. 57. Fulford's drawing (1963a, fig. 147) of a 4-lobed leaf from a plant from Dominica is a species of sect. *Telaranea*.

DISTRIBUTION—Brazil, Cuba. None of the published statements of distribution can be relied upon (see below). Reported (as *A. confervifolia*) from Guadeloupe by Pagan (1942). *Telaranea sejuncta* is reported for Tasmania by Stephani (1909), almost certainly in error.

Plants lax and delicate, the cells collapsed when dry. Only ventral-intercalary branching observed, leafy. Stems fragile and delicate, the cortical cells short-rectangular, firm walled, in cross section in 6 rows, their exposed wall thickened; medullary cells in 3 rows, smaller, thin-walled. Shoots with 3–4 cortical cells intervening between successive leaves on either side. Rhizoids often produced from cells of the underleaves and from distal cells of the leaf lobes. Leaves laxly spreading, the insertion transverse to weakly succubous (Fig. 57: 1), asymmetrically bilobed or at times monocru-

rous. Lobes rather flaccid, uniseriate to the base, often unequal in length, the dorsal lobe 9–12 (14) cells long and 1–2 cells longer than the ventral, the ventral lobe more slender (particularly at the base) and often producing rhizoids from its tip. Lobe cells short and rather turgid in appearance, the basal cells (29) 42–50  $\mu\text{m}$  wide  $\times$  (78) 85–94 (114)  $\mu\text{m}$  long, the next cell 42–48  $\mu\text{m}$  wide  $\times$  (72) 88–96  $\mu\text{m}$  long, the terminal cell small, elliptical, at times becoming detached; lobe cells thin-walled and rather delicate, the transverse septa not or scarcely thickened in the corners and the lobes distinctly constricted at the septa (submoniliform); cuticle smooth to faintly striolate. Underleaves small and inconspicuous, bifid, consisting of two basal cells, each with 1–2 curved cylindrical cells(s), terminating in a slime papilla.

Autoecious. Androecia terminal or becoming intercalary in position on leading shoots, second, the bracts strongly dorsally assurgent, with the dorsal lobe biseriate at the base; bracts bilobed, the basal cells coherent to about 0.6 their length, both lobes with a geminate base or the bracts asymmetric, with the ventral lobe uniseriate to the base. Antheridia solitary, the stalk uniseriate. Gynoecia on short ventral-intercalary branches; bracts with a low disc, 1–1.5 cells high, the lobes with a geminate base and 1–2 additional biseriate tiers in some lobes, the uniseriate row 8–10 cells long.

The concept of *Telaranea sejuncta* adopted here differs from almost all previously published applications of the name. It was equated with *T. nematodes* (sect. *Telaranea*) by Arnell (1963) and Fulford (1963a, 1966), and this synonymy has been widely adopted. *Telaranea sejuncta* is probably widely distributed in the Neotropics, but all published statements of distribution, descriptions and illustrations of "*T. sejuncta*" (apart from the type) are suspect, since they may include some or all of the taxa formerly included in "*T. nematodes*" (see p. 171), as well as *T. diacantha*, when in fact, it is none of these.

According to Grolle (1975, p. 490), *T. sejuncta* is conspecific with *A. diacantha*. Based on an examination of the types of both species, however, *T. sejuncta* differs from *T. diacantha* in several important respects. Chiefly, *T. sejuncta* has short, inflated lobe cells, as much as 50  $\mu\text{m}$  in diameter, and the lobes are distinctly contracted at the septa (Fig. 57: 2–6). By contrast, *T. diacantha* has elongate, subcapillary lobe cells (Fig. 46: 6, 7), which scarcely exceed 24  $\mu\text{m}$  in diameter. In addition,

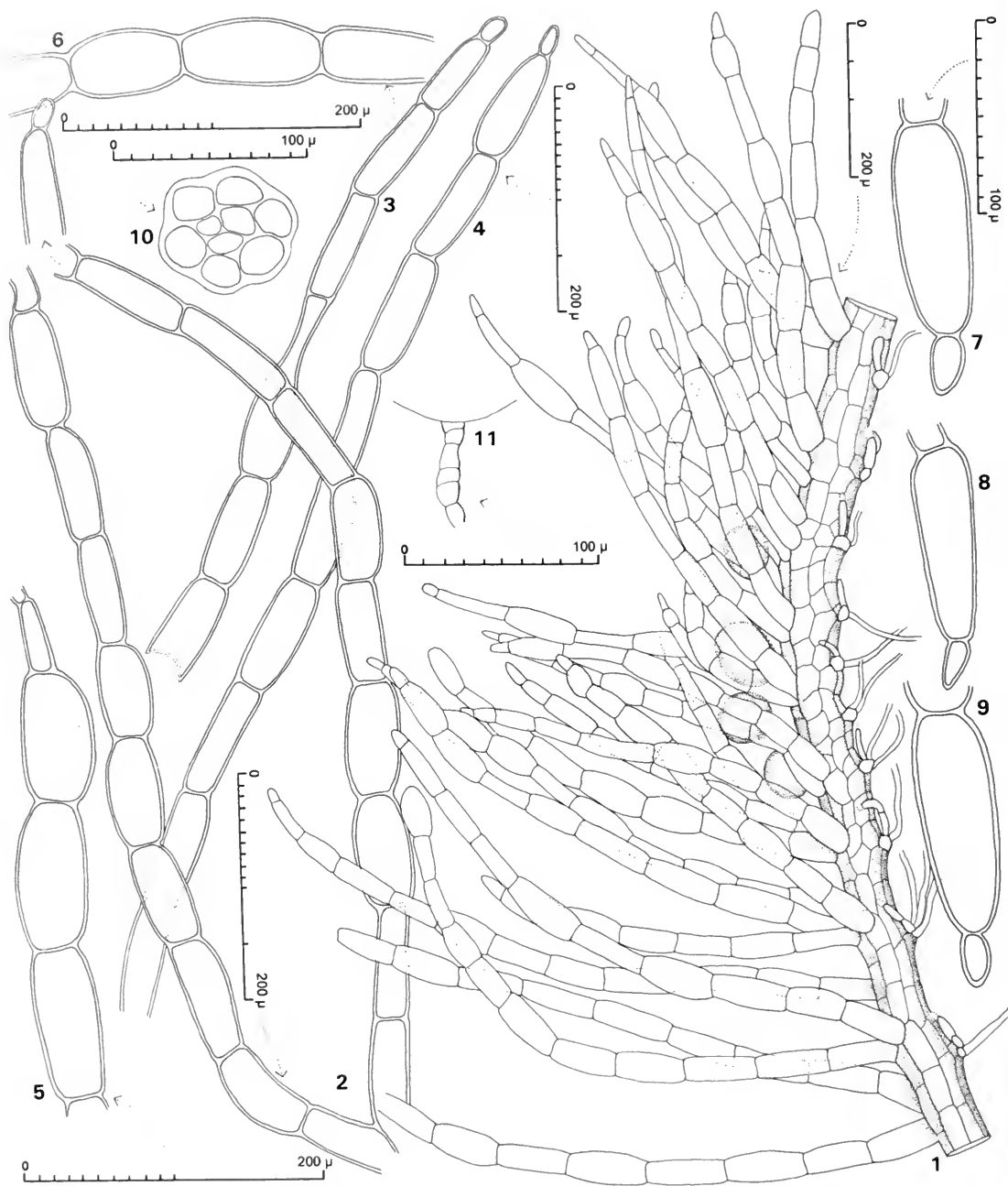


FIG. 57. *Telaranea sejuncta* (Ångstr.) S. Arnell. 1. Portion of shoot, lateral view, showing an intercalary androecium. Note subisodiametric cortical cells in region of androecium vs. elongate cortical cells in vegetative sectors. Note also variation ♂ bract bases, i.e., both lobes geminate at base vs. bracts with 1 lobe geminate at base + the other lobe uniseriate throughout. Note the weakly succubous insertion of both leaves and ♂ bracts. 2. Leaf. 3, 4. Leaf lobes. 5, 6. Portions of leaf lobes showing turgid cells. 7–9. Lobe tips; note minute terminal cell. 10. Stem, cross section. 11. Antheridial stalk. (All from type of *Blepharostoma sejunctum* Ångstr.)

*T. diacantha* appears to be dioecious, whereas *T. sejuncta* (and *T. coactilis*) are monoecious.

*Telaranea coactilis* and *T. sejuncta* (including *A. confervifolia*) are treated here as distinct, although they are alike in being autoecious and having cells of the leaf lobes short and rather broad in proportion to their length. The lobe cells are comparable in width, but somewhat shorter (1.5–2:1 vs. 2–3.5:1 in *T. coactilis*). In both species the insertion of the leaf lobes is usually weakly but plainly succubous, with 3–4 cortical cells between leaves on each side of the stem, and the lobes tend to be of unequal length, the dorsal lobe 1–2 cells longer than the ventral. Howe (1902) recorded lobes up to 14 cells in length in the type of *A. confervifolia*, but typically the lobes are 10–12 cells long. In *T. sejuncta* the basal cell of the ventral lobe often appears more slender than its dorsal counterpart.

According to Howe (1902, p. 289), the type of *A. confervifolia* is “essentially identical with the typical *A. coactilis*,” although he allows that plants of the former are more “flaccid” than those of *T. coactilis*. The lobe cells in *T. sejuncta* are thin-walled and delicate (vs. moderately thick walled and firm in *T. coactilis*), and in *T. sejuncta* the lobes are distinctly constricted at the septa and submoniliform.

In the type of *T. sejuncta*, an androecium was observed in an intercalary position on a leading shoot, which had a gynoeceum borne on a ventral-intercalary branch near its base. The stem in the androecial sector is noticeably thickened and the cortical cells isodiametric (Fig. 57: 1; see Fulford, 1963a, fig. 139, also drawn from the type). Male bracts resemble leaves of sect. *Telaranea* species in having both lobes with a geminate base, or the bracts may be asymmetric, with the ventral lobe uniseriate to the base (Fig. 57: 1). Androecia and perianths are abundant in the type of *T. confervifolia*, but we could demonstrate a physical connection only once, a result of the delicacy of the plants, which form thin, intricately interwoven mats on fragments of bark. The androecium was at the tip of a leading shoot and the gynoeceum a short distance further down the same shoot, on a short ventral-intercalary branch. Schuster (2000, p. 455) says *A. confervifolia* is dioecious; we can confirm Howe’s observation that the type is monoecious. By comparison, the androecia in the type of *T. coactilis* were borne on short ventral-intercalary branches in close proximity to the gynoeceal branch.

Fulford’s (1963a) illustrations of *T. sejuncta*,

“drawn from a portion of the type (G)” suggest a mixture of two different species. One is *T. sejuncta*, as understood here, while the other is a species of sect. *Telaranea* with short, tapering leaf lobes, leaf lobes geminate at the base (fig. 134), and a stem cross section of 9 + 16 cells (fig. 137).

Schuster’s (2000) disposition of *T. sejuncta* is unclear. He appears to accept both *T. diacantha* and *T. sejuncta* as distinct (see *Arachniopsis* key, p. 451), although in a footnote he says “*A. diacantha* and *A. sejuncta* may prove to be identical.” On p. 452, he refers to “weak phases of *A. sejuncta* [including the type of *A. coactilis*],” but his fig. 191, drawn from the type of *A. coactilis*, is labelled *Arachniopsis diacantha*.

Stephani’s (1909) *Lepidozia sejuncta* included *L. bicurvis* (p. 125) as a synonym. The leaves as described by Stephani are 2–3-lobed to the base, the lobes 6 cells long and biseriate at the base. Vanden Berghen (1973) listed *T. sejuncta* from Gabon, and refers to another report from Zaire by Pearson. The plant illustrated as *T. sejuncta* by Vanden Berghen (1972, fig. 1) is a species of sect. *Telaranea*, with lobes biseriate at the base. As in many species of that section (*T. longifolia*, Fig. 51: 1) the terminal, *Frullania*-type branches are *Arachniopsis*-like, with lobes uniseriate to the base (fig. 1: A, B).

SPECIMEN SEEN—BRAZIL: Sao Paulo, near Rio Grande on “Sao Paulo Railway,” 800 m, *Schiffner* as *Telaranea sejuncta* (Crypto. exsicc. Mus. Hist. Nat. Vin-dobon. no. 4400) (F).

*Telaranea semperiana* (Steph.) Del Ros.

*Lepidozia semperiana* Steph., Spec. Hep. 3: 612. 1909. *Telaranea semperiana* (Steph.) Del Ros., Philipp. J. Sci. 100: 238. 1973 (1971). Lectotype (nov.): Philippines, Luzon, *Semper* (G!).

ILLUSTRATIONS—Del Rosario (1973, figs. 39–42, type). Stephani, Icones, *Lepidozia* 245.

DISTRIBUTION—Philippines, Sri Lanka (Ceylon). Reported from Borneo (Mizutani, 1974).

Plants irregularly 1(2)-pinnate with a straggling appearance, the branches elongate, terminal, *Frullania* type, the half-leaf bilobed; first branch underleaf undivided and ventral lateral or median in position at the branch base. Ventral-intercalary branches common, often becoming leading shoots. Stem cortical cells in surface view thick walled, in section much larger than the medullary cells, in 12–15 rows, thick-walled and firm, the

medullary cells ca. 45, with incrassate walls. Leaves of the main shoot approximate to weakly imbricate, subtransversely to weakly incubously inserted, 4-lobed. Leaf lobes biseriate at the base, with a uniseriate row 7–11 cells long, constricted at the septa, the lobe cells thin (type) to thick walled, ca. 2:1 or a little longer, becoming gradually shorter toward the tip, the terminal cell about the same length as the penultimate cell, broadly rounded at the summit; cuticle densely papillose, the papillae small and well defined (type) or cuticle smooth. Disc two cells high, with a single tier of cells plus the basal cells of the lobes, the cells thin-walled (type) to rather thick-walled and rounded, with distinct trigones. Branch leaves resembling the stem leaves, densely imbricate, incubous, 4-lobed, the disc two cells high, the lobes with a uniseriate row of 6–9 cells. Stem underleaves various, 4-lobed, the lobes all short, or with the lateral lobes to 6 cells long and the median pair short, terminating in a slime papilla, the disc 2 cells high; branch underleaves 2–3-lobed, the lobes with a uniseriate row up to 10 cells long, when 3-lobed the branch essentially isophyllous, when 2-lobed the underleaves distinctively pincer-like in appearance.

Androecia on ventral-intercalary branches or at the tips of  $\pm$  elongate *Frullania*-type branches, rather loosely bracteate, the bracts subfoliose, 2–3-lobed to 0.5, the lobes caudate, 4 cells wide at the base, followed by a biseriate tier of cells and a uniseriate row 6 cells long, the disc 2–3 cells high. Gynoecia not seen.

*Telaranea semperiana* and *T. lawesii* are notable for the length of the uniseriate row of the leaf lobes, up to 11 cells in length. As in many species of sect. *Transversae*, the underleaves of *T. semperiana* are often unequally lobed, a type of underleaf usually associated only with *Kurzia* species (see p. 231). See Mizutani (1974) for remarks on this species, based on an examination of the type, in the form of a key differentiating this species from *T. lawesii* and *T. neesii*.

The type consists of somewhat flaccid shoots; the disc and lobe cells are thin-walled vs. rather thick-walled in the Meijer plant cited below. The disc cells of the type, however, have minute trigones.

SPECIMENS SEEN—SRI LANKA (CEYLON): ex hb. Jack, syntype of *L. semperiana* (G); Radrapura District, Morapitiya Forest Preserve, *Meijer 2041*—c. ♂ (F).

## *Telaranea seriatitexta* (Steph.) Engel

*Lepidozia seriatitexta* Steph., Bih. Kongl. Svenska Vetenskapsakad. Handl. 26 (III, 6): 53. 1900. *Neolepidozia seriatitexta* (Steph.) Fulf., Mem. New York Bot. Gard. 11: 215. 1966. *Telaranea seriatitexta* (Steph.) Engel, Bryologist 79: 514. 1976. Type: Chile, Prov. Magallanes, Isla Newton, *Dusen 21* (G!, NY!); Seno Molyneux, June 1896, *Dusen 62* (NY!); Prov. Chiloë, Isla Guaitecas, April 1897, *Dusen 396* (NY!).

*Lepidozia husnotii* Steph., Spec. Hep. 6: 329. 1922 ("Husnoti"). *Neolepidozia husnotii* (Steph.) Fulf. & J. Tayl., Brittonia 11: 85. 1959. Type: Chile, "Fretum magellanicum," *sin. coll.*, ex hb. Husnot (G!).

DESCRIPTIONS—Stephani (1909); Fulford (1966).

ILLUSTRATIONS—Fulford (1966, pl. 46, fig. 2, type of *L. seriatitexta*). Stephani, Icones, *Lepidozia* 141, 157 (*L. husnotii*).

DISTRIBUTION—South Georgia; Southern South America (Magellanian and Valdivian zones north to 40° 07' S). Reported for New South Wales by Watts (1902), almost certainly in error.

Plants irregularly once-pinnate, typically whitish pale green, dull, glaucous and distinctly water repellent; branches terminal, *Frullania* type, short or at times whiplike and flagelliform throughout; branch half-leaves bifid; first branch underleaf laminar and undivided (very rarely bilobed), ventral-lateral in position at branch base; ventral-intercalary branches occasional, leafy or stoloniform. Leaves strongly decurved when dry, the margins broadly inflexed, contiguous to imbricate, when moist plane to distinctly convex and with lobes inflexed, symmetrically to more typically asymmetrically 4-lobed to 0.4 (median sinus), often bisbifid, the dorsal lobes  $\pm$  paired, the insertion incubous, becoming somewhat hooked at dorsal end, often somewhat decurrent at ventral end; branch leaves 3–4-lobed. Lobes acute, somewhat tapering, 3–4 cells wide at base, with up to 3(4) biseriate tiers and a short uniseriate row of 2–3 cells. Disc asymmetrically cuneate, the dorsal margin often distinctly curved and sinuate, the ventral margin straight to incurved and somewhat decurrent, the disc 6–9 cells high, 8–10(12) cells wide in basal portion, (10)14–16(21) cells wide distally; disc cells  $\pm$  evenly thick-walled and firm,  $\pm$  isodiametric below, 48–62  $\mu$ m wide, short rectangular and 31–39  $\mu$ m wide in upper portion as a result of additional divisions; cuticle distinctly glaucous, the cell surface typically appearing fine-



ly granular at high magnifications. Underleaves somewhat smaller than the leaves but rather leaf-like in appearance, 1.5–2.2× stem width, ± erect to weakly spreading, plane, 4-lobed to 0.5, the lobes narrowly acute to subacuminate, 2–4 cells wide at base and biseriate for 1–3 tiers, ending in a uniseriate row of 2–3 cells, terminating in a slime papilla, or the lobe blunt, lacking a uniseriate row and ending in two paired cells; disc symmetrically broadly cuneate (wider than high), 3–5(6) cells high (median sinus), 11–12(14) cells wide at widest point. Rhizoids produced from distal tier of disc cells and basal cells of lobes.

Androecia on abbreviated terminal, *Frullania*-type branches and short ventral-intercalary branches, tightly spicate and somewhat curved, the bracts in 4–5 series, distinctly concave, 2–3-lobed to ca. 0.3, the dorsal margin at times with a tooth with a terminal slime papilla, the lobes broadly acute; antheridia 1 per bract, the stalk uniseriate. Gynoecia on short ventral-intercalary branches; bracts in 3 series, the outermost lobulate, the inner broadly ovate, with 3–4 broad teeth, the tooth margins crenulate, the marginal cells ± sinuous and crowded, the lamina margins weakly and irregularly crenulate, the marginal cells elongate and overlapping, forming an indistinct border. Perianth long-cylindrical, bluntly trigonous below, narrowed and deeply plicate in upper third, the mouth sinuous-crenulate, the cells elongate and sinuous like those of the margins of the bracts; perianth 3–4(5)-stratose in basal portion.

Seta rather short, the capsule exerted a short distance beyond the perianth mouth, in cross section with 8 large outer cells and an inner core of ca. 28 cells. Capsule oblong, 560 × 1435 µm, the valves 4- or locally 5-stratose, 37–38 µm thick, the outer layer about ½ the thickness of the valve; outer layer of cells ± uniform, rectangular, with two-phase development, the wall thickenings confined to the secondary longitudinal walls, continuous, sheet-like, pigmented, with nodule-like to short spine-like projections, the primary (first phase) longitudinal and transverse walls entirely devoid of thickenings; inner layer of cells narrowly rectangular, the longitudinal walls with thin continuous sheets of wall material, the semianular bands mostly complete but narrow and widely spaced, only sporadically incomplete.

Spores 12–14.4 µm in largest diam., reddish brown, papillose-vermiculate, the surface marked by closely spaced irregular ridges which only sporadically coalesce to delimit areolae. Elaters near-

ly straight, 12–13.4 µm wide, only slightly tapering and loosely bispiral to the tips, the spirals 3.8–4.3 µm wide.

*Telaranea seriatitexta* differs from *T. oligophylla* primarily in the more deeply lobed leaves, with broad-based medium acute lobes, and disc becoming 10–16(21) cells wide distally. The leaves in *T. oligophylla* (Fig. 54: 1–4) have abbreviated lobes, 2(3) cells wide at the base with a single terminal cell or a short uniseriate row of 2 cells, and the disc is ± parallel-sided and 8 cells wide throughout. The leaf labeled “Fretum magell. Husnot” in Stephani’s *Icones* 141 is *T. oligophylla*. For differences between *T. seriatitexta* and *T. disticha* of Juan Fernández, see comments under the latter species.

Apart from the glaucous cuticle, *T. seriatitexta* is remarkably like *T. consobrina* of Tasmania, in particular the asymmetric leaves with broad-based lobes (Fig. 8: 1–5, *T. consobrina*), the dorsal lobes often paired; the broad, undivided first branch underleaf (Fig. 8: 6, 8); and the large underleaves, which are similar in appearance to the leaves (Fig. 8: 6, 7).

*Telaranea seriatitexta* is placed in sect. *Cancellatae*, notwithstanding the glaucous cuticle. Another species in this section, *T. grossiseta* of Tasmania, is also glaucous and water repellent, but with these two exceptions, glaucous taxa are limited to sect. *Ceraceae*. Capsule valves 4–5 cells thick condition are found in *T. plumulosa*, and 5-stratose valves are reported in *T. pulcherrima*, both species of sect. *Tricholepidozia*; capsule valves in *T. tetrapila* (sect. *Cancellatae*) are typically 4-stratose, while those of *T. seriatitexta* are 4- and only locally 5-stratose.

ECOLOGY—In southern South America rather common but not abundant in the Magellanian and Valdivian zones north to 40° 07' S. Typically a forest species, the species occurs on very rotted, decorticated logs and stumps particularly where soil and other bryophytes have accumulated, and may be admixed with *Leptoscyphus aequatus*, *Acromastigum laetivirens*, *Riccardia* sp. and *Adelanthus* sp. (Engel 4961D, Puerto Alert). Also on bryophyte-covered tree trunks, e.g., admixed with *Schistochila laminigera*, *Adelanthus lindenberghii*, *Acromastigum anisostomum*, *Leptoscyphus* sp. and *Riccardia* sp. on *Nothofagus dombeyi* (Engel 4056G, Refugio Antillanca), over soil of the forest floor, rather frequently in protected hollows, and on soil of stream banks. The species only rarely occurs over rock. In the southern part of its range

it occurs at sea level, but is present at increasingly higher elevations northward. It is present at or near sea level in Prov. Magallanes, and occurs, for example in forests of *Nothofagus betuloides*, *Berberis ilicifolia* and *Desfontainea* in a very shaded ravine at Puerto Churruca (Isla Desolación), or at the fringe of a dense mossy forest of *Drimys*, *Nothofagus betuloides*, *Pilgerodendron* and *Podocarpus* near the shore of Bahía Wide (Isla Juan). Northward found at sea level to 320 m in Prov. Chiloé, occurring, for example, in a mossy forest of *Drimys*, *Myrceugenia* and *Lauralia* at Puerto Ballena (Isla Mulchey). In Prov. Osorno the species was found at 400–885 m in, e.g., a forest of *Nothofagus dombeyi*, *Drimys*, *Podocarpus*, *Laurelia*, *Saxegothaea* and *Flotowia* at Lago Toro (Refugio Antillanca area). The species reaches the its highest known elevation (1000 m) in a *Fitzroya* forest at the summit of El Mirador on Cordillera Pelada (Prov. Valdivia).

SELECTED SPECIMENS SEEN—SOUTH GEORGIA: *Skoutsberg* as *L. oligophylla* (G). CHILE. PROV. MAGALLANES: Isla Desolación, Puerto Churruca, peninsula on N side of Fondeadero Nassau, *Engel* 5922 (F, MSC); N shore of Caleta Amalia, Fiordo Peel; *Engel* 5432 (F, MSC); E side of Isla Juan (Bahía Wide), near shore, *Engel* 5280—c. per. (F, MSC); Puerto Charrúa (S side of Isla Wellington), *Engel* 4855 (F, MSC); Puerto Alert (Isla Mornington), *Engel* 5026 (MSC); Puerto Edén (Isla Wellington, Canal Messier), *Engel* 4570 (MSC); near shore at SE point of Isla Williams (Bahía Tribune, Canal Messier), *Engel* 4504 (F, MSC). PROV. AISEN: Puerto Island (Península Swett), *Engel* 4319 (F, MSC). PROV. CHILOÉ: Puerto Ballena (Isla Mulchey), along shore of harbor, *Engel* 4187 (F, MSC); Isla Chiloé, Cocauque area, across Estero Yaldad from village of Yaldad, sea level, *Engel* 11979 (F); *ibid.*, Loncomilla (Alto de la Virgen), E of Cucao near SW end of Lago Cucao, 75 m, *Engel* 12128 (F); *ibid.*, Cordillera San Pedro, Río Puidi, near aserradero at San Pedro, 320 m, *Engel* 11877 (F); *ibid.*, Aguas Buenas area, 4.7 km. E along Aguas Buenas road from Ancud-Quemchi road, ca. 100 m, *Engel* 12194 (F). PROV. OSORNO: 12.1 km. by road below Refugio Antillanca, 550 m, *Engel* 11533—c. sporo. (F); just above Lago Toro, on road to Refugio Antillanca, 885 m, *Engel* 4056G (MSC); Agua Caliente, near falls, along Río Chanleufú, 4 km from Termas de Puyehue along road to Refugio Antillanca, 400 m, *Engel* 11458—c. ♂ (F). PROV. VALDIVIA: 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* 12282—c. ♂ (F); Cordillera Pelada, summit of El Mirador, near road between La Union and Punta Hueicolla, 1000 m, *Engel* 12402 (F).

*Telaranea setosa* Engel & Merr., sp. nov.

Species lobis foliorum brevis sinuosis sive tortilis,

cellulis seriei uniseriatae elongatis incrassatis cum septis projectis, disco 0.5 cellulas alto distincta.

Holotype: Chile, Prov. Valdivia, E slope of Cordillera Pelada, 7.1 km by road E of El Mirador on road between La Union and Punta Hueicolla, 840 m, *Engel* 12423 (F).

DISTRIBUTION—Chile (Valdivia; Magellanean, north of 50° 39' S in Prov. Magallanes).

Plants minutely prickly in appearance, loosely creeping as individuals over substrate or, occasionally, forming pure mats, whitish pale green, highly nitid and polished when dry. Branching of *Frullania* type very common, irregularly bipinnate, the branches occasionally becoming flagelliform, also becoming leading shoots; branch half-leaf bifid or undivided; first branch underleaf at base of branch, asymmetrically 2–3-lobed, the ventral 1 or 2 lobes smaller and parallel with branch, consisting of a pair of small basal cells and a uniseriate row of 2–3 cells, the dorsalmost lobe stiffly spreading, leaf-lobe like, consisting of a pair of small basal cells and a uniseriate row of 5–6 cells. Ventral-intercalary branching rather common, both stoloniform and leafy and becoming leading shoots. Stems appearing rather stout in relation to the size of the leaves, the branches more slender than the main shoot; stem cortical cells rather large, rectangular, thin-walled but firm, in section the cortical cells in 12 rows, much larger than the numerous (ca. 50), thin-walled medullary cells, the outermost ring of medullary cells somewhat larger than the internal ones. Leaves of the main shoot distant, transversely inserted, the insertion extending dorsally to the midline of the stem, leaves symmetrically to somewhat asymmetrically (3)4–5-lobed nearly to the base (ventral lobe at times a little longer), the lobes setaceous, variously spreading and oriented, the dorsalmost lobes suberect, straight or at times sinuous and even spirally twisted, the ventral lobe straight and often stiffly spreading  $\pm$  at right angles to the stem; branch leaves similar, (2)3(4)-lobed, the insertion extending dorsally to the midline of the branch. Leaf lobes divergent, bristle-like,  $\pm$  evenly tapering from the base, the uniseriate row 3–5(6) cells long, the dorsal lobe cells often individually (adaxially) arched, accounting for the sinuous appearance of the lobe, the septa thickened in the corners and straight or somewhat bulging; basal cell of the uniseriate row 24–37  $\mu$ m wide  $\times$  48–66  $\mu$ m to (type) 108–140  $\mu$ m

long, the next cell shorter, 20–29  $\mu\text{m}$  wide and up to 90–112  $\mu\text{m}$  long, the terminal cell about equal to the penultimate cell, but typically appearing secondarily divided; cuticle of lobe cells smooth or indistinctly roughened. Disc consisting of the paired, very short to  $\pm$  isodiametric basal cells of the lobes, the basal cells (particularly in the branch leaves) often incrassate. Underleaves 4(5)-lobed,  $\pm$  appressed to stem, the lobes consisting of 2–3 long, narrowly cylindric cells, hooked at the tip, ending in a terminal slime papilla; disc 1 cell high, becoming subdivided both transversely and vertically into as many as 4 tiers of rhizoid initials.

Androecia on short, determinate, *Frullania*-type branches, compactly spicate;  $\sigma$  bracts in 4 pairs, suberect, dorsally assurgent;  $\sigma$  bracts deeply concave, 2–3-lobed, asymmetric, the lobes 4 cells wide at the base, the uniseriate row of 3–6 firm-walled cells, occasionally with a biseriate tier, the disc 4 cells high dorsally, 2 cells high ventrally, occasionally with a small, 1-celled tooth in the sinus between lobes, the dorsal margin inflexed, with a prominent cilium 3–4 cells long; antheridia 1 per bract, the stalk uniseriate. Gynoecia on short ventral-intercalary branches, only young  $\text{f}$  seen.

The short, bristle-like leaf lobes with prominent septa and the often markedly thick-walled cells of the uniseriate row are highly distinctive. The lobes are widely spreading and oriented at odd angles, and the lobe cells (particularly in the dorsal-most lobes) are individually curved; consequently the lobes appear sinuous, or at times, even spirally twisted. The disc is 0.5 cells high, consisting of the short, often incrassate basal cells of the lobes. The underleaves of *T. apiahyna* are also large and 4(5)-lobed, with a disc one cell high, but this species and *T. setosa* are not likely to be confused. The basal paired cells of the leaf lobes in *T. apiahyna* are  $\pm$  elongate rather than nearly isodiametric, and the disc may be 1.5 cells long, with a partial or complete tier of disc cells along the insertion; some lobes may be more than 2 cells wide at the base, with additional biseriate tiers, and the uniseriate row is up to 7 cells long. Another unusual feature of *T. setosa* is that the outermost layer of medullary cells is weakly differentiated, the cells somewhat larger in diameter than the internal ones.

ECOLOGY—Known from several scattered localities, all at lower elevations north of 50° 39' S in Prov. Magallanes, as well as at sea level on Isla

Chiloé (Prov. Chiloé), and the type (the northernmost station) at 840 on Cordillera Pelada (Prov. Valdivia). In the southern portion of its range the species occurs in forests, for example, of *Drimys*, *Podocarpus*, *Pilgerodendron*, *Nothofagus betuloides* (Bahía Wide) or scrub forest of *Drimys*, *Weinmannia*, and *Blechnum* (Puerto Edén), while at the Cordillera Pelada site it grows in forests of mostly *Nothofagus* and *Drimys* with some *Saxegothea*. This species is able to tolerate considerable light, and occurs, for example, in a *Sphagnum* moor with *Marsippospermum* and scattered small *Nothofagus* (Puerto Edén), and in *Berberis-Pernettya* scrub along a river at the forest edge (Puerto Alert). The species grows on soil and may be admixed with *T. oligophylla*, *Leptoscyphus aequatus*, and *Plagiochila* spp. on stream banks, or with *Blepharidophyllum clandestinum* and *Riccardia* spp., or on tree bases under the overhang of exposed roots or (type) over litter of the shaded forest floor.

SPECIMENS SEEN—CHILE. PROV. MAGALLANES: Isla Chatham, N shore of Bahía Wide, *Engel 5305C* (MSC); Puerto Alert (Isla Mornington, Canal Trinidad), head of fiord W of Mte Markham, *Engel 4995* (F, MSC); Puerto Edén (Isla Wellington, Canal Messier), *Engel 4558—c.*  $\sigma$  (F, MSC). PROV. CHILOE: Isla Chiloé, Cocauque area, across Estero Yaldad from village of Yaldad, sea level, *Engel 11997A—c.*  $\sigma$  + young  $\text{f}$  (F).

*Telaranea tenuifolia* (Schust.) Engel & Merr., comb. nov.

*Arachniopsis tenuifolia* Schust., Nova Hedwigia Beih. 118: 461. f. 193B: 8–15, 193C. 2000. Type: Brazil, “Rio Negro, E of Santa Isabel,” *Schuster 79-8-187* (NY, cited in legend, fig. 193C).

ILLUSTRATIONS—Schuster (2000, figs. 193B: 8–15; 193C).

DISTRIBUTION—Brazil (Rio Negro).

Schuster (2000, p. 459) remarked, “*A. tenuifolia* is highly unusual in *Arachniopsis* (if it fits in that genus) in that, on the remote-leaved, leading stems one can find trifid leaves.” Several characters, including that of trifid leaves, are reminiscent of *T. chaetophylla* (sensu type). The main shoot has leaves wide-set, leaving the 2-cell wide median strip of cortical cells broadly exposed. The similarity to the leaf-free strip found on primary branches of *T. chaetophylla* is particularly striking (Fig. 42: 2). Both species have 3-fid leaves (occasionally in *T. tenuifolia*, 3(4)-lobed in *T. chaetophylla*), as well as an asymmetrical first

branch underleaf and an undivided half-leaf. Leaf (lobe) insertion in *T. tenuifolia* is distinctly incubous (Schuster, 2000, fig. 196C: 11, 12).

Androecial bracts (Schuster, 2000) are 2–3-lobed, with the uniseriate row of the lobes to 5 long; the disc is to 3 cells high. Antheridial stalks are uniseriate.

The capsule wall is 2-stratose. The outer capsule wall layer has a two-phase development: the longitudinal walls have thin continuous sheets of material and appear sinuous, alternating with walls devoid of thickenings (Schuster, 2000, fig. 193C: 1, 2). The inner layer has  $\pm$  irregularly spaced nodular to pale spurlike thickenings and occasional semiannular bands (Schuster, 2000, fig. 193C: 3). Capsule wall anatomy is thus identical to that of *T. chaetophylla* (Fig. 43: 10–12).

The seta in *T. tenuifolia* is 8+4 in section (Schuster, 2000, fig. 193B: 8). Schuster is “tempted to see a phylogenetic association” between this species and *Telaranea*, because of the occasional 3-fid leaves and *Frullania*-type branching, but dismisses these similarities as the result of “chiefly parallel reduction.” He describes the species as an *Arachniopsis* because an 8+4 seta “has never been seen in a *Telaranea*”; an 8+4 seta may also occur in *T. herzogii* (Fig. 36: 5).

**NOMENCLATURE**—This species is the type of *Arachniopsis* sect. *Tenuifoliae* (Schuster, 2000, p. 461). The status of the section is somewhat clouded by the fact that on p. 461, Schuster says that *A. tenuifolia* “surely deserves segregation into its own section,” but on p. 463, he refers to *A. diplopoda*, *A. dissotricha* and *A. tenuifolia* as “here placed in the Dissotrichae.” On p. 450, these three species are keyed together under “Sect. Dissotrichae.” Section *Tenuifoliae* is the only available sectional epithet in the *Arachniopsis*-group, and is provided with a Latin description and citation of a type species, *A. tenuifolia*, which is published in accordance with the ICBN. We are accepting the name sect. *Tenuifoliae*, but using it in a much broader sense, corresponding to the former genus *Arachniopsis*. The other two species, *A. dissotricha* and *A. diplopoda*, are assigned to here to *Amazoopsis* gen. nov. (p. 242).

#### *Telaranea trichocoleoides* (Herz.) Schust.

*Lepidozia trichocoleoides* Herz., Trans. Brit. Bryol. Soc. 1: 314, f. 31. 1950. *Telaranea trichocoleoides* (Herz.) Schust., J. Hattori Bot. Lab. 26: 256. 1963. Type: NW Borneo, Sarawak, Dulit Trail, ca. 750 m, Richards 2576 (JE!).

**ILLUSTRATIONS**—Herzog (1950, fig. 31); Piippo (1986, fig. 3a, b); Fig. 58.

**DISTRIBUTION**—Borneo, Papua New Guinea (Piippo, 1986).

Resembling *T. pulcherrima* of Australasia (p. 76) in almost all respects, with fanlike, 8–11-lobed leaves. The most startling feature of the species is the coarsely papillose cuticle of the leaf lobes, plainly visible in the type (JE!) even under the dissecting microscope. The papillae are guttulate (Stearn, 1966; Engel & Merrill, 1997): coarse, high, and spherical, resembling spherical droplets of oil or resin (Fig. 58: 3), a type unique in the genus. The disc cells and stem cortical cells are finely, longitudinally striolate (Fig. 58: 5).

Plants of *T. trichocoleoides* are bipinnately branched, with the aspect of a miniature *Trichocolea*, the primary and secondary branches terete and woolly, with densely imbricate leaves and matted, interwoven capillary leaf lobes. The stem cortical cells are similar in size to the medullary cells and ca. 24 in number (Fig. 58: 4), with 2 disc cells of the basal tier inserted on each cortical cell (Fig. 58: 4). Stem leaves in the type are somewhat distant, incubously inserted and distinctly decurrent ventrally, the insertion curved and becoming almost transverse in the dorsal half. Branch leaves are densely imbricate and  $\pm$  transversely inserted and the underleaves are similar in size and form to the leaves, a condition seen also in *T. kaindina* (p. 161). The septa of the leaf lobes are thickened in the corners, but the lobes are straight or weakly constricted at the septa (Fig. 58: 3). The tip cell of the leaf lobes is uniformly elongate, 12–18  $\mu$ m wide  $\times$  78–114  $\mu$ m long, and is parallel-sided or at most slightly tapered (Fig. 58: 3), the summit rounded. The leaf disc is 3 cells high in *T. trichocoleoides* (Fig. 58: 1, 2) vs. 4–5 cells high in the dorsal sector in *T. pulcherrima* (Fig. 25: 2, 3). The branch half-leaves are 4–5-lobed; the first branch underleaves are 2–3-lobed, inserted on the ventral side of the branch base.

One of the specimens examined (Kokawa & Hotta 2505) is a somewhat less robust plant with 6-lobed leaves, leaf disc 2 cells high, and papillae less strongly developed. Another (Kokawa & Hotta 2051) has the main shoots subsiphylous and similar in appearance to the branches, the stem leaves densely imbricate and  $\pm$  transversely inserted.

**SPECIMENS SEEN**—SABAH: Tenom, N ridge of Mt.

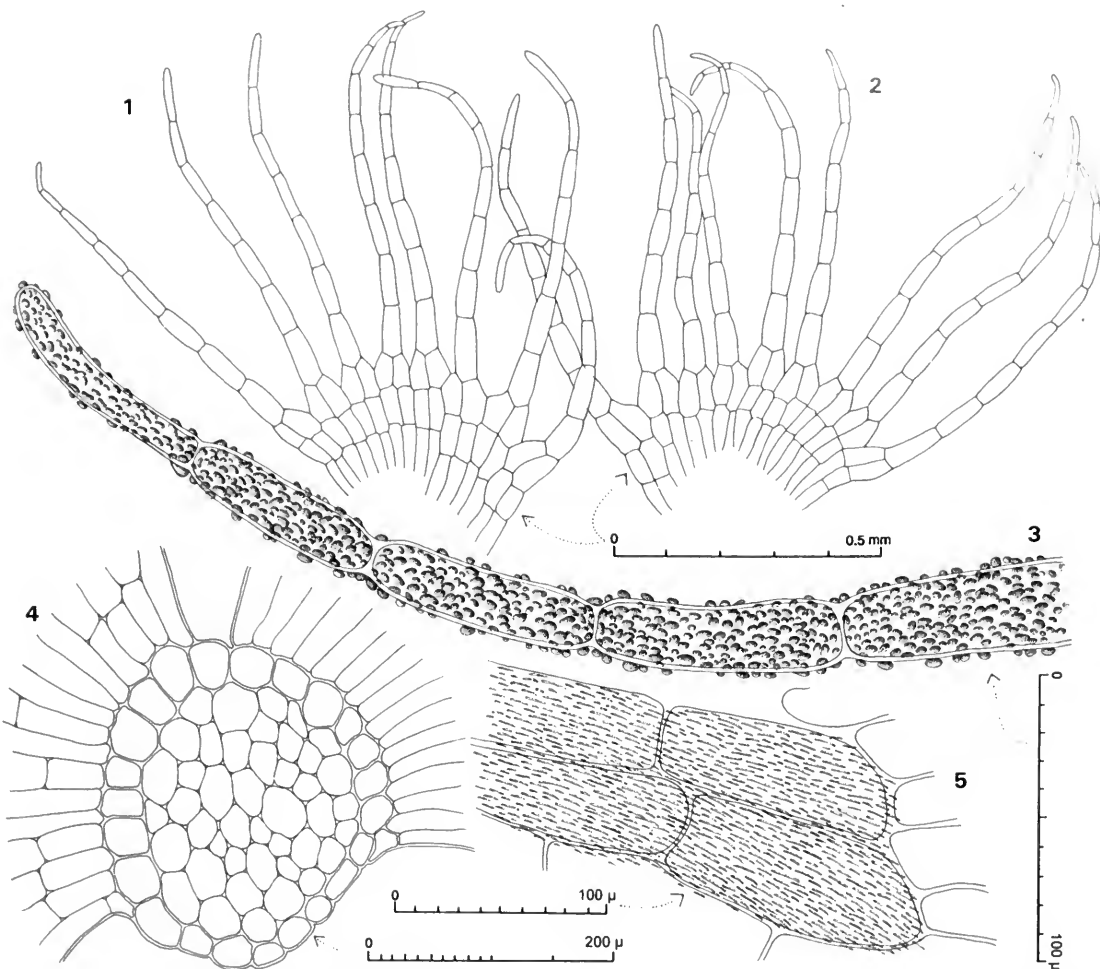


FIG. 58. *Telaranea trichocoleoides* (Herz.) Schust. 1, 2. Leaves (cuticle not shown). 3. Portion of leaf lobe showing papillae. 4. Stem, cross section, with basal row of cells of opposing leaves. 5. Stem cortical cells showing striae and, to right, outline of basal cells of leaf. (Figs. 1–3, 5 from type; 4 from *Kokawa & Hotta 2051*, Sabah, Penampang Gunong Alab.)

Malutut, about 15 km N of Tenom, *Kokawa & Hotta 2505* (OSA); Penampang, Gunong Alab, 1600–1930 m, *Kokawa & Hotta 2051* (OSA); Kinabalu National Park, eastern ridge, Poring, 600–1800 m. *Kokawa & Hotta 5105 bis* (OSA).

DISTRIBUTION—Known from the type (Rwanda) and from Zaire (Fischer, 1993), where it was collected only in swamps and peat bogs at 2330 to 2350 m, and from Uganda (Pócs and Lye, 1999).

#### *Telaranea trifida* (Steph.) Schust.

*Lepidozia trifida* Steph. in Mildbraed, Wiss. Ergebn. Deutsch. Zentr.-Afrika Exped. 2: 120, fig. 20. 1911, non *Lepidozia trifida* Steph., Spec. Hep. 6: 344. 1922, *hom. illeg.* (Art. 64.1) (New Caledonia). *Telaranea trifida* (Steph.) Schust., Hep. Anthoc. N. Amer. 1: 105. 1966; Beih. Nova Hedwigia 118: 211. 2000. Type: Rwanda, “Rugege-Wald: Waldmoor, 1800 m, (n. 813 ex parte)” (G!).

ILLUSTRATIONS—Stephani (1911a); Schuster (2000, fig. 79A). Stephani, *Icones, Lepidozia* 18.

Leaf insertion in the type of *T. trifida* varies from very weakly to distinctly succubous and the leaves are (3)4-lobed. The lobes are 3–4 cells wide at the base, just as in Stephani’s illustration, and the uniseriate row is 4–5 cells long. The disc is cuneate, 3–4 cells high, and the areolation is somewhat irregular. The half-leaf of *Frullania*-type branching is bifid, and the first branch underleaf is asymmetrically 2(3)-lobed (or only rarely undivided), with 1 lobe small and underleaf lobe-like, the other lobe large and leaf lobe-like.

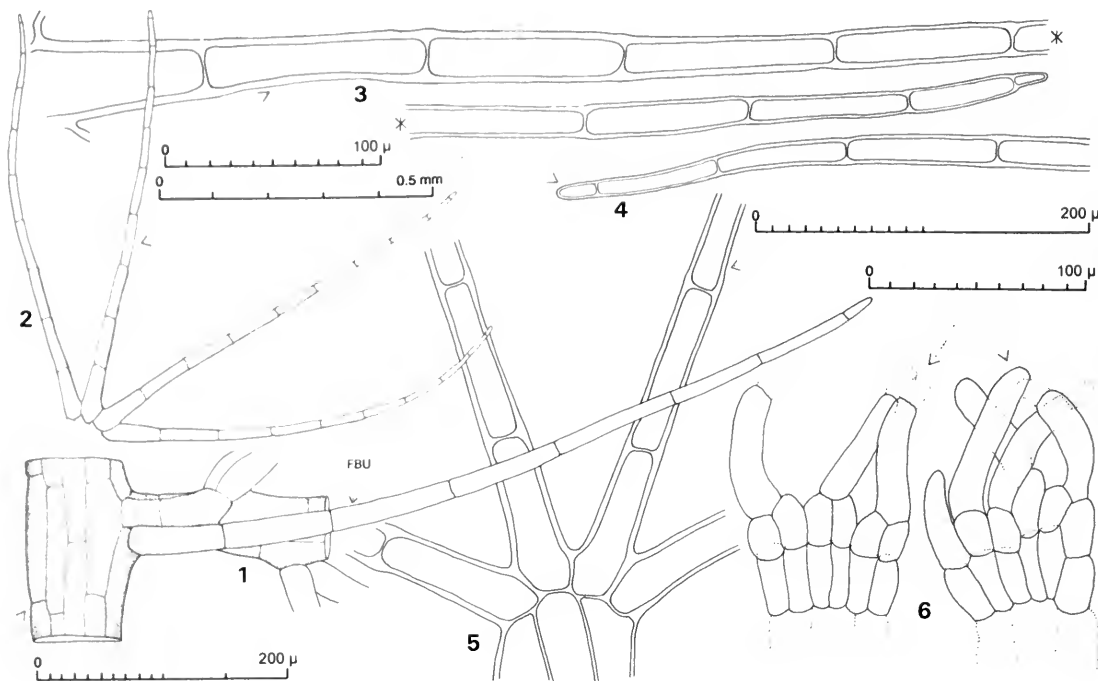


FIG. 59. *Telaranea trisetosa* (Steph.) Grolle. 1. Sector of main shoot showing base of terminal branch, ventral view (FBU = first branch underleaf). 2. Leaf. 3. Leaf lobe of 10 cells, the distal portion shown immediately below (joined at point indicated by asterisk). 4. Distal portion of leaf lobe. 5. Leaf base. 6. Underleaves. (All from Norris 59859, Papua New Guinea, Morobe Prov., Rawlinson Range.)

*Acromastigium*-type branches are also present, though exceptional. The underleaves are 4-lobed, the disc 2 cells high, and the lobes consist of a uniseriate row of 2 cylindric cells very large for the underleaf stature.

Stephani's plant (as witness the name) was described and illustrated as 3-lobed, and the underleaves bilobed (Stephani, 1911a; Icones 18). Plants of the type are quite flaccid. Schuster's illustration (Schuster, 2000, fig. 79A) is based on a De Sloover collection from Rwanda, which appears to be a more robust plant. The leaves are  $\pm$  symmetrically 4–5(6)-lobed to about 0.75 and transversely to distinctly succubously inserted. The lobe cells are plainly constricted at the septa. The stem cross section has a distinct hyaloderm and a many-celled medulla.

The De Sloover plant is autoecious, with the gynoeceium (apparently) on a ventral-intercalary branch and the androeceia borne on secondary *Frullania*-type branches (Schuster, 2000, fig. 79A: 3).

This species was transferred to *Telaranea* by Schuster (1966) in the bibliography to his manual of North American Hepaticae. Based on an ex-

amination of the type, Vána et al. (1979) referred this species to *Telaranea* subg. *Neolepidozia*, as did Pócs (1984); it is placed here in sect. *Cancellatae*. Succubous leaf insertion is rare in *Telaranea*, present in *T. redacta* (sect. *Telaranea*) and in many members of sect. *Tenuifoliae*.

#### *Telaranea trisetosa* (Steph.) Grolle

*Lepidozia trisetosa* Steph., Spec. Hep. 3: 607. 1909.  
*Telaranea trisetosa* (Steph.) Grolle, J. Hattori Bot. Lab. 29: 280. 1966. Lectotype (*vide* Grolle, 1966): New Guinea, in Catena montis Yule, 2300 m, 1895, Kowald 138 (G!).

DESCRIPTIONS—Grolle (1966); Piippo (1984).

ILLUSTRATIONS—Grolle (1966, fig. 2a–g). Stephani, Icones, *Lepidozia* 254; Fig. 59.

DISTRIBUTION—Endemic to New Guinea (1570–2350 m).

A striking species with slender, wiry stems, transversely inserted 3–4-lobed leaves divided nearly to the base, and stiff, ciliiform leaf lobes up to 10–11 cells long (Fig. 59: 2, 3, the terminal cell abbreviated and much smaller than the pen-

ultimate cell (Fig. 59: 3, 4). The lobes are widely divergent, the lobe bases uniseriate (Fig. 59: 2, 5) or biseriate, often on the same leaf (Grolle, 1966, fig. 2b) and connate for less than half their length. The cells are thick-walled and firm, and the septa thickened in the corners and at times weakly projecting (Fig. 59: 3). The stem cortical cells in surface view and in cross section are moderately thick-walled and somewhat larger than the medullary cells. The first branch underleaf (Fig. 59: 1) is monocrurous and identical to one of the lobes of a leaf, except a little shorter (7–8 cells long). An unusual feature of the species is the underleaves (Fig. 59: 6; Grolle, 1966, fig. 2d–f), which have an almost rectangular disc 6–8 cells wide and 2 cells high, 3–4-lobed, with the lobes either obsolete or consisting of a single narrowly cylindric cell terminating in a slime papilla.

The original material included collections from Java (leg. Fleischer), and New Guinea (leg. Kowald); Grolle (1966) lectotyped the species and excluded the Javan element. The species was placed in subg. *Chaetozia* by Grolle (1966), but later excluded (Grolle, 1968).

**SPECIMEN SEEN**—PAPUA NEW GUINEA: Morobe Prov., Rawlinson Range, near Ogeramnang airstrip, 5 km NNW of Ogeramnang, 1800–1900 m, *Norris 59859* (F).

*Telaranea verruculosa* Engel & Merr., sp. nov.

*T. patentissima* aemulans, cuticula valde papillosa, foliis ramulorum fere lateraliter insertis cellulae dorsales surculorum conspicue expositis optime distincta.

**Holotype**: Australia, Queensland, Kuranda, Wright's Lookout Surprise to Creek Track, 9 Jul 1994, *Scott s.n.* (MELU 1668); **isotype**: (F).

**ILLUSTRATION**—Fig. 60.

**DISTRIBUTION**—Known only from Queensland, Australia.

Plants soft, the stems rather straight, loosely prostrate in thin mats, pale green, moderately nitid when dry; plants medium, to 5 mm wide, including branches. Branching loosely 1 (rarely 2)-pinate, the leafy branches terminal, *Frullania* type, leafy or flagelliform, the branches determinate, short and subequal in length; branch half-leaf 2-lobed; first branch underleaf ventral in position on branch base, undivided, typically with 3 biseriate basal cell tiers and a uniseriate row of 2–3 cells, ending in a slime papilla. Terminal, *Acromastig-*

*um*-type branches (1 seen) stoloniform, the first appendage at base of branch, identical to the first branch underleaf of the *Frullania*-type branches. Ventral-intercalary branches occasional, stoloniform or leafy and becoming leading shoots. Stem cortical cells rectangular (2–3:1) in surface view, moderately thick-walled, in section in 11 rows, firm walled, but the exposed wall moderately thickened, larger than the 25–26, firm-walled medullary cells. Leaves of main shoot somewhat distant, the insertion incubous, the insertion reaching the stem midline; leaves 265–310(340)  $\mu\text{m}$  wide (measured between lobe tips)  $\times$  265–360  $\mu\text{m}$  long, symmetrically 4(5)-lobed to ca. 0.6, the lobes a little longer than the disc. Branch leaf distinctly obovate in outline, equal to the stem leaves in size or a little longer,  $\pm$  symmetrically 3-lobed, bilobed distally, imbricate, complanate, broadly decurved, strongly incubous to at times almost laterally inserted, the two median rows of cortical cells rather broadly exposed. Lobes divergent, narrowly triangular to  $\pm$  parallel-sided for much of their length, 2–3(4) cells wide at the base, with 1–3 biseriate tiers, the uniseriate row to 5 cells long (shorter in lobes with several biseriate tiers); lobe cells subquadrate to short rectangular, firm-walled, moderately to distinctly contracted at the septa, the basal cell of the uniseriate row 27–32  $\mu\text{m}$  wide  $\times$  30–36  $\mu\text{m}$  long; cuticle distinctly papillose, the papillae rounded to short elliptical. Lobes of branch leaves 2–4 cells wide at base (sometimes with an additional 3-celled tier) and up to 3–4 biseriate tiers, the uniseriate row of 3–4 cells. Disc of stem leaves  $\pm$  symmetrically, moderately cuneate, 4–5 cells high, 8 cells wide at the insertion, to 13 cells wide at base of lobes. Disc of branch leaves 5–6 cells high, broadest above the middle, with additional longitudinal cell divisions, becoming up to 11 cells wide. Cells of disc firm-walled, lacking trigones, in regular rows and tiers, uniformly quadrate to short-rectangular, (28)30–36  $\mu\text{m}$  wide  $\times$  38–44  $\mu\text{m}$  long; disc papillose, the papillae hemispherical near lobe bases and distinctly elongated and striolate below, especially evident along the dorsal edge of the disc. Underleaves erect-spreading, equal to the stem in width or a little wider, plane, 4-lobed to 0.3–0.4, the lobes biseriate at base, with a single cell or a uniseriate row of 2–3 cells, terminating in a slime papilla; disc rectangular, 3–4 cells high, 8 cells wide throughout; rhizoids sparingly produced, from basal cells of lobes. Branch underleaves small, bilobed, and pincer-like (3-lobed at base of branch), the disc 2–3 cells high.

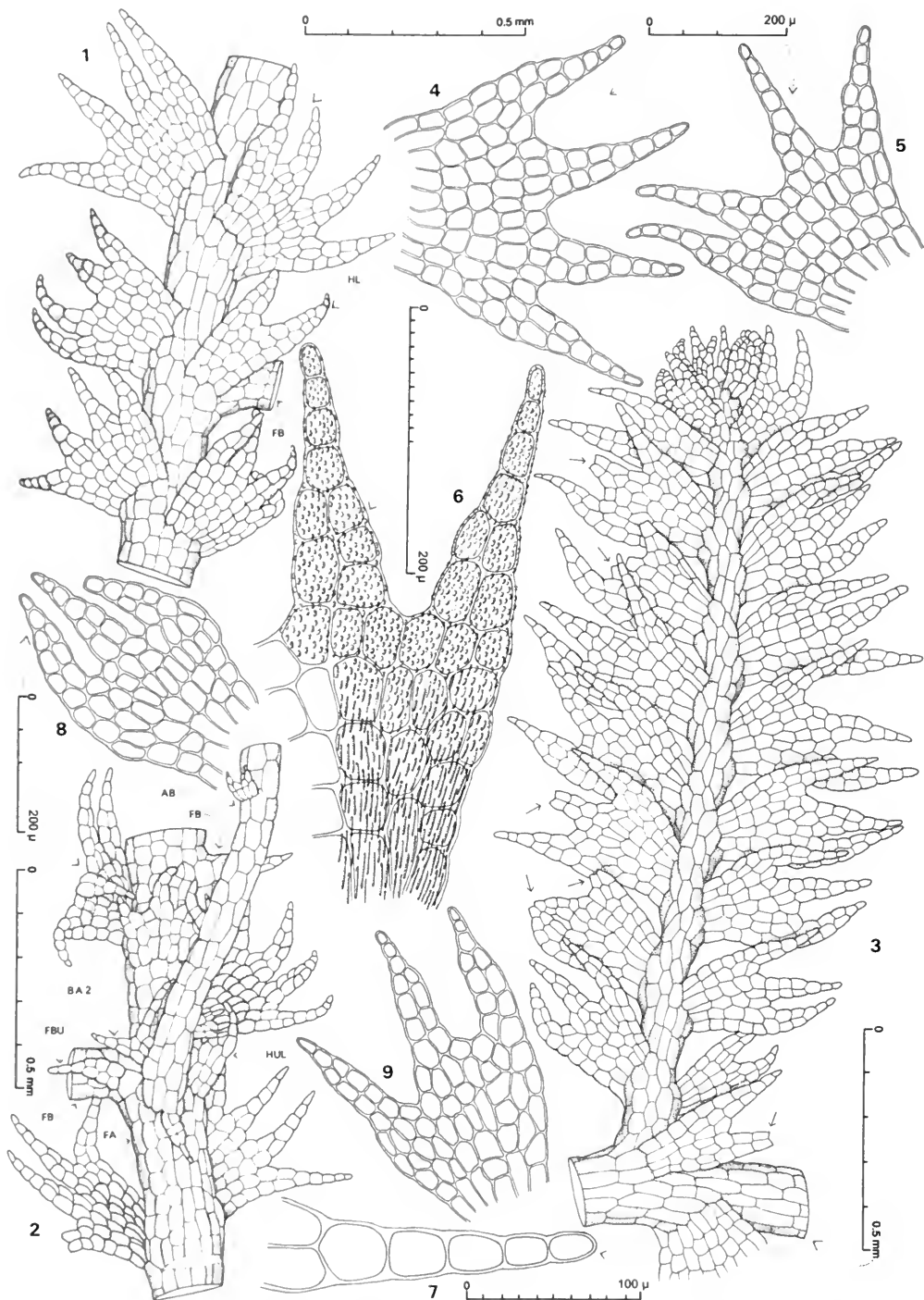


FIG. 60. *Telaranea verruculosa* Engel & Merr. 1. Portion of main shoot with *Frullania*-type branch (= FB; hl = half-leaf). 2. Portion of main shoot with an *Acromastigum*-type stoloniform branch (= AB) and 2 *Frullania*-type branches (= FB, only extreme bases included). Note that the half-underleaf (= hul) of the ventral terminal branch is bilobed (one lobe is beneath a microphyllous leaf), and that the first branch appendage (= fa) is similar in shape and form to the first branch underleaf (= fbu) of the *Frullania*-type branch, and, like the fbu, is inserted at the extreme base of the branch. Also note that the second branch appendage (= BA2) of the ventral-terminal branch is comparatively large, and that the remaining appendages of the branch are microphyllous. 3. Primary *Frullania*-type branch.



Androecia not seen. Only very young gynoecia seen, on short ventral-intercalary branches.

This species is notable for the markedly papillose cuticle of the leaves, which is plainly visible even at lower magnifications of the dissecting microscope (Fig. 60: 6). The papillae are short-elliptical on the lobes and lobe bases, and distinctly elongated and striolate on the surface as well as the edges of the disc (Fig. 60: 6). The lobe tips in several other species (*T. patentissima*, *T. tetrapila*) are finely papillose, and in *T. patentissima* var. *zebrina* at least a portion of the disc is also papillose (Fig. 17: 1, 9). There, however, the markings on the lobes consist of fine, short striae ("hatch marks") vs. the rounded to short-elliptical papillae of *T. verruculosa* (Fig. 60: 6). Moreover, in *T. patentissima* the branch leaves are plainly incubous and their insertion extends to the branch midline. *Telaranea praenitens* of New Zealand has strongly papillose lobes, but the disc is essentially smooth, and unlike in *T. verruculosa*, the lobes and disc margins are bluntly denticulate by virtue of the conspicuously projecting septa. *Telaranea verruculosa* is assigned to sect. *Cancelatae*.

*Telaranea disparata*, another Queensland species described here, differs by having 4–6-lobed stem leaves, asymmetrically lobed branch leaves (Fig. 47: 1, 10–12), and a smooth cuticle. The branch leaves in *T. verruculosa* are  $\pm$  symmetrically lobed and broadest at or above the middle (Fig. 60: 3, 8, 9). The leaf lobes in *T. disparata* are short acuminate, with no more than one additional biseriate tier (Fig. 47: 1, 5–8, 11, 12); the lobes of *T. verruculosa*, particularly of the branch leaves, are sublinear, with up to 4 biseriate tiers (Fig. 60: 1, 3, 9). Moreover, in *T. disparata* both the stem and branch leaves are widely set, exposing the two median rows of cortical cells (Fig. 47: 1); in *T. verruculosa* the insertion of the stem leaves reaches the stem midline (Fig. 60: 1).

DISTRIBUTION AND ECOLOGY—Endemic to Queensland, Australia. The type was collected on a roadside bank in a mesophyll vine forest. The Stone collection from Cardstone Road occurred "on bark fallen from tree."

SPECIMENS SEEN—AUSTRALIA. QUEENSLAND: Murray Falls, near Cardwell, *Stone s.n.* (MELU); Cardstone Road, Cardwell, Tully River, *Stone s.n.* (MELU); Fishery Falls National Park, *Stone s.n.* (MELU); Mt. Mackay State Forest, near Tully, *Stone s.n.* (MELU); Worpen Creek, near Tully, *Stone s.n.* (MELU); Cape York, Captain Billy Landing, *Duigan s.n.* as *T. disparata*—c. per. (MELU).

*Telaranea wallichiana* (Gott.) Schust.

*Lepidozia wallichiana* Gott. in G. L. & N., Syn. Hep. 204. 1845. *Mastigophora wallichiana* (Gott.) Trev., Mem. Ist. Lomb. Sci. Lett. III. 4: 416. 1877. *Neolepidozia wallichiana* (Gott.) Fulf. & J. Tayl., Brittonia 11: 84. 1959. *Telaranea wallichiana* (Gott.) Schust., Phytologia 45: 419. 1980. Lectotype (*fide* Piippo, 1984): Nepal, inter *Mastigobryum inaequilaterum* (W, *non vidi*); isolectotype: leg. Wallich, ex hb. Jack (G!).

*Lepidozia variifolia* Steph. in Gehceeb, Biblioth. Bot. 8. Heft 44(2): 29. 1898. *syn. nov.* Type: Borneo, Ins. Blitoeng, in Mte. Sagem, *Teysman 11137*—c.  $\delta$  + per., ex hb. Beccari 1886 (G!).

*Lepidozia tenera* Steph., Spec. Hep. 3: 608. 1909. Type: Java, *Jungluhn*, ex hb. Nees (G!).

*Lepidozia expansa* Steph., Spec. Hep. 6: 346. 1922. Type: Philippines, Luzon, Laguna Prov., Mt. Maquilang, Dec. 1912, *Robinson*, ex Merrill (G!).

DESCRIPTIONS—Jovet-Ast (1947, type), Piippo (1984).

ILLUSTRATIONS—Lindenberg and Gottsche (1846, tab. 4); Jovet-Ast (1947, fig. 3, type); Del Rosario (1977, fig. 76: a, b); Piippo (1984, fig. 4: a, b, c, type). Stephani, Icones, *Lepidozia* 256a; 256b, type; 249a, b (*L. tenera*); 209 (*L. expansa*).

DISTRIBUTION—Nepal, Java, Borneo, Sumatra. Reported from Japan, Taiwan, India, Nepal, Sri Lanka, Java, Amboina, Borneo, Philippines, New Guinea, Solomon Is. (Piippo, 1984). If true, this is arguably the *Telaranea* species with the widest distribution, extending from the Himalayas to Japan, south to Ceylon and the Solomon Is. Previously published statements of distribution can be reevaluated once this complex is better understood. Our experience with specimens determined as *T. wallichiana* indicates that a number of distinct taxa are probably involved, rather than a single widely distributed, polymorphic species (see below). *Telaranea papulosa*, for example, is a distinct species, as stated by Kitagawa (1973). Col-

Note the branch leaves are strongly incubous to  $\pm$  laterally inserted,  $\pm$  symmetrically 3-lobed, but near the branch tip are bilobed (note also the caducous leaf tips, at arrows). Note also that the two median rows of cortical cells are broadly exposed. 4, 5. Leaves of main shoot. 6. Dorsal half of leaf; note the "welt-like" cuticular papillae of lobes and at lobe bases and the elongate striolae toward base of disc. 7. Leaf lobe, cuticular detail not shown. 8, 9. Branch leaves; note symmetry of lobing and broadly arched margins (drawn to same scale). (All from type.)

lections from Japan cited by Hattori & Mizutani (1958) are best referred to *T. planifolia*, which is maintained here as distinct from *T. wallichiana*; plants of *T. planifolia* from Taiwan are autococious. Specimens reported as *L. tenera* from New Guinea (Hattori, 1951) have been referred to *T. wallichiana* by Piippo (1984) and Grolle & Piippo (1984).

**NOMENCLATURE**—The identity of *Lepidozia massartiana* Schiffn. has been widely misunderstood. Schiffner (1900) cites a Massart collection from Java (1158 pp.), "Urwald von Tjibodas, an faulem Holze; c. per." as the basis of his "*Lepidozia Massartiana* Schiffn. n. sp.," without providing a description of the species. Schiffner's material was excluded from the protologue by Stephani (1909, p. 611), who cited specimens from Amboina, New Caledonia, and Tahiti, all apparently sterile; Kitagawa (1973, p. 266) erroneously cites the Massart collection as the type of *L. massartiana*. Our concept of Schiffner's plant is based on authentic material, collected by him at or near the original locality.

Stephani's illustration of *L. massartiana* (Icones, *Lepidozia* 227) is based on the plants from Amboina (leg. Karsten) and Tahiti (leg. Nadeaud). The Tahitian plant is represented by a branch in ventral view, with leaves ventrally decurrent ("postice decurrentia"). The leaf lobes are broad at the base, resembling those of *T. cuneifolia*. According to Hürlimann (1985), *L. massartiana* does not occur in New Caledonia, although New Caledonia is cited by Stephani in the protologue. We are treating *L. massartiana* Steph. as a probable synonym of *T. cuneifolia*, and Schiffner's plant as *T. wallichiana*. We have intentionally avoided lectotypifying *L. massartiana* Steph. because of the confusion surrounding this name and its distribution.

Plants of *T. wallichiana* are rather loosely once pinnate, with ribbon-like leafy branches regularly interspersed with whiplike, flagelliform, *Frullania*-type branches. The habit of the species is illustrated elegantly by Lindenberg and Gottsche (1846, tab. 4). The type of *L. wallichiana* (G!) has distant main shoot leaves and contiguous to imbricate branch leaves, just as in the illustration. Leaves of both stem and branches are  $\pm$  symmetrically lobed, the lobes consistently 2 cells wide at base with a uniseriate row 3 cells long (Jovet-Ast, 1947, fig. 3: b, c, type). The lobe tips are plane to strongly decurved and often distinctly papillose. The disc of the stem leaves is 3–4 cells

high and 8 cells wide throughout; the branch leaves are not much larger than the stem leaves, with a disc 4–5 cells high. The half-leaves are bifid; the first branch leaf is undivided and ventrally positioned at the base of the branch. The underleaves of *T. wallichiana* (Jovet-Ast, 1947, fig. 3: d, e; Piippo, 1984, fig. 4: e) are rather small, with a disc 2–3 cells high and abbreviated lobes, the lobes typically consisting of 1 or at most 2 cells and terminating in a slime papilla.

*Telaranea cuneifolia* differs by the more strongly differentiated branch leaves, variable in shape but typically ligulate, asymmetrical, often subfalcate, with a disc up to 10 cells high (Piippo, 1984, fig. 4: c, h) vs. shorter,  $\pm$  symmetrically lobed, and a disc 4–5 cells high in *T. wallichiana*. The areolation of the branch leaf disc tends to be rather lax and the cells somewhat irregular in shape. In addition, the lobes of the branch leaves are broader than those of *T. wallichiana*,  $\pm$  triangular in shape and evenly tapering from a base 3–4 cells wide vs. slenderly acuminate and 2 cells wide at the base in *T. wallichiana*. The underleaves tend to be larger than those of *T. wallichiana*, with a disc to 4 cells high (Icones; Piippo, 1984, fig. 4: f), and better developed lobes, 2–3 cells wide at the base and a uniseriate row up to 4 cells long.

The Schiffner specimens of *T. wallichiana* cited below bear both gynoecia and sporophytes. The  $\varnothing$  bracts are shallowly 4-lobulate to 0.25 or less, with each lobe terminating in a long, contorted cilium, the disc margins with a few short, hooked teeth. The perianth is terete below and strongly plicate below the mouth. The cilia of the perianth mouth are subcapillary, spirally twisted to contorted, 4–7 cells long, the cells elongate and thick-walled, with moderately to strongly projecting septa. The cells of the perianth surface are elongate, marked by conspicuous cuticular striae. By contrast, in our fruiting specimen of *T. cuneifolia* from New Guinea (Koponen 35935) the perianth mouth bears crowded, short, rigid teeth consisting of a single elongate cell or a uniseriate row only 2 cells long, with not or only weakly projecting septa. The lobes of the  $\varnothing$  bracts terminate in a uniseriate row of 3–4 cells.

The collections cited below, distributed as *T. wallichiana* from Taiwan (Lai 11539) and Iriomote Is. (Mizutani & Yoshimura 5357 and Hepaticae Japonicae Exsiccatae 1027) have a disc areolation like that of *T. heterotexta* of New Caledonia, in which the two dorsal longitudinal rows of disc cells form a  $\pm$  distinct border along the

dorsal margin. Admixed with the latter are plants with bulging leaf disc and lobe cells resembling *T. papulosa*, which is not reported for Japan or Taiwan by Kitagawa (1973).

**SPECIMENS SEEN**—**JAVA**: Prov. Preanger, in decliv. austral. montis Pangerango, in sylvis primaevae supra Tjibodas, regio nubium, 1510–1560 m, 21–24 Apr 1894 (4 specimens), *Schiffner*—c. sporo. (F). **SUMATRA**: Mt. Sago, summit region, 2000–2200 m, *Meijer 8665* (F). **TAIWAN**: Nantou Co., Chitou, ca. 1100, *Lai 11539* (F). **JAPAN**: Iriomote Is., between Funatsuki-ba and Mariudo-no-taki, along Urauchi-gawa, 1–70 m, *Mizutani & Yoshimura 5357*—c. per. + ♂; same loc., 50 m, *Mizutani & Yoshimura* (Hepaticae Japonicae Exsiccatae 1027).

## Systematics

Progress in phylogenetic systematics of bryophytes has lagged behind that of other major groups of plants and animals, but in recent years there has been increasing interest in cladistics as a tool to reconstruct bryophyte phylogenies and refine existing classifications. Considerable progress has been made in outlining phylogenetic relationships between bryophytes and tracheophytes, and among the major bryophyte clades (Capesius & Bopp, 1997; Garbary & Renzaglia, 1998; Goffinet, 2000; Hedderson et al., 1998; Lewis, Mishler & Vilgalys, 1997), but there have been few cladistic studies dealing specifically with leafy hepatics, comparable in number and in scope to those in marchantioid hepatics (Long et al., 2000; Wheeler, 2000), sphagna (Shaw, 2000), and mosses (Buck et al., 2000; Cox & Hedderson, 1999; Cox et al., 2000; De Luna, 1995; De Luna et al., 1999; De Luna et al., 2000; Goffinet & Cox, 2000; Hedenäs, 1997, 1998; Hedenäs & Buck, 1999; Hyvönen et al., 1998; La Farge et al., 2000; Lewinsky-Haapasaari & Hedenäs, 1998; Newton et al., 2000). Among the few examples of cladistic studies of leafy hepatics at the genus level are those of *Balantiopsis* (Engel & Merrill, 1997) and *Pleurozia* (Thiers, 1993).

The evolution and classification of leafy hepatics have been extensively reviewed and discussed by Schuster (1966, 1973, 1979, 1984, 2000). Major attention has been devoted to the identification of primitive character states, the establishment of “credible intraordinal groups,” and the “orienting” of taxa within these groups (Schuster, 2000, p. 33). In essence, Schuster’s classification of leafy hepatics is a synthesis of former systems (see Schuster, 1966, p. 647), with a number of

additions and modifications supported by a variety of “phylogenetic” arguments and interpretations. There are, however, major differences between Schuster’s unique approach to the understanding of relationships and the methods and concepts of phylogenetic analysis as generally practiced and understood.

Using empirical methods, phylogenetic analysis attempts to develop a hypothesis of common ancestry relationships. Shared, derived character states (synapomorphies) are used to indicate relationships and identify sister groups. The resulting hierarchy of relationships is presented as a phylogenetic tree, or cladogram. Decisions concerning character polarity and reconstructions of character evolution are not attempted until a tentative phylogeny has first been established.

Schuster’s system is an “edifice of phylogenetic speculation” (Schuster, 1979, p. 47). In the Besseyan tradition, the process begins with the selection of a set of characters which appear to be important indicators of relationship. These assumptions are embodied in a series of “phylogenetic criteria,” which are used as a guide to understanding and interpreting relationships (Schuster, 1973, p. 330–331). Schuster’s emphasis throughout is on “plesiomorphic taxa” and primitive character states (plesiomorphies). By contrast, cladistics focuses on the search for synapomorphies, and considers shared plesiomorphies to be useless as indicators of relationships, except at the most basal levels. Schuster tends to regard similarities between derived taxa as evidence of widespread and pervasive convergence and parallelism.

At issue is not the choice of characters used, but the use of global criteria to understand relationships, the reliance on “phylogenetically significant” characters, and the fact that alternative explanations are usually not explored. The method also provides no reliable way to distinguish between homology and homoplasy. Cladistics offers an empirical means of sifting through the mass of accumulated data and identifying those characters which are most informative in a given situation.

Schuster seems to regard phylogeny primarily as a teleological process of character transformation from primitive to derived character states. Schuster’s criteria also include a number of broad evolutionary generalizations which are presumed applicable to all organisms. One of the oddest of these is that variability in itself is primitive. Since “rigidly fixed” features are phylogenetically advanced, organisms which are “malleable” with

respect to a given character—such as those with “plastic” branching—must be “relatively low phylogenetically” (Schuster, 1979, p. 64; 2000, p. 36). The result is an arrangement of taxa in order of increasing evolutionary complexity, from “structurally generalized” taxa to those whose morphology is more rigidly defined (Schuster, 1979, p. 65).

In Schuster’s view, the phylogeny of leafy hepatics cannot be expressed as a phylogenetic tree (Schuster, 1973, p. 64). Instead, it must be represented as a “bush-like” polytomy (Schuster, 1973, tab. 2), as a consequence of a “very early fragmentation into a number of units that retain primitive features” (Schuster, 1973, p. 326). Each of the major groups (suborders) begins with an “essentially isophyllous prototype,” leading to a succession of forms, which have undergone a similar sequence of character transformations independently. If a suborder contains no isophyllous members, it is assumed that they once existed but are now extinct (Schuster, 1979, p. 66). The aim is to present a sense of relationships between these “basement” groups and the suborders derived from them, but the inescapable conclusion is that all of the characters involved are homoplasies, which is theoretically possible, but not the most parsimonious solution. If this were a phylogenetic tree—given two polytomies, one with 9 branches and one with 3 (Schuster, 1973, tab. 2)—it represents a number of alternative classifications equal to the product of the number of trees possible for each polytomy,  $(2,027,025)(3)$ , or 6,081,075 (see Felsenstein, 1977).

In Schuster’s discussions of relationships between taxa, a sense of shared ancestry as the underlying basis for similarity is often conspicuously absent. Instead—in the language of traditional taxonomy—species and groups of species are “circumscribed” by “perimeters,” “limits,” and “bounds.” The notion of “contacts,” “bridges,” and “interfaces” between taxa, on the other hand, defies phylogenetic interpretation. If evolution has occurred, organisms must be related by a hierarchy of genealogic descent. A true phylogenetic classification must reflect these relationships, which is what cladistics is designed to do.

## Choice of Taxa

For this portion of our study, in addition to the Australasian species of *Telaranea*, we surveyed

and reevaluated most of the extraterritorial species of the genus published to date (for discussion and descriptions of these species, see p. 120). Representatives of three other related genera of Lepidoziaceae, *Arachniopsis*, *Kurzia*, and *Lepidozia*, were included in the analysis as outgroups (Madison et al., 1984; Watrous & Wheeler, 1981). This was done to assist in resolving relationships within *Telaranea*, as well as to clarify relationships between these four genera. To represent *Kurzia*, we selected the following: *K. calcarata*, *K. helopila* and *K. hippuroides* (Figs. 60, 61), representing sect. *Microlepidozia*; *K. fragilifolia*, *K. quadriseta*, *K. quadriseta* var. *trilobata* (sect. *Leucolepidozia*, Schuster, 1980); and *K. bisetula* and *K. quinquespina* (Fig. 34; subg. *Nanolepidozia*, Schuster, 1980). As placeholders for *Lepidozia*, we selected *L. obtusiloba* (Figs. 62–64), a species for which sporophyte details are known, and *L. spinosissima* (Fig. 66), widely regarded as a primitive member of the genus. *Arachniopsis* is represented by *A. diacantha* (Fig. 46).

We selected *Triandrophyllum symmetricum* (Figs. 67, 68) as an additional outgroup, because it is clearly not a member of the Lepidoziaceae but is sufficiently similar in gross morphology to allow polarization of most of the characters used in the analysis. *Triandrophyllum* occupies a near basal position relative to other leafy hepatics in the arrangement of Schuster (1966, 1979). Data were available for *T. symmetricum* on all of the characters used in the analysis. The 56 taxa included in the analysis are listed in Table 1.

All data used in the analysis were verified by examination of herbarium specimens. All characters were treated as unordered, in order to avoid making *a priori* assumptions concerning character polarity. Characters were scored as inapplicable when the structure in question was absent (e.g., characters of the first branch underleaf when terminal branches are lacking, as in *T. symmetricum* and *A. diacantha*). Taxa with more than one state of a given character were treated as polymorphic with respect to that character and assigned both values. PAUP 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

1. *Frullania*-type branching. Terminal-lateral (*Frullania*-type) branches occur in all of the taxa

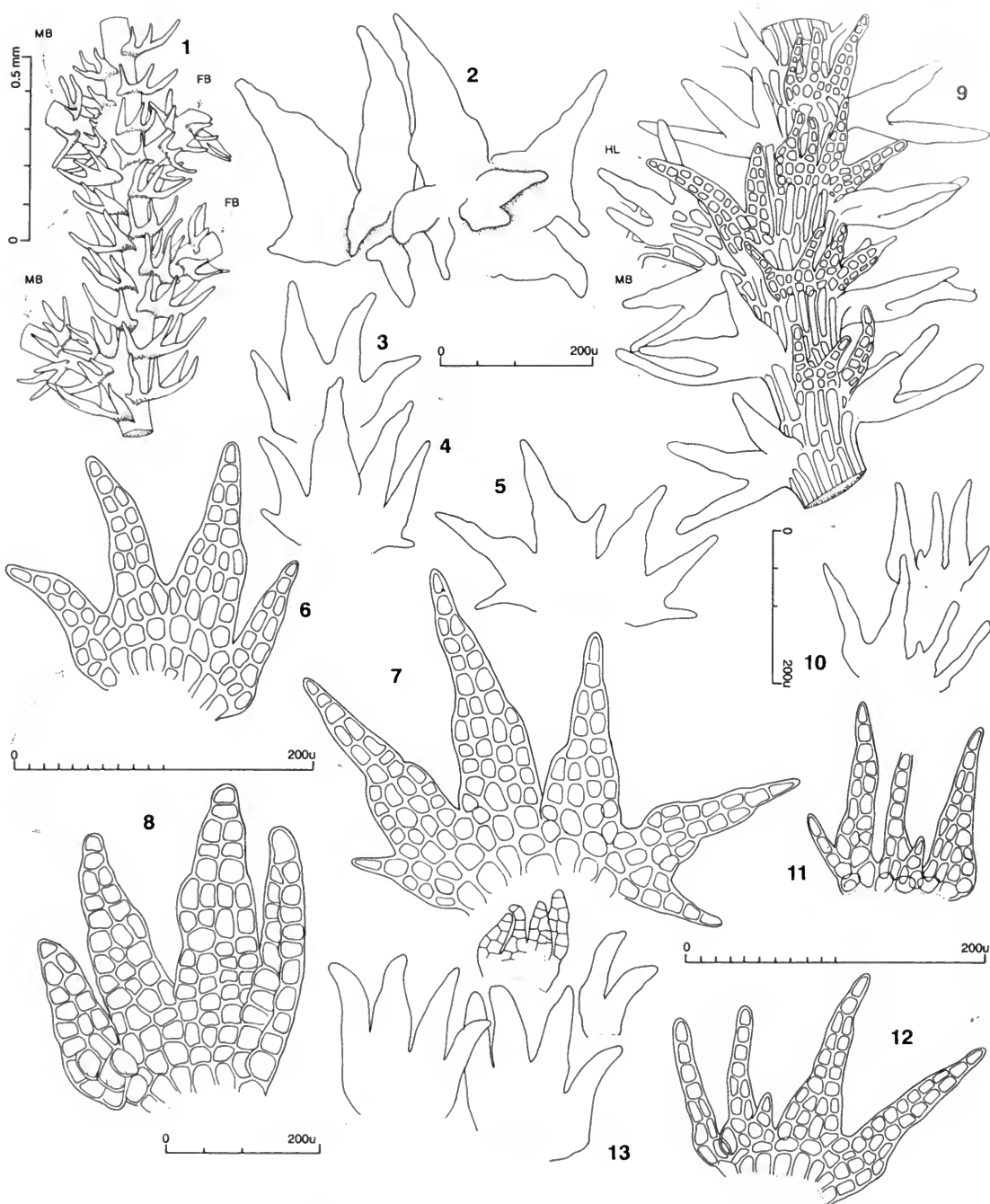


FIG. 61. *Kurzia hippuroides* (Hook. f. & Tayl.) Grolle. 1. Sector of main shoot, dorsal view; *Frullania*-type branches (= FB) at right and *Microlepidozia*-type branch (= MB) at left, dorsal view. 2-5. Leaves. 6-8. Leaves, cellular detail. 9. Sector of main axis, with *Microlepidozia*-type branch (= MB), ventral view. 10. Underleaves. 11-12. Underleaves, cellular detail. 13. Two leaves and (above) an underleaf (lobes with cellular detail), and a half-leaf. (Figs. 1, 3, 6, 9 from type of *K. hippuroides*; 2 from type of var. *ornata*; 4-5, 7, 10-12 from Engel 18690, New Zealand, South Is., Fiordland Natl. Park, Borland Road; 8, 13 from type of *K. allisonii*.)

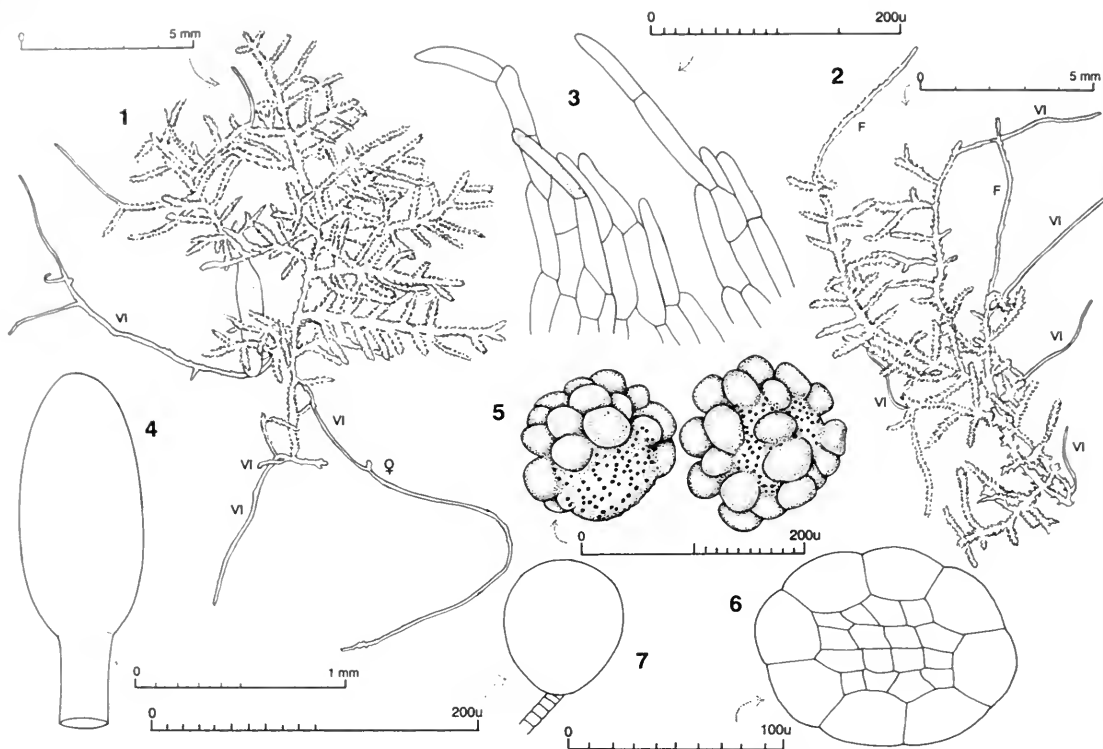


FIG. 62. *Kurzia hippuroides* (Hook. f. & Tayl.) Grolle. 1, 2. Plants, all branches terminal unless otherwise indicated (F = *Frullania*-type branch; vi = ventral-intercalary branch; ♀ = juvenile gynoeccium; note that leading shoots may become flagelliform and that perianth (in fig. 1) originates from leafless stolon. 3. Portions of perianth mouth. 4. Capsule profile. 5. Spores, proximal face shown at left. 6. Seta, cross section. 7. Antheridium. (Figs. 1–2, 4–6 from Engel 19001, New Zealand, South Is., Westland Prov., track to Alex Knob; 3 from Engel 17727, New Zealand, South Is., Otago Prov., summit of Mt. Maungatua; 7 from Engel 19293, New Zealand, South Is., Westland Prov., Paparoa Range, Croesus Track.)

included in the matrix, with two exceptions: *Triandrophyllum* and *Arachniopsis diacantha*. Taylor (1962) reported *Frullania*-type branching in *A. diacantha*, but we chose to score *A. diacantha* as lacking terminal branches, since this species was included in the analysis as the exemplar for *Arachniopsis*, and the absence of terminal branching has often been cited as a difference between *Arachniopsis* and *Telaranea*. Later in the study, we also observed occasional *Frullania*-type branching in *A. diacantha*, but did not change the way the species was scored.

*Frullania*-type branching is treated as a binary character: 0 = absent; 1 = present.

2. *Microlepidozia*-type branching. Terminal-lateral, *Microlepidozia*-type branches have not been reported in the genus *Telaranea*, but are present in all species of *Kurzia* included in the analysis.

*Microlepidozia*-type branches are relatively rare in Jungermanniales, and occur in two sub-

orders, Lepidoziinae (Lepidoziaceae, Calypogeiaceae) and Herbertinae (Trichocoleaceae). The single exception is *Pachyschistochila reflexistipula* (Engel & Schust.) Schust. & Engel, suborder Perssoniellinae (see Schuster & Engel, 1985).

*Microlepidozia*-type branching is treated as a binary character: 0 = absent; 1 = present.

3. *Acromastigum*-type branching. In most species of *Telaranea*, branches originating from the ventral merophyte are of the ventral-intercalary type. In *T. blepharostoma* (Fig. 39: 1), *T. clatritexta* (Fig. 1: 7) and *T. grossiseta* (Fig. 13: 2), however, terminal-ventral (*Acromastigum*-type) branches are also present, in addition to those of the ventral-intercalary and *Frullania* type. *Acromastigum*-type branches are associated with a "half-underleaf," analogous to the "half-leaf" of the *Frullania*-type branch. This type of branching is present in several *Telaranea* species and in *Lepidozia spinosissima*. *Acromastigum*-type branch-

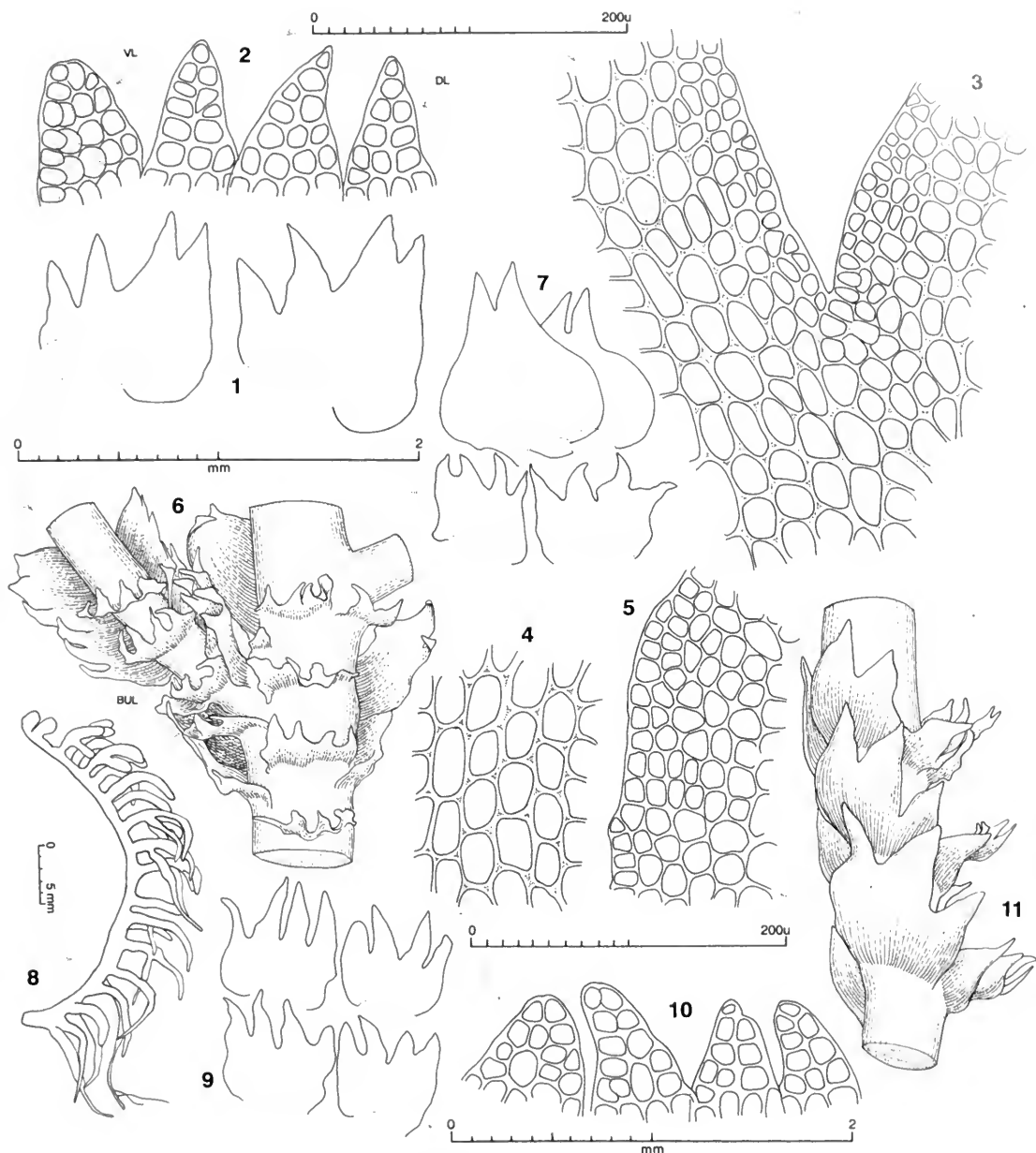


FIG. 63. *Lepidozia obtusiloba* Steph. 1. Leaves. 2. Apical sectors of 4 lobes from same leaf (vl = ventral lobe; dl = dorsal lobe). 3. Base of median sinus of leaf showing border of smaller cells. 4. Median disc cells. 5. Sector of ventral margin of leaf disc showing border of smaller cells. 6. Sector of main shoot with 2 *Frullania*-type branches, ventral view (BUL = first branch underleaf). 7. Half-leaves and, below, 2 first branch underleaves. 8. Outline of shoot at low magnification, lateral view. 9. Underleaves. 10. Apical sectors of 4 lobes from same underleaf. 11. Sector of main shoot, lateral view. (All from Engel 17843, New Zealand, South Is., Westland Prov., Mt. Aspiring Natl. Park, off track to Mt. Brewster.)

ing has also been reported in *Arachniopsis confervoides* (Schuster, 1988, fig. 1: 1, 2; see p. 143).

*Acromastigum*-type branching is treated as a binary character: 0 = absent; 1 = present.

4. Lateral-intercalary (*Plagiochila*-type) branching. Lateral-intercalary branching, in which branches originate in the axil of a lateral leaf, is present in *Telaranea tasmanica*, *Kurzia fragilifol-*

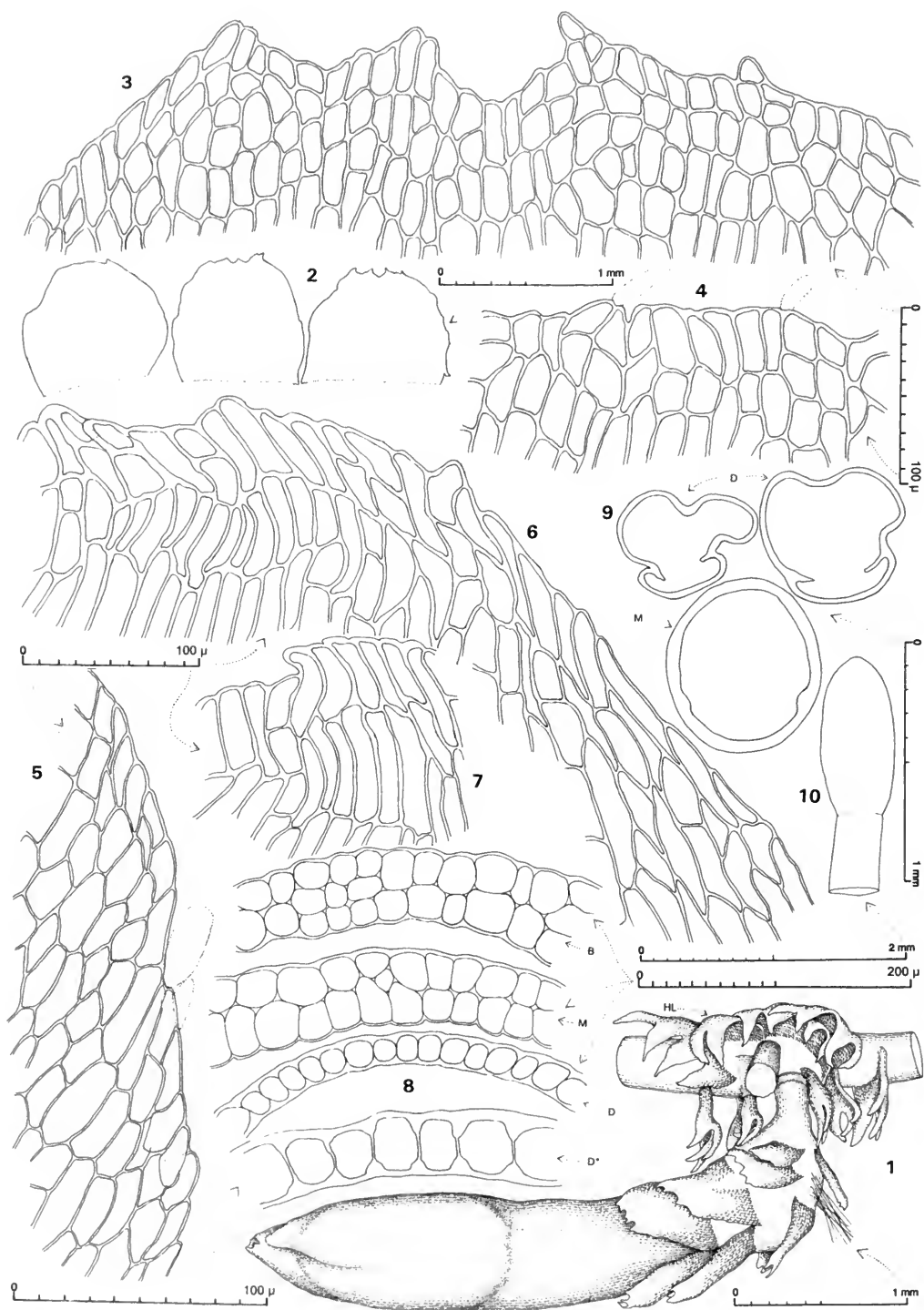


FIG. 64. *Lepidozia obtusiloba* Steph. 1. Portion of main shoot with mature gynoeceum; base of terminal branch shown, but with initial leaves and underleaves removed from branch for clarity (hl = half-leaf); lateral view. 2. Innermost bracts and bracteole. 3. Apex of innermost bract. 4. Portion of apex of innermost ♀ bract showing obsolete median pair of teeth, each represented by a slime papilla. 5. Portion of lateral margin of innermost bract showing nearly entire condition. 6. Perianth mouth, the summit at upper left. 7. Portion of perianth mouth. 8. Perianth, cross sections (top to bottom) through basal (= b), median (= m) and distal (= d) sectors; d\* drawn at higher magnification.



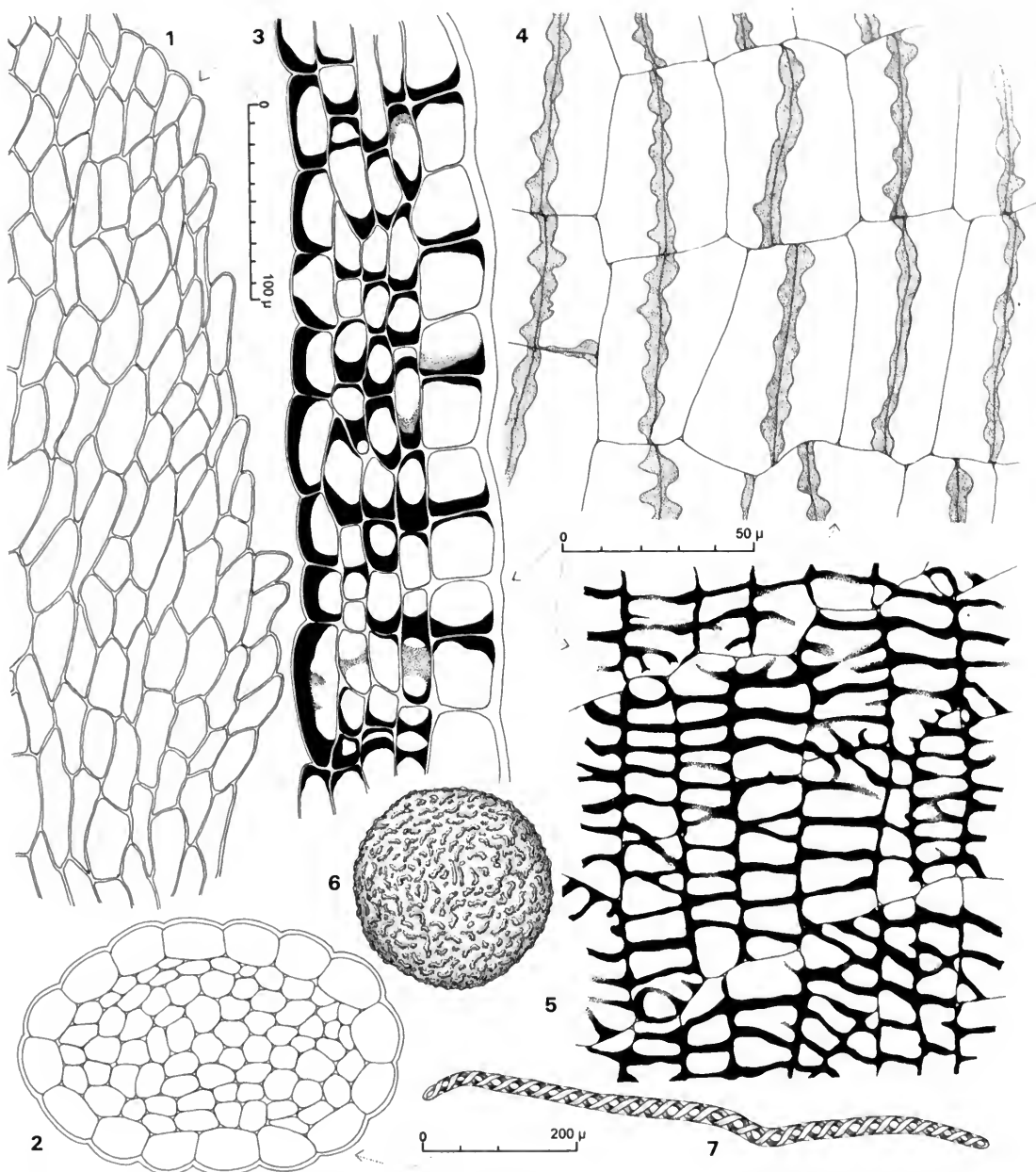


FIG. 65. *Lepidozia obtusiloba* Steph. 1. Portion of lateral margin of innermost ♀ bract showing crenulate-denticulate condition. 2. Seta, cross section. 3. Capsule wall, cross section. 4. Capsule wall, outer layer. 5. Capsule wall, inner layer. 6. Spore ( $\times 1880$ ). 7. Elater ( $\times 233$ ). (All from *Engel 17565*, New Zealand, South Is., Otago Prov., S side of Mt. Cargill.)

9. Perianth, cross sections through median (= m) and distal portions (= d). 10. Capsule profile. (All from *Engel 17565*, New Zealand, South Is., Otago Prov., S side of Mt. Cargill.)



FIG. 66. *Lepidozia spinosissima* (Hook. f. & Tayl.) Mitt. 1. Plant showing androecia on primary and secondary branches, the main axis with 9 androecia from ventral face of stem between arrows a and b, the plant also with a number of androecia (not shown) between the plant base and those drawn (these basal  $\delta$  not included appear older, at times broken and presumably from a previous year of growth). 2. Main shoot with androecium, ventral view (the leaf at lower left not shown); note also terminal branch and position of first branch underleaf. 3. Antheridium. 4. Portion of plant with perianth, ventral view; note primary and secondary terminal branches and the position of the

ia, *K. trilobata*, *K. quinquespina* and *Triandrophyllum*.

Lateral-intercalary branching is treated as a binary character: 0 = absent; 1 = present.

5. Differentiated stem cortex. Large, thin-walled stem cortical cells, or "hyaloderm," is traditionally a distinguishing feature of the genus *Telaranea* (Schuster & Blomquist, 1955; Fulford & Taylor, 1959, in *Neolepidozia*), although the same condition is found in other Lepidoziaceae (e.g., *Arachniopsis*, *Kurzia* subg. *Nanolepidozia*, *Zoopsis*). In *T. pulcherrima*, however, the cortical layer is only weakly differentiated (Fig. 25: 11). In *T. capilligera* (Fig. 3: 8), *T. tridactylis* (Fig. 7: 15), and *Kurzia quinquespina* (Fig. 34: 8, 9) the cortical cells are larger than the medullary cells, but are also thicker-walled. In most outgroup taxa the cortical cells are equal in size or smaller than the medullary cells and thick-walled. Cell size and wall thickening are therefore best treated as two distinct characters.

Differentiated cortex is treated as a binary character: 0 = undifferentiated (cortical cells about the same diameter as the medullary cells); 1 = differentiated (cortical cells larger).

6. Cortical wall thickening. This character pertains to wall thickness, irrespective of cell size, the cortical cells either thin- or  $\pm$  distinctly thick-walled.

Cortical wall thickening is treated as a binary character: 0 = thin-walled and hyaline, 1 = thick-walled.

7. Leaf symmetry. Most species of *Telaranea* have either equally lobed leaves (*T. patentissima*), or varying degrees of asymmetry of the *Lepidozia* type, in which the dorsalmost lobes are larger than the ventral, and  $\pm$  paired (*T. paludicola*). In *T. clatritexta* and *T. pennata*, however, the dorsal leaf lobe is the smallest, and the 2 ventral lobes are larger and often  $\pm$  paired. Such leaves are a mirror image of the typical *Lepidozia*-type leaf. This is the usual condition in liverworts with incubously inserted leaves. For example, in *Isotachis* (Balantiopsaceae), with incubous leaf insertion, the dorsal lobe is largest. In *Balantiopsis*, with succubously inserted leaves, the dorsal lobe is de-

cidedly smaller. Asymmetry with respect to lobe size is often accompanied by asymmetry of the disc, and leaves of the *Lepidozia* type commonly have the dorsal margin longer than the ventral. In *T. grossiseta*, which is scored as (7,2), the lobes are not markedly different in length, but the dorsalmost lobe differs in being more slender (1–2 seriate at base), and the dorsal margin of the disc is distinctly shorter than the ventral.

Leaf symmetry is treated as a multistate character with 3 states: 0 = asymmetric, ventralmost lobe smallest; 1 = symmetric; 2 = asymmetric, dorsalmost lobe smallest.

8. Lobe number. Most species of *Telaranea* have 4-lobed leaves, but in some species (*T. lindenbergii*, *T. tetrapila*) 5–6-lobed leaves also occur. Leaves are consistently 3-lobed in *T. martinii*, and 2-lobed in *Kurzia quinquespina*. Leaves are consistently 2-lobed in *T. inaequalis* and *T. tasmanica*, and variably 2–3 lobed in *T. herzogii*. In *T. pulcherrima* the leaves are 9–12-lobed. Monocurous leaves occur in *Arachniopsis pecten*, which was not included in the matrix.

Lobe number is treated as a multistate character with 3 states: 0 = 4–6; 1 = 2–3; 2 = 8 or more.

9. Leaf decurvature. In some *Telaranea* species (*T. clatritexta*, *T. meridiana*) the leaf lobes (and to some extent the disc) are ventrally decurved and "clawlike." In these species the leaves are also longitudinally inserted and oriented, lending a distinctive aspect to these plants.

Leaf decurvature is treated as a binary character: 0 =  $\pm$  straight; 1 = decurved and clawlike.

10. Lobe width at base. Leaf lobes in *Telaranea* are typically broadest at the base, and gradually or  $\pm$  abruptly tapering to a uniseriate row of cells of varying length. The lobe base varies from an extreme of 5–8 cells wide in *T. pennata* to 2–4 cells wide (*T. elegans*, *T. lindenbergii*, *T. pulcherrima*). In a few species, the undivided portion of the leaf consists of the lobe bases themselves, which are connate for less than their full length. Here the lobe bases may be geminate, consisting of a pair of cells (*T. chaetophylla*, Fig. 42: 1, 4; *T. tasmanica*, Fig. 32: 5, 6; *Kurzia quin-*

first branch underleaves. 5. Innermost bracts and bracteole. 6. Bract lobes. 7. Perianth, cross sections through median sector (a), distal 0.2 (b) and near apex (c). 8. Portion of perianth mouth. 9. Two leaves and (at right) an underleaf of main axis (DS = dorsal sinus). 10. Half-leaf. 11. First branch underleaves. (Figs. 1–3 from *Braggins 98/311*, New Zealand, North Is., North Auckland Prov., E edge of Waipoua Forest, Mataraurau Plateau; 4–8 from *Cameron 3797a*, New Zealand, South Auckland Prov., Coromandel Ranges, SW side of Maunapaki, *Cameron 3797a*; 9–1 from *Engel 21109*, New Zealand, North Is., North Auckland Prov., SE corner of Waipoua Forest, just N of Tutamoe.)

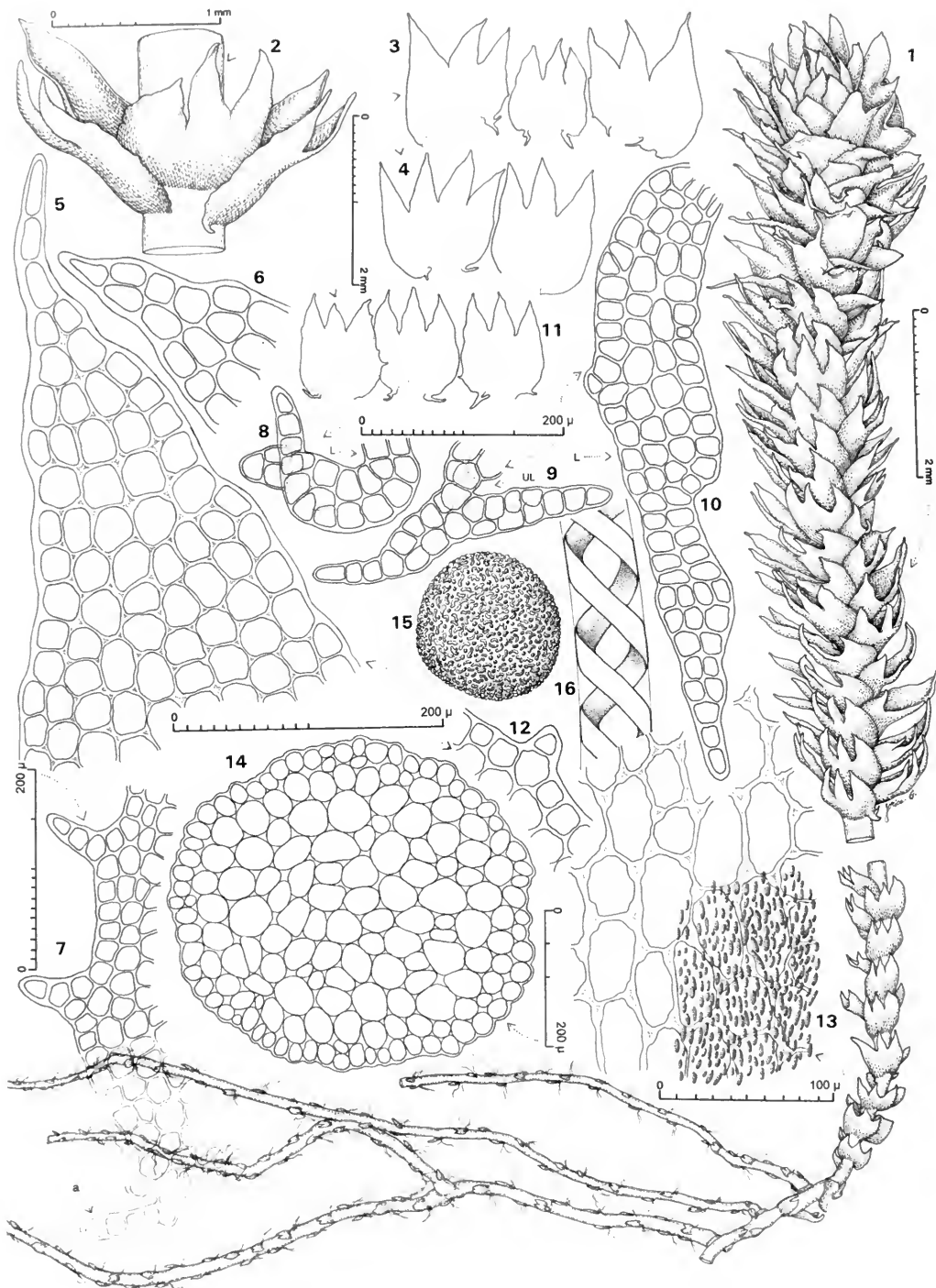


FIG. 67. *Triandrophyllum symmetricum* Engel. 1. Shoot with basal, horizontal, leafless stolons, ventral view. 2. Two leaves and an underleaf, ventral view. 3. Two leaves and, in middle, an underleaf (flattened). 4. Two leaves (flattened). 5. Lobe of leaf. 6. Portion of middle lobe of leaf (drawn at same scale as fig. 5). 7. Ventral margin of leaf showing 3 teeth and, at base, an appendage (= a). 8-10. Appendages of leaf (= l) and underleaf (= ul) bases. 11. Underleaves. 12. Tooth of underleaf lobe. 13. Median leaf cells, the cuticle shown in part. 14. Seta, cross section. 15. 16. Spore and portion of elater drawn at same scale ( $\times 1235$ ). (All from type.)

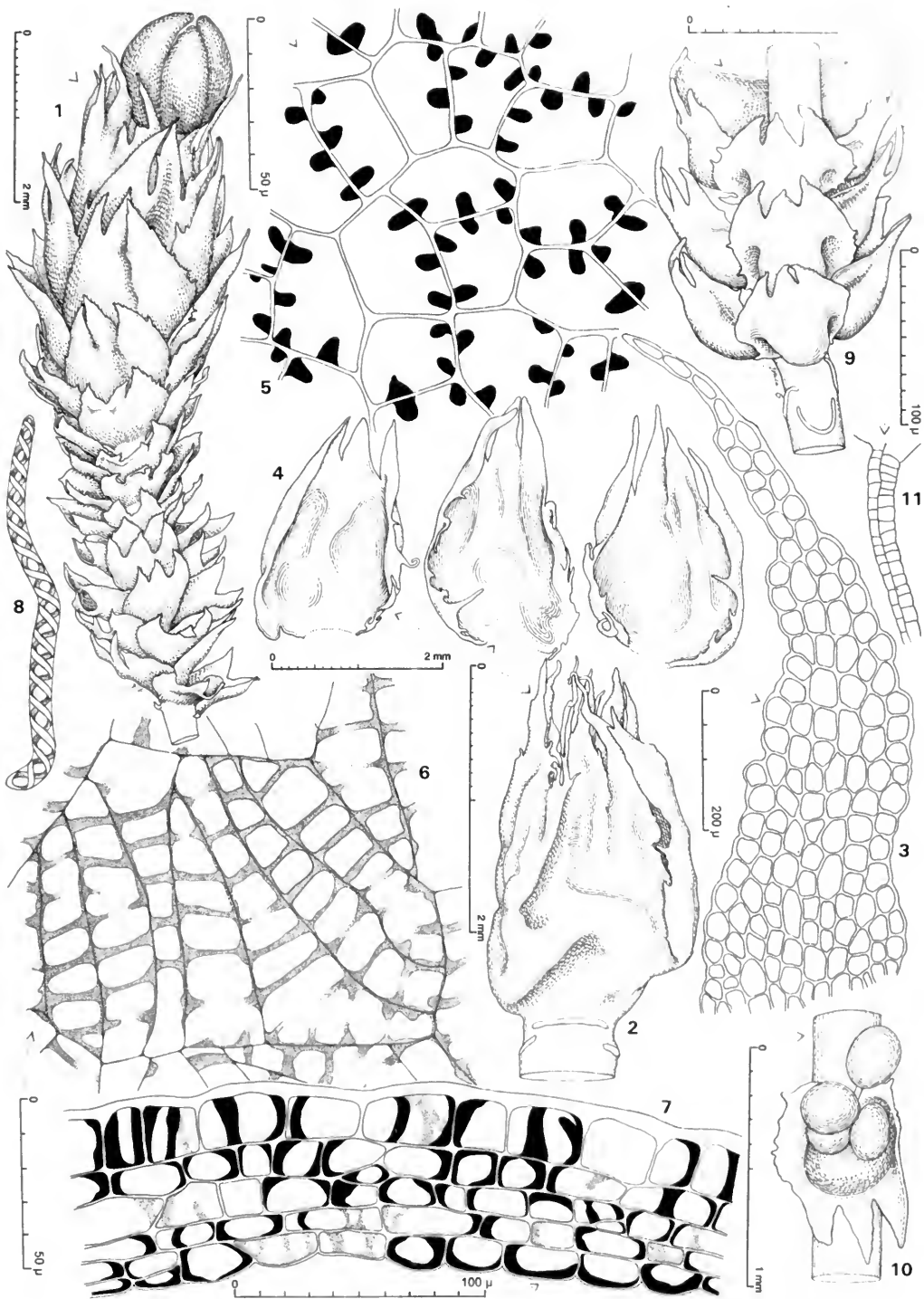


FIG. 68. *Triandrophyllum symmetricum* Engelm. 1. Gynoecium with mature sporophyte, ventral view. 2. Perianth (bracts and bracteole removed), ventral view. 3. Lobe of perianth mouth. 4. Innermost ♀ bracts, and in middle, bracteole (adaxial view). 5. Capsule wall, outer layer. 6. Capsule wall, inner layer. 7. Capsule wall, cross section. 8. Elater ( $\times 480$ ). 9. Portion of main shoot with 3 gyres of antheridia-bearing bracts and bracteoles, ventral view. 10. ♂ Bracteole with 4 antheridia, ventral view. 11. Antheridial stalk. (All from type.)

TABLE 1. Taxa included in systematic analysis.

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<i>Arachniopsis diacantha</i> (Mont.) Howe
<i>Kurzia bisetula</i> (Steph.) Grolle
<i>Kurzia calcarata</i> (Steph.) Grolle
<i>Kurzia fragilifolia</i> Schust.
<i>Kurzia helophila</i> Schust.
<i>Kurzia hippuroides</i> (Hook. f. & Tayl.) Grolle
<i>Kurzia pallescens</i> Grolle
<i>Kurzia quinespina</i> Engel & Merr.
<i>Kurzia trilobata</i> (Schust.) Schust.
<i>Lepidozia obtusiloba</i> Steph.
<i>Lepidozia spinosissima</i> (Hook. f. & Tayl.) G. L. & N.
<i>Telaranea blepharostoma</i> (Steph.) Fulf.
<i>Telaranea capilligera</i> (Schwaegr.) Schust.
<i>Telaranea centipes</i> (Tayl.) Schust.
<i>Telaranea chaetocarpa</i> (Pears.) Grolle
<i>Telaranea chaetophylla</i> (Spruce) Schiffn.
<i>Telaranea claritexta</i> (Steph.) Engel & Merr.
<i>Telaranea consobrina</i> Engel & Merr.
<i>Telaranea elegans</i> (Col.) Engel & Merr.
<i>Telaranea gibbsiana</i> (Steph.) Hodgs.
<i>Telaranea granulata</i> Engel & Merr.
<i>Telaranea grossiseta</i> (Steph.) Engel & Schust.
<i>Telaranea herzogii</i> (Hodgs.) Hodgs.
<i>Telaranea hodgsoniae</i> Engel & Merr.
<i>Telaranea inaequalis</i> Schust. ex Engel & Merr.
<i>Telaranea iriomotensis</i> Yam. & Miz.
<i>Telaranea kaindina</i> Grolle
<i>Telaranea kogiana</i> (Steph.) Grolle
<i>Telaranea lawesii</i> (Steph.) Grolle
<i>Telaranea lindenberghii</i> (Gott.) Engel & Merr.
<i>Telaranea longifolia</i> (Howe) Engel & Merr.
<i>Telaranea longitudinalis</i> (Herz.) Schust.
<i>Telaranea martinii</i> (Hodgs.) Schust.
<i>Telaranea meridiana</i> (Hodgs.) Hodgs.
<i>Telaranea neesii</i> (Lindenb.) Fulf.
<i>Telaranea nivicola</i> Schust.
<i>Telaranea oligophylla</i> (Lehm. & Lindenb.) Engel
<i>Telaranea palmata</i> Engel & Merr.
<i>Telaranea paludicola</i> (Hodgs.) Hodgs.
<i>Telaranea patentissima</i> (Hook. f. & Tayl.) Hodgs.
<i>Telaranea pennata</i> Engel & Merr.
<i>Telaranea perfragilis</i> Engel & Merr.
<i>Telaranea plumulosa</i> (Lehm. & Lindenb.) Fulf.
<i>Telaranea praenitens</i> (Hook. f. & Tayl.) Hodgs.
<i>Telaranea pseudozoopsis</i> (Herz.) Fulf.
<i>Telaranea pulcherrima</i> (Steph.) Schust.
<i>Telaranea quadrifida</i> (Steph.) Engel & Merr.
<i>Telaranea remotifolia</i> Hodgs.
<i>Telaranea tasmanica</i> (Steph.) Engel & Merr.
<i>Telaranea tetradactyla</i> (Hook. f. & Tayl.) Hodgs.
<i>Telaranea trichocarpa</i> (Hook. f. & Tayl.) Engel & Merr.
<i>Telaranea trichocoleoides</i> (Herz.) Schust.
<i>Telaranea tridactylis</i> (Lehm. & Lindenb.) Engel & Merr.
<i>Telaranea trisetosa</i> (Steph.) Grolle
<i>Telaranea tuberifera</i> Engel & Schust.
<i>Triandrophyllum symmetricum</i> Engel

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*quespina*, Fig. 34: 6, 7), or the lobes may be uniseriate to the insertion (*T. herzogii*, Fig. 35: 1, 5; *Arachniopsis diacantha*, Fig. 46: 5).

Leaf lobe width is treated as a multistate character with 4 states: 0 = more than 4 cells wide; 1 = 2–4 cells wide; 2 = lobe base geminate; 3 = lobe base uniseriate.

11. Lobes fragmenting. A tendency toward fragmentation of the leaf, probably as a form of asexual reproduction, is confined to a few species (*T. centipes*, *T. tuberifera*, *Kurzia fragilifolia*). The extreme condition occurs in *T. perfragilis*, where not only the lobes but also the distal portion of the disc are missing (Fig. 20: 7, 10).

Lobes fragmenting is treated as a binary character: 0 = not fragmenting; 1 = fragmenting.

12. Lobe tip cells divided. In several species of *Telaranea* (*T. tetrapila*, Fig. 18: 4–6; *T. patentissima*, sporadically in a few other species) the terminal cell of the lobe is short, and the transverse wall between the terminal cell and the penultimate cell is noticeably thinner than those between the other cells of the uniseriate row, giving the impression that this division occurred later. Repeated divisions of the apical lobe cells occur in *T. inaequalis* (Fig. 37: 7–11). In some species (*T. inaequalis* (Fig. 37: 5) the lobes terminate in a very small, button-like cell, which is much shorter than the penultimate cell.

Lobe tip cells divided is treated as a multistate character with 3 states: 0 = not divided; 1 = secondarily divided; 2 = cap cell.

13. Septa of uniseriate row. In the leaf lobes of some *Telaranea* species (*T. chaetocarpa*, Fig. 40: 6, 7; *T. gibbsiana*, Fig. 11: 7; *T. praenitens*, Fig. 10: 5) the transverse septa in the cell angles of the uniseriate row are swollen and projecting ("vorgewölbt," see Grolle, 1966, fig. 1: i, k, *T. chaetocarpa*). In others the septa do not protrude, and the lobes are either straight-sided or are moderately to distinctly constricted at the septa (*T. pulcherrima*, Fig. 25: 7; *T. tetradactyla*, Fig. 27: 5). In *T. praenitens* the marginal cells of the leaf disc also have projecting septa (Fig. 10: 5, right).

Projecting septa is treated as a binary character: 0 = not swollen; 1 = swollen and projecting.

14. Lobe cell shape. Lobe cell shape is treated as a multistate character with 4 states: 0 =  $\pm$  isodiametric (at most 1.5:1); 1 = short-rectangular (1.6–3:1); 2 = elongated (3–5:1); 3 = capillary (6–9:1).

15. Leaf insertion. Leaf insertion was treated as a multistate character with 3 states: 0 = incubous; 1 = transverse; 2 =  $\pm$  longitudinal.

TABLE 2. Data matrix used in cladistic analysis of *Telaranea* and outgroup taxa.

	1	2	3	4	5	6	7	8	9	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	1				
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	
T. symmetricum	0	0	0	1	0	1	0,11	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	?	?	?	?	2	0	3	4	
L. spinosissima	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	?	?	
L. obtusiloba	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0,20	0	2,3	
K. hippuroides	1	1	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	2	0	0	1	0	1	0	0	0	0	0	0	2	1	0,1	
K. pallescens	1	1	0	0	1	1	1	0	0	1	0	0	0	1,2	1	0	2	1	0	1	1	1	1	1	0	0	0	?	0	1	1	1	
K. trilobata	1	1	0	1	1	1	1	1	0	1	0	0	0	1	1	1	0	2	1	0	1	1,2	1	1,20,10	0,1?	0,2?	?	?	?	?	?	?	
K. fragilifolia	1	1	0	1	1	0	1,2	1	0	2	1	0	0	1,2	1	0	1,2	1	0	1	1	1	1	1	0,10	1	?	?	2	?	?	?	
K. bisetula	1	1	0	0	1	1	0,11	0	2	0	0	0	0	1	1	1	?	1	1	0	1	1	1	0	2	?	?	?	?	?	?	2	
K. helophila	1	1	0	0	0	1	1	0	0	0	0	0	0	0,10	0	0	0	0	0	1	0	1	0	1	0	0	0	?	0	0	?	?	
K. calcarata	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	2	1	?	?	
K. quinquespina	1	1	0	1	1	1	1	1	0	2	0	1	1	2	1	1	?	1	1	0	0	1	1	1	2	1	0	0	?	0	1	2	
A. diacantha	0	0	0	0	1	0	1	1	0	3	0	2	0	3	1	1	?	1	1	0	1	2	0	2	?	?	?	?	0,20	1	2	0	
chaetophylla	1	0	0	0	1	0	1	1	0	2	0	1	0	2	1	1	?	1	1	0	1	1	0	1	1	0	2	0,10	2	0	0	1	2
longifolia	1	0	0	0	1	0	1	1	0	2	0	0	0	2	1	1	0	1,2	1	0	1	1	0	1	2	0,10	2	0	0	1	1	1	
chaetocarpa	1	0	0	0	1	1	1	0,10	2	0	0	1	2	1	1	?	1	1	0	1	1	0	1	0	1	0	1	0	1,20,10	1	2	1,2	
trisetosa	1	0	0	0	1	1	1	0,10	2,30	1	0,12	1	1	1	?	1	1	0	1	1	0	1	1	0	1	0,10	1	0	0	1	?	?	
neesii	1	0	0	0	1	0	1	0	1	1	0	0	0	1	0	1	0	2	1	0	0	1	0	1	0	0	0	1	2	1	?	?	
kogiana	1	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	1	2	1	0	1	1	0	1	0	0	1	1	2	1	?	?	
lawesii	1	0	0	0	1	0	1	0	0	1	0	2	0	1	1	1	0	2	1	0	1	1	0	1	0	0	1	1	2	1	?	?	
kaindina	1	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1	0	2	1	0	1	1	1	1	?	0	1	1	0	1	?	?	
blepharostoma	1	0	1	0	1	0	1	1	0	1	0	0	1	1	1	1	2	1	0	0	1	1	1	0	0	2	1	2	?	?	?	?	
oligophylla	1	0	0	0	1	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0,10	0	?	0	?	?	?	?	
plumulosa	1	0	0	0	1	0	1	0	0	1	0	0	1	1	1	1	0	0,2	1	0	0	1	0	0	0	0	0	0	1	0	?	2,3	
pseudozoopsis	1	0	0	0	1	0	1	1	0	1	0	0	0	1	1	?	1	1	0	1	1	0	1	0	2	0	0	2	0	0	?	?	?
longitudinalis	1	0	0	0	1	1	1	0	1	1	0	0	0	2	0	1	0	1	0	1	1	0	1	0	0	0	0	1	0	0	?	?	?
trichocoleoides	1	0	0	0	0	0	1	2	0	1	0	0	0	1	0	1	0	2	1	0	0	1	0	0	0	0	0	0	0	2	0	?	?
iriomotensis	1	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1	1	2	1	0	1	1	0	1	0	0	0	0	1	2	1	?	?
capilligera	1	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	0	2	0	0	1	0	0	0	0	0	0	1	1	0	?	?	?
tridactylis	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	2	0	0	1	0	0	0	0	0	0	1	1	0	1	1	1
palmata	1	0	0	0	1	0	1	0	0	1	0	0	1	0	1	0	2	0	0	1	0	0	0	0	0	0	0	1	1	0	1	?	?
centipes	1	0	0	0	1	0	1	0	0	1	0	0	0	2	1	1	0	1	1	1	1	1	0	1	0	1	1	1	1	0	?	?	?
perfragilis	1	0	0	0	1	0	1	0	0	1	1	0	0	0	2	1	1	0	1	1	1	1	0	1	0	0	1	1	1	0	?	?	?
tuberifera	1	0	0	0	1	0	1	0	0	1	1	0	0	1	2	1	1	0	1	1	1	1	0	1	0	0	1	1	1	?	?	?	?
elegans	1	0	0	0	1	0	1	0	0	1	0	0	0	1	2	1	1	0	1	0	1	1	0	1	0	0	1	1	1	?	?	?	?
tetrapila	1	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	1	0	0	1	1	0,11	0	0	0	0	0	1	1	2	1	1	2
paludicola	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0	1	1	0	?	?	?
gibbsiana	1	0	0	0	1	0	1	0	0	1	0	0	1	2	0	1	0	0	0	1	0	1	0	0	0	0	0	1	?	0	1	?	1,2
grossiseta	1	0	1	0	1	0	2	0	0	0	0	0	1	3	0	1	0	0	0	1	0	1	0	0	0	0	1	1	1	1	?	?	?
herzogii	1	0	0	0	1	0	0	1	0	3	0	0	0	1	2	1	1	?	1	1	0	1	2	0	2	1	0	2	0	0	?	?	?
tasmanica	1	0	0	1	1	0	1	1	0	2	0	1	1	1	1	?	?	1	1	0	1	1	0,12	1	0	2	0	0	?	?	?	?	?
inaequalis	1	0	0	0	1	1	0	1	0	3	0	2	1	2	1	1	?	1	1	?	1	2	0	2	1	0	0	0	0	?	?	?	?
clatritexta	1	0	1	0	1	0	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0,10,10	0	0	0	0	0	0	1	1	0	?	?	?
meridiana	1	0	0	0	1	0	1	0	1	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	?	?
hodgsoniae	1	0	0	0	1	0	1	0	0	1	0	1	0	0	0	1	1	0	1	1	1	1	0	0	0	0	0	1	1	0	1	?	?
nivicola	1	0	0	0	1	0	0	1	0	1	0	0	0	1	1	1	?	?	1	1	1	1	1	0	2	1	0	2	0	0	?	?	?
pennata	1	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	?	0	?	?	?
praenitens	1	0	0	0	1	0	1	0	0	1	0	0	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0	1	?	2	1	1	1
pulcherrima	1	0	0	0	0	0	1	2	0	1	0	0	0	3	1	1	0	2	1	1	0	1	0	0	0	0	0	0	0	0	?	?	3
remotifolia	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	1	2	1	1	1	1	0	1	0,10	2	?	2	0	?	?	?	?
lindenberghii	1	0	0	0	1	0	1	0	0	1	0	0	1	1	1	1	0	2	1	0	1	1	0	1	0	0	1	0,10	1	1	1	1	1
tetradactyla	1	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	2	1	0	1	1	0	1	0	0	1	1	0	1	?	?	?
quadrisseta	1	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	2	1	0	1	1	0	1	0	0	1	0	0	1,13	1	?	?
granulata	1	0	0	0	1	0	1	0,10	2	0	1	0	1	0,11	0	2	1	0															

16. Leaf width at base. In *T. clatritexta* and *T. meridiana* the leaf insertion is up to 18 cells wide, and bears no definite relationship to the number of leaf lobes. In other species of *Telaranea* the number of cells along the insertion is almost al-

ways twice the number of lobes: 8 cells wide at the insertion in 4-lobed leaves, 6 in 3-lobed branch leaves, 10 in 5-lobed leaves, and up to 23 cells in *T. pulcherrima*, corresponding to a lobe number of 9–12. When the basal cells of the lobes



form the "disc" (*T. inaequalis*, *T. tasmanica*, *T. herzogii*), disc width has been scored as definite (16,1).

Leaf width at base is treated as a binary character: 0 = indefinite; 1 = definite (8, 10, 12 cells, etc.).

17. Disc shape. Leaf disc shape varies in *Telaranea* from  $\pm$  parallel-sided (*T. elegans*) to cuneate (*T. capilligera*, *T. praenitens*).

Disc shape is treated as a binary character: 0 = disc cuneate (disc cells more numerous in distal portion); 1 = disc parallel-sided (8 cells wide throughout).

18. Leaf disc height. Disc height varies from an extreme of 9–13 cells high in *T. oligophylla* (Fig. 54: 1–4) to a disc only 2 cells high (*T. lindenbergii*, Fig. 26: 2, 3), consisting of a single tier of cells along the insertion, plus the tier of paired cells at the base of each lobe. In most *Telaranea* species, however, the disc is of medium height, 3–4 cells high (*T. tridactylis*, Fig. 6: 6, 7). When the basal cells of the lobes themselves form the "disc," the disc is scored as 0 cells high (18,1), whether the lobe bases are geminate (*T. tasmanica*, *Kurzia quinquespina*) or uniseriate (*T. herzogii*, *Arachniopsis diacantha*).

Disc height is treated as a multistate character with 3 states: 0 = 5 cells or more; 1 = disc height 0; 2 = 2–4 cells high.

19. Disc areolation. The common condition in *Telaranea* is for disc cells  $\pm$  precisely arranged in longitudinal rows and tiers (*T. centipes*, Fig. 21: 2). In some species (*T. capilligera*, Fig. 3: 1, 3; *T. clatritexta*, Fig. 1: 2, 3), however, the leaves resemble the condition in *Lepidozia*, in which the cells of the disc are compact and irregularly arranged.

Disc areolation is treated as a binary character: 0 = irregular; 1 = regular rows and tiers.

20. Disc cell width. Some species of *Telaranea* have relatively small cells, lending the leaves a dense, subopaque appearance (*T. pennata*, *T. tridactylis*). Others have much larger cells (to 70  $\mu$ m in *T. tetrapila*) and lax areolation, the entire plant with a turgid,  $\pm$  translucent quality. Although cell size is essentially quantitative, cell width ranges in different species showed a discontinuity at about 40  $\mu$ m, which was used as a basis for scoring this character. For consistency, measurements reflect the average width of median disc cells. In species in which disc height is scored as 0 (as for example, *T. chaetophylla*, *T. herzogii*, character 18,1), measurements of disc cell size apply to the basal cells of the lobes.

Disc cell width is treated as a binary character: 0 = less than 35  $\mu$ m; 1 = 40  $\mu$ m or more.

21. Symmetry. Radial symmetry in leafy hepatics in general is regarded as primitive, and the differentiation of underleaves from leaves *per se* is generally explained as a corollary of shoot orientation, in hepatics as well as in other groups (e.g., *Selaginella*). In Balantiopsaceae, however (see Engel & Merrill, 1997, pp. 27, 44), there are indications that subisophylly may be related to habitat-related factors rather than supposed primitiveness.

Pronounced anisophylly is typical of most leafy hepatics, and most *Telaranea* species are moderately to distinctly anisophyllous. Strict isophylly, in which underleaves are undistinguishable from leaves, is rather uncommon. Approaches to the isophyllous condition can be seen in *Triandrophyllum* and *Lepidozia spinosissima*, two of the outgroups chosen for this study. *Telaranea* also includes some subisophyllous species (*T. pulcherrima*, *T. oligophylla*, *T. plumulosa*) with underleaves only slightly smaller than the leaves and resembling them in form; in a few cases (*T. tridactylis*) the two are similar in form, but the underleaves are much smaller.

Underleaves may differ from leaves in other ways, apart from relative size. In some *Telaranea* species, underleaf lobes are acute and resemble the lobes of the leaves (22,0). In other species the underleaf lobes are essentially uniseriate to the base (22,1 and 22,2), but this type is not restricted to species with capillary leaf lobes. The areolation of the underleaf disc may or may not show the orderly arrangement of cells in the leaves. The height of the underleaf disc (24) is usually less than that of the leaves. Rhizoids typically originate from a  $\pm$  well-defined field of small quadrate cells, either at the underleaf base (28,0) or forming a distal "pad" at the base of the lobes (28,1). The underleaves of some species are asymmetrically lobed (23,1), where one or more lobes is short and uniseriate and the other(s) resemble leaf lobes.

Symmetry is treated as a binary character: 0 = subisophyllous; 1 = anisophyllous.

22. Underleaf lobe base. Underleaf lobes in *Telaranea* vary from acute or acuminate, 3–4 cells wide or more at the base, often with an additional biseriate tier, and a usually rather short uniseriate row (*T. meridiana*, *T. clatritexta*), to uniseriate except for a basal pair of cells (*T. tuberifera*, *T. lindenbergii*). In some species the underleaf "disc" is formed by the connate basal cells of the lobes;



in these the basal cells are either geminate (*T. chaetophylla*, *T. nematodes*), or undivided (*T. herzogii*).

Underleaf lobe base is treated as a multistate character with 3 states: 0 = acute, 3–4 or more cells wide at base; 1 = capillary, inserted on two basal cells; 2 = basal cells undivided.

23. Underleaf lobe differentiation. In many *Kurzia* species and in a few *Telaranea* species (*T. blepharostoma*, Fig. 39: 1, 4), underleaf lobes are dimorphic, with one or more lobes shorter and mostly uniseriate, and other lobes  $\pm$  resembling the leaf lobes in form (although at times with a terminal slime papilla).

Underleaf lobe differentiation is treated as a binary character: 0 = lobes similar; 1 = lobes dissimilar.

24. Underleaf disc height. In general, underleaf disc height is expressed as in the leaf (see character 18). Thus, when the lobes are uniseriate and inserted on a pair of basal cells, the latter are counted as part of the disc. Some species have underleaves with a well-developed disc 3–4 or more cells high (to 7 cells in *T. clatritexta*, Fig. 1: 10). In others (*T. lindenberghii*, *T. remotifolia*) the underleaf disc is only 2 cells high, with a single tier of (true) disc cells, in addition to the basal cells of the lobes. When the underleaf “disc” consists solely of the connate basal cells of the lobes (*T. chaetophylla*, *T. herzogii*) it is counted as 1 cell high.

Disc height is treated as a multistate character with 3 states: 0 = 3 or more cells; 1 = 2 cells high; 2 = 1 cell high.

25. Half-leaf lobing. The stem leaf associated with terminal branches in the Jungermanniales is formed from the dorsal half (*Frullania* type) or ventral half (*Microlepidozia* type) of a lateral apical cell derivative, the other half giving rise to the branch. As a general rule, the number of half-leaf lobes is half that of the leaves, for example in *T. pulcherrima*, which has 9–12-lobed leaves, the half-leaf is 4–5(6)-lobed (Fig. 25: 1). In most species of *Telaranea*, half-leaves are 2–4-lobed, or undivided (*T. martinii*, Fig. 29: 1, 10; *T. herzogii*).

Half-leaf lobing is treated as a binary character: 0 = 2–4-lobed (or more); 1 = undivided.

26. First branch underleaf (FBU) position. In most of the taxa included in the analysis, the first underleaf produced at the base of a *Frullania*-type branch is located at or near the branch base. In a few species (*T. clatritexta*, Fig. 1: 7; *T. grossiseta*, Fig. 14: 1) the FBU often appears displaced, and

inserted some distance below the base of the branch.

FBU position is treated as a binary character: 0 = at or near base of branch; 1 = displaced on stem. A species is scored 26,1 if a displaced position has been observed in that species.

27. First branch underleaf (FBU) lobing. The first branch underleaf takes several forms, often differing from the normal underleaves of the shoot and branches in shape, symmetry, and number of lobes. In most *Telaranea* species the FBU is undivided and subulate. A less common type of FBU, first noted in *T. longifolia* by Schuster and Blomquist (1955, as *T. nematodes*) is asymmetrically bilobed, with one lobe shorter and ending in a slime papilla (*T. herzogii*, *T. remotifolia*). In a few *Telaranea* species (*T. pulcherrima*, Fig. 25: 9), and in most outgroup taxa, the FBU is  $\pm$  equally and symmetrically 2–4-lobed.

FBU type is treated as a multistate character with 3 states: 0 =  $\pm$  equally 2–4-lobed; 1 = undivided or only sporadically 2-lobed; 2 = 2 dissimilar lobes.

28. Rhizoid origin. In *Telaranea*, rhizoids originate from the cells of the underleaf disc. Transverse and vertical tangential divisions of the lobe cells give rise to a transverse strip of small quadrate cells, termed rhizoid initials; often divisions in the plane of the disc produce a bi- or multi-stratose pad of initials. In *T. clatritexta* these arise from cells at the base of the underleaf. In all other species the rhizoidal initials form a distinct strip at the distal portion of the underleaf disc (*T. tetrapila*, Fig. 18: 8), sometimes from the basal cells of the lobes as well. Species in which the underleaf disc is only one cell high, excluding the basal cells of the lobes (*T. herzogii*, Fig. 35: 4) were scored as basal. In *Arachniopsis coactilis*, rhizoids at times originate from terminal cell(s) of the leaf lobes (Fig. 44: 3–10) as well as from the basal cells of the underleaves.

Rhizoid origin is treated as a multistate character with 3 states: 0 = on or near basal cells of underleaf disc; 1 = from distal cells of underleaf disc; 2 = from leaf lobe tips.

29. Cuticle. Leaf cells in *Telaranea* may be smooth, or the surface may be variously papillose, scabrous, or glaucous. In a few species, all Australasian (*T. centipes*, *T. grossiseta*), the cells are obscured by a  $\pm$  uniform, densely granular deposit, and the plants are glaucous and often highly water repellent. The glaucous condition also occurs in other regional Lepidoziaceae (*Bazzania taylorii*, *Lepidozia glaucophylla*). A papillose cu-

icle (29,2) is characterized by discrete, wartlike surface projections. These may be rounded or somewhat elongate, forming longitudinal striae (*T. patentissima* var. *zebrina*, Fig. 17: 1, 9). In *T. quadricilia* the cuticle is finely and evenly scabrous with minute, sharp prickles (Fig. 28: 3). A rough, papillose cuticle also occurs in several out-group taxa. In most *Telaranea* species both disc and lobes appear smooth, even under the highest magnification of the light microscope. Cuticular roughening may be limited to a portion of the leaf. For example, in *T. quadricilia* (Fig. 28: 3) and *T. remotifolia* (Fig. 24: 1–7) the lobe cells are papillose, but the disc cells are smooth.

Cuticle is treated as a multistate character with 4 states: 0 = smooth; 1 = glaucous; 2 = papillose; 3 = granular/scabrous.

30. Antheridial stalk. Biseriate antheridial stalks occur in *T. meridiana*, in *T. centipes* and *T. perfragilis*, as well as in *T. pulcherrima* and *T. trichocoleoides*. The stalk is uniseriate in other *Telaranea* species for which androecia are known, as well as in *Arachniopsis diacantha*. Biseriate antheridial stalks occur in *Triandrophyllum*, *Lepidozia spinosissima*, *L. obtusiloba*, and *Kurzia helophila*, but in other *Kurzia* species included in the analysis they are uniseriate.

Antheridial stalk is treated as a binary character: 0 = 2-seriate; 1 = uniseriate.

31. Seta cross section. In Lepidoziaceae the outer layer of cells of the seta is composed of 8 or 16 rows of cells that are much larger than the more numerous interior cells (Schuster, 1969, p. 9). In all *Telaranea* species for which seta structure is known the outer layer consists of 8 large cells (5–7 in *T. tuberifera*) surrounding 15–24(34) medullary cells or fewer. The seta section in *Telaranea* is thus similar to the section of the stem, with a differentiated “hyaloderm” of larger cells. A seta with as few as 4 inner cells occurs in a few species (*T. herzogii*, *Kurzia quinquespina*) which also have stems with a small number of medullary cells. In *Lepidozia obtusiloba* the seta has 16 outer cells and ca. 40 medullary cells (Fig. 65: 2); in *Triandrophyllum* the outer cells are ca. 60 in number and smaller than the medullary cells (Fig. 68: 14).

Seta section is treated as a multistate character with 4 states: 0 = outer layer 16 + inner  $\pm$  40; 1 = outer layer ca. 8 + medullary cells 15–30; 2 = outer layer ca. 8 + medullary 12 or less; 3 = outer layer numerous, inner larger.

32. Capsule valve thickness. The capsule wall is 4–5 strato in *T. plumulosa* (Fig. 56: 12), 5–

strato in *T. pulcherrima* (Schuster, 2000, fig. 81: 5), and 4–5-strato in *Lepidozia obtusiloba* (Fig. 65: 3). In *Triandrophyllum*, the wall is 5–6-strato (Fig. 68: 7). In *T. lindenberghii*, *T. praenitens*, *T. herzogii*, *T. centipes*, and *T. tuberifera* the wall is 2–3 strato. We decided to score the number of wall layers observed, which resulted in multiple state assignments for some species.

Capsule valve thickness is treated as a multistate character with 5 states: 0 = 2-strato; 1 = 3-strato; 2 = 4-strato; 3 = 5-strato; 4 = >5-strato.

## Other Potential Characters

SPORE SCULPTURING—Reticulate spore sculpturing was illustrated by Schuster & Blomquist (1955, fig. 4) in *T. longifolia*, and has often been cited as a generic character of *Telaranea*. For example, Schuster (1969, p. 31) noted for the genus that “. . . without exception at least the outer spore face is always delicately reticulate, being covered by a close-meshed web of fine, anastomosing ridges.”

Of the 23 species of *Telaranea* for which sporophyte data is available, spores were observed in 19. Of these, 13 were examined under the scanning electron microscope. Unfortunately, this was not done until late in the study, and consequently, spore ornamentation is not included as a character in the matrix.

The type of the genus, *T. chaetophylla* (Fig. 69: 1), has “reticulate-areolate” spores, with low ridges enclosing irregular polygonal areolae. The ridges form a more or less closed reticulate pattern and the surface of the areolae (ground) is essentially smooth. *Arachniopsis diacantha* (Fig. 69: 2, 3) has almost identical reticulate-areolate spores, although Schuster (2000, p. 448), described the spores of *Arachniopsis* as “densely granular, verruculose or granular-papillate.”

The spores of *T. lindenberghii* (Fig. 69: 4), *T. longifolia* (Fig. 69: 5, 6) and *T. nematodes* (Fig. 70: 1, 2) are also reticulate-areolate, but with the ground roughened by scattered, minute papillae. *Telaranea europaea* (Fig. 70: 3, 4) and *T. tuberifera* (Fig. 70: 5, 6) have distinctly reticulate spores with prominent ridges.

Not all species of *Telaranea* have areolate spores, however. At one extreme, in *T. tridactylis* (Fig. 71: 1, 2) the spore surface is “rough plastered,” with closely spaced, irregular broad elevations, covering the spore surface. In *T. paten-*

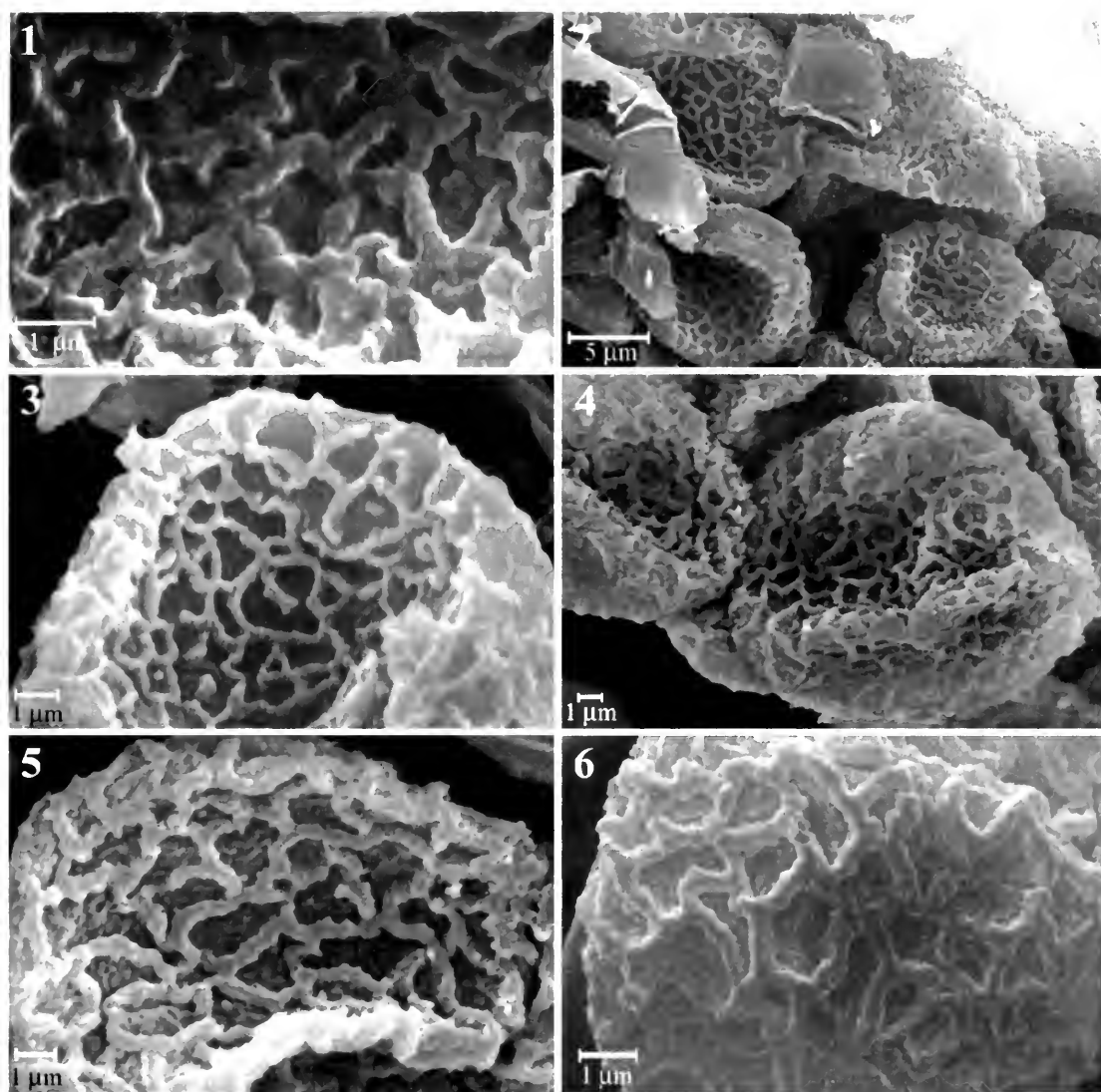


FIG. 69. SEM micrographs of spores. Reticulate-areolate type. 1. *Telaranea chaetophylla* (Spruce) Schiffn. 2, 3. *Telaranea diacantha* (Mont.) Howe. 4. *Telaranea lindenberghii* (Gott.) Engel & Merr., ground surface roughened by scattered, minute papillae. 5, 6. *Telaranea longifolia* (Howe) Engel & Merr., ground with scattered, minute papillae. (Fig. 1 from type of *Lepidozia chaetophylla* Spruce (BM); 2, 3 from Crosby 2393, Trinidad, trail to Morne Bleu from summit of Arima-Blanchisseuse Rd.; 4 from type of *T. lindenberghii* var. *complanata*; 5, 6 from Schuster F-101, Florida, Highland Hammock State Park.)

*tissima* (Fig. 71: 3, 4), *T. tetrapila* (Fig. 71: 5, 6), *T. plumulosa* (Fig. 72: 1) and *Arachniopsis coactilis* (Fig. 72: 2–4, the type of the genus *Arachniopsis*), the spores are “papillose-vermiculate,” marked by irregular short ridges which appear to be formed by coalescing papillae. The ridges are discontinuous, however, and do not delimit areolae. Spores of *Lepidozia obtusiloba* (Fig. 65: 6) and *Triandrophyllum* (Fig. 67: 15) appear papil-

lose-vermiculate as seen with the light microscope.

In the outgroup taxon, *Kurzia hippuroides* (Fig. 62: 5), the spore surface has prominent, dome-shaped, coarse bosses, with the intervening wall surface papillose. In *K. quadriseta* (Fig. 72: 5, 6), the spores are papillose-vermiculate and resemble those of *Telaranea patentissima* (Fig. 71: 3, 4) and *T. tetrapila* (Fig. 71: 5, 6). The spores of *K.*

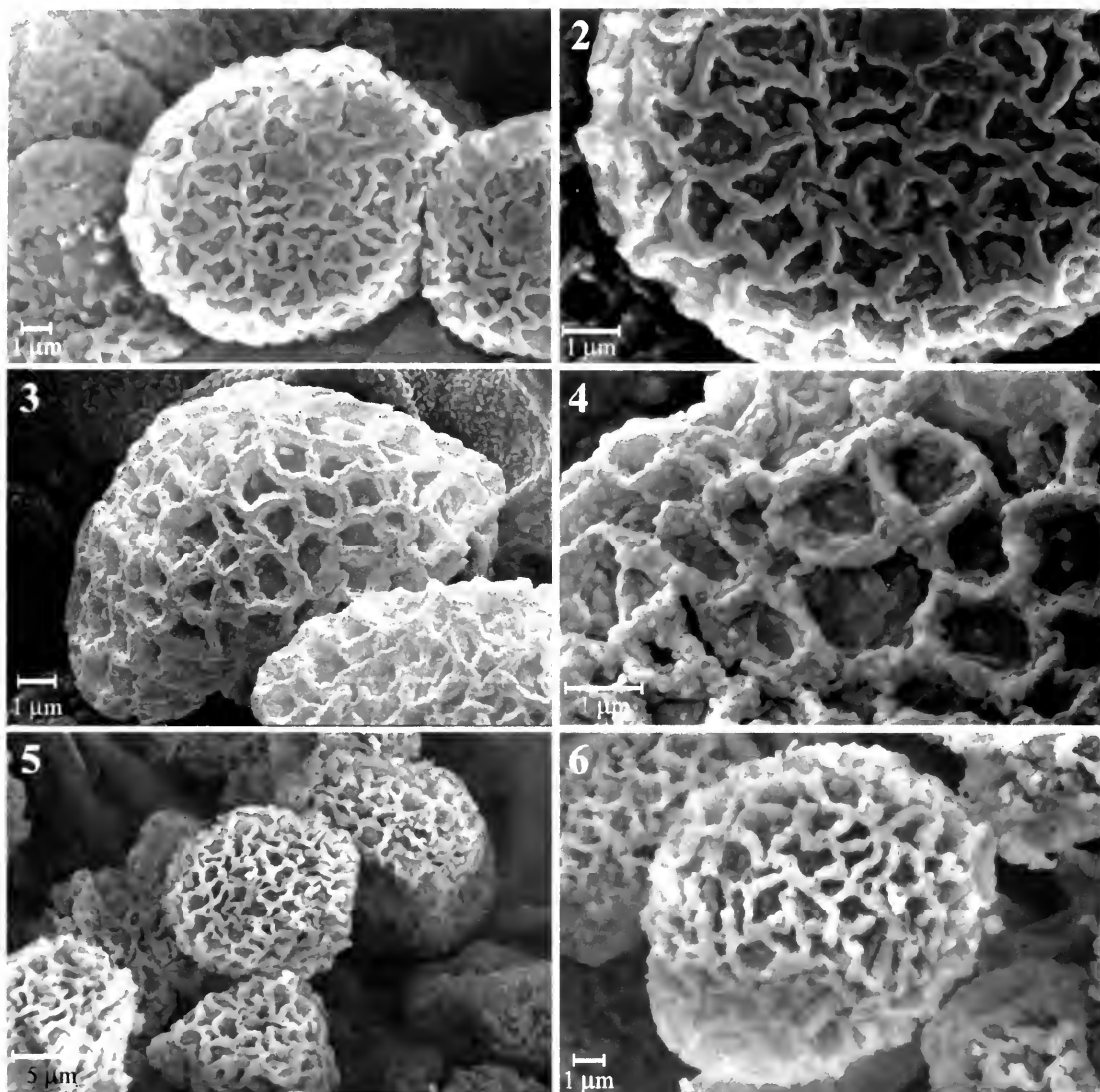


FIG. 70. SEM micrographs of spores. Reticulate-areolate type. 1, 2. *Telaranea nematodes* (Gott. ex Aust.) Howe, ground surface roughened by scattered, minute papillae. 3, 4. *Telaranea europaea* Engel & Merr., note high, prominent ridges, especially where displayed in profile note, and (fig. 4) dense cover of nanogranules on ridges and to a lesser extent on the intervening ground between the ridges. 5, 6. *Telaranea tuberifera* Engel & Schust., with prominent ridges. (Figs. 1, 2 from type of *Cephalozia nematodes* Gott. ex Aust. [NY]; 3, 4 from type of *T. europaea*; 5, 6 from Engel 19307, New Zealand, South Is., Paparoa Range, Croesus Track.)

*quinquespina* (Fig. 34: 16) are also papillose-vermiculate.

♀ BRACTS—Schuster (2000) remarked (p. 240) that unlobed, dentate ♀ bract apices are characteristic of subg. *Tricholepidozia* (as well as in *T. rectangularis*, of subg. *Neolepidozia*). In other *Telaranea* species, bracts are said to be “usually deeply quadrifid and/or lacinate or ciliate.” In fact, bracts with a dentate or lobulate apex are

found rather widely in the genus, e.g., in *T. centipes* (Fig. 21: 12), *T. gibbsiana* (Fig. 12: 4), *T. plumulosa* (Fig. 56: 7–10) and *T. tridactylis* (Fig. 7: 7). Dentate-lobulate bract apices also occur in the outgroup species *Lepidozia obtusiloba* (Fig. 64: 1–3) and *L. spinosissima* (Fig. 66: 4, 5).

Distinctly lobed ♀ bracts, but with a relatively high disc (divided to less than ca. 0.5), occur in *T. lindenberghii* (Fig. 26: 11), *T. martinii* (Fig. 30:

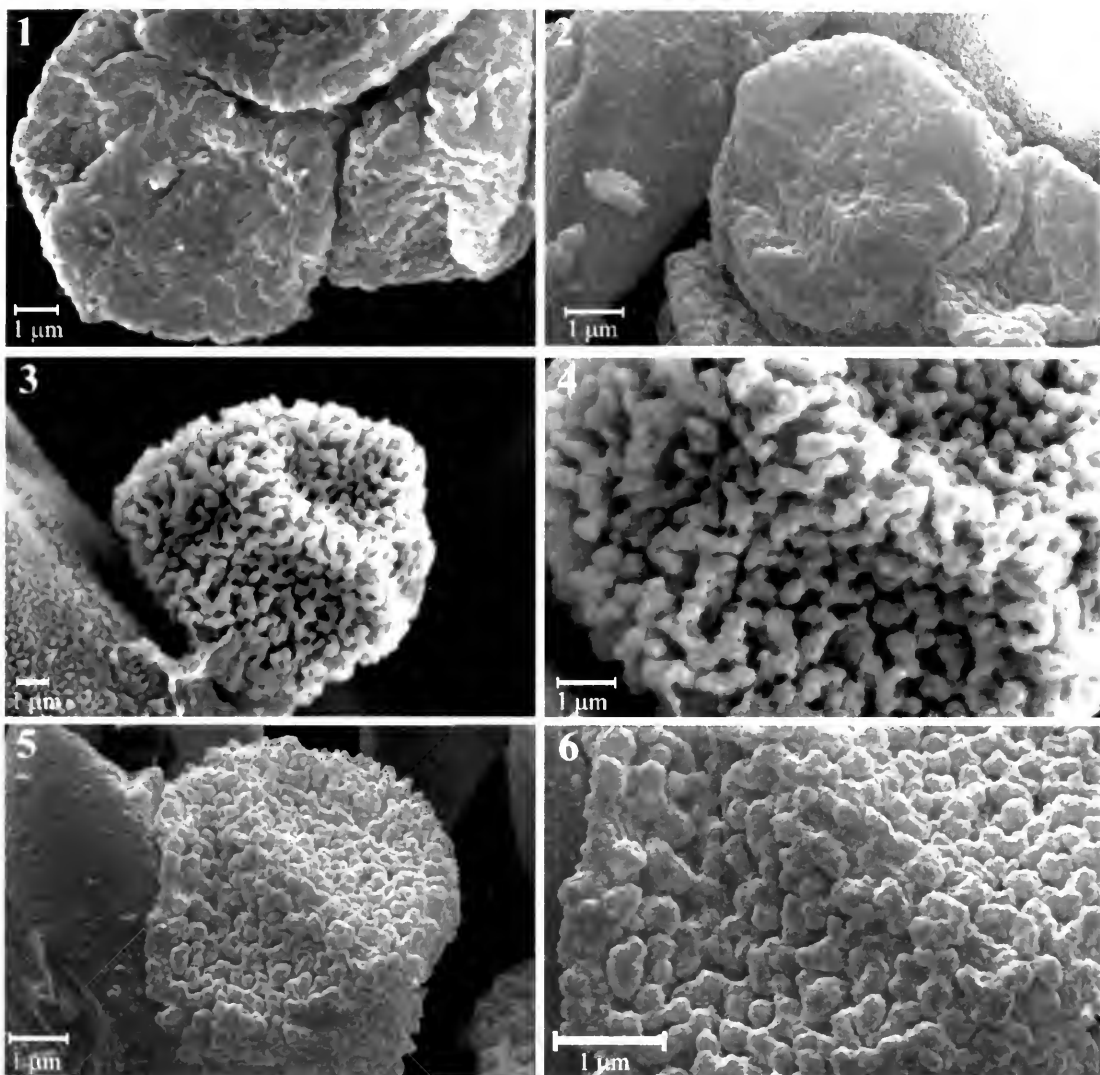


FIG. 71. SEM micrographs of spores. 1, 2. *Telaranea tridactylis* (Lehm. & Lindenb.) Engel & Merr., "rough plastered" surface with closely spaced, irregular broad elevations. 3, 4. *Telaranea patemissima* (Hook. f. & Tayl.) Hodgs., papillose-vermiculate type, with irregular, discontinuous, short ridges. Note areolae not delimited and (fig. 4) nanogranules on the ridges. 5, 6. *Telaranea tetrapila* (Hook. f. & Tayl.) Engel & Merr., papillose-vermiculate surface; note (fig. 6) dense cover of nanogranules on ridges and also the intervening ground between the ridges with scattered, minute papillae. (Figs. 1, 2, from Engel 19446, Tasmania, Surprise Valley; 3, 4, from Engel 17984, New Zealand, South Is., Mt. Aspiring Natl. Park, summit area of Haast Pass, 570 m; 5, 6, from Engel 18469, New Zealand, South Is., Arthur's Pass Natl. Park, Bealey River.)

1, 6), *T. tasmanica* (Fig. 33: 1, 2) and *T. tetradactyla* (Fig. 26: 12). *Kurzia quinquespina* has ♀ bract apices divided to 0.4 (Fig. 34: 10). Deeply divided bracts are found in such dissimilar taxa as *T. chaetocarpa* (Fig. 41: 1, 5), *T. chaetophylla* (disc 2–3 cells high, Fig. 43: 1), *T. herzogii* (Fig. 36: 2), and *T. quadricilia* (Fig. 28: 9), and in all of the *Arachniopsis* species examined in the

course of this study (*A. coactilis*, Fig. 44: 21, 22, *A. diacantha*, Fig. 46: 17).

**OIL-BODIES**—Oil-bodies are known for about nine species. Oil-bodies in *Telaranea* are for the most part hyaline or, in a few species, pale, smokey grey (*T. herzogii*, *T. remotifolia*). The surface is variable within the genus, ranging from  $\pm$  homogeneous in *T. nivicola* (Schuster, 2000, fig. 72: 11)

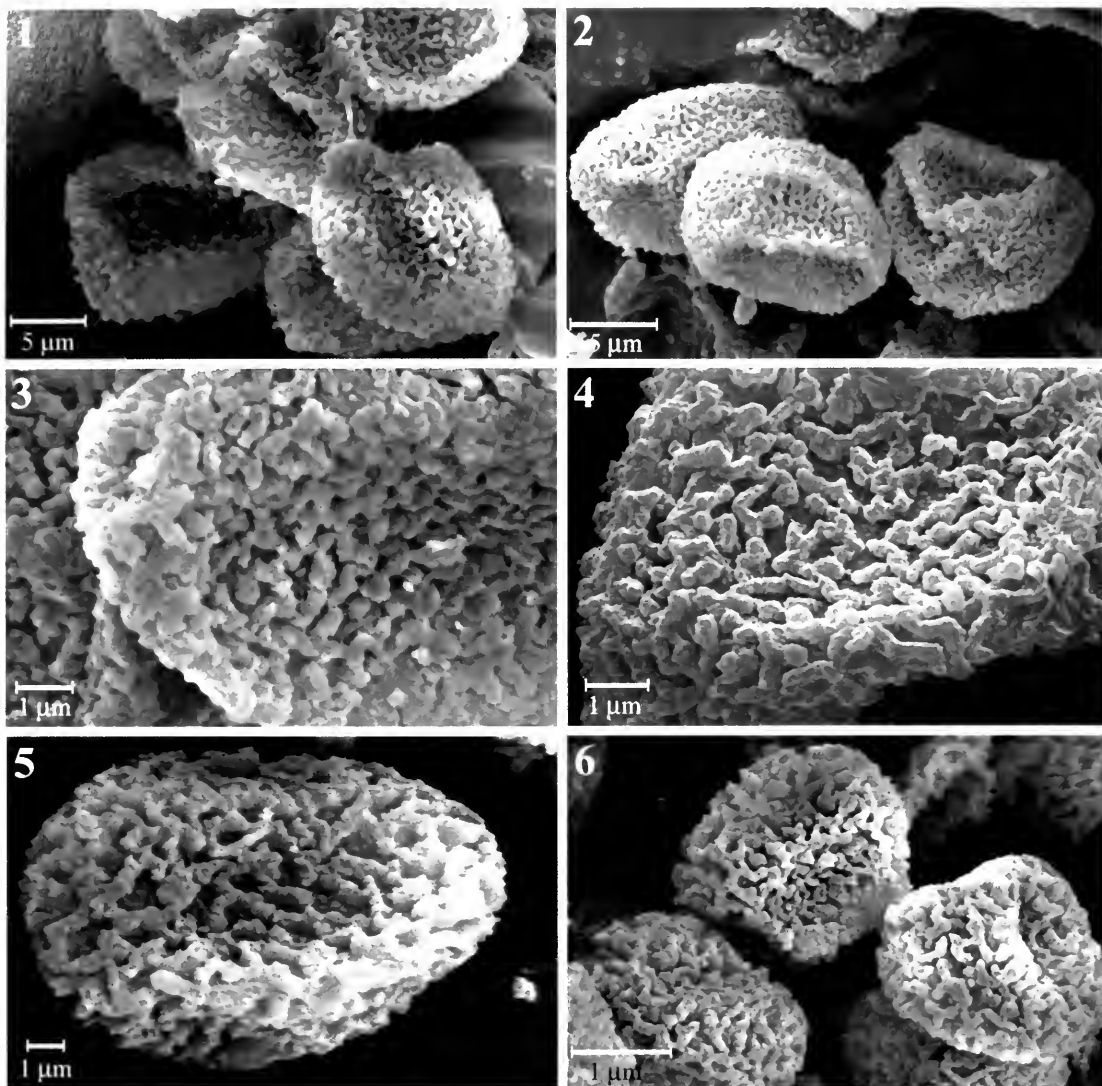


FIG. 72. SEM micrographs of spores. Papillose-vermiculate type. 1. *Telaranea plumulosa* (Lehm. & Lindenb.) Fulf. 2–4. *Telaranea coactilis* (Spruce) Engel & Merr., note (figs. 3, 4) ridges with covering of nanogranules. 5, 6. *Telaranea pallescens* (Grolle) Engel & Merr., note (fig. 6) ridges with nanogranules and the intervening ground between the ridges with scattered, minute papillae. (Fig. 1, from Engel 2240A, Chile, Brunswick Peninsula, Puerto Cutter; 2–4, from type of *Arachniopsis coactilis* [NY]; 5, 6, from Engel 19032, New Zealand, South Is., Paparoa Range, immediately N of Sewell Peak.)

to finely granular (*T. herzogii*, Schuster, 2000, fig. 78; 7) to more coarsely granular (*T. martinii*, Fig. 72A: 4) to coarsely papillose *T. remotifolia*, Fig. 72A: 2, 3; *T. tetrapila* Fig. 72A: 1). Most species fall within the 5–9 per cell range (e.g., ca. 6 in *T. remotifolia*, Fig. 72A: 2, 3; and 8–11 per cell in *T. tetrapila*, Fig. 72A: 1). *Telaranea pulcherrima* has 9–12 oil-bodies per cell (Schuster, 2000).

## Results

We used MacClade 3.04 (Maddison & Maddison, 1992) for entering our data and editing the data matrix, and PAUP\* 4.0 Beta Version (Swofford, 1998) for searching for most parsimonious trees. Both programs were used to analyze and interpret the resulting cladograms. In addition,



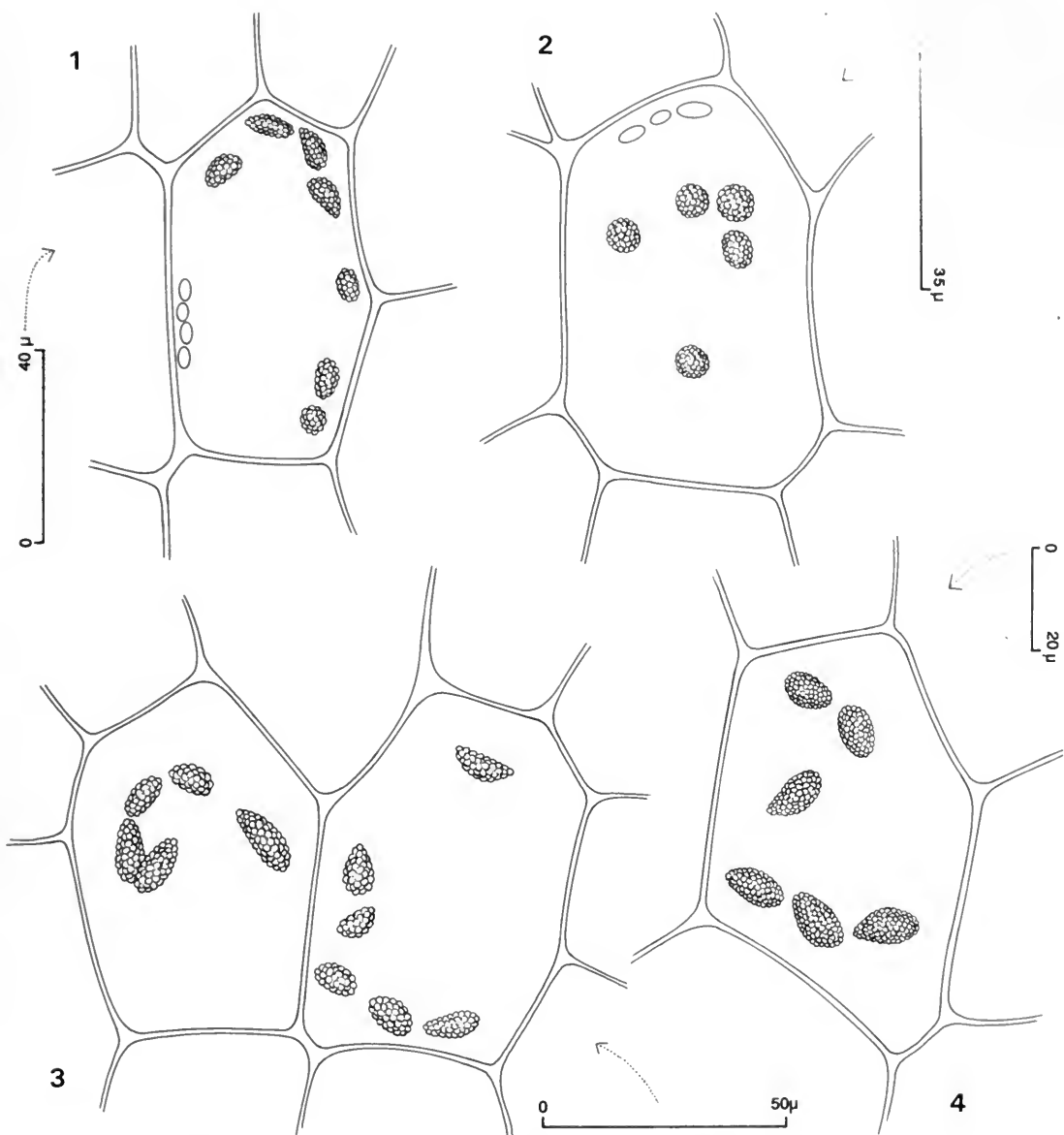


FIG. 72A. Oil-bodies. 1. *Telaranea tetrapila* var. *cancellata* (Col) Engel & Merr. Median cells of disc, the outline of a few chloroplasts included. 2, 3. *Telaranea remotifolia* Hodgs. Median cells of disc and cells at base of median sinus, respectively. 4. *Telaranea martinii* (Hodgs.) Schust. Median cells of disc. (Fig. 1, from Engel 25127, New Zealand, North Is., Herangi Range, Whareorino Forest; 2, 3, from Engel 24055, New Zealand, Stewart Is. Rakiura Natl. Park, Fern Gully Track; 4, from Engel 24773, New Zealand, South Is., Westland Prov., Cascade Rd, just W of Jackson River.)

PAUP was used to generate trees using the neighbor-joining (NJ) method for comparison with the phylogenetic trees. For the main analysis, PAUP was run on a Sun E3500 Enterprise Server, and for shorter runs on a Macintosh Quadra 610. Unrooted arrays were generated with TreeView (Page, 1996, 2000).

Analysis of the full data set of 56 taxa and 32

characters was attempted, using the heuristic search option of PAUP, with tree-bisection-reconnection (TBR) branch-swapping performed. Multistate taxa were interpreted as polymorphism; all characters were parsimony-informative. The search was truncated after generating 485,487 most parsimonious trees, with a score (length) of 213 steps. Strict consensus and majority (50%)

strict consensus of 485487 trees, len = 213

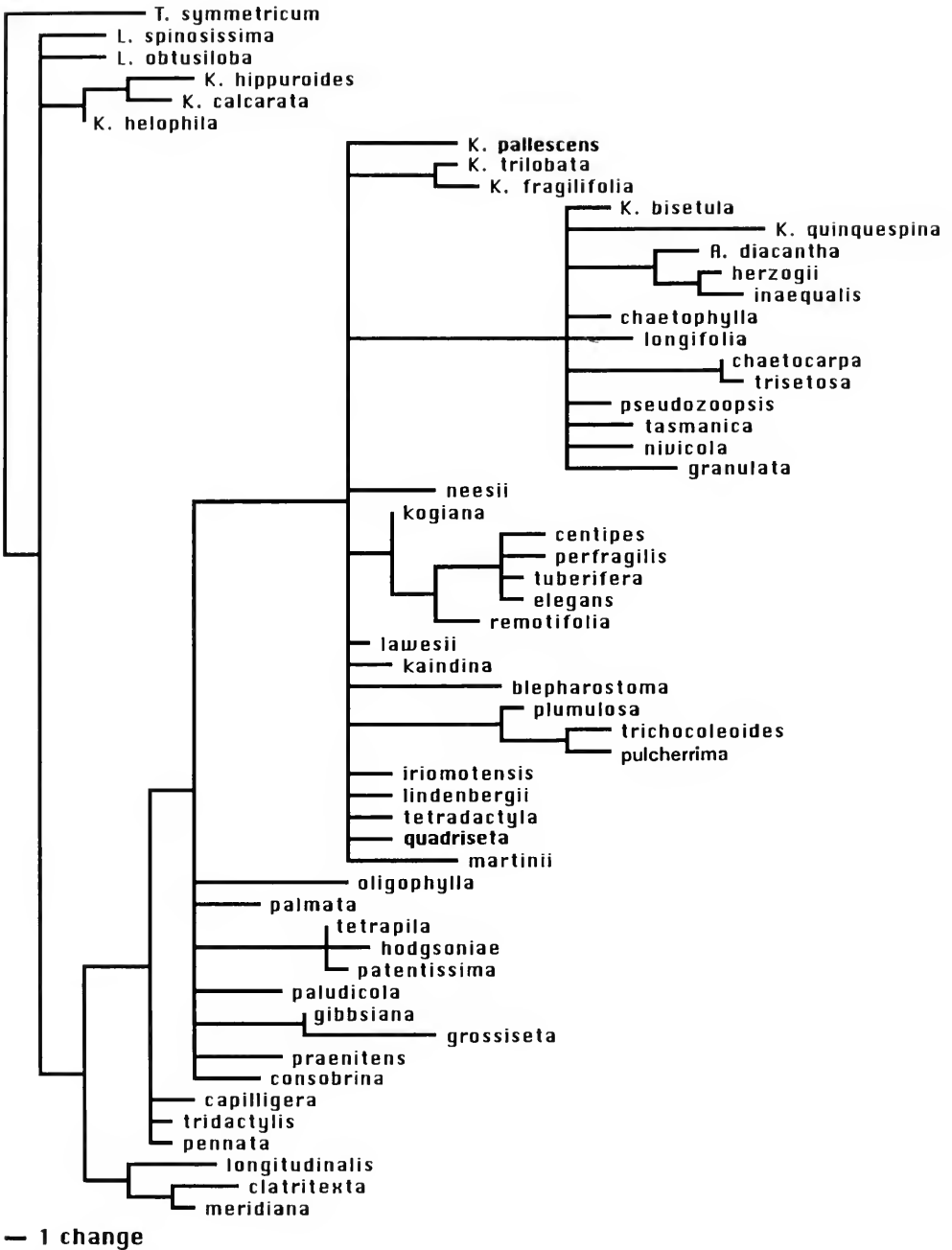


FIG. 73. Strict consensus of 485,487 most parsimonious trees. The length of a branch is proportional to the number of character changes occurring on that branch. Branches of zero length have no supporting apomorphies. Compare with fig. 77, illustrating the marked improvement of resolution resulting from elimination of *Triandrophyllum* from the data set.



majority consensus of 485487 trees, len = 213

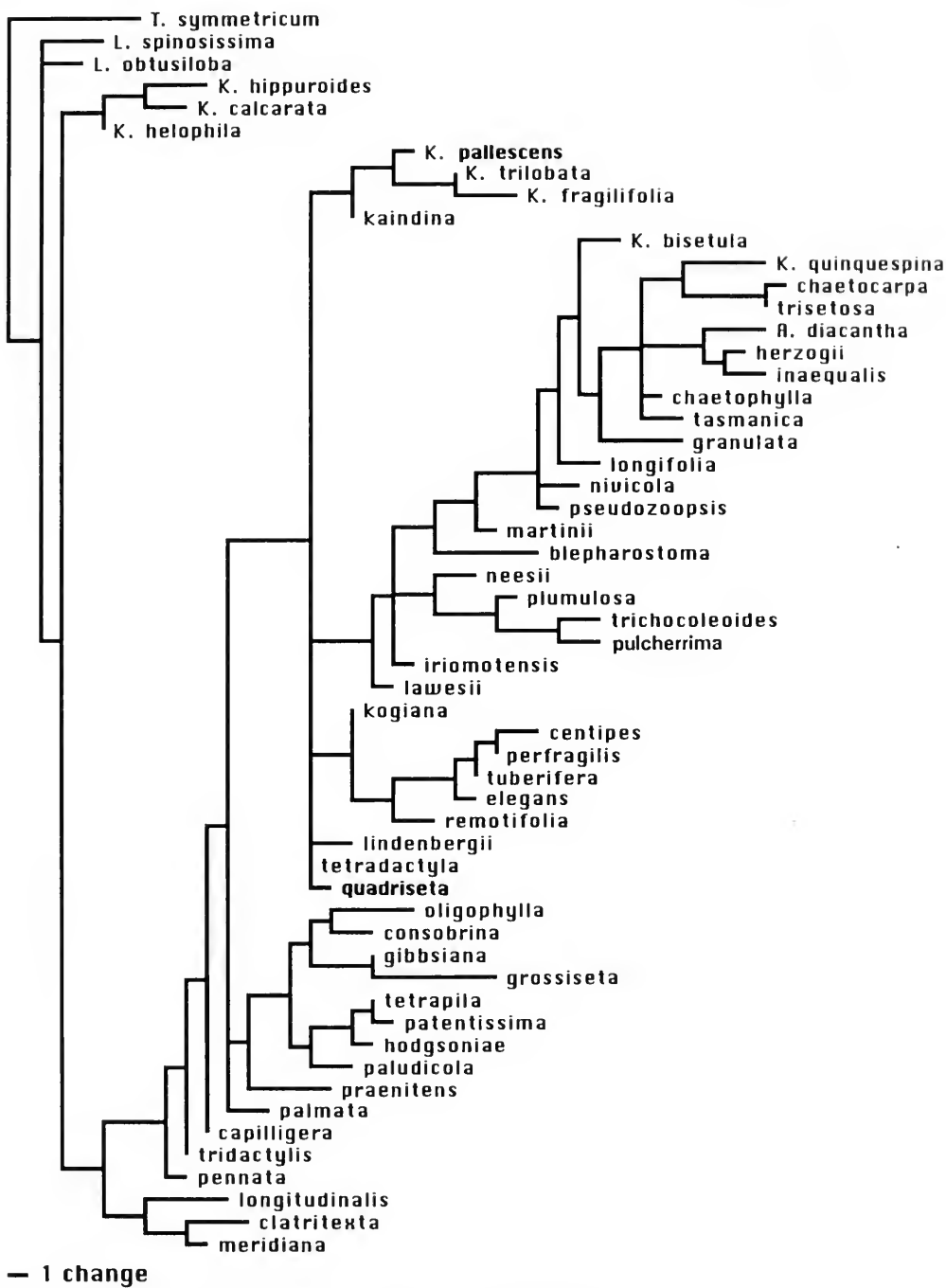


FIG. 74. Majority rule (50%) consensus of 485,487 most parsimonious trees.

consensus of these trees are shown in Figs. 73 and 74, respectively. The trees are drawn as phylograms, with the length of branches proportional to the number of character changes occurring on that branch. For clarity, the ingroup is represented as monophyletic, with the outgroup as paraphyletic to the ingroup taxa.

To test for the possibility of shorter trees, a run of 10,000 replicates was then made. PAUP was instructed to save no more than one tree of length greater than or equal to 210 in each replicate, with a random addition sequence, and nearest-neighbor interchange (NNI) branch-swapping performed. The length of the best tree found (Fig. 75) was 215 steps, with a consistency index (CI) of 0.4208, a homoplasy index (HI) of 0.7647, a retention index (RI) of 0.6735, and a rescaled consistency index (RC) of 0.2834. Bootstrapping (Felsenstein, 1985) was not attempted.

In an attempt to obtain a clearer picture of evolutionary trends and relationships, we selected two subsets of taxa for analysis and comparison. The first included only those species with sporophytes. Analysis of these 22 taxa yielded three most parsimonious cladograms (Fig. 76: 1–3). In this subset of the data, 2 of the 32 characters (#3 and #11) were parsimony-uninformative, and 1 character (#9) was constant. Each tree had a length of 121 steps, with a CI = 0.5785 (0.5714 with uninformative characters excluded), an HI = 0.5868 (0.4286), RI = 0.6277, and RC = 0.3632. The three cladograms are identical except for the resolution in the portion of the tree involving *T. gibbsiana*, *T. patentissima*, *T. praenitens* and *T. tetrapila*.

The other subset consisted of 21 taxa. Compared with the first group, in which selection was determined entirely by the availability of sporophyte data, the choice of taxa was more subjective, with preference given to taxa known from actual specimens examined vs. published descriptions, and completeness of data, including androecia as well as sporophytes. In this subset, 29 characters were parsimony-informative. The analysis yielded a single most parsimonious cladogram (Fig. 76: 4) with a length of 120 steps, with a CI = 0.5917 (0.5812 with uninformative characters excluded), HI = 0.5750 (0.4188), RI = 0.6370, and RC = 0.3769.

By eliminating *Triandrophyllum* as an outgroup, the overall topology remained unchanged but the resolution was dramatically improved. The analysis yielded 306 most parsimonious trees with a length of 215 steps. A strict consensus of these

trees is shown in Fig. 77, rooted at *L. spinosissima*. The trees were almost identical (see legend). One character (#1) was parsimony uninformative. A representative tree (#22) had a CI = 0.4186 (0.4159 with uninformative characters excluded), HI = 0.7674 (0.5841), RI = 0.6667, and RC = 0.2791. Figure 78 depicts the same tree, presented as an unordered array, with the subgenera and sections of *Telaranea* recognized in this study superimposed on the tree (see figure legend).

In addition to the phylogenetic analyses, trees were calculated using the neighbor-joining option of PAUP\*. The resulting NJ tree, based on total character distance, is shown in Fig. 79, with the length of branches proportional to the number of changes occurring on that branch.

## 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, 1998). 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. For the most part, the comments which follow are based on DELTRAN reconstructions, and are based on Fig. 75, the best tree from 10,000 replicates. Selected character changes are also indicated in Fig. 78, the strict consensus of 306 mp trees.

1. *Frullania*-type branching, CI = .500. The species of *Triandrophyllum* chosen lacks *Frullania*-type branching, but at least one other species of this genus has it. With *Triandrophyllum* omitted (Fig. 77), this character becomes an autapomorphy, CI = 1.00. Terminal, *Frullania*-type branching has been lost in *T. diacantha* (0), as this species was scored in the analysis.

The different branching types in leafy hepatics are all plesiomorphies to a greater or lesser degree. Variability in branching *per se* (Schuster, 1979, p. 64) is not a valid “phylogenetic criterion,” since it involves different types of branching in different combinations (see p. 201). The

10000.tre 1 tree held at each step, 10000 reps len = 215

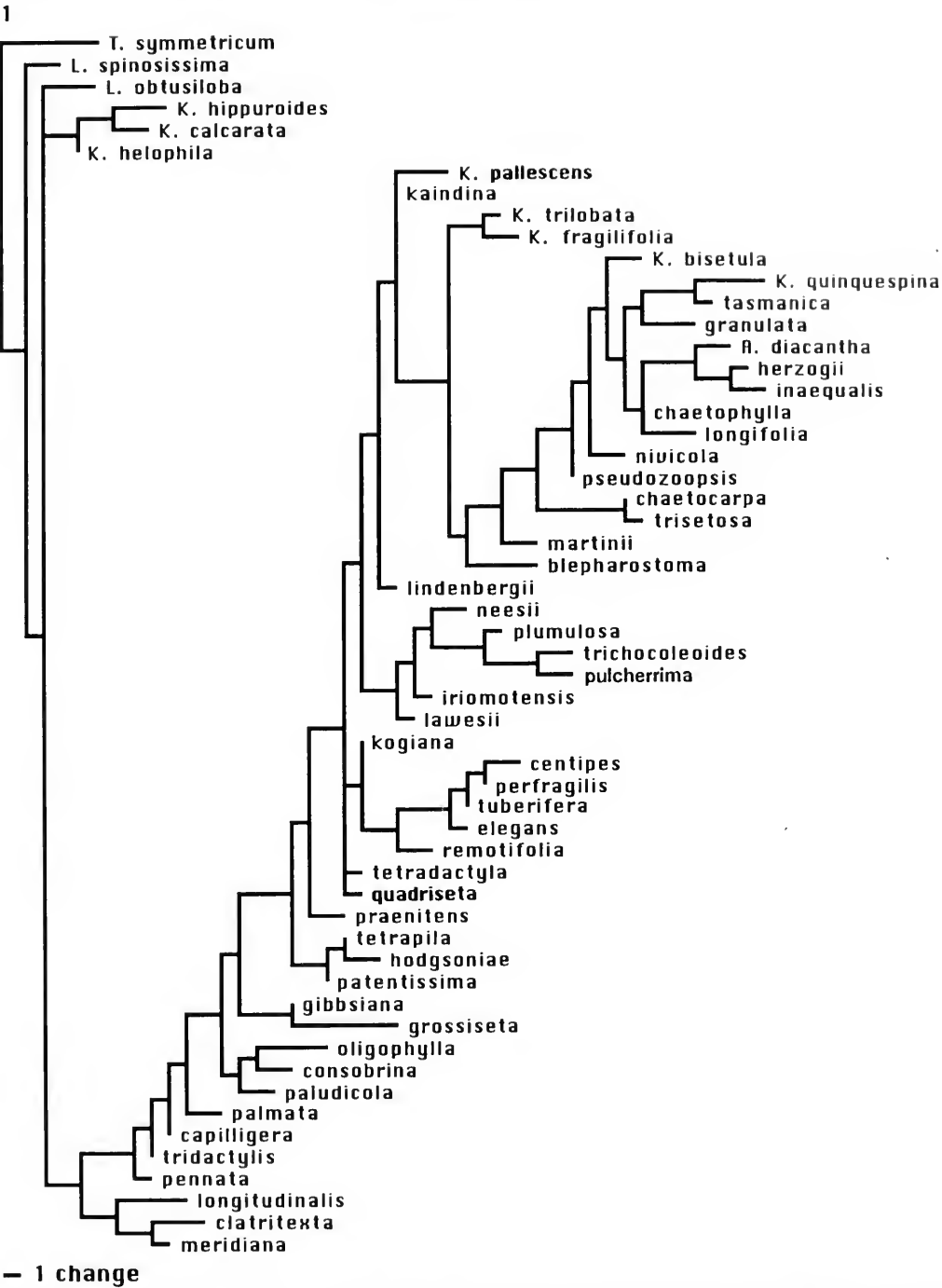


FIG. 75. Best tree (length = 215) from 10,000 replicates, one tree saved in each replicate, based on full data set. For explanation, see text.

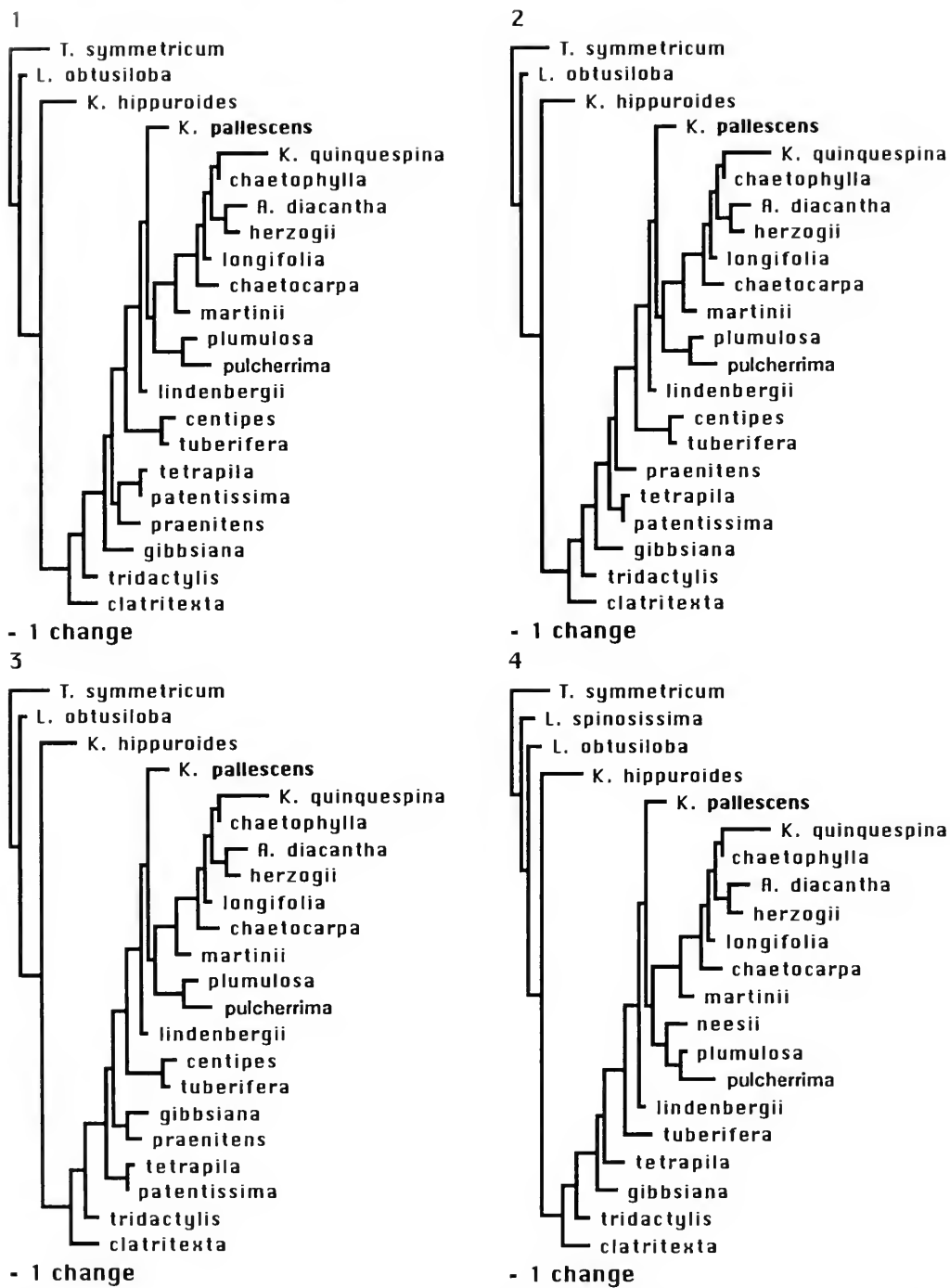


Fig. 76. Cladograms obtained from subsets of data. 1–3, three most parsimonious cladograms (length = 121) from data subset including the 22 species in the data set known with sporophytes. Cladograms 1–3 are identical except for the portion of the tree, involving *T. gibbsiana*, *T. patentissima*, *T. praenitens*, and *T. tetrapila*. 4. Cladogram based upon 21 taxa chosen by selected criteria (see text).

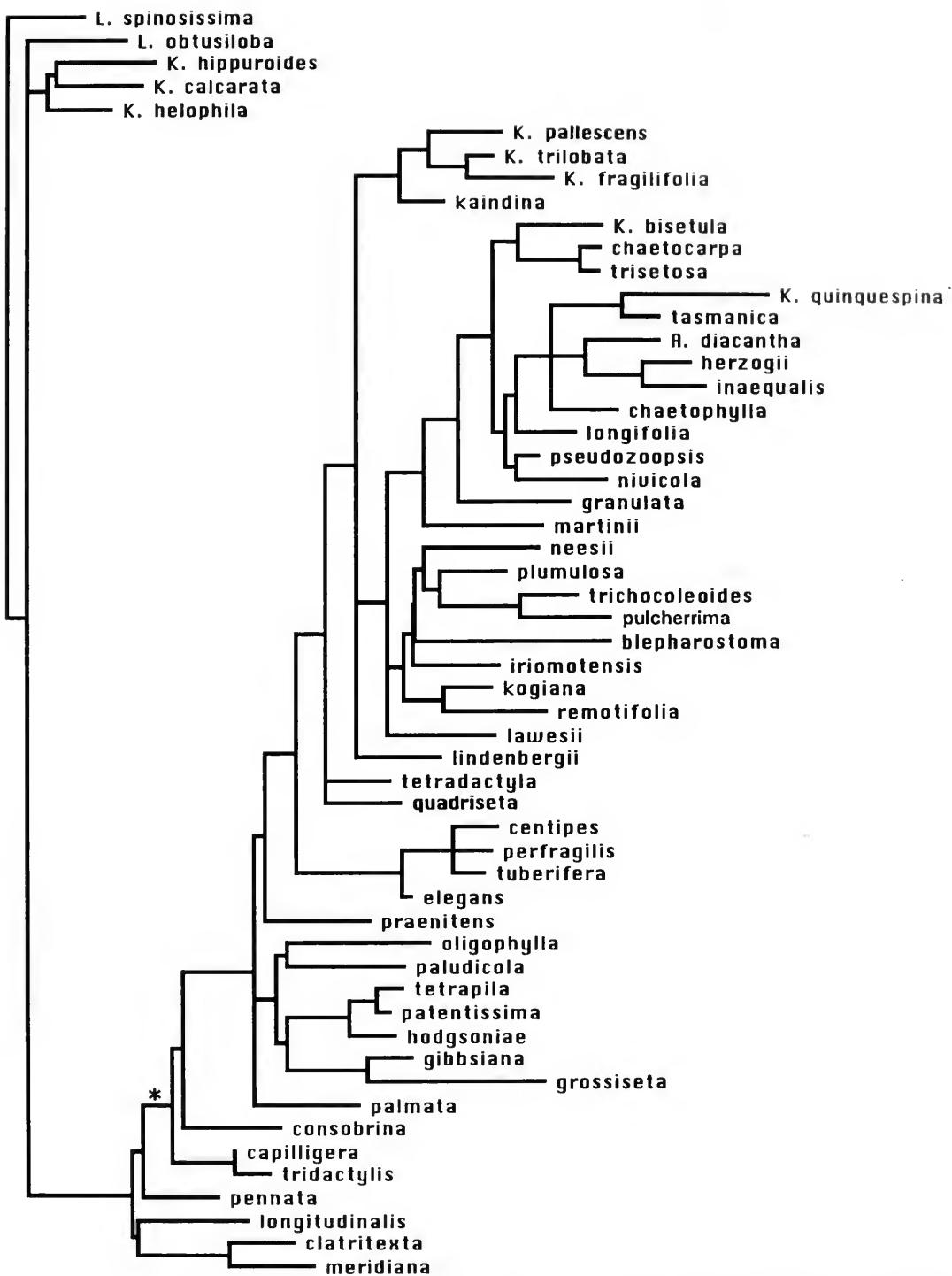


FIG. 77. Strict consensus of 306 most parsimonious trees (len = 215) obtained by eliminating *Triandrophyllum* as an outgroup. Percentages are 51% at node indicated by \*; all other nodes are 100%. The same tree is shown as an unrooted array in fig. 78.

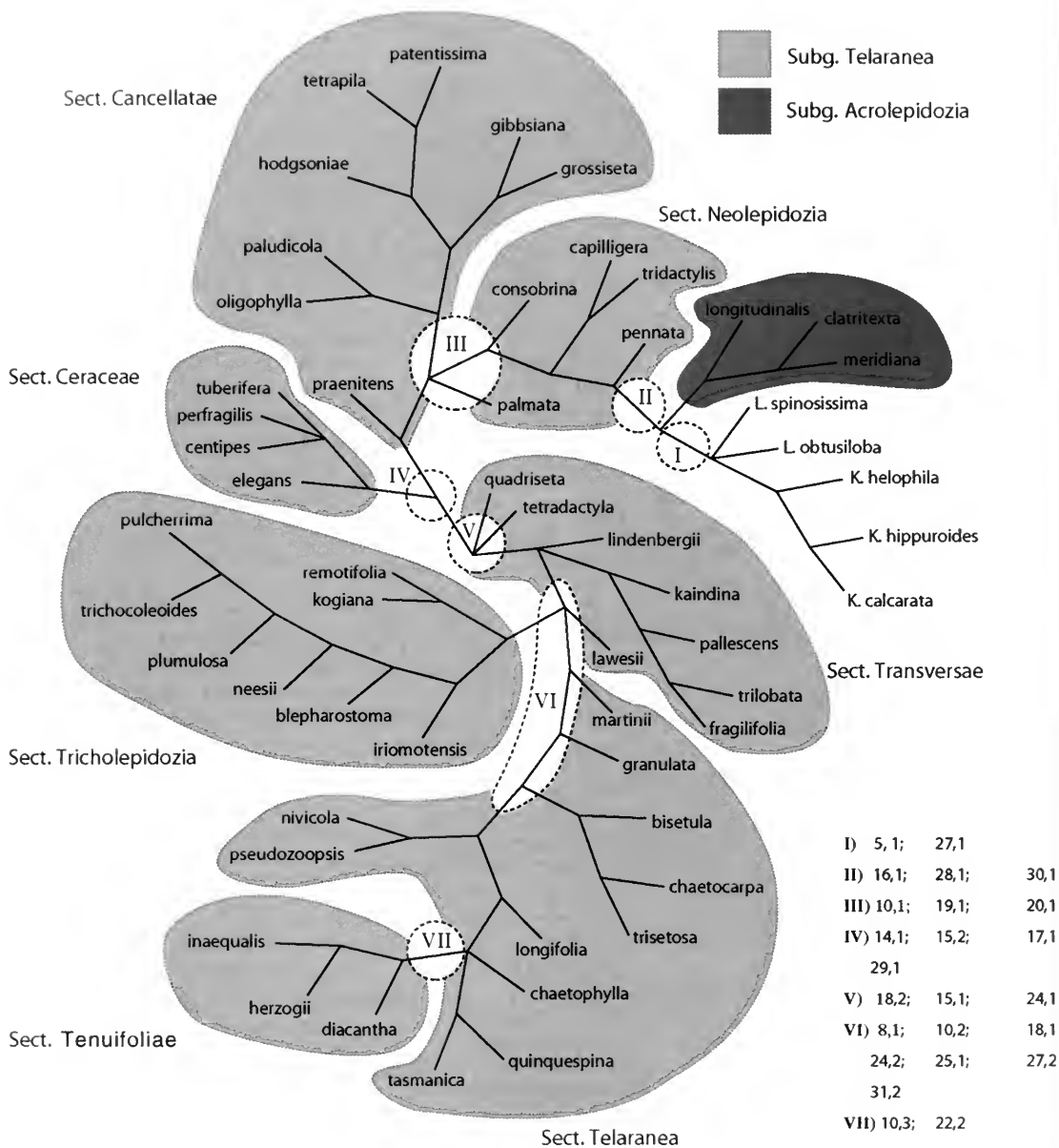


FIG. 78. Unrooted array based on strict consensus of 306 trees (shown as a phylogram in fig. 77), indicating "hot spots" (I-VI) where significant concentrations of character transformations occur and the areas of the tree (shaded) corresponding to the subgenera and sections of *Telaranea* discussed in the text.

absence of a particular type of branching is informative when the same branch type is present in the sister group, as in sect. *Tenuifoliae*.

2. *Microlepidozia*-type branching, CI = .200. The cladogram does not support a genus *Kurzia* based on this type of branching alone. *Microlepidozia*-type branching is shown originating independently 4 times (in *T. pallezens*, *T. triloba*-

*ta-T. fragilifolia*, *T. bisetula*, and in *T. quinquespina*), as well as in the 3 outgroup *Kurzia* species. For a reconstruction involving another "Kurzia character," see underleaves with dissimilar lobes (23,1).

*Microlepidozia*-type branching is a plesiomorphy at this level. However, it may well be a synapomorphy of a larger group which includes the

Lepidoziaceae, as well as the Trichocoleaceae, in which this type of branching is known to occur (see p. 204).

3. *Acromastigum*-type branching, CI = .250. This type of branching is also plesiomorphic in leafy hepatics. Here, it appears as a homoplasy, evolving independently in *T. clatrertexta*, *T. grossiseta*, and *T. blepharostoma*, as well as in *Lepidozia spinosissima*. The same holds true whether the outgroup is *Triandrophyllum*, which lacks *Acromastigum*-type branches, or *L. spinosissima*, which has them. This type of branching also occurs in *T. confervoides*, and may well be present in other *Telaranea* species.

4. Lateral-intercalary branching, CI = .333. Like *Acromastigum*- and *Microlepidozia*-type terminal branching, lateral-intercalary (*Plagiochila*-type) branching is a plesiomorphy, and this too appears to be a homoplasy in *Telaranea*. It appears as a synapomorphy in 2 species pairs, *T. tasmanica*-*T. quinquespina* and *T. trilobata*-*T. fragilifolia*, as well as in *Triandrophyllum*.

5. Differentiated stem cortex, CI = .500. An undifferentiated cortex (5,0) is characteristic of all the outgroup taxa. A hyaloderm (5,1) is a synapomorphy of *Telaranea*, reversing only once, in *T. pulcherrima* and *T. trichocoleoides*. Absence of a hyaloderm (5,0) in these species might otherwise have been misinterpreted as plesiomorphic in *Tricholepidozia*. Moreover, *T. plumulosa*, the sister species of *T. pulcherrima* and *T. trichocoleoides*, has a well-developed hyaloderm.

6. Thick-walled cortical cells, CI = .125. This character is highly homoplasious and thus relatively uninformative. A differentiated cortex of relatively thick-walled cells is characteristic of sect. *Neolepidozia* (*T. tridactylis*). A similar type of cortex occurs in several species of *Kurzia* (sect. *Leucolepidozia*, sect. *Nanolepidozia*), which our analysis indicates belong in *Telaranea*. For example, *T. pallescens*, a species which in most respects is similar to *T. lindenberghii*. The result confirms our decision to consider cortical differentiation and cell wall thickness as separate characters (see p. 209).

7. Leaf symmetry, CI = .455. Symmetric leaves (7,1) are plesiomorphic, and are characteristic of most species of *Telaranea*. Two types of assymetry were scored, namely ventral lobe smallest (7,0) and dorsal lobe smallest (7,2). Significantly, these are indicated as alternative states, both derived from symmetrical leaves (polarity 0 < 1 > 2). Dorsal lobe smaller occurs in *T. cla-*

*tritexta* and *T. pennata*, both near basal in position on the cladogram, and in *T. grossiseta*.

8. Lobe number, CI = .833. This character proved to be highly informative. Lobes 4–6 in number (8,0) are the plesiomorphic state, present in *Telaranea*, as in many Lepidoziaceae. The polarity of character 8 is 1 < 0 > 2. Six-lobed leaves, particularly on robust shoots, are a frequent occurrence in both sect. *Transversae* (*T. lindenberghii*, *T. pallescens*) and sect. *Tricholepidozia* (*T. neesii*, *T. plumulosa*). Lobes 8 or more (8,2) occurs in the terminal clade comprising *T. pulcherrima* and *T. trichocoleoides*, and is best interpreted as derived from the quadrifid condition, as implied by Schuster (1984, p. 813, fig. 15 legend).

The transition to 2–3 lobed leaves (8,1) can be considered a synapomorphy of “*Telaranea* s. str.” (see p. 239), even though a few species (*T. chaetocarpa*, *T. trisetosa*) can have 4- as well as 3-lobed leaves, and some species of sect. *Tenuifoliae* have monocrurous leaves.

9. Leaf decurvature, CI = .250. Leaves which are ventrally decurved and claw-like (9,1) lend a distinctive aspect to plants of *T. longitudinalis* and *T. meridiana*, which occupy a near basal position in the cladogram. Elsewhere, this relatively uninformative character occurs in two widely separated terminal taxa, *T. neesii* (sect. *Tricholepidozia*) and *T. oligophylla* (sect. *Cancellatae*).

10. Lobe width at base, CI = .400. Reconstruction of character state changes shows a progressive reduction in leaf lobes, from acute lobes 4 cells or more wide at the base, to 2–3 cells wide, to a pair of cells (geminate) at the base, to uniseriate throughout. This character, along with several others in both gametophyte (18, 22, 24) and sporophyte (31, 32) generations, documents an almost relentless “reduction” in morphological complexity in *Telaranea*, a concept which was articulated early (Howe, 1902; Fulford, 1963a; see Introduction, p. 5).

Reduction in lobe width at base is essentially unidirectional (0 <> 1 > 2 > 3), with reversals (1 > 0) occurring only in two terminal taxa (*T. consobrina* and *T. grossiseta*). Lobes with a geminate base (10,2) are limited to sect. *Telaranea*, and uniseriate (10,3) is a synapomorphy of sect. *Tenuifoliae*. Lobes with a 2–3 celled base is shown as independently derived in *Kurzia hippuroides* and does not support inclusion of this and similar species in *Telaranea* (sensu Müller).

11. Lobes fragmenting, CI = .333. Fragmenting lobes occurs independently in two species of

sect. *Ceraceae* and in *T. fragilifolia*. As such, it is not particularly phylogenetically informative.

12. Lobe tip cells secondarily divided, CI = .250. Lobe tip cells are undivided in most species of *Telaranea*. Secondarily divided tip cells (12,1) occur independently in several parts of the cladogram, in sect. *Cancellatae*, sect. *Telaranea*, and sect. *Tenuifoliae*, but also occurs in *T. lawesii* (p. 162). Button-like terminal cells occur in sect. *Transversae* (*T. lawesii*) as well as in sect. *Tenuifoliae*.

13. Swollen septa of uniseriate row, CI = .200. This is a highly homoplasious character. It is, however, a synapomorphy in three species pairs: *T. gibbsiana* and *T. grossiseta*, *T. quinquespina* and *T. tasmanica*, *T. herzogii* and *T. inaequalis*. A few other scattered species (*T. blepharostoma*, *T. lindenbergii*, *T. palmata*, *T. plumulosa*, *T. praenitens*) also exhibit this feature.

14. Lobe cell shape, CI = .417. Lobe cells  $\pm$  isodiametric (14,0) is the plesiomorphous state, persisting throughout subg. *Acrolepidozia* and sections *Neolepidozia* and *Cancellatae* of subg. *Telaranea*. The transition to short rectangular lobe cells (14,1) occurs as a synapomorphy of a large clade which includes all the remaining sections of the genus (Fig. 78). The transition to elongated lobe cells (14,2) occurs within sect. *Telaranea*. Capillary lobe cells (14,3) have a widely scattered distribution, in *T. grossiseta* (Fig. 14: 6), *T. pulcherrima* (Fig. 25: 4), and *T. diacantha* (Fig. 46: 5–7). Unexpectedly, this character proves to be quite informative, and essentially unidirectional (0 > 1 > 2 > 3), reversing (1 > 0) only in *T. centipes* (Fig. 21: 11) and *T. perfragilis* (Fig. 20: 8).

15. Leaf insertion, CI = .364. Incubous leaf insertion (15,0) is plesiomorphic. Evolution of  $\pm$  longitudinal insertion (15,2) occurs twice, as a synapomorphy of two major groups, subg. *Acrolepidozia* and sect. *Ceraceae*. Transverse leaf insertion (15,1) evolves at the base of the large clade which includes sect. *Transversae*, sect. *Tricholepidozia*, and all the remaining sections of the genus (see Fig. 78).

Transverse and longitudinal leaf insertion are both independently derived from incubous (polarity 1 < 0 > 2). *Telaranea* sensu Müller (see Introduction, p. 2) is not supported, since transverse insertion in *Kurzia hippuroides* is independently derived (see also character 10). The incubous condition in *T. martinii* is a reversal (1 > 0).

Insertion of the uniseriate leaf lobes in *T. diacantha* and its sister taxa, *T. herzogii* and *T. inaequalis* (sect. *Tenuifoliae*), was scored in the ma-

trix as transverse, but is in fact transverse to weakly succubous. We experimented with adding an additional (succubous) state for this character, and scoring these three species as polymorphic. This had little effect on the overall topology of the resulting trees, but predictably, insertion succubous was introduced as an apomorphy of this clade, derived from transverse.

16. Leaf width at base, CI = 1.000. The distinctive architecture of the *Telaranea* leaf, in which the number of cells along the insertion is twice the number of lobes (16,1) is a synapomorphy of subg. *Telaranea*.

17. Disc shape, CI = .143. Evolution from cuculate (17,0) to parallel-sided (17,1) is relatively uninformative phylogenetically, although it is a synapomorphy of sect. *Ceraceae*. This character was not scored in taxa which lack a disc (disc height 0, see 18,1).

18. Disc height, CI = .500. Polarity in this character is essentially unidirectional (0 <> 2 > 1), another example of the “progressive reduction” in the genus (see character 10, above). Disc 2–4 cells high (18,2) is a synapomorphy of the large clade which includes sections *Transversae*, *Telaranea*, and *Tenuifoliae*. The change to disc height 0 (18,1) occurs early in *Telaranea* sens. str. (excl. *T. martinii*).

19. Disc areolation, CI = .333. Irregular arrangement of disc cells is plesiomorphic. The regular alignment of disc cells in rows and tiers (19,1) is one of the distinctive features of *Telaranea* species. The transition from irregular to regular arrangement (0 > 1) occurs at the base of sect. *Cancellatae*.

20. Disc cell width, CI = .125. In the ACCT-RAN reconstruction, larger leaf cells (more than 40 $\mu$  wide) is a synapomorphy of a major clade which includes all of subg. *Telaranea* except the basal sect. *Neolepidozia*. Scattered reversals occur in both reconstructions, which render this character relatively uninformative.

21. Symmetry, CI = .300. Anisophylly is plesiomorphic, with subisophylly in scattered taxa (e.g., *T. blepharostoma*, *T. oligophylla*), as well as in most species of sect. *Tricholepidozia*, including *T. plumulosa*, the species characterized by Fulford (1963a) as primitively subisophyllous.

Tirradial forms are considered primitive, according to the most important of Schuster’s “phylogenetic criteria” (see p. 201), but these exhibit a confusing mix of characters found in various “highly derivative” groups. Schuster resolves this by treating the similarities between the derived



axa as evidence of parallelism and convergence, rather than as potential synapomorphies. The alternative (and more parsimonious) explanation is that subisophyly is not always primitive. For example, Engel and Merrill (1997) treated *Isotachis* as the sister group to *Balantiopsis*, and the *Isotachis* perigynium and the marsupium of *Balantiopsis* as homologous. Subisophyly in *Isotachis* species is interpreted as habitat-related, and not as a persistence of a primitive trait.

22. Underleaf lobe base, CI = .667. Leaves and underleaves undergo a similar reduction. Most species of *Telaranea* are anisophyllous, and this character is the first of several which contrast differentiation of leaves vs. underleaves. Here, as in leaf lobes, an acute lobe base (22,0) is plesiomorphic. However, in the case of leaves, reduction of the lobe base to 2–3 cells wide (10,1) occurs somewhat earlier. By contrast, lobes uniseriate throughout occurs simultaneously in both leaves (10,3) and underleaves (22,2), both synapomorphies of sect. *Tenuifoliae*. Polarity of this character is essentially unidirectional ( $0 > 1 > 2$ ).

23. Underleaf lobes dissimilar, CI = .333. One of the two “*Kurzia* characters” scored in the data set, asymmetrically-lobed underleaves occur in at least 3 *Telaranea* which lack this type of branching (*T. blepharostoma*, *T. kaindina*, and *T. tasmanica*). Two of these are sister species of “*Kurzia*” taxa: *T. kaindina* and the former species of *Kurzia* subg. *Leucolepidozia*, as well as *T. tasmanica* and *T. quinquespina*.

24. Height of underleaf disc, CI = .750. Reduction in disc height from 3 or more cells high to 2 cells high (24,0 > 1) is found at the base of the clade which includes sections *Ceraceae* and *Transversae* and *Telaranea* s. str. However, reduction in leaves and underleaves is not synchronous. Underleaves with a disc to 1 cell high (24,2) are confined to sect. *Telaranea* and *Tenuifoliae*, but many species of sect. *Transversae* already have a leaf disc only 1 cell high. Polarity of this character is also essentially unidirectional ( $0 > 1 > 2$ ).

25. Half-leaf lobing, CI = .889. This character is highly informative, even though a number of terminal taxa (e.g., *T. oligophylla*, *T. remotifolia*, *T. trilobata*) were scored as polymorphic with respect to this character. An undivided half-leaf (25,1) is a synapomorphy of *Telaranea* sens. str.

26. First branch underleaf (FBU) position, CI = .333. Displaced FBU (26,1) evolves indepen-

dently in *T. centipes*, and *T. grossiseta*, and as a synapomorphy of the species pair, *T. clatritexta* and *T. meridiana*. As such, it is relatively uninformative phylogenetically.

27. First branch underleaf (FBU) lobing, CI = .333. In the 306 mp trees equally 2–4 lobed (27,0) is the outgroup condition, and the undivided FBU (27,1) is a synapomorphy of the genus *Telaranea*. The 2–4 lobed condition occurs in sect. *Tricholepidozia*, probably as a consequence of the increased number of lobes in both leaves and underleaves in this group. With the exception of *T. remotifolia* (sect. *Tricholepidozia*), the asymmetrically bilobed FBU (27,2) is confined to sections *Telaranea* and *Tenuifoliae*. *Telaranea diacantha* lacks terminal branches, and therefore has no FBU. Equally bilobed FBU's in *T. inaequalis*, *T. pallescens*, *T. quinquespina* are reversals.

28. Rhizoid origin, CI = .667. Basal origin (28,0) is the plesiomorphic condition, retained in subg. *Acrolepidozia* (except *T. meridiana*). Distal origin (28,1) is a synapomorphy of subg. *Telaranea*. A reversion to basal origin occurs in sect. *Telaranea*, as an artifact of scoring these species as basal, despite the fact that the underleaf disc is only 1 cell high, excluding the basal cells of the lobes (24,2).

29. Cuticle, CI = .312. Cuticular ornamentation is relatively uninformative, with both parallelism and reversals at many points in the cladogram. Smooth cuticle (29,0) is the plesiomorphic condition. Papillose cuticle (29,2) occurs in several of the outgroup taxa, and in scattered species in several sections of the genus, e.g., *T. tetrapila*, *T. trichocoleoides*, *T. trilobata*. Glaucous cuticle (29,1) is a synapomorphy of sect. *Ceraceae*. Only one other species in the genus, *T. grossiseta* (sect. *Cancellatae*), is glaucous. Note that glaucous evolves from smooth, and not from the papillose condition, suggesting that a different type of surface deposit may be involved. *Telaranea granulata* and *T. quadriseta*, the 2 species with scabrous cuticle (29,3) are not closely associated in the cladogram.

30. Antheridial stalk, CI = .250. Antheridial stalk uniseriate (30,1) is a synapomorphy of subg. *Telaranea*. The biseriate condition (30,0) is plesiomorphic and is retained in *T. meridiana*, the only species of the basal subg. *Acrolepidozia* in which antheridia are known. Biseriate stalks occur also in the sister species *T. centipes* and *T. perfragilis* (sect. *Ceraceae*) and *T. pulcherrima* and *T. trichocoleoides* (sect. *Tricholepidozia*). Evolu-

tion from biseriate to uniseriate stalks ( $0 > 1$ ) occurs independently within *Kurzia* s. str. (see p. 238).

31. Seta cross section, CI = .600. A seta of 8 outer cells and 15–30 inner cells (31,1) is the plesiomorphic condition. The condition in *Lepidozia obtusiloba* (31,0) is unique to this outgroup species. In the 306 mp trees, the reduction to 8+12 or less (31,2) in the common ancestor of sect. *Telaranea* and sect. *Tricholepidozia* (see Fig. 78). A massive seta, cited as the “generalized” condition by Schuster (1973), is an autapomorphy of *Triandrophyllum* (31,1). This character state is not present in the 306 mp trees with elimination of *Triandrophyllum* as an outgroup.

32. Capsule wall section, CI = .818. The 3-stratose condition (32,1), is the plesiomorphic condition, and persists throughout most of the genus *Telaranea*. In the ACCTRAN reconstruction, 5-stratose capsule wall (32,3) is optimized as a synapomorphy of sect. *Tricholepidozia*. Evolution to a 4-stratose capsule wall (32,1 > 2) is shown as a synapomorphy of sect. *Cancellatae* in the ACCTRAN reconstruction, but in DELTRAN this is merely a synapomorphy of the sister species, *T. tetrapila*, and *T. patentissima*.

Reduction to a 2-stratose wall (32,0), occurs in sect. *Telaranea* and sect. *Tenuifoliae*, but also occurs independently within *Kurzia hippuroides*, which was scored as polymorphic (32,0 & 1) with respect to this character. A massive capsule wall is cited as the “generalized” condition in hepatics as a whole (Schuster, 1973), however valves 5-stratose and more (32,4) is an autapomorphy in *Triandrophyllum*. This last state is not represented in the set of 306 mp trees.

## Discussion of Phylogenetic Relationships

“*Telaranea* is a large genus, so complicated that it is impracticable to subdivide it into subgenera” (Hodgson, 1965, p. 70).

Cladograms obtained from the parsimony analysis of the full data set (Figs. 73–75, 77) and data subsets (Fig. 76), as well as the NJ tree (Fig. 79) are strikingly similar in topology. The overall similarity between all these analyses lends further support to the species relationships within *Tela-*

*anea* which are embodied in the arrangement proposed below.

Comparison of an existing arrangement with a phylogeny is possible if both are expressed in tree form (Wiley et al., 1991). Figure 77: 1–4 shows the implied relationships of the four genera of Lepidoziaceae represented in our dataset, based on the arrangements of Spruce (1885), Müller (1956), Fulford (1966, 1968), and Schuster (2000), respectively (see Introduction). In the first two, *Microlepidozia* (*Kurzia*) and *Telaranea* are sister groups (see Müller, 1956, p. 1133). Fulford places *Arachniopsis* and *Telaranea* in separate families, Schuster in separate subfamilies, but in each case, *Lepidozia*, *Telaranea*, and *Kurzia* are shown as a polytomy since the genealogical relationships of these genera are not specified. The 3 possible dichotomous trees (classifications) which can be derived from a polytomy of 3 branches are shown in Figure 80: 5–7. None of these trees is consistent with the phylogenetic relationships of the genera, shown in Figure 80: 8. Most importantly, *Arachniopsis* is indicated as the sister group to *Telaranea*.

Figure 81: 1 shows the implied relationships of subgenera and sections of *Arachniopsis* and *Telaranea* according to Schuster (2000). Subgenus *Acrolepidozia* is included in Schuster’s key (p. 208) but is not treated further. Here there are two polytomies, one with 4 branches and one with three branches. The number of possible classifications is (15)(3), or 45, the product of the number of trees possible for each polytomy (see Felsenstein, 1977). The relationships of these taxa indicated by the phylogeny are shown in Figure 81: 2.

*Telaranea* presents a picture of progressive reduction in morphological complexity. The intuitive recognition of this central evolutionary tendency in *Telaranea* by earlier workers (Howe, 1902; Fulford, 1963a; see Introduction, p. 5) is strongly supported. This reduction is marked by episodes of character transformations, often involving combinations of several characters (see Fig. 78).

Monophyly of *Telaranea* is supported by the presence of a hyaloderm (5,1), as well as by an undivided first branch underleaf (27,1). Two subgenera, subg. *Acrolepidozia* and subg. *Telaranea*, are strongly supported in all the cladograms presented here. The division between these two subgenera, however, is highly asymmetrical. In addition, we recognize a number of sections within

total character distance

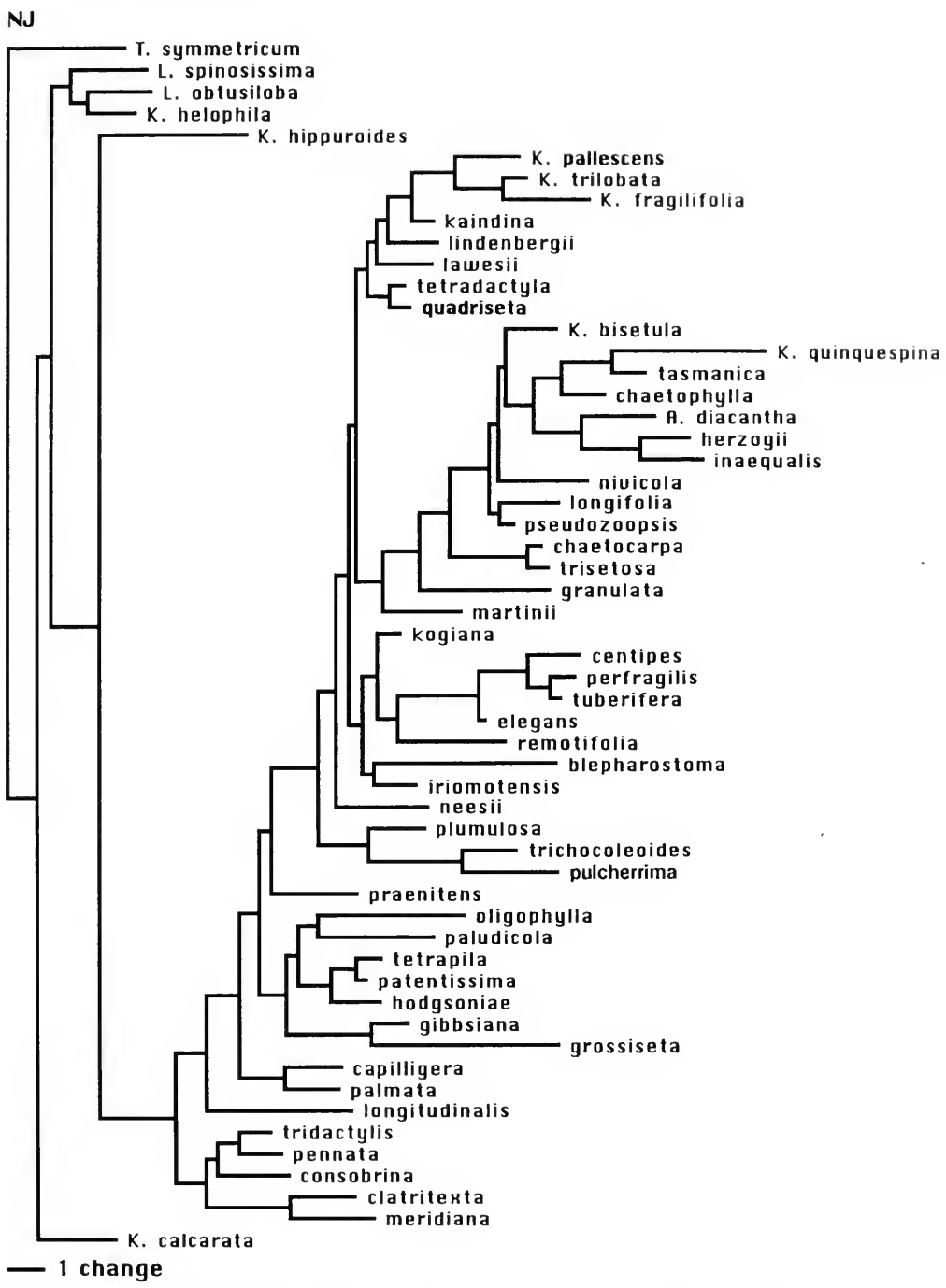


FIG. 79. Distance tree calculated using the neighbor-joining (NJ) option of PAUP\*, based on total character distance. The length of branches is proportional to the number of changes occurring on that branch.

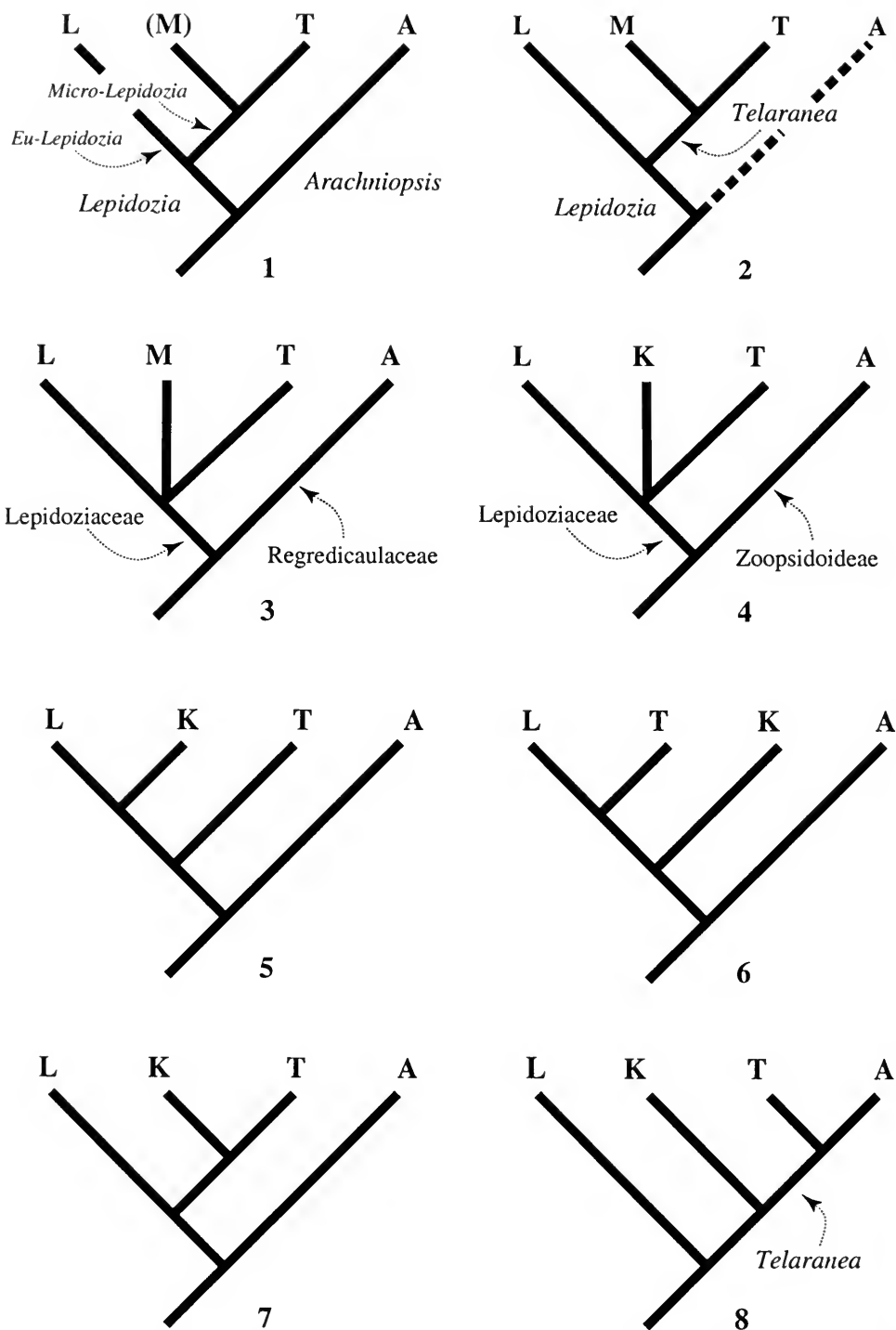


FIG. 80. Comparison of classifications (see text). 1. Arrangement of Spruce (1885) expressed in tree form. 2. Müller (1956, position of *Arachniopsis* conjectural). 3. Fulford (1966, 1968). 4. Schuster (2000). 5-7. The three possible phylogenies for the relationships implied in figs. 3 and 4. 8. Cladogram showing phylogenetic relationships of these genera, where K denotes *Kurzia* s. str. (see p. 238). (A = *Arachniopsis*; K = *Kurzia*; M = *Microlepidozia*; L = *Lepidozia*; T = *Telaranea*.) Note that figs. 1, 2, and 7 are identical, as are figs. 3 and 4.

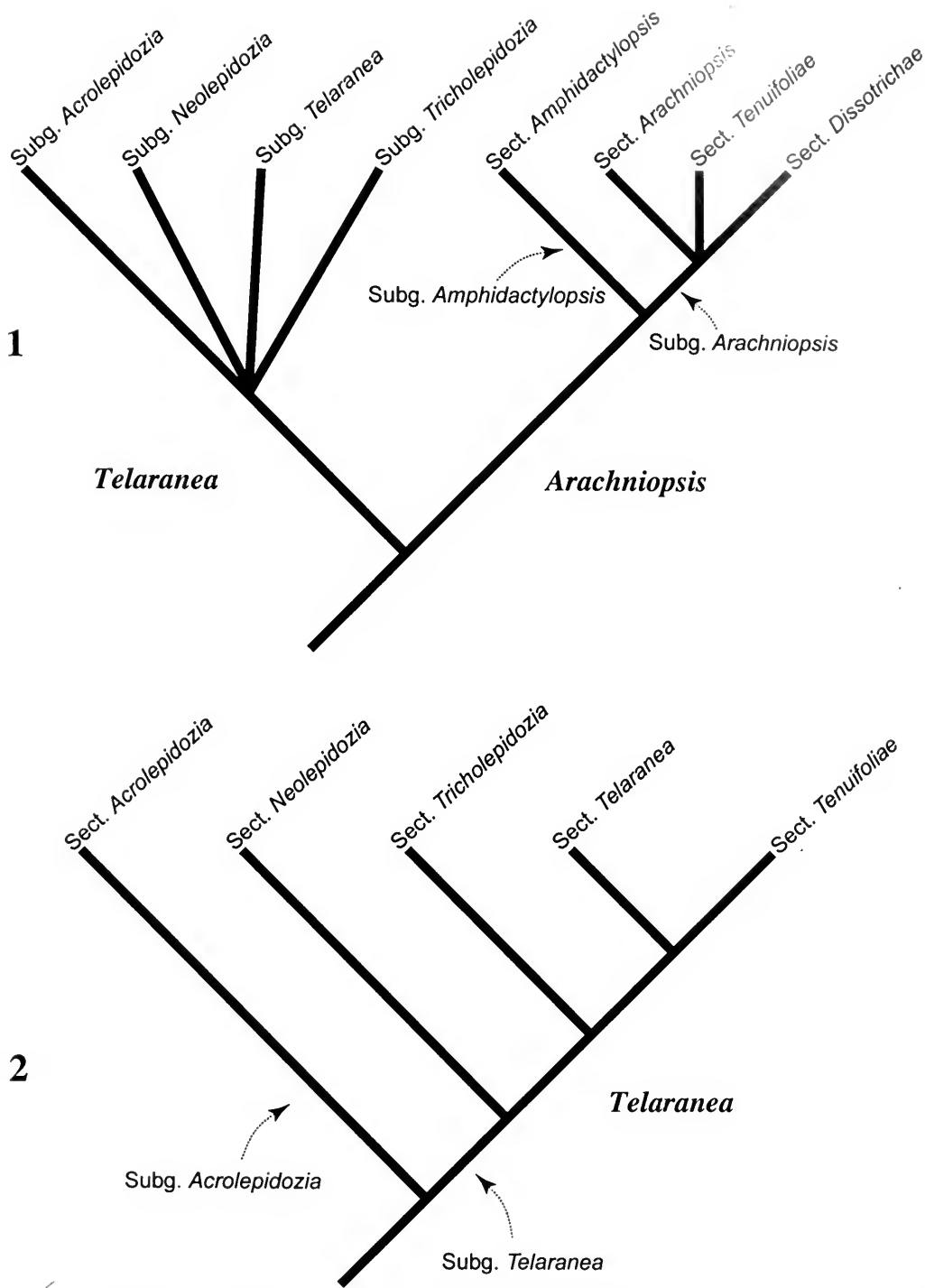


FIG. 81. Comparison of classifications. 1. Subgenera and sections of *Arachniopsis* and *Telaranea* (Schuster, 2000) expressed in tree form. The number of possible phylogenies is 104, or 45 if all trees are dichotomous (see text). 2. Cladogram showing phylogenetic relationships. Sections *Cancellatae*, *Ceraceae*, and *Transversae* not shown; Schuster's "sect. *Dissotrichae*" (*Amazoopsis* Engel & Merr.) is excluded.

subg. *Telaranea* (see Fig. 78). While not strictly monophyletic, these sections represent our attempt to reflect the pattern of character transformations indicated by the cladogram, and incorporate this important information in the classification.

Synoptic Key to the Subgenera and Sections of *Telaranea*

- 1. Number of cells at leaf base with no fixed relationship to lobe number; rhizoids originating from basal cells of underleaf disc; antheridial stalk biseriate ..... Subg. *Acrolepidozia*
- 1. Number of cells at leaf base equal to twice the number of lobes; rhizoids originating from distal cells of underleaf disc (when disc 2 or more cells high); antheridial stalk typically uniseriate. Subg. *Telaranea* ..... 2
- 2. Leaf disc 2 or more cells high ..... 3
- 3. Leaves densely areolate, the disc cells not in regular rows and tiers; disc cells small, less than 35  $\mu$ ; leaf lobes acute in some species; plants small and wiry,  $\pm$  opaque .... sect. *Neolepidozia*
- 3. Leaves laxly areolate, the disc cells in  $\pm$  regular rows and tiers; disc cells larger, more than 40  $\mu$ ; leaf lobes typically uniseriate except at base; plants typically more robust, with a translucent appearance ..... 4
- 4. Leaf typically 4-lobed; leaf insertion oblique to longitudinal; leaf disc 5 or more cells high (exc. *T. remotifolia*) ..... 5
- 5. Plants nitid, not glaucous (exc. *T. grossiseta*, *T. seriatitexta*); leaf insertion oblique ... sect. *Cancellatae*
- 5. Plants glaucous and water repellent, dull and opaque; leaf insertion  $\pm$  longitudinal. Leaf lobes in some species fragmenting, caducous. Antheridial stalk biseriate ..... sect. *Ceraceae*
- 4. Leaf 4–6- or more lobed; leaf insertion transverse; leaf disc mostly 2–4 cells high (including basal cells of lobes) ..... 6
- 6. Capsule wall (where known) 3-stratose; stem cortex well differentiated, a distinct hyaloderm always present; leaves 4–6-lobed; plants with a prickly appearance ..... sect. *Transversae*
- 6. Capsule wall (where known) 5-stratose; stem cortex in some species weakly differentiated; leaves in some species with multiple lobes (up to 13); plants often with a *Trichocolea*-like appearance. Antheridial stalk biseriate in some species ..... sect. *Tricholepidozia*
- 2. Leaf disc 1.5–0.5 cells high or less ..... 7
- 7. Main shoot (exc. *T. tenuifolia*) without a broadly exposed median strip (median strip when present confined to branches, e.g., *T. chaetophylla*); leaves 2–3(4)-lobed, the lobes divergent ..... 8
- 8. Leaves 2–3(4)-lobed, the lobes biseriate at base. *Frullania*-type branching always present ..... sect. *Telaranea*
- 8. Leaves 2- (rarely 3) lobed or monocrurous, the lobes uniseriate to the base. *Frullania*-type branching lacking in some species ..... sect. *Tenuifoliae*
- 7. Main shoot with 2 rows of cortical cells broadly exposed and forming a prominent median strip; leaves bilobed, the lobes parallel and closely approximated ... [*Amazoopsis* gen. nov.]

A discussion of subgenera and sections follows. The systematic disposition of individual species is shown in the Conspectus of *Telaranea*, Tab. 3.

basal cells of underleaf disc; leaf insertion longitudinal; leaf decurved and claw-like; antheridial stalk biseriate.

**Subgenus *Acrolepidozia*** (Schust.) Schust.

Width of leaf disc at base with no fixed relationship to lobe number; rhizoids originating from

The subgenus is supported by one apomorphy, leaf insertion longitudinal (15,2). The group includes three species, distinguished from subg. *Telaranea* primarily by plesiomorphies which are

shared with outgroup taxa. Most importantly, the leaf is broadly inserted (up to 18 cells wide), with no definite relationship between the number of cells along the insertion and the number of leaf lobes (16,0; Fig. 1: 2, 3, *T. cladritexta*). In addition, leaf lobes are typically acute, and 4 or more cells wide at the base (10,0).

The nomenclatural type, *T. longitudinalis*, is similar in many respects to species of sect. *Cancellatae* (subg. *Telaranea*; see below), which is reflected in the placement of this species in the NJ tree (Fig. 79). Nevertheless, in cladograms, *T. longitudinalis* is consistently resolved with *T. cladritexta* and *T. meridiana* (e.g., Fig. 77).

*Acrolepidozia* was distinguished as a genus from *Lepidozia* by Schuster (1963), but later reduced to a subgenus of *Telaranea* (Schuster, 1969; see Introduction, p. 4). It is used here in a somewhat different sense, for a taxon equivalent to our sect. *Latifoliae* (Engel & Merrill, 1996a). Subgeneric rank seems more appropriate than recognition of *Acrolepidozia* as a genus, since this would raise questions of relationship with other genera of Lepidoziaceae which are not addressed here. The situation is similar in some respects to that of *Stereocolea* Schust. in relation to *Balan-tiopsis* (Engel & Merrill, 1997, p. 49).

### Subgenus *Telaranea*

Width of leaf disc at base with a fixed relationship to lobe number (twice the number of lobes); leaf lobes 2–4 cells wide at base; rhizoids originating from distal cells of underleaf disc; antheridial stalk uniseriate.

Monophyly of the subgenus is supported by 3 synapomorphies: leaf width at base definite (16,1); antheridial stalk uniseriate (30,1); and rhizoid origin from distal cells of the underleaf disc (28,1). Recognition of a single subgenus for all of *Telaranea* (except subg. *Acrolepidozia*) represents a departure from previous classifications (see Introduction). Schuster (1963), divided the genus into three subgenera, *Neolepidozia*, *Tricholepidozia*, and *Telaranea*. Piippo (1984) removed *Neolepidozia* from the genus, and placed it as a section of *Lepidozia*. These taxa are recognized here (along with several others) at the sectional level.

While there is considerable diversity within the subgenus (for example, compare Figs. 18, 19, *T. tetrapila* with Figs. 42, 43, *T. chaetophylla*), the differences are the result of progressive reduction

in almost all features of the plant, including the height of the leaf and underleaf disc, lobe number, transition from acute lobes to uniseriate (capillary) lobes with a 2–4-celled base, seta anatomy, and capsule valve thickness.

The distinctive areolation of the *Telaranea* leaf was attained in two stages. First, in sect. *Neolepidozia*, the number of cells at the leaf base becomes fixed in relation to the number of lobes. Then, in sect. *Cancellatae*, the disc cells become regularly aligned in longitudinal rows and horizontal tiers.

In Fig. 73, the strict consensus of 485K trees, subg. *Telaranea* contains several nested clades. The most conspicuous clade is one that excludes sect. *Neolepidozia* but includes all of the other sections. The synapomorphies of this clade are cortical cells thin-walled (6,0) and lobes 2–4 cells wide at base (10,1). Nested within this larger clade is a smaller one, corresponding to “*Telaranea* sens. str.” (see discussion below, p. 239).

### Section *Neolepidozia* (Fulf. & J. Tayl.) Engel & Merr.

Plants small, wiry; stem cortical cells differentiated but thick walled; leaf lobes acute in some species; disc cells small (less than 35 $\mu$ ), the areolation dense and cells not in regular rows and tiers.

Small cell size and irregular disc areolation distinguishes this section from the rest of subg. *Telaranea*. As a rule, most *Telaraneas* have relatively large cells and a more or less translucent appearance. Two of the species (*T. pennata*, *T. tridactylis*) have acute leaf lobes, in common with subg. *Acrolepidozia*. Acute leaf lobes were an important historical distinction between “*Neolepidozia*” and *Telaranea* in the sense of Müller (1914); see Introduction, p. 2.

The ♀ bracts of *T. tridactylis* (Fig. 7: 7, 11) are dentate-lobulate, as in the outgroup *Lepidozia* species. This type of bract probably represents the plesiomorphic state by outgroup comparison, although such bracts are also found in sect. *Cancellatae* (*T. tetrapila*) and sect. *Tricholepidozia* (*T. plumulosa*). Bracts in more derived species of *Telaranea* (e.g., *T. chaetophylla*, Fig. 43: 1) are deeply lobed, with a disc only 2–3 cells high. The spores of *T. tridactylis* are “rough plastered” (Fig. 71: 1, 2) and strikingly different from the papillose-vermiculate or reticulate-areolate spores seen in other members of the genus.

## Section *Cancellatae* Engel & Merr.

Plants robust, lax, nitid, often appearing translucent; disc cells large, in regular rows and tiers, often turgid and "pillow-like."

A generally higher disc, 5 or more cells high (18,0), and larger disc cells, 40  $\mu\text{m}$  or more wide (20,1) distinguish this section from sect. *Neolepidozia*. The sectional name, *Cancellatae*, is a reference to the conspicuous grid-like arrangement of the disc cells in regular rows and tiers in members of this section, not to the species name, *T. cancellata* Col. (*T. tetrapila* var. *cancellata*, p. 57).

From an Australasian perspective, the species of this section include many of the "typical" representatives of the genus. Eight species of the section occur there. Included are *T. tetrapila* and *T. patentissima*, both common and conspicuous members of the Australasian flora.

In Fig. 78, the section has 3 constituent clades. Of these, *T. gibbsiana* and *T. grossiseta* are sister taxa in all the cladograms. *Telaranea tetrapila*, *T. patentissima*, and *T. hodgsoniae* also consistently form a clade. In the strict consensus (Fig. 73), this clade is supported by 2 autapomorphies: lobe tip cells secondarily divided (12,1) and 4-stratose capsule wall (32,2).

The spores of both representatives of sect. *Cancellatae* examined with the SEM, *T. patentissima* (Fig. 71: 3, 4) and *T. tetrapila* (Fig. 71: 5, 6), are papillose-vermiculate.

## Section *Ceraceae* Engel & Merr.

Plants glaucous; shoots strongly anisophyllous, plano-distichous, the leaves with  $\pm$  longitudinal leaf insertion; leaf disc high and parallel-sided; leaf lobes fragile, caducous; first branch underleaf often displaced.

This section forms a clade, supported by a three apomorphies: leaf insertion longitudinal (15,2), disc parallel-sided (17,1), and glaucous cuticle (29,1). Elsewhere, a distinctly glaucous cuticle occurs only twice, in *T. grossiseta* of Tasmania and *T. seriatitexta* of southern South America. The higher disc (5–10 cells high) allies this section with sect. *Cancellatae*. Spores of *T. tubrifera* are reticulate-areolate, with prominent ridges bounding the areolae (Fig. 70: 5, 6). This spore type is characteristic of *Telaranea* sens. str., and

is also found in sect. *Transversae* (*T. lindenbergii*), but not in more basal members of the genus.

## Section *Transversae* Engel & Merr.

Plants with a prickly appearance, often with regular bipinnate branching; branches tending to be subsophyllous; *Microlepidozia*-type branching in some species; leaves transversely inserted, 4–6 lobed, the lobe cells short rectangular; leaf disc 1.5(2)–4 cells high; underleaf disc 2 cells high.

One of the more significant outcomes of this analysis has been the recognition that *Kurzia*, as traditionally constituted, is polyphyletic. One group of *Kurzia* species (*K. calcarata*, *K. helophila*, and *K. hippuroides*) is consistently resolved as a clade, supported by two apomorphies, *Microlepidozia*-type branching (2,1) and underleaf lobes differentiated (21,1), both homoplasies. This clade represents *Kurzia* s. str. (*Kurzia* sect. *Microlepidozia*, sensu Schuster, 1980). The evolution of uniseriate antheridial stalks (30,1) occurs independently within *Kurzia* s. str., biseriate in *K. helophila* and uniseriate in the other two species. Additional features found in this group include dense areolation, thick-walled cells and small cell size, and leaves and underleaves armed with spurs or teeth.

In the strict consensus of 306 mp trees (Fig. 77), the three species of *Kurzia* sect. *Leucolepidozia* Schust. (Schuster, 1980), together with *T. kaindina*, form a clade. All but *T. kaindina* have *Microlepidozia*-type branching, and all have unequally lobed underleaves, with one or more lobes short and uniseriate, and the others resembling leaf lobes (Grolle, 1968, fig. 3a, *T. kaindina*). Underleaves of this type are not confined this clade. Both *Kurzia* s. str. and *T. blepharostoma* (Fig. 39: 1, 3, 4) have similar underleaves. Neither *T. blepharostoma* nor *T. kaindina* has been associated with *Kurzia* because they lack *Microlepidozia*-type branching. The strong resemblance between *Kurzia pallescens* and *T. lindenbergii* has been noted elsewhere (see p. 88). The position of *T. blepharostoma* in the cladograms varies, either within the clade corresponding to sect. *Tricholepidozia* (Fig. 78), or at the base of the clade identified here as sect. *Telaranea* (Figs. 74, 75).

Unequally bilobed underleaves occur in two former *Kurzia* species, *T. bisetula* and *T. quinquespina* (Fig. 34: 1, 3, 4), placed here in sect. *Telaranea*. Both have *Microlepidozia*-type branching, and were formerly placed in *Kurzia*



subg. *Nanolepidozia* Schust. (Schuster, 1980; Engel & Merrill, 1996b). *Nanolepidozia* is not supported in the cladogram (see Fig. 78). Two other species with similar underleaves, *T. anomala* (Schuster, 2000, fig. 196: 5, 7, 8) and *T. monocera* (fig. 194: 4) were formerly placed in *Arachniopsis* subg. *Amphidactylopsis* Schust. (Schuster, 1965), which is not recognized here. The branch underleaves of *T. chaetocarpa* are either equally or unequally bilobed (Fig. 40: 1). In some species of sect. *Telaranea* the underleaves are equally lobed, but the first branch underleaf is unequally lobed.

The spores of the two species of sect. *Transversae* examined with the SEM have differing surface patterns. In *T. pallescens* (Fig. 72: 5, 6) the spores are papillose-vermiculate, vs. reticulate-areolate in *T. lindenberghii* (Fig. 69: 4).

### Section *Tricholepidozia* (Schust.) Engel & Merr.

Plants medium to large, much-branched, many with *Trichoclea*-like appearance, with both main shoot and branches tending to be subisophyllous; stem thick, the cortex weakly differentiated, of numerous cells; leaf insertion transverse; leaves with multiple lobes; seta 8+12 or less; capsule valves 5-stratose.

This section includes several species in which the prevailing tendency in the genus towards reduction in structural complexity is reversed. This is manifest in all parts of the plant, and includes such features as leaf, underleaf and first branch underleaf lobe number, stem cortical cell number, and in the sporophyte generation, capsule wall thickness. Apart from lobe number, the leaves of *T. pulcherrima* are strikingly similar to species of sect. *Transversae*, such as *T. tetradactyla*.

Reduction in the seta from 8 outer cells plus 15–30 medullary cells (31,1) to 8+12 or less (31,2) occurs in the common ancestor of sect. *Telaranea* and sect. *Tricholepidozia*, and serves as evidence from the sporophyte generation of relationship between these two groups.

Included in this section is *T. neesii*, a common and widespread Malesian species. Not included in the data set, but clearly belonging here, is *T. octoloba* of the Philippines. The core group of species, consisting of the southern South American *T. plumulosa*, *T. trichocoleoides* of Borneo, and *T. pulcherrima*, constitutes a clade supported by 3 apomorphies: underleaf disc 3 or more cells high (24,0); first branch underleaf equally 2–4 lobed (27,0); and 5-stratose capsule valves (32,2).

The biseriate antheridial stalk of *T. plumulosa*, another feature shared with *T. pulcherrima*, was not discovered until after the analysis was completed and is not scored in the matrix. Thus, a group which was previously thought to be restricted to temperate Australasia and the palaeotropics is now known to be amphipacific in distribution.

Schuster (2000, p. 240) cited the unlobed, dentate ♀ bracts of *T. pulcherrima* as an indication of the "taxonomic isolation" of the *Tricholepidozia* group, but this type of bract is also found in sect. *Neolepidozia*, sect. *Cancellatae*, and sect. *Ceraceae*, as well as in the outgroup *Lepidozia* species. Another species of sect. *Tricholepidozia*, *T. plumulosa*, also has erose-dentate bracts (Fig. 56: 7–10).

Members of the section appear to be heterogeneous with respect to spore ornamentation. The single species of sect. *Tricholepidozia* examined with the SEM (*T. plumulosa*, Fig. 72: 1) has papillose-vermiculate spores, the surface marked by irregular ridges which are discontinuous, and do not delimit areolae. However, the spores of *T. pulcherrima* illustrated by Schuster (2000, fig. 81: 3) appear reticulate, and thus similar to those of *T. lindenberghii*, as well as of members of "*Telaranea* sens. str." (e.g., *T. chaetophylla*, the type of the genus).

### Section *Telaranea*

Plants slender and wire-like, with irregular branching; half-leaf undivided; first branch underleaf asymmetrically bilobed in most species; leaves 2–3 lobed, the lobes geminate at base; leaf disc 1.5–0.5 cells high or less; underleaf disc 1 cell high; mostly monoecious; seta 8 + 12 or less; capsule wall bistratose.

Collectively, the species of sect. *Telaranea* and sect. *Tenuifoliae* ("*Telaranea* s. str.") form a clade, supported by leaves 2–3 lobed (8,1), half-leaf undivided (25,1), lobes geminate at base (10,2), disc less than one cell high (18,1), and rhizoids originating from basal cells of the disc (28,0) (see Fig. 77, the strict consensus of 306 trees). In the best tree from 10,000 replicates (Fig. 75), members of this clade have as apomorphies lobes geminate at base (10,2), disc less than one cell high (18,1), underleaf disc 1 cell high (24,2), first branch underleaf asymmetrically bilobed (27,2), rhizoids originating from basal cells of the disc (28,0), seta 8 + 12 or less (31,2), and capsule valves bistratose (32,0).

*Telaranea* s. str. corresponds to the original concept of the genus (Spruce, 1885), but includes species with a low disc (1.5 cells high or less, e.g., *T. longifolia*, *T. nivicola*), as well as species in which the "disc" is further reduced, consisting only of the partially connate basal cells of the lobes (*T. chaetophylla*, Fig. 42: 1, 4; *T. tasmanica*, Fig. 32: 5, 6). The exception is *T. martinii*, the basal species (see Fig. 77), which has a disc 2–4 cells high (Fig. 29: 1–4).

In general, the ♀ bracts in sect. *Telaranea* (as well as in sect. *Tenuifoliae*) are deeply dissected, with a disc only a few cells high, but there are exceptions. However, *Telaranea martinii*, which occupies a basal position in sect. *Telaranea*, has 2–4-lobulate bracts (Fig. 30: 1, 6). The bracts of *T. quinquespina* (Fig. 34: 10) are quite similar to those of *T. tetradactyla* (sect. *Transversae*, Fig. 26: 12).

The species of sect. *Telaranea* examined with the SEM all have the classic reticulate-areolate spore type so often cited as typical of the genus. These include the type, *T. chaetophylla* (Fig. 69: 1), as well as *T. nematodes* (Fig. 70: 1, 2) and *T. longifolia* (Fig. 69: 5, 6). The spores of *T. chaetocarpa* are also strikingly reticulate-areolate, even as seen under the light microscope. The spores of *T. quinquespina*, however, would be characterized as papillose-vermiculate (Fig. 34: 16), in common with such diverse species as *T. patentissima*, *T. plumulosa*, and *T. pallescens*.

### Section *Tenuifoliae* (Schust.) Engel & Merr.

Plants extremely slender and thread-like, with a cobwebby appearance; terminal, *Frullania*-type branching lacking in some species; stems typically reduced (to as few as 4 cortical cells and a single medullary cell in *T. pecten*); leaf insertion transverse to weakly succubous (incubous in *T. tenuifolia*); leaves bilobed or monocrurous, with long narrow lobe cells, the lobes uniseriate to the base.

*Telaranea diacantha* and its sister taxa, *T. herzogii* and *T. inaequalis*, form a clade supported by three apomorphies: lobes of both leaves and underleaves (10,3; 22,2) uniseriate to the base, and button-like lobe tip cells (12,2). Succubous leaf insertion becomes an additional apomorphy for this clade when these species are scored as such (p. 230). Spores of *T. diacantha* (Fig. 69: 2, 3) are reticulate-areolate and almost identical to those of *T. chaetophylla* (Fig. 69: 1), but the

spores of *T. coactilis* (Fig. 72: 2–4) are papillose-reticulate.

*Arachniopsis* was described by Spruce (1882), and publication of this name thus predates the valid publication of the genus *Telaranea* Spruce ex Schiffn. (Schiffner, 1893). Therefore, a proposal has been made to conserve *Telaranea* over *Arachniopsis* (Engel & Merril, 2002). The necessary transfers will be found in the section on Extra-Australasian Taxa (p. 120).

No support was found for maintaining *Arachniopsis* as a genus distinct from *Telaranea*. Schuster (1965) considered *Arachniopsis* to be derived from *Telaranea*-like ancestors by loss of terminal branching, and yet maintained the two as distinct, consistent with the historic emphasis on branching types as decisive characters in hepatic classification (Evans, 1912; Schuster, 1982). It now appears that terminal, *Frullania*-type (and rarely, *Acromastigum*-type) branching does occur in many species of sect. *Tenuifoliae*. For an analogous situation involving branching, see comments above concerning *Microlepidozia*-type branching in *Kurzia* (p. 238). For treatment of another generic segregate, see the discussion of *Anisotachis* in Engel and Merrill (1997, p. 54).

In most members of sect. *Tenuifoliae* the insertion of the two leaf lobes is transverse to weakly succubous. This is best seen in ventral aspect, where the ventral lobe is inserted slightly above (distal to) the dorsal lobe (Fig. 57: 1, *T. sejuncta*; Fig. 44: 1, *T. coactilis*). Lobe insertion in *T. tenuifolia*, however, is distinctly incubous (Schuster, 2000, fig. 193C: 11, 12).

The following key summarizes the distinctions between species of sect. *Tenuifoliae*, based on the literature and the examination of selected specimens, including the types of several critical species. *Telaranea inaequalis* and *T. herzogii* are given full treatments in the first section of this paper, and are included in the key to Australasian species (p. 6). Members of the section fall into 4 groups, including one with asymmetrical underleaves (2 species), one with 2–3-lobed leaves (2 species), including the type, *T. tenuifolia*, and one with monocrurous leaves (3 species). The fourth, and largest group, includes *T. diacantha* and a number of similar species with predominately bilobed leaves. These differ in branching, cortical cell number, length of leaf lobes, size, shape and proportions of the lobe cells, and sexuality. Additional details on individual species are given in the section on Extra-Australasian Taxa (p. 120).

## Key to Species of Sect. *Tenuifoliae*

1. Leaves 2–3-lobed ..... *T. herzogii*, *T. tenuifolia*
1. Leaves bilobed or monocrurous, never 3-lobed ..... 2
2. Leaves 2-lobed (1-lobed on poorly-developed shoots or on lower portion of shoots); stem thicker (4+1 in sectors with 1-lobed leaves) ..... 3
3. Underleaves symmetric, caliper-like (2 basal cells + 1–2 cylindric lobe cells + slime papillae) or rudimentary, consisting of 2 adjacent cells capped by slime papillae. Neotropics; tropical Africa, South Africa; Madagascar, Mascarenes; Melanesia (Malacca, Borneo, New Guinea); Tasmania, New Zealand ..... *T. diacantha*, *T. major*, *T. inaequalis*, *T. microstipulata*, *T. coactilis*, *T. sejuncta*
3. Underleaves variable, asymmetrically lobed, with one lobe resembling a leaf lobe (occas. symmetrical in *T. monocera*) ..... 4
4. Cortical cells narrowly rectangular, with 2 cortical cells intervening between successive leaves; medullary cells 2. Malacca, Sumatra, New Guinea, Solomon Is. .... *T. monocera*
4. Cortical cells  $\pm$  isodiametric, with 3–4 cortical cells between leaves; medullary cells 4. Venezuela ..... *T. anomala*
2. Leaves monocrurous; stem 4+1. Neotropics ..... *T. pecten*, *T. confervoides*

### The Status of *Arachniopsis* subg. *Monodactylopsis* Schust.

Excluded from this treatment are two neotropical species which formerly comprised the subg. *Monodactylopsis* (Schuster, 1965), recently raised to generic rank as *Monodactylopsis* in the subfamily Zoopsidoideae (Schuster, 1999).

Fulford (1968) transferred Spruce's *Cephalozia monodactyla* to *Regredicaulis*, which Grolle (1983, p. 45) treated as a synonym of *Zoopsidella*. Schuster (1999, p. 523) suggested that *Monodactylopsis* may be "derived from *Zoopsidella*-like ancestral types," and that (Schuster, 2000, p. 435) "placing such a reduced organism in the proper phylogenetic context is a virtual impossibility." *Zoopsidella* species have essentially bilobed leaves with a broad, well-developed lamina. We think it equally likely that *Monodactylopsis* is allied to *Telaranea* sect. *Tenuifoliae*, but for the present it remains an element whose phylogenetic affinities are uncertain. Gradstein et al. (2001, p. 181) list *Monodactylopsis* as a synonym of *Arachniopsis*.

*Monodactylopsis minima* Schust. ex Engel & Merr., sp. nov.

*Arachniopsis minima* Schust., Nova Hedwigia 10: 24. 1965, nom. inval. (Art. 42.1). *Monodactylopsis minima* Schust., Tropical Bryology 2: 247. 1990; Nova Hedwigia 69: 520. 1999, nom. inval. Type:

Brazil, San Gabriel et San Carlos, Rio Negro, Spruce.

Foliis ad unicum segmentum reducta abbreviatis 2–4 cellulas formatis, caules 4+1, setis 8+4.

DESCRIPTIONS—Schuster (1999).

ILLUSTRATIONS—Schuster (1988, p. 250, fig. 2; 1999, figs. 31, 32; 2000, figs. 185, 186).

DISTRIBUTION—Brazil, Rio Negro; also reported from Sao Paulo (Vital and Visnadi, 1994).

The species is autoecious (Schuster, 1999), and apparently confined to the Rio Negro area, Brazil. Fulford (1968) listed *A. minima* as a synonym *Arachniopsis pecten* Spruce (p. 178), probably because the latter species, a *Telaranea* with monocrurous leaves, was earlier included by Schuster (1965) in subg. *Monodactylopsis*.

NOMENCLATURE—Cited as the type of *Arachniopsis* subg. *Monodactylopsis* Schust. (Schuster, 1965). The species was not validly published, since the subgenus and species are given a single description. Combined descriptions of infrageneric taxa and species are not sanctioned in the Code (Art. 42.1; see comment under *Telaranea monocera*, p. 168).

*Monodactylopsis monodactyla* (Spruce) Schust.

*Cephalozia monodactyla* Spruce, On Cephalozia: 28. 1882. *Zoopsis monodactyla* (Spruce) Sieph., Spec. Hep. 3: 282. 1908. *Arachniopsis monodactyla* (Spruce) Schust., Nova Hedwigia 10: 30. 1965. *Re-*

*gredicaulis monodactylus* (Spruce) Fulf., Mem. New York Bot. Gard. 11: 359. 1968. *Monodactyloopsis monodactyla* (Spruce) Schust., Nova Hedwigia 69: 523. 1999. Original material: Brazil, "in sylvis fl. Negro superioris" Spruce.

DESCRIPTIONS—Fulford (1968); Schuster (1999).

ILLUSTRATIONS—Fulford (1968, pl. 95, fig. 2, as *Regredicaulis monodactylus*); Schuster (1999, fig. 33; 2000, fig. 186A).

DISTRIBUTION—Puerto Rico (Fulford, 1968), Costa Rica (Gradstein et al., 1994), Brazil (Rio Negro, Rondonia, Reese; see Schuster, 1999), Guyana (Roraima, Gradstein and Florschütz-de Waard, 1989, as "*Zoopsideella monodactyla*").

### The systematic position of *Arachniopsis* "sect. *Dissotrichae*."

Schuster (2000, p. 463) discussed three species, *A. dissotricha*, *A. diplopoda*, and *A. tenuifolia* in connection with this section, which was not formally described. The latter species is the type of *Telaranea* sect. *Tenuifoliae* Schust. (see p. 194). The other two species are strikingly similar in the position and orientation of the leaves: laterally inserted, leaving the two median dorsal rows of cortical cells broadly exposed, the leaf lobes essentially parallel, closely approximated and oriented in an almost horizontal plane. As in other "*Arachniopsis*" species, the lobes are free except at the extreme base, and uniseriate throughout. Both species produce stoloniform ventral branches (Figs. 83: 3; 85: 5), which are said to be lacking in other *Arachniopsis* species (Schuster, 2000, p. 451, key). Both species also appear to be dioecious, whereas *T. tenuifolia* is autoecious.

These two species differ, however, in several respects. When dry, *A. diplopoda* is "glass-like" in appearance: strongly nitid, with the cortical cells and lobe cells uniformly collapsed. When moist, the plants appear somewhat fleshy (Fig. 82: 1), due to the rather large and turgid cortical cells of the stem. In *A. dissotricha* the cortical cells are incrassate and obliquely oriented, giving the surface of the stem a unique scaly appearance (Fig. 85: 1, 2). Leaf insertion in *A. dissotricha* is succubous (Fig. 85: 1) and in *A. diplopoda* incubous

(Fig. 82: 1), but the manner of insertion is otherwise strikingly similar. Branching in both species is almost exclusively ventral, but in *A. dissotricha* appears to be predominately terminal, *Acromastigium*-type, vs. ventral-intercalary in *A. diplopoda*. In addition, we have observed *Fruilania*-type branching in several populations of *A. diplopoda* (Fig. 82: 4), as well as in a new species, *A. gracilis*, described below.

We are treating this group as a genus whose phylogenetic relationships are not known.

### *Amazoopsis* Engel & Merr., gen. nov.

*Arachniopsis* sect. *Dissotrichae* Schust., Beih. Nova Hedwigia 118: 450, 459. 2000, nom. inval. sin. descr. lat.

Dioicae. Cellulae dorsales surculorum conspicue expositus, insertio foliorum in una specie vix succuba, aequae in altera incubae, foliis plano-distichis, 2-fidis, lobis binatim approximatis: surculi ventrales stoloniformes praebens.

Type: *Arachniopsis dissotricha* Spruce.

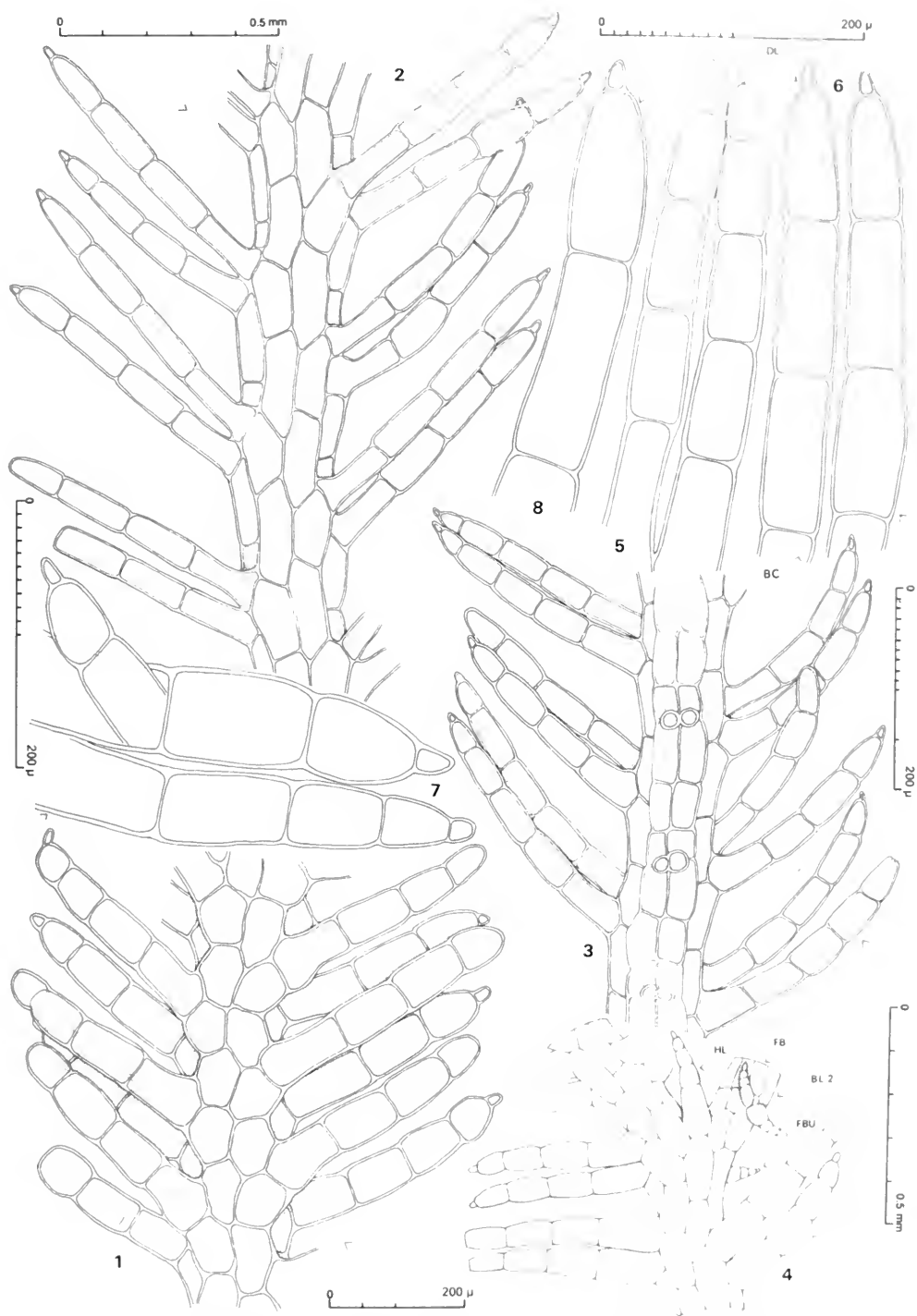
Dioecious; main shoot with 2 prominent dorsal rows of broadly exposed cortical cells; stoloniform ventral branches produced; leaves laterally inserted, plano-distichous, bilobed, the 2 lobes  $\pm$  parallel and closely approximated, lying in an almost horizontal plane. Underleaves minute and inconspicuous, consisting of a pair of small,  $\pm$  spherical cells inserted along the transverse wall between cortical cells, each cell crowned with a slime papilla.

Three species of the genus are distinguished as follows.

### Key to the Species of *Amazoopsis*

1. Leaves succubous; branches differentiated from leading shoots, feather-like, with leaves inserted at the distal end of every cortical cell (leading shoots with two cortical cells between successive leaves); dorsal cortical cells incrassate

FIG. 82. *Amazoopsis diplopoda* (Pócs) Engel & Merr. 1. Portion of shoot, dorsal view; note incubous insertion of leaves, and the often subisodiametric cortical cells with subtransverse end walls. Note also the often caducous terminal cells of lobes. 2. Portion of leading shoot (dorsal view) drawn at 25% less magnification than fig. 1; note



the more elongated cells of both stem cortex and leaf lobes. 3. Portion of main shoot, ventral view. 4. Portion of main shoot with *Frullania*-type branch (= FB), dorsal view; note half-leaf (= hl), first branch underleaf (= fbu), and second branch leaf (= BL2), the two lobes free at the base. 5, 6. Two leaves from different shoots (dl = dorsal lobe; bc = basal cell). 7. Two leaf lobes and, above, distal portion of a third lobe (all at same scale). 8. Distal portion of leaf lobe. (Figs. 1, 4, 7, from type of *Arachniopsis diplopoda*; 2, 3, 5, 6, 8, from Pócs et al. 90113/L, Madagascar, Prov. Antsiranana, Reserve Integrale Nationale de Marojejy.)

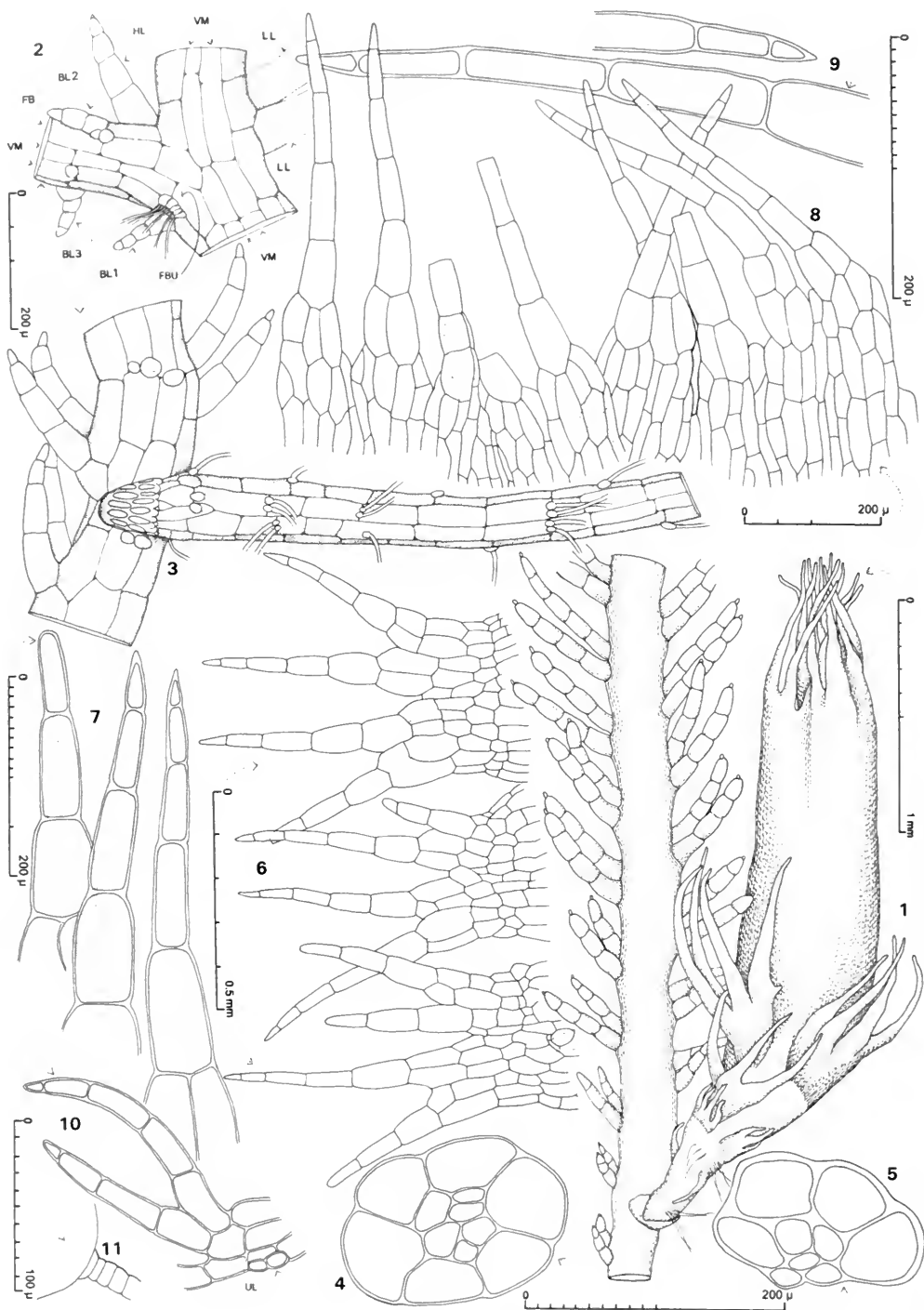


FIG. 83. *Amazoopsis diplopoda* (Pócs) Engel & Merr. 1. Portion of shoot with mature gynoeceum. 2. Portion of main shoot with *Frullania*-type branch (= FB); note position of the first branch underleaf (= fbu); the cells have subdivided, with each rhizoid initial producing a rhizoid. Note also the monocurous first branch leaf (= BL1), the strongly asymmetric second branch leaf (= BL2), and, following, an underleaf and 1 lobe of the third branch leaf (= BL3), the other lobe not visible. The half-leaf (= hl) is clearly visible in the branch axil. Note the ventral merophyte cells of the main shoot and the first appearance of two rows of ventral merophyte cells of the branch (shown on both main shoot and branch with arrows, = VM). An underleaf of main shoot not shown, the position indicated by stippled

sate, those of feather-like branches trapezoidal in shape, the end walls strongly oblique, lending the stem a scaly appearance; branching terminal, *Acromastigum*-type and ventral-intercalary. Neotropics (Brazil, Peru) . . . . .

- ..... *A. dissotricha*  
1. Leaves incubous; branches not differentiated, two cortical cells intervening between successive leaves on either side of shoot; dorsal cortical cells thin- to firm-walled, turgid, the end walls subtransverse; branching ventral-intercalary and terminal, *Frullania*-type . . . . . 2  
2. Plants distinctly complanate-distichous; leaf lobes arranged in comb-like fashion,  $\pm$  parallel, broadly decurved, dactyloid (finger-like), scarcely tapering, to 665  $\mu$ m long; lobe cells short and broad (often 2:1). Africa (Zaire), Madagascar, Comores Is. . . . .  
..... *A. diplopoda*  
2. Plants bristly in appearance; leaf lobes  $\pm$  divergent, slender, distinctly tapering, to 840  $\mu$ m long; lobe cells elongate (4–5:1 or more). Rhizoids from subapical cells of leaf lobes. Réunion, Seychelles Is. . . . .  
..... *A. gracilis*

*Amazoopsis diplopoda* (Pócs) Engel & Merr., comb. nov.

*Arachniopsis diplopoda* Pócs in Vána, Proceedings of the Third Meeting of the Bryologists from Central and East Europe, p. 114, f. 2–3. 1984. Holotype: Madagascar, Prov. Diego Suarez, Normandia-Nord, 50 m, *Cremers 2733b* (hb. Onraedt); isotypes: (BR, EGR[!], hb. E.W. Jones).

ILLUSTRATIONS—Pócs (1984, figs. 2–3); Schuster (2000, fig. 193D: 1, 6). Figs. 82, 83.

DISTRIBUTION—Madagascar, Comores Is., Réunion; also from Zaire, leg. *Mansuet-Andre* (BR), represented by a single stem in a tuft of *Sprucella succida* (Pócs, 1984); see maps in Gradstein, Pócs and Vána (1983) and Pócs (1995). Pócs (1995, p. 255) describes *A. diplopoda* as a “Lemurian” (endemic Indian Ocean island) species, with a wide altitudinal range from sea level to high mossy

montane rainforest. According to Pócs, the species “shows a distinct preference for an acidic soil substrate,” in contrast to *Telaranea diacantha*, which is more common on wood than soil.

Plants slender, rather soft and flexuous, freely and irregularly branched, pale green, highly nitid when dry, the cortical cells and leaf lobe cells all collapsed, when moist, the shoots strongly complanate, the leaves (lobes) lying in one plane, to 1225  $\mu$ m wide with leaves. Branching frequent, the branches not differentiated, predominantly ventral-intercalary, both leafy and stoloniform, the stoloniform rootlets often arising immediately at the base of a leafy ventral-intercalary branch. Terminal, *Frullania*-type branches occasional, the half-leaf and first branch appendage monocurrous; first few leaves of branch often also monocurrous or asymmetrically bilobed. Stems with a turgid appearance, the cortical cells in 6 rows (4 in axes with monocurrous leaves), thin- to firm-walled, subquadrate to  $\pm$  elongate, the end walls subtransverse to somewhat oblique, the ventral cortical cells narrower and forming a conspicuous ventral strip or similar in size and shape to the dorsal; medullary cells in 3–6 rows, much smaller, thin walled. Shoots with 2 cortical cells intervening between successive leaves on either side of shoot. Rhizoid initials formed from divisions of the underleaf cells. Leaves approximate to contiguous, bifid to the base or sporadically monocurrous, 340–415  $\mu$ m long (type) to as much as 525–665  $\mu$ m long, typically regularly arranged in a comb-like fashion, broadly and gently decurved, laterally inserted, the two median dorsal rows of cortical cells broadly exposed; leaf insertion incubous or at times nearly longitudinal, the dorsal lobe positioned nearest shoot apex and inserted slightly to distinctly above the ventral. Lobes uniseriate to the base, 4–5(7) cells long, in regular ranks,  $\pm$  equal in length, touching or somewhat divergent, typically oriented in an almost horizontal plane, the tip cell (and sometimes the distal lobe cells) caducous. Cells of lobes thin- to firm-

←  
transverse walls of cortical cells in distal portion of figure (LL = leaf lobes of main shoot). 3. Ventral-intercalary stoloniform branch subtended by an underleaf in the basal portion of a leading ventral-intercalary leafy branch. 4, 5. Stem, cross sections. 6. Innermost  $\varnothing$  bracts. 7. Three lobes of  $\varnothing$  bracts showing both rounded and sharply acute terminal cells. 8. Portion of perianth mouth. 9. Distal portion of perianth mouth lobe and (above) a lobe apex. 10.  $\sigma$  Bract, *in situ* (ul = underleaf). 11. Antheridium. (Figs. 1, 3, 4, 6–9, from Pócs *et al.* 90113/L, Madagascar, Prov. Antsiranana, Reserve Integrale Nationale de Marojejy; 2, 5, from type of *Arachniopsis diplopoda*; 10, 11, from Lübenau 22, Madagascar, Prov. Antananarivo, NR Ambohetantely, Ankazobe.)

walled, the transverse septa at most moderately thickened in the corners and straight sided to somewhat constricted, the basal cells 48–67  $\mu\text{m}$  wide  $\times$  110–132  $\mu\text{m}$  long, the next cell 50–77  $\mu\text{m}$  wide  $\times$  96–110  $\mu\text{m}$  long, the subapical cell shorter, the tip cell minute, often caducous, sharp-pointed, often somewhat curved, resembling a candle flame, or at times narrowly ovate; cuticle smooth or finely striolate. Underleaves consisting of a pair of rounded, button-like, moderately thick- or merely firm-walled cells (rarely with an additional short-cylindric cell), each lobe terminating in an elongate slime papilla. Asexual reproduction by fragmenting leaf tips.

Dioecious. Androecia on short, spicate ventral-intercalary branches or less often intercalary in position on leading shoots, basket-like, enclosing the conspicuous, whitish antheridia, the bracts falcate-secund, strongly dorsally assurgent, asymmetrically bilobed (ventral lobe 5 cells long, the other 4), the lobes uniseriate to the base, their basal cells united for about 0.6 their length, the cells resembling the uniseriate row of the lobes of the  $\varnothing$  bracts; antheridial stalk uniseriate. Gynoecia on short, ventral-intercalary branches from main shoot; bracts much larger than the leaves, 4-lobed to about 0.7, the disc 2.5–3.5 cells high, the cells subquadrate, thin walled, the lobes strikingly different from those of the leaves, consisting of a basal pair of elongate, turgid, thin-walled cells and a bristle-like uniseriate row of 4–5 thick-walled cells, the septa distinctly thickened in the corners but not bulging, the terminal cell narrowly triangular, sharp-pointed and thickened in the tip (less often rounded), the tips at times caducous. Perianth slenderly fusiform, subterete below, obtusely trigonous and tri-plicate above the middle, weakly contracted to the 12-lobulate-ciliate mouth, the cilia caudate, resembling the lobes of the  $\varnothing$  bracts, with a base 4–5 cells wide, 1 or 2 biseriate tiers and a bristle-like uniseriate row of 5 elongate cells, no accessory cilia or spurs, the distal portion at times caducous.

Sporophyte not seen.

The species is somewhat variable in the proportions of the leaf lobe and dorsal cortical cells, and the degree of differentiation of the ventral merophyte row (compare Fig. 83: 4 and 5). The leaf lobe cells (particularly the penultimate cell), are typically short (as little as 2:1). A conspicuous strip of narrow ventral merophyte cells is evident in the type, but in other material the ventral cells are similar in size and shape to the dorsal (Fig.

82: 3; also compare Fig. 83: 4 with 5, as seen in cross section).

Plants of *A. diplopoda* are highly nitid when dry, the cortical cells and leaf lobe cells often all collapsed. When moist, the shoots are strongly complanate, the leaves (lobes) lying in one plane and slightly decurved toward the substrate (Fig. 82: 2). Stoloniform rootlets (ventral-intercalary branches) are frequent, often arising immediately at the base of a leafy v.i. branch (Fig. 83: 3).

In contrast to *A. dissotricha*, branches are not differentiated from leading shoots, the branching appearing much less regular as a result of the predominance of ventral-intercalary branches, vs. terminal, *Acromastigum*-type branches in *A. dissotricha*. Two cells intervene between leaf insertions dorsally, and leaf insertion is clearly incubous (Fig. 82: 2). Underleaves (Fig. 82: 3) typically consist of a pair of small spherical cells, inserted along the transverse wall between cortical cells, each cell crowned with an elongate slime papilla. The minute terminal cell of the leaf lobes tapers to a distinct tip, the cell often resembling a candle flame (Fig. 82: 5, 6), and is often caducous.

Terminal, *Frullania*-type branching occasionally occurs in *A. diplopoda* but has not been observed in *A. dissotricha*. A *Frullania*-type branch from the type of *A. diplopoda* is illustrated in Figs. 82: 4; 82: 2. The situation is similar to that in *A. gracilis* (see below), but the first branch underleaf has produced a fascicle of rhizoids, the first leaf (BL1) is abbreviated and the leaves of the next several cycles are asymmetrically bilobed with abbreviated lobes.

SPECIMENS SEEN—MADAGASCAR: Prov. Antsiranana, Reserve Integrale Nationale de Marojejy, 1350 m, *Pócs, Randrianasolo, Magill & Lafarge-England 90115/K* (EGR); *ibid.*, Reserve Integrale Nationale de Marojejy, ridge N of Andampibe Falls, 400 m, *Pócs, Magill & Lafarge-England 90113/L*—c. per. (EGR, F). Prov. Antananarivo, NR Ambohetantely, Les Hautes Plateaux, Ankazobe,  $\pm$  1500 m, *Liubenau 22*—c.  $\delta$  (EGR). COMORO ARCHIPELAGO: W end of Mwali (Moheli) Is., SSW ridge leading to the summit with Chalet St. Antoine, 600–660 m, *Pócs, Magill & Rupf 92100/D* (EGR, F); Ndouzani (Anjouan) Is., SE summit ridge of Mt. Ntringi (N'Tingui), 1325 m, *Pócs, Magill & Rupf 9274/A* (EGR, F). REUNION ISLAND: Takamaka gorge, 13 km W of Ste Anne, around the Cascade de l'Arc en Ciel, 520–800 m, *Orbán 9436/W* (EGR, F).

*Amazoopsis gracilis* Engel & Merr., sp. nov.

Plantae minute aculeatae, foliis 2-fidis vel (raro) simplicibus, lobis foliorum  $\pm$  divergentibus gracilibus dis-



tincte angustatis, cellulis loborum subcapillaribus, subtiliter striolatis.

Holotype: Réunion, E edge of Cirque de Ma-fate, NW slope of Piton Marmite, 1610 m, 26 Aug. 1994, *Vojtkó 9431/X* (EGR); isotype: (F).

DISTRIBUTION—Réunion, Seychelles Is.

Plants slender, bristly in appearance due to  $\pm$  divergent leaf lobes, freely branched, pale whitish green, strongly complanate, the leaves (lobes) lying in one plane, 1330 mm wide with leaves. Branching in aerial shoots chiefly of terminal, *Frullania*-type (primary and rarely secondary branches present), the half-leaf and first branch appendage monocurrous, the first few leaves of branch often also monocurrous or asymmetrically bilobed. Ventral-intercalary branches common, stoloniform. Stems with a rather turgid appearance, the cortical cells in 6 rows (4 in monocurrous axes), firm-walled, subisodiametric to short rectangular, the end walls transverse to somewhat oblique, the ventral cortical cells narrower and forming a conspicuous ventral strip; medullary cells in 4–5 rows, much smaller, thin walled. Shoots with 2 cortical cells intervening between successive leaves on either side of shoot. Rhizoids from basal underleaf cells as well as from subapical cells of leaf lobes. Leaves approximate, bifid to the base, sporadically or (in weaker shoots) regularly monocurrous, 595–840  $\mu\text{m}$  long, laterally inserted, the two median dorsal rows of cortical cells broadly exposed; lobe insertion distinctly incubous. Lobes slender, distinctly tapering, uniseriate to the base, the two lobes at times completely free from one another at insertion, 5–6 cells long, subequal in length, lying in an almost horizontal plane. Cells of lobes thin to moderately thick-walled, elongate (4–5:1 or more), 29–50  $\mu\text{m}$  wide  $\times$  120–161  $\mu\text{m}$  long, the next cell 29–38  $\mu\text{m}$  wide  $\times$  120–163  $\mu\text{m}$  long, the transverse septa moderately thickened in the corners, the lobes somewhat constricted at the septa; cuticle smooth. Underleaves consisting of a pair of basal cells, each with a short-cylindric cell, terminating in a slime papilla (or with a slime papilla directly on the basal cell).

Dioecious. Androecia elongate, terminal on leading shoots, bracts stiffly dorsally assurgent, bilobed, the lobes uniseriate to the base, their basal cells united for about 0.3–0.5 their length. Gynoeceia not seen.

The two *Amazoopsis* species with incubously

inserted leaves differ strikingly in aspect. The shoots of *A. gracilis* are rather bristly in appearance, the leaf lobes more divergent, slender, and distinctly tapering, vs. lobes arranged in comb-like fashion, closely approximated, finger-like and scarcely tapering in *A. diplopoda*. The lobe cells are elongate and firm-walled (4–5:1 or more) vs. short and broad (often 2:1) in *A. diplopoda*. Rhizoids are produced from subapical cells of leaf lobes.

Terminal, primary and (rarely) secondary *Frullania*-type branches (Fig. 84: 2) are freely produced in *A. gracilis*. The first branch underleaf consists of a single underleaf-like lobe, with a small basal cell and an elongate slime papilla (Fig. 84: 2, FBU). The fbu is positioned at the point where the two rows of ventral merophyte cells of the branch become differentiated; the basalmost ventral cell of the branch is undivided and similar to adjoining cells of the main axis. The first leaf (BL1) is monocurrous and is inserted on the ventral lateral merophyte cell row (Fig. 84: 2). The next leaf (BL2) is bilobed, but the two lobes are inserted some distance apart.

SPECIMENS SEEN—SEYCHELLES: Mahe, Morne Blanc, ca. 550 m, *Onraedt 74.S.073*—c. ♂ (F); *ibid.*, La Misère, versant Grand Anse, ca. 400 m, *Onraedt 74.S.416* (F). Both specimens previously determined as *Arachniopsis diacantha*.

*Amazoopsis dissotricha* (Spruce) Engel & Merr., comb. nov.

*Arachniopsis dissotricha* Spruce, On Cephalozia: 86. 1882. Original material: Brazil, Fl. Uaupés, Panuré, Spruce (NY!).

DESCRIPTION—Fulford (1968, p. 364).

ILLUSTRATIONS—Fulford (1968, pl. 97, fig. 4, type); Pócs (1984, fig. 1, type); Schuster (2000, fig. 193B: 1–7); Fig. 85. Stephani, Icones, *Arachniopsis* 3.

DISTRIBUTION—Brazil (Uaupés, type), Peru (see map in Gradstein, Pócs and Vána, 1983).

Plants slender but rather rigid, irregularly branched to loosely pinnate with flattened, feathery branches, highly nitid when dry, the branches to 700  $\mu\text{m}$  wide with leaves. Branching frequent from ventral merophytes, predominantly terminal, *Acromastigum*-type, both leafy and stoloniform. Ventral-intercalary branches apparently also produced. Stem cortical cells thick-walled, in 6 rows; medullary cells in 7–8 rows, much smaller, the

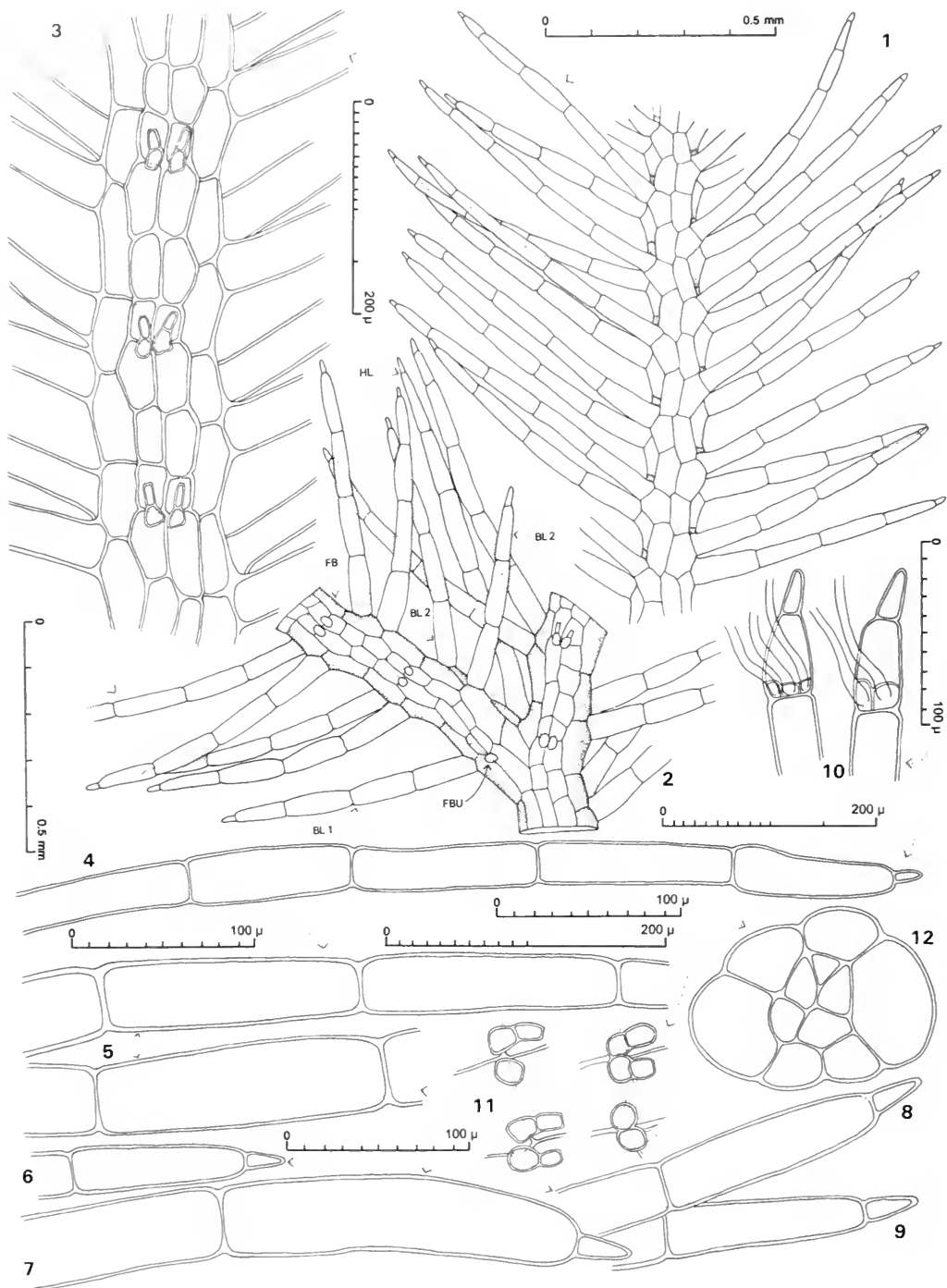


FIG. 84. *Amazoopsis gracilis* Engel & Merr. 1. Portion of main shoot, dorsal view; note some leaves with unattached lobes. 2. Portion of main shoot with *Frullania*-type branch (= FB); note the position of the first branch underleaf (= FBU), the monocurrous first branch leaf (= BL1), and the second branch leaf (= BL2), with lobes some distance apart (HL = half-leaf). Note the two underleaves of the main shoot, one with button-like cells each capped by a slime, the other with a cylindrical cell between button-like cell and slime papilla. 3. Portion of main shoot, ventral view. 4. Complete leaf lobe. 5. Portions of 2 leaf lobes showing constricted septae. 6-9. Distal portions of leaf lobes. 10. Distal portions of lobes of same leaf, each with rhizoids originating from subapical cells. 11. Underleaves. 12. Stem, cross section. (All from type.)

walls  $\pm$  equal in thickness to those of the cortical cells. Leading shoots with 2 (very rarely 3) cortical cells intervening between successive leaves on either side of shoot; feather-like branches with dorsal lobes inserted at the upper end of every cortical cell. Rhizoid initial cells formed from divisions of the underleaf cells. Leaves contiguous, bifid to the base, (lobes) 265–310  $\mu\text{m}$  long, on the branches very regularly arranged in comb-like fashion (leaves similar but more distant on leading shoots), broadly decurved, laterally inserted, the two median dorsal rows of cortical cells broadly exposed; leaf insertion nearly longitudinal but plainly succubous, the dorsal lobe inserted slightly above the ventral. Lobes uniseriate to the base, 4(5) cells long, tapering, in regular ranks,  $\pm$  equal in length, touching or weakly divergent, oriented in an almost horizontal plane, the apical cell (and sometimes the distal lobe cells) caducous (particularly in older parts of plant). Cells of lobes  $\pm$  thick-walled, the transverse septa strongly thickened in the corners but nearly always  $\pm$  constricted (particularly at base of tip cell), the basal cells 36–48  $\mu\text{m}$  wide  $\times$  120–144  $\mu\text{m}$  long, the next cell 34–46  $\mu\text{m}$  wide  $\times$  120–130  $\mu\text{m}$  long, the subapical cell shorter, the tip cell minute, narrowly ovate, at times becoming detached; cuticle finely striolate. Underleaves minute and inconspicuous, consisting of a pair of very thick-walled cells each capped by a slime papilla. Asexual reproduction by fragmenting leaf tips.

Dioecious (Spruce, 1882, 1885). Androecia (Spruce) flattened and assurgent-second, at the tips of branches; bracts similar to the leaves, monandrous. Perianth (Spruce) 5 $\times$  longer than broad, linear-fusiform, trigonous, the mouth with 12 long cilia.

This species is notable for the succubous insertion of the leaves (Fig. 85: 1), vs. incubous in *A. diplopoda*. The two species also differ in the number of cortical cells intervening between successive leaves. In *A. diplopoda* there appear to be regularly two cells between a leaf and the leaf next above it (Fig. 82: 1, 2), whereas in the feather-like branches of *A. dissotricha* every dorsal cortical cell has a leaf inserted at its upper end, and the stem in dorsal view has a distinctive scale-like appearance (Fig. 85: 1, 2). However, there are also leading shoots with more distant leaves, which have 2 (locally 3) cortical cells intervening between successive leaves. The result is a plant that can appear loosely pinnate, with a main axis and feathery branches.

In contrast to *A. diplopoda*, branching in *A. dissotricha* appears to be predominantly (if not exclusively) of the terminal, *Acromastigum*-type. In fact, the differentiation of branches in this species argues for their being terminal in origin, just as terminal, *Frullania*-type branches are variously differentiated from leading shoots in many *Telaranea* species (e.g., *T. chaetophylla*, p. 137, Fig. 42: 2). In fact, leafy "intercalary branches" are not branches at all, but are best thought of as adventitious leading shoots. In many cases the origin of these branches is unequivocal, with the branch clearly inserted on one ventral merophyte row, and the other row unaffected, with its button-like half-underleaf lying alongside the branch base. Paired *Acromastigum*-type branches from adjacent ventral merophyte rows are not uncommon. Branches may be normally leafy or stoloniform, whip-like, and greatly simplified in structure (Fig. 85: 5). Ventral-intercalary branches are evidently also produced, but all branches are strongly contracted to the base, the cells of the base confluent with the adjacent cortical cells, with no evident collar. A single, arguably ventral-intercalary branch was observed, with the paired underleaf cells positioned directly beneath the branch.

The cuticle of the leaves is finely striolate in the type, more strongly so in the Peruvian specimen. A slip of paper in the type at NY has the notation "Panur —in rivuli ripis umbrosis."

SPECIMEN SEEN—PERU: Rio Mayo, near Tarapoto, Spruce 4736 (NY).

## Phytogeography and Ancestral Areas

An ancestral area analysis was undertaken as part of this study in an attempt to explain the present geographical distribution of *Telaranea* species. The geographical distribution of each taxon is shown graphically in Fig. 86, in which the cladogram shown in Fig. 77 has been converted into an area cladogram by substituting for each taxon the geographical areas where each occurs.

The area cladogram conclusively points to temperate Australasia as the ancestral area for the genus *Telaranea*, i.e., to the portion of Gondwanaland that included present Australasia. With one exception (*T. longitudinalis* of Borneo), the earliest, basally divergent lineages on the cladogram (subg. *Acrolepidozia*, sect. *Neolepidozia*) are exclusively temperate Australasian. Moreover, all

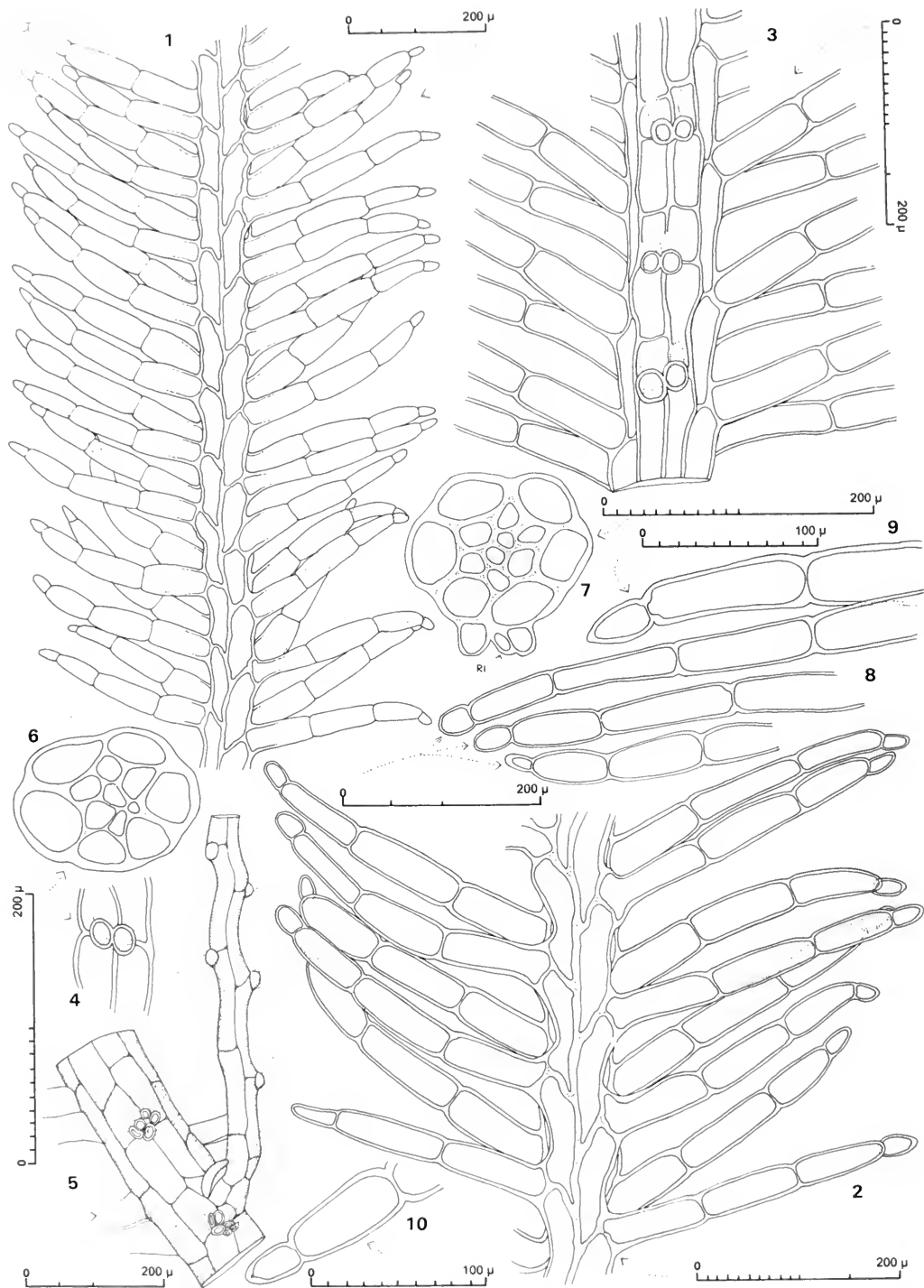


FIG. 85. *Amazopsis dissotricha* (Spruce) Engel & Merr. 1. Portion of shoot (dorsal view); note succubous insertion of leaves, with a dorsal lobe inserted at the distal end of every cortical cell. Note also the incrassate dorsal-cortical cells, with oblique end walls. 2. Portion of shoot, dorsal view. 3. Portion of shoot, ventral view; note underleaves consisting of a pair of thick-walled cells each with a slime papillae. 4. Underleaf. 5. Portion of shoot with *Acromastigium*-type stoloniform branch, ventral view; note that the remaining underleaf cell has repeatedly subdivided to produce several rhizoid initials, each giving rise to a rhizoid. Note cells of other main shoot underleaf

sections of the genus are represented in temperate Australasia, from the most basal to the most derived. The situation in *Telaranea* contrasts with that suggested for another Gondwanalandic genus, *Balantiopsis* (Engel & Merrill, 1997), in which temperate South America was proposed as the most probable ancestral area for the genus. The situation in *Telaranea* is relatively unambiguous, and resort to ancestral area analysis, such as reversible parsimony (Ronquist, 1994), appears unnecessary. For further description of this methodology and its applicability to the biogeography of antipodal hepatics, see the discussion in Engel and Merrill (1997).

Several examples of amphi-Pacific species relationships in *Telaranea* are evident in the area cladogram. *Telaranea plumulosa* of southern South America is the sister species to *T. pulcherrima* (temperate Australasia), and *T. trichocoleoides* (Borneo), suggesting a common Gondwanalandic origin for this clade. *Telaranea coactilis* (sect. *Tenuifoliae*) arguably occurs both in tropical America and in Africa (see legend, Fig. 86); this species and *T. nematodes* (sect. *Telaranea*) are the only instances of amphi-Atlantic distribution in the genus. Evidence of dispersal to remote oceanic islands in the south Atlantic and Indian Ocean is limited. *Telaranea oligophylla* is reported from South Georgia (Herzog, 1926, p. 381), possibly based on the same collection cited as *T. seriaticulata* by Fulford (1966), and *T. breviseta* is reported from Tristan da Cunha by Arnell (1958). Grolle (2002) lists no species of *Telaranea* from the subantarctic and temperate oceanic islands of the eastern Southern Hemisphere. *Telaranea tetradactyla*, a New Zealand species, has apparently been introduced by human agency to Britain.

Section *Cancellatae* has a widespread distribution, including numerous Old World as well as American species, indicating that the evolution of sectional diversity in subg. *Telaranea* took place early, before the breakup of Gondwanaland. Included in this section is (reputedly) the most wide-ranging *Telaranea* species, *T. wallichiana*, extending from western Melanesia (Solomon Is.) to Ceylon, north to the Himalayas and Japan.

*Telaranea* sect. *Ceraceae* is exclusively temperate Australasian, although a glaucous, water-repellent cuticle is not confined to species of this

group. Section *Transversae* is chiefly an Old World group, but the section is also represented in southern South America by 4 species (*T. fernandeziensis*); this group is absent from tropical America.

The most reduced taxa in the genus are the most widely distributed geographically and essentially pantropical. Section *Telaranea* is present in Australasia (*T. tasmanica*) and Malaysia (*T. chaetocarpa*); temperate South America (*T. setosa*), tropical America (*T. chaetophylla*), eastern North America (*T. longifolia*), Europe and Macaronesia (*T. europaea*); and in southern Africa (*T. tenuis*). Section *Tenuifoliae* (essentially the former genus *Arachniopsis*), including the most highly reduced taxa, is also widely distributed. In this connection, Schuster (1988, p. 243), noted that the Lepidoziaceae of the lowland tropics are mostly highly specialized, including *Arachniopsis* in lowland Amazonia. *Telaranea diacantha* is reported from tropical America, and similar species occur in tropical and southern Africa (*T. coactilis*), and in tropical Asia (*T. major*, Ceylon to Malaysia to New Hebrides, and New Guinea). Section *Tenuifoliae* is not confined to the tropics, however, occurring also in temperate Australasia (*T. herzogii*, *T. inaequalis*). No species of sect. *Tenuifoliae* is known to occur in south temperate South America, or in the north temperate zone.

The 98 species included in the Conspectus (Table 3) are distributed as follows: subg. *Acrolepidozia* (3), sect. *Neolepidozia* (7), sect. *Cancellatae* (25), sect. *Ceraceae* (4), sect. *Transversae* (18), sect. *Tricholepidozia* (7), sect. *Telaranea* (22), and sect. *Tenuifoliae* (12).

Distribution of *Telaranea* species by major geographical regions is as follows: Australasia (36), paleotropical (30), temperate South America (13), neotropical (13), African (4), and north temperate (4, one species each in eastern North America and Japan, 2 in Europe). The geographical distribution of the sections and numbers of species in each region are shown in Table 4. The conclusions based on the area cladogram are confirmed: the largest number of species is Australasian, with an almost equal number of species in the paleotropics, followed by temperate South America and the neotropics. It should be noted that only about 1/3 of the paleotropical species are

←  
have subdivided to form several rhizoid initials. 6, 7. Stem, cross sections; note (fig. 7) underleaves and rhizoid initial (ri). 8. Four- and 5-celled leaf lobes. 9, 10. Distal portion of leaf lobes. (All from type of *Arachniopsis dissotricha*.)

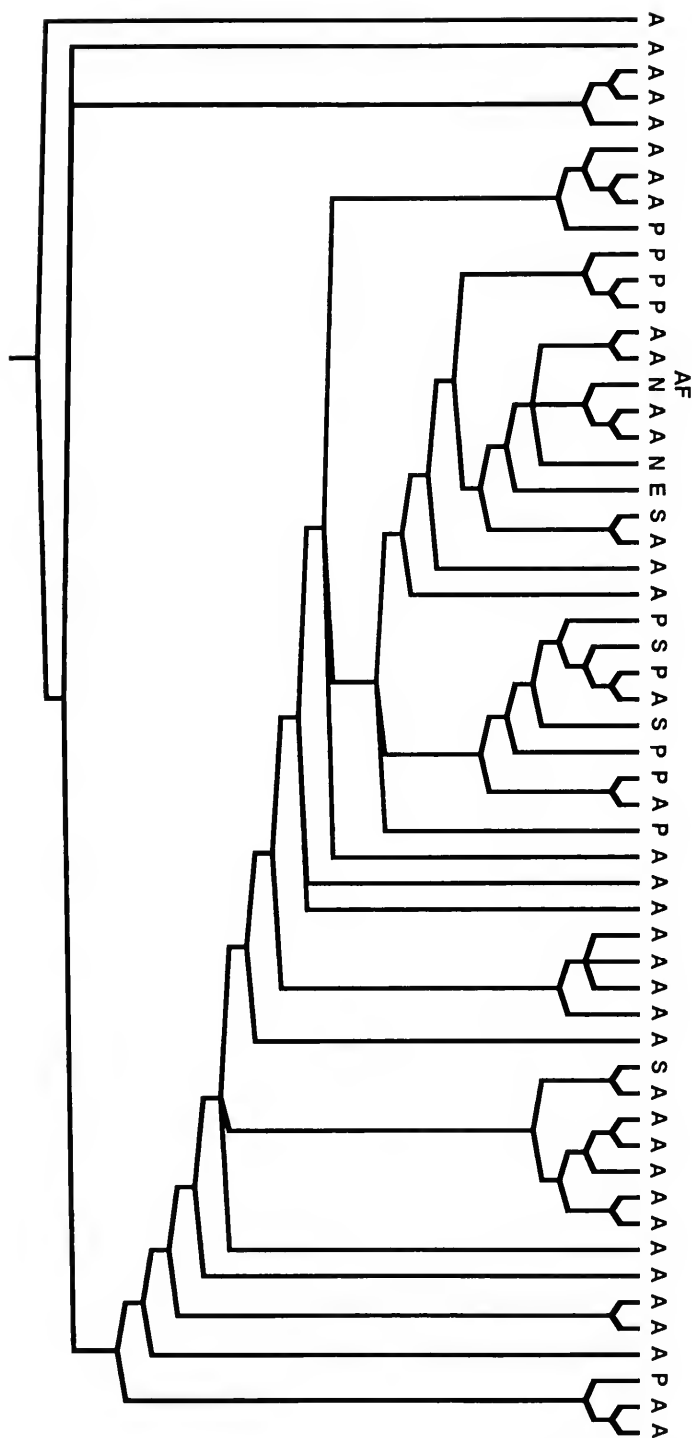


FIG. 86. Area cladogram showing the distribution of each terminal taxon in the data set (based on fig. 77) with the geographical distribution substituted for the name of the taxon (A = Australasia, S = temperate South America, P = Paleotropics, N = Neotropics, E = eastern North America, AF = Africa). Note that the basally divergent taxa are almost exclusively Australasian. *Telaranea diacantha* is indicated as African (AF) as well as neotropical (N) in distribution, based on literature reports. However, African material is probably referable to *T. coactilis* (see p. 140).

TABLE 3. Conspectus of *Telaranea* Spruce ex Schiffn.

In general, taxa are listed in order of branching in Fig. 77, following the listing convention of Nelson (1972). Species not included in the data matrix are assigned to sections based on comments in the Discussion of Extraterritorial Taxa (p. 120), and are placed in sequence close to similar species.

Subg. *Acrolepidozia* (Schust.) Schust.

- T. clatritexta* (Steph.) Engel & Merr.  
*T. meridiana* (Hodgs.) Hogs.  
*T. longitudinalis* (Herz.) Schust.

Subg. *Telaranea*Sect. *Neolepidozia* (Fulf. & J. Tayl.) Engel & Merr.

- T. pennata* Engel & Merr.  
*T. disparata* Engel & Merr.  
*T. quadrastipula* (Steph.) Engel & Merr.  
*T. tridactylis* (Lehm. & Lindenb.) Engel & Merr.  
*T. capilligera* (Schwaegr.) Schust.  
*T. consobrina* Engel & Merr.  
*T. palmata* Engel & Merr.

Sect. *Cancellatae* Engel & Merr.

- T. gibbsiana* (Steph.) Hodgs.  
*T. grossiseta* (Steph.) Engel & Schust.  
*T. hodgsoniae* Engel & Merr.  
*T. patentissima* (Hook. f. & Tayl.) Hodgs.  
*T. verruculosa* Engel & Merr.  
*T. tetrapila* (Hook. f. & Tayl.) Engel & Merr.  
*T. paludicola* (Hodgs.) Hodgs.  
*T. praenitiens* (Lehm. & Lindenb.) Hodgs.  
*T. autoica* Engel & Merr.  
*T. rectangularis* Schust.  
*T. oligophylla* (Lehm. & Lindenb.) Engel  
*T. seriatitexta* (Steph.) Engel  
*T. disticha* (Steph.) Solari  
*T. trifida* (Steph.) Schust.  
*T. wallichiana* (Gott.) Schust.  
*T. cuneifolia* (Steph.) Engel & Merr.  
*T. planifolia* (Steph.) Engel & Merr.  
*T. papulosa* (Steph.) Engel & Merr.  
*T. leratii* (Steph.) Engel & Merr.  
*T. mamilliosa* (Schiffn.) Engel & Merr.  
*T. parvifolia* (Steph.) Engel & Merr.  
*T. heterotexta* (Steph.) Engel & Merr.  
*T. aubertii* (Jovet-Ast) Engel & Merr.  
*T. pruinosa* (Herz.) Engel & Merr.  
*T. ophiria* (Steph.) Engel & Merr.

Sect. *Ceraceae* Engel & Merr.

- T. elegans* (Col.) Engel & Merr. Engel & Merr.  
*T. tuberifera* Engel & Schust.  
*T. centipes* (Tayl.) Schust.  
*T. perfragilis* Engel & Merr.

Sect. *Transversae* Engel & Merr.

- T. tetradactyla* (Hook. f. & Tayl.) Hodgs.  
*T. quadristea* (Steph.) Engel & Merr.  
*T. murphyae* J. A. Paton  
*T. fissifolia* (Steph.) Hürl.  
*T. melanesica* H. A. Mill.  
*T. jowettiana* H. A. Mill.  
*T. semperiana* (Steph.) Del Ros.  
*T. lindenbergi* (Gott.) Engel & Merr.  
*T. fernandeziensis* (Steph.) Engel & Merr.

*T. marginata* Engel & Merr.

- T. kaindina* Grolle  
*T. longicaulis* (Piippo) Engel & Merr.  
*T. pallescens* (Grolle) Engel & Merr.  
*T. trilobata* (Schust.) Engel & Merr.  
*T. fragilifolia* (Schust.) Engel & Merr.  
*T. lawesii* (Steph.) Grolle  
*T. blepharostoma* (Steph.) Fulf.  
*T. ferruginea* Engel & Merr.

Sect. *Tricholepidozia* (Schust.) Engel & Merr.

- T. remotifolia* Hodgs.  
*T. kogiana* (Steph.) Grolle  
*T. neesii* (Lindenb.) Fulf.  
*T. plumulosa* (Lehm. & Lindenb.) Fulf.  
*T. octoloba* Del Ros.  
*T. pulcherrima* (Steph.) Schust.  
*T. trichocoleoides* (Herz.) Schust.

Sect. *Telaranea*

- T. martinii* (Hodgs.) Schust.  
*T. granulata* Engel & Merr.  
*T. bisetula* (Steph.) E. Campb.  
*T. chaetocarpa* (Pears.) Grolle  
*T. trisetosa* (Steph.) Grolle  
*T. nivicola* Schust.  
*T. pseudozoopsis* (Herz.) Fulf.  
*T. pellucida* Engel & Merr.  
*T. longifolia* (Howe) Engel & Merr.  
*T. europaea* Engel & Merr.  
*T. apialhyna* (Steph.) Fulf.  
*T. chaetophylla* (Spruce) Schiffn.  
*T. nematodes* (Gott. ex Aust.) Howe  
*T. setosa* Engel & Merr.  
*T. bicruris* (Steph.) Howe  
*T. breviseta* (Herz.) Engel & Merr.  
*T. redacta* (Steph.) Engel & Merr.  
*T. fragilis* Miz.  
*T. tasmanica* (Steph.) Engel & Merr.  
*T. quinquespina* Engel & Merr.  
*T. panchoi* Del Ros.  
*T. rosarioana* H. A. Mill.

Sect. *Tenuifoliae* (Schust.) Engel & Merr.

- T. sejuncta* (Ångstr.) S. Arnell  
*T. coactilis* (Spruce) Engel & Merr.  
*T. microstipulata* Schust.  
*T. tenuifolia* (Schust.) Engel & Merr.  
*T. herzogii* (Hodgs.) Hodgs.  
*T. inaequalis* Schust. ex Engel & Merr.  
*T. diacantha* (Mont.) Engel & Merr.  
*T. major* (Herz.) Engel & Merr.  
*T. anomala* Schust. ex Engel & Merr.  
*T. monocera* Mitt. ex Engel & Merr.  
*T. pecten* (Spruce) Engel & Merr.  
*T. confervoides* (Schust.) Engel & Merr.

TABLE 4. Geographical distribution of major taxa of *Telaranea* and numbers of species in each region.

	Austral- asia	Paleo- tropics	Tem- perate South America	Neo- tropics	Africa	Japan	Europe	Eastern North America	Total Species
<i>Tenuifoliae</i>	2	2	—	8	1	—	—	—	13
<i>Telaranea</i>	5	6	4	4	2	—	1	1	23
<i>Tricholepidozia</i>	2	4	1	—	—	—	—	—	7
<i>Transversae</i>	7	6	4	—	—	—	1	—	18
<i>Ceraceae</i>	4	—	—	—	—	—	—	—	4
<i>Cancellatae</i>	8	10	4	1	1	1	—	—	25
<i>Neolepidozia</i>	7	—	—	—	—	—	—	—	7
<i>Acrolepidozia</i>	2	1	—	—	—	—	—	—	3

included in the area cladogram, whereas all of the Australasian species are included. However, the poor representation of the basal groups in the paleotropics (subg. *Acrolepidozia*, 1 species) is immediately apparent. Section *Neolepidozia* is exclusively Australasian. These two groups are absent from temperate South America and the neotropics, and elsewhere. The most derived groups have a decidedly different distribution. The largest number of species of sect. *Tenuifoliae* occurs in the neotropics (8). Section *Telaranea* is the only section represented in all areas.

### *Telaranea* Excludenda

- 1) *Telaranea dispar* (Mont. ex Tayl. & Hook. f.) Hodgs.

*Jungermannia dispar* Mont. ex Tayl. & Hook. f. in Hooker, Bot. Antarc. Voy. 1: 158. (ante May) 1845. *Jungermannia dispar* Mont. ex Hook. f. & Tayl., London J. Bot. 3: 388. 1844, nom. nud. *Lepidozia dispar* (Mont. ex Tayl. & Hook. f.) Mont. in Dumont d'Urville, Voy. Pôle Sud, Bot. 1: 248 (Aug.) 1845; Ann. Sci. Nat., Bot. III, 4: 353. (Dec.) 1845. *Mastigophora dispar* (Mont. ex Tayl. & Hook. f.) Trev., Cat. Herb. Crypt. 2: 30. 1853. *Telaranea dispar* (Mont. ex Tayl. & Hook. f.) Hodgs., Rec. Domin. Mus. 4: 107. 1962. Lectotype (*vide* Engel & Merrill, 1996b): Auckland Is., *Hombroon*, ex herb. Montagne (FH!).

The name *Telaranea dispar* is reported for Auckland and Campbell Islands by Hodgson (1962), and for Victoria, Australia by Scott and Bradshaw (1986, see p. 147, *T. disparata*). Engel and Merrill (1996b) placed the species as a new synonym of *Kurzia hippuroides* (Hook. f. & Tayl.) Grolle, var. *hippuroides*.

- 2) *Telaranea fusifera* (Spruce) Schiffn.

*Lepidozia fusifera* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 364. 1885. *Telaranea fusifera* (Spruce) Schiffn. in Schiffner & Arnell, Oesterr. Akad. Wiss., Math.-Naturwiss. Kl., Denkschr. 111: 78. 1964. Original material: Peru, Mat. Campana & Guayrapurina, 1000 m, *Spruce*.

Stephani's illustration of *L. fusifera* (Icones, *Lepidozia* 59), based on original material, illustrates a plant with strongly asymmetric leaves with reversed symmetry (see p. 209), the ventral lobe 4 cells wide at the base, and the dorsal lobe uniseriate for all or most of its length. This species is placed in the synonymy of *Kurzia verrucosa* (Steph.) Grolle (Grolle, 1964) and as a synonym of *Kurzia* ("*Microlepidozia*") *capillaris* (Sw.) Grolle by Fulford (1966). *Kurzia verrucosa*, according to Grolle (1964) occurs in southeast Brazil, Bolivia to Mexico.

- 3) *Telaranea longiscypha* (Tayl.) Schust.

*Jungermannia longiscypha* Tayl., London J. Bot. 5: 280. 1846. *Lepidozia longiscypha* (Tayl.) Carring. & Pears., Proc. Linn. Soc. New South Wales 12: 1047. 1888. *Telaranea longiscypha* (Tayl.) Schust., J. Hattori Bot. Lab. 26: 256. 1963. *Hyalolepidozia longiscypha* (Tayl.) Grolle, Rev. Bryol. Lichénol. 32: 179. 1964 (1963). *Paracromastigum longiscyphum* (Tayl.) Schust. & Engel, Brittonia 48: 167. 1996. Original material: Western Australia, Swan River, *Drummond*.

This species is a *Paracromastigum* and is endemic to New Zealand (see Schuster & Engel, 1996).

- 4) *Telaranea setacea* (Web.) K. Müll. (Freib.)

*Jungermannia setacea* Web., Spicilegium Flor. Goet-



tingensis 155. 1778. *Blepharostoma setacea* (Web.) Dum., Recueil Observ. Jung. 18. 1835. *Lepidozia setacea* (Web.) Mitt., J. Proc. Linn. Soc., Bot. 5: 103. 1861. *Microlepidozia setacea* (Web.) Joerg., Bergens Mus. Skr. 16: 303. 1934. *Telaranea setacea* (Web.) K. Müll. (Freib.), Rabenhorst, Kryptogamenfl. Deutschland ... (ed. 3) 6: 1134. 1956. *Kurzia setacea* (Web.) Grolle, Rev. Bryol. Lichenol. 32: 171. 1964 (1963). Original material: Baumannshöhle, Harz, Germany.

This Northern Hemisphere species belongs to *Kurzia* s. str. (see p. 238); for distribution see Schuster (1969, as *Microlepidozia setacea*).

#### 5) *Telaranea succulenta* (Sim) Grolle

*Lepidozia succulenta* Sim, Trans. Roy. Soc. South Africa 15: 90, fig. 138. 1926. *Arachniopsis succulenta* (Sim) S. Arnell, Bot. Not. 108: 309. 1955, *comb. inval.* (Art. 33.2). *Microlepidozia succulenta* (Sim) S. Arnell, Bot. Not. 115: 204. 1962. *Telaranea succulenta* (Sim) Grolle, Rev. Bryol. Lichen. 32: 178. 1963. *Paracromastigum succulentum* (Sim) Engel & Merr., Bryologist 104: 151. 2001. Type: South Africa, Cape, Table Mt., Slongoli, 1500 ft., *Sim* (PRE!).

Grolle (1963) and Schuster (2000, p. 211) included the species in *Telaranea*; it belongs to *Paracromastigum* and is endemic to South Africa (see Engel & Merrill, 2001).

#### 6) *Telaranea sylvatica* (Evans) K. Müll. (Freib.)

*Lepidozia sylvatica* Evans, Rhodora 6: 186, pl. 57. 1904. *Microlepidozia sylvatica* (Evans) Joerg., Bergens Mus. Skr. 16: 305. 1934 ("sylvatica"). *Telaranea sylvatica* (Evans) K. Müll. (Freib.), Rabenhorst, Kryptogamenfl. Deutschland ... (ed. 3) 6: 1136. 1956 ("sylvatica"). *Kurzia sylvatica* (Evans) Grolle, Herzogia 3: 77. 1973. Original material: Connecticut, Westville, *Evans*.

The species belongs to *Kurzia* s. str. and occurs suboceanic in eastern North America and western Europe. For details of distribution see Schuster (1969, as *Microlepidozia sylvatica*).

#### 7) *Telaranea trichoclados* (K. Müll. (Freib.)) K. Müll. (Freib.)

*Lepidozia trichoclados* K. Müll. (Freib.), Hedwigia 38: 197. 1899. *Telaranea trichoclados* (K. Müll. (Freib.)) K. Müll. (Freib.), Rabenhorst, Kryptogamenfl. Deutschland ... (ed. 3) 6: 1138. 1956. *Kurzia trichoclados* (Web.) Grolle, Rev. Bryol. Lichenol. 32: 171. 1964. Original material: Germany, "im Zastlerthale am Feldbert ...," K. Müller.

This is also a species of *Kurzia* s. str. and occurs in Europe.

#### 8) *Lepidozia vastiloba* Steph.

We have seen two specimens from Stephani's herbarium (G) labeled as *L. vastiloba*. Neither, apparently, represents the original material cited in the protologue, but one collection, from New South Wales, leg. Watts, is probably the plant illustrated in Stephani's Icones 112 ("N. S. Wales, Watts leg."). A second specimen, from Tasmania, leg. Waymouth, is the same species, and both agree with the protologue. The leaves are deeply concave, symmetrically 3-lobed to ca. 0.5 or somewhat less, the insertion varying from transverse to weakly succubous. The lobes are acute, 4 cells wide at the base, ending in a single cell. Stephani's drawing suggests a disc as much as 12 cells wide at the base. The disc and lobe cells are thin-walled, with the tips of the lobes tinged a clear reddish to brownish red. No *Microlepidozia*-type branches were observed, but *Acromastigum*-type branches are common, with *Frullania*-type branches somewhat less so. The stem cortical cells are in 11–12 rows, surrounding 18 somewhat smaller medullary cells, all thin-walled. We are treating this species as a *Paracromastigum*, rather than a *Telaranea*.

*Paracromastigum vastilobum* (Steph.) Engel & Merr., *comb. nov.*

*Lepidozia vastiloba* Steph., Sp. Hep. 3: 581. 1909. Original material: New South Wales, *Forsyth*; Tasmania, *Moore*.

SPECIMENS EXAMINED—Tasmania, W. Coast, Rindeena, Mt. Lyell Railway, *Weymouth* 899, Hb. Levier no. 3669 (G); Australia, New South Wales, Blue Mountains, Katoomba Falls, *Watts* 563, Hb. Levier no. 3391 (G).

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## Literature Cited

- ALLISON, K. W., AND J. CHILD. 1975. The liverworts of New Zealand. Univ. of Otago Press, Dunedin, pp. 1–300.
- ALLORGE, P. 1939. Le *Telaranea nematodes* dans les Pyrénées basques. Bull. Soc. Bot. France, **86**: 425–426.
- ARNELL, S. 1956. Hepaticae collected by K. Byström in Fernando Po and Annobón, West Africa, 1953. Svensk Bot. Tidskr., **50**: 527–534, f. 1–3.
- . 1958. Hepatics from Tristan da Cunha. Results Norweg. Sci. Exped. to Tristan da Cunha 1937–1938, **3**(42): 1–76, f. 1–30.
- . 1963. Hepaticae of South Africa. Norstedt & Söner, Stockholm, pp. 1–411, f. 1–290.
- AUSTIN, C. F. 1879. Notes on hepaticology. Bull. Torrey Bot. Club, **6**: 301–306.
- BASTOW, R. A. 1888. Tasmanian Hepaticae. Pap. & Proc. Roy. Soc. Tasmania, **1887**: 209–289, pl. 1–35.
- BUCK, W. R., B. GOFFINET, AND A. J. SHAW. 2000. Novel relationships in pleurocarpous mosses as revealed by cpDNA sequences. Bryologist, **103**: 774–789.
- CAMPBELL, E. O. 1971. Liverworts collected in Fiji by A. C. Smith and W. Greenwood. J. Roy. Soc. New Zealand, **1**: 7–30.
- CAPESIUS, I., AND M. BOPP. 1997. New classification of liverworts based on molecular and morphological data. Pl. Syst. Evol., **207**: 87–97.
- COLENSO, W. 1886. A description of some newly-discovered cryptogamic plants; being a further contribution towards the making known the botany of New Zealand. Trans. & Proc. New Zealand Inst., **18**: 219–255. (Hepaticae-Anthocerotae, pp. 236–255).
- COX, C. J., AND T. A. J. HEDDERSON. 1999. Phylogenetic relationships among the ciliate arthrodontous mosses: Evidence from chloroplast and nuclear DNA sequences. Pl. Syst. Evol., **215**: 119–139.
- , B. GOFFINET, A. E. NEWTON, A. J. SHAW, AND T. A. J. HEDDERSON. 2000. Phylogenetic relationships among the diplolepidous-alternate mosses (Bryidae)

- inferred from nuclear and chloroplast DNA sequences. *Bryologist*, **103**: 224–241.
- DE LANGE, P. J., P. B. HEENAN, B. D. CLARKSON, AND B. R. CLARKSON. 1999. Taxonomy, ecology and conservation of *Sporodanthus* (Restionaceae) in New Zealand. *New Zealand J. Bot.*, **37**: 413–431.
- DE LUNA, E. 1995. The circumscription and phylogenetic relationships of the Hedwigiaceae (Musci). *Syst. Bot.*, **20**(3): 347–373.
- , W. R. BUCK, H. AKIYAMA, T. ARIKAWA, H. TSUBOTA, D. GONZALEZ, A. E. NEWTON, AND A. J. SHAW. 2000. Ordinal phylogeny within the hypnobryalean pleurocarpous mosses inferred from cladistic analyses of three chloroplast DNA sequence data sets: trnL-F, rps4, and rbcL. *Bryologist*, **103**: 242–256.
- , A. E. NEWTON, A. WITHEY, D. GONZALEZ, AND B. D. MISHLER. 1999. The transition to pleurocarpy: A phlogenetic analysis of the main diplolepidous lineages based on rbcL sequences and morphology. *Bryologist*, **102**: 634–650.
- DEL ROSARIO, R. M. 1973 (1971). New and noteworthy Philippine liverworts. *Philipp. J. Sci.*, **100**: 227–242.
- . 1977 (1975). Philippine liverworts, III. Calobryales and Herbertales of the Philippines. *Philipp. J. Sci.*, **104**: 93–209.
- EGGERS, J., AND A. SCHÄFER-VERWIMP. 1987. Some liverworts new to Sri Lanka (Ceylon). *J. Bryol.*, **14**: 531–534.
- ENGEL, J. J. 1978. A taxonomic and phytogeographic study of Brunswick Peninsula (Strait of Magellan) Hepaticae and Anthocerotae. *Fieldiana, Bot.*, **41**: i–viii, 1–319.
- . 1990. Falkland Islands (Islas Malvinas) Hepaticae and Anthocerotophyta: A taxonomic and phytogeographic study. *Fieldiana, Bot. N. S.*, **25**: i–viii, 1–209.
- ENGEL, J. J., AND G. L. S. MERRILL. 1996a (1995). Austral Hepaticae 23. New taxa and new combinations in *Telaranea* Spruce ex Schffn. (Lepidoziaceae). *Phytologia*, **79**: 250–253.
- . 1996b. Studies of New Zealand Hepaticae. 14–19. *Kurzia* and *Lepicolea*. *J. Hattori Bot. Lab.*, **80**: 217–231, f. 1–3.
- . 1997. Austral Hepaticae. 22. The genus *Balantiopsis* in New Zealand, with observations on extraterritorial taxa and a phylogeny of *Balantiopsis* and the Family Balantiopsaceae (Jungermanniales). *Fieldiana, Bot.*, **37**: i–iii, 1–62, f. 1–18.
- . 1999. Austral Hepaticae 29. More new taxa and combinations in *Telaranea* (Lepidoziaceae) and a new name for *Frullania caledonica* (Schust.) Schust. (Frullaniaceae) from New Caledonia. *Novon*, **9**: 339–344, f. 1–3.
- . 2002. Proposal to conserve *Telaranea* against *Arachniopsis* (Hepaticae). *Taxon* **51**: 571–572.
- ENGEL, J. J., AND R. M. SCHUSTER. 2001. Austral Hepaticae 33. *Paracromastigum succulentum* (Sim) Engel & Merr., *comb. nov.* (Lepidoziaceae, Jungermanniales). *Bryologist*, **104**: 151–153, f. 1.
- . 1973. On some tidal zone Hepaticae from south Chile, with comments on marine dispersal. *Bull. Torrey Bot. Club*, **100**: 29–35.
- . 1983. Austral Hepaticae XVIII. Studies toward a revision of *Telaranea* subg. *Neolepidozia* (Lepidoziaceae). *Fieldiana Bot. N.S.*, **14**: i–v, 1–7, f. 1–3.
- EVANS, A. W. 1912. Branching in the leafy Hepaticae. *Ann. Bot.*, **26**: 1–37, f. 1–36.
- . 1939. The classification of the Hepaticae. *Bot. Rev. (Lancaster)*, **5**: 49–96.
- FELSENSTEIN, J. 1977. The number of evolutionary trees. *Syst. Zool.*, **27**: 27–33.
- . 1985. Confidence limits on phylogenetics: An approach using the bootstrap. *Evolution*, **39**: 783–791.
- FERNÁNDEZ ORDÓÑEZ, C., AND M. A. COLLADO PRIETO. 2000. Flora briofítica rara y amenazada en la cuenca del Río de Nueva (Llanes, Asturias). *Bol. Cien. Nat. R.I.D.E.A.*, **46**: 133–143.
- FISCHER, E. 1993. Taxonomic Results of the Bryotrop expedition to Zaïre and Rwanda. 10. Trichocoleaceae, Geocalycaceae, Acrobolbaceae, Balantiopsidaceae, Lepidoziaceae (*Telaranea*, *Arachniopsis*), Calypogeiaceae, Adelantheaceae, Porellaceae, Jubulaceae, Marchantiaceae (*Dumortiera*), Polytrichaceae. *Trop. Bryol.*, **8**: 83–98.
- FRYE, T. C., AND L. CLARK. 1937–47. Hepaticae of North America. Univ. Wash. Publ. Biol., **6**: 1–1018.
- FULFORD, M. 1963a. Segregate genera of the *Lepidozia* complex (Hepaticae). Part 4. *Telaranea* and a review of the Lepidoziaceae. *Brittonia*, **15**: 65–86.
- . 1963b. Manual of the Leafy Hepaticae of Latin America. Part I. Mem. New York Bot. Gard., **11**: 1–172, pl. 1–37 (unnumbered).
- . 1966. Manual of the Leafy Hepaticae of Latin America. Part II. Mem. New York Bot. Gard., **11**: 173–276, pl. 38–65.
- . 1968. Manual of the Leafy Hepaticae of Latin America. Part III. Mem. New York Bot. Gard., **11**: 277–392, pl. 66–107.
- . 1971. The ecology of an elfin forest in Puerto Rico. 15. A study of the leafy hepatic flora of the Luquillo Mountains. *J. Arnold Arbor.*, **52**: 435–458.
- . 1972. Hepaticae. In Steyermark, J., and B. Maguire. The flora of the Meseta del Cerro Jaua. Mem. New York Bot. Gard., **23**: 838–845, f. 1–3.
- FULFORD, M., AND J. TAYLOR. 1959. The segregate genera of the *Lepidozia* complex (Hepaticae) Part 1. *Spruella* Steph. and *Neolepidozia* gen. nov. *Brittonia*, **11**: 77–85, f. 1–41.
- GARBARY, D. J., AND K. S. RENZAGLIA. 1998. Bryophyte phylogeny and the evolution of land plants: Evidence from development and ultrastructure. pp. 45–63. In Bates, J. W., N. W. Ashton, and J. G. Duckett, eds., *Bryology for the Twenty-First Century*. Maney Publishing and British Bryological Society.
- GIBBS, L. S. 1911. The hepatics of New Zealand. *J. Bot.*, **49**: 261–266.
- GLENNY, D. 1998. A revised checklist of New Zealand liverworts and hornworts. *Tuhinga*, **10**: 119–149.
- , AND A. FIFE. 1996. Additions to the bryophyte flora of the Antipodes Islands. *Australas. Bryolog. Newslett.*, **34**: 7–9.
- GOFFINET, B. 2000. Origin and phylogenetic relationships of bryophytes, pp. 124–149. In Shaw, A. J., and

- B. Goffinet, eds., *Bryophyte Biology*. Cambridge University Press.
- GOFFINET, B., AND C. J. COX. 2000. Phylogenetic relationships among basal-most arthrodontous mosses with special emphasis on the evolutionary significance of the Funariineae. *Bryologist*, **103**: 212–223.
- GOOD, R. 1964. The geography of the flowering plants. Longmans, London, pp. i–xvi, 1–518.
- GOTTSCHKE, C. M., J. B. G. LINDENBERG, AND C. G. NEES AB ESENBECK. 1844–47. *Synopsis Hepaticarum*. Meissner, Hamburg, pp. 1–834. (Fasc. I, pp. 1–144, 1844; Fasc. II–III, pp. 145–464, 1845; Fasc. IV, pp. 465–624, 1846; Fasc. V, pp. 625–834, 1847).
- GRADSTEIN, S. R., S. P. CHURCHILL, AND N. SALAZAR-ALLEN. 2001. Guide to the bryophytes of tropical America. *Mem. New York Bot. Gard.*, **86**: i–viii, 1–577, f. 1–219.
- GRADSTEIN, S. R., AND J. FLORSCHÜTZ-DE WAARD. 1989. Results of a botanical expedition to Mount Roraima, Guyana. I. Bryophytes. *Trop. Bryol.*, **1**: 25–54, f. 1–6.
- GRADSTEIN, S. R., A. LÜCKING, M. I. MORALES, AND G. DAUPHIN. 1994. Additions to the hepatic flora of Costa Rica. *Lindbergia*, **19**: 73–86.
- GRADSTEIN, S. R., T. PÓCS, AND J. VÁNA. 1983. Disjunct Hepaticae in tropical America and Africa. *Acta Bot. Hung.*, **29**: 127–171.
- GROLLE, R. 1964 (1963). Über *Kurzia* v. Martens. *Rev. Bryol. Lichénol.*, **32**: 166–180, pl. 1–2.
- . 1966. Lebermoose aus Neuguinea. 5. *Telaranea*. *J. Hattori Bot. Lab.*, **29**: 279–289, pl. 1–4.
- . 1967. Lebermoose aus Neuguinea. 6. Dritte Fundliste. *J. Hattori Bot. Lab.*, **30**: 113–118, pl. 1–2.
- . 1968. Lebermoose aus Neuguinea. 7. Vierte Fundliste. *J. Hattori Bot. Lab.*, **31**: 1–12, f. 1–3.
- . 1969. Grossdisjunktionen in artarealen Latein-amerikanischer Lebermoose, pp. 562–582, f. 1–11. In Fittkau, E. J., J. Illies, H. Klinge, G. H. Schwabe, and H. Sioli, eds., *Biogeography and Ecology in South America*. W. Junk, The Hague.
- . 1975. Miscellaneous hepaticologica 141–150. *J. Bryol.*, **8**: 483–492, f. 1.
- . 1978. Die Lebermoose der Seychellen. *Wiss. Z. Friedrich-Schiller-Univ. Jena, Math.-Naturwiss. Reihe*, **27**: 7–17.
- . 1983. Nomina generica Hepaticarum; references, types and synonymies. *Acta Bot. Fenn.*, **121**: 1–62.
- . 1995. The Hepaticae and Anthocerotae of the East African Islands. An annotated catalogue. *Bryophytorum Bibliotheca*, **48**: 1–178.
- . 2002. The Hepaticae and Anthocerotae of the subantarctic and temperate islands in the eastern Southern Hemisphere (90° E to 0°): An annotated catalogue. *J. Bryol.*, **24**: 57–80, f. 1.
- , AND D. G. LONG. 2000. An annotated check-list of the Hepaticae and Anthocerotae of Europe and Macaronesia. *J. Bryol.*, **22**: 103–140.
- , AND M. ONRAEDT. 1974. Lebermoose aus Madagaskar und den Maskarenen. *Lindbergia*, **2**: 230–233.
- , AND S. PIIPPO. 1984. Annotated catalogue of Western Melanesian bryophytes. I. Hepaticae and Anthocerotae. *Acta Bot. Fenn.*, **125**: 1–86, f. 1–2.
- HAMLIN, B. G. 1972. Hepaticae of New Zealand, Parts I and II. Index of binomials and preliminary checklist. *Rec. Domin. Mus.*, **7**: 243–366.
- HÄSSEL DE MENÉNDEZ, G. G. 1984. The bulbils of the Lepidoziaceae. *J. Hattori Bot. Lab.*, **56**: 105–114.
- HATTORI, S. 1951. On a small collection of Hepaticae from Dutch New Guinea. *Bot. Mag. (Tokyo)*, **64**: 112–119.
- HATTORI, S., AND M. MIZUTANI. 1958. A revision of the Japanese species of the family Lepidoziaceae. *J. Hattori Bot. Lab.*, **19**: 76–118, f. 1–X.
- HEDDERSON, T. A., R. L. CHAPMAN, AND C. J. COX. 1998. Bryophytes and the origins and diversification of land plants: New evidence from molecules, pp. 65–77. In Bates, J. W., N. W. Ashton, and J. G. Duckett, eds., *Bryology for the Twenty-First Century*. Maney Publishing and British Bryological Society.
- HEDENÄS, L. 1997 (1996). A cladistic overview of the "Hookeriales." *Lindbergia*, **21**: 107–143.
- . 1998 (1997). An evaluation of phylogenetic relationships among the Thuidiaceae, the Amblystegiaceae, and the temperate members of the Hypnaceae. *Lindbergia*, **22**: 101–133.
- , AND W. R. BUCK. 1999. A phylogenetic analysis of the Sematophyllaceae. *Lindbergia*, **24**: 103–132.
- . 1926. *Geographie der Moose*. Gustav Fischer, Jena, pp. x–xi, 1–439, f. 1–151, pl. 1–8.
- . 1937. Neue Hepaticae aus Südamerika. *Broteria*, **6**: 17–23, f. 1–4.
- . 1938. Descriptions of new species of New Zealand hepatics, II. *Trans. Roy. Soc. New Zealand*, **68**: 40–46, pl. 3–7.
- . 1942. Die foliosen Lebermoose der Juan Fernandez-Inseln und der Osterinsel, pp. 697–752, f. 1–14. In Skottsberg, C., *Nat. Hist. Juan Fernandez, Easter Island 2* (5).
- . 1950. Hepaticae Borneenses. (Oxford University Expedition to Sarawak, 1932). *Trans. Brit. Bryol. Soc.*, **1**: 275–326, f. 1–38.
- . 1952. Miscellaneous Bryologica. III. Memoranda Soc. Fauna Fl. Fenn., **27** (1950–1951): 92–110, f. 39–50.
- . 1954. Zur Bryophytenflora Chiles. *Rev. Bryol. Lichénol.*, **23**: 27–99, f. 1–24. (Hepaticae, pp. 28–66).
- HODGSON, E. A. 1956. New Zealand Hepaticae (Liverworts)—IX. A review of the New Zealand species of the genus *Lepidozia*. *Trans. Roy. Soc. New Zealand*, **83**: 589–620, f. 1–2.
- . 1962. Hepatics from the subantarctic islands of New Zealand including "Cape Expedition" collections from the Auckland and Campbell Islands. *Rec. Domin. Mus.*, **4**: 101–132.
- . 1964. Revised generic keys to the hepatic flora of New Zealand. With introduction and relevant notes. *Tuatara*, **12**: 1–13. (Part 2)
- . 1965. New Zealand Hepaticae (Liverworts)—XVI. A miscellany of new genera, new species and notes, part I. *Trans. Roy. Soc. New Zealand, Bot.*, **3**: 67–97, f. 1–2.
- HOOKE, J. D. 1867. Hepaticae, pp. 497–549, 750–755.

- In Handbook of the New Zealand Flora. Reeve & Co., London.
- HOOKER, J. D., AND T. TAYLOR. 1844. Hepaticae antarcticae; being characters and brief descriptions of the Hepaticae discovered in the southern circumpolar regions during the Voyage of H. M. Discovery Ships *Erebus* and *Terror*. London J. Bot., **3**: 366–400, 454–481, 556–582.
- HOWE, M. A. 1902. Notes on American Hepaticae. Bull. Torrey Bot. Club, **29**: 281–289.
- HÜRLIMANN, H. 1985. Hepaticae aus dem Gebiete des südlichen Pazifik. VIII. Bauhinia, **8**: 101–118.
- HYVÖNEN, J., T. A. HEDDERSON, G. L. SMITH MERRILL, J. G. GIBBINGS, AND S. KOSKINEN. 1998. On phylogeny of the Polytrichales. Bryologist, **101**: 489–504.
- INFANTE, M. 2000. Las hepáticas y antocerotas (Marchantiophyta y Anthocerotophyta) en la Comunidad Autónoma del País Vasco. Guineana, **6**: 1–345.
- INOUE, H. 1979. Studies on the oil-bodies of some Papua New Guinean hepatics. Pp. 19–32, pl. 1–6. In Kurokawa, S., ed., Studies on Cryptogams of Papua New Guinea. Academia Scientifica Book Inc., Tokyo.
- JOVET-AST, S. 1947. A propos du *Lepidozia Aubertii* Jovet-Ast (= *L. Wallichii* Steph. ms.). Candollea, **11**: 31–35, f. 1–4.
- . 1949. Hépatiques australiennes.—Notes diverses. Rev. Bryol. Lichénol., **18**: 179–180.
- . 1951. Hépatiques des Nouvelles-Hébrides. Récoltes de E. Aubert de la Rüe, 1934. Rev. Bryol. Lichénol., **20**: 96–98.
- KITAGAWA, N. 1973. Miscellaneous notes on little-known species of Hepaticae, 26–50. J. Hattori Bot. Lab., **37**: 263–273.
- KORNERUP, A., AND J. H. WANSCHER. 1981. Methuen Handbook of Colour. 3rd Ed. (Pavey, D., ed.) Eyre Methuen Ltd., London, pp. 1–252.
- KÜHNEMANN, O. 1937. Contribución al catálogo briológico argentino. I. Revista Centro Estud. Doct. Ci. Nat., Buenos Aires, **1**: 85–97, 155–181.
- . 1949. Catalogo de las hepáticas Argentinas. Lilloa, **19**: 319–375.
- LA FARGE, C., B. D. MISHLER, J. A. WHEELER, D. P. WALL, K. JOHANNES, S. SCHAFER, AND A. J. SHAW. 2000. Phylogenetic relationships within the haplolepidous mosses. Bryologist, **103**: 257–276.
- LEHMANN, J. G. C. 1844–47. Plantae Preissianae, sive enumeratio plantarum quas in Australasia occidentali et meridionale-occidentali annis 1830–1841 collegit Ludovicus Preiss, ... Vol. 2. Meissner, Hamburg. (Hepaticae pp. 120–129, 1846).
- LEWINSKY-HAAPASAARI, J., AND L. HEDENÄS. 1998. A cladistic analysis of the moss genus *Orthotrichum*. Bryologist, **101**: 519–555.
- LEWIS, L. A., B. D. MISHLER, AND R. VILGALYS. 1997. Phylogenetic relationships of the liverworts (Hepaticae), a basal embryophyte lineage, inferred from nucleotide sequence data of the chloroplast gene *rbcl*. Molecular Phylogenetics and Evolution, **7**: 377–393.
- LINCOLN, M. S. G., AND S. LAGRECA. 2002. A new, northern location for the liverwort *Telaranea nematodes* (Gottsche ex Austin) M. A. Howe. Evansia, **19**: 69–70, f. 1.
- LINDENBERG, J. B. G., AND C. M. GOTTSCHKE. 1846. Species Hepaticarum. Fasc., VI–VII: 1–78. Bonn. (*Lepidozia*).
- LONG, D. G., M. MOLLER, AND J. PRESTON. 2000. Phylogenetic relationships of *Asterella* (Aytoniaceae, Marchantiopsida) inferred from chloroplast DNA sequences. Bryologist, **103**: 625–644.
- MADDISON, W. P., M. J. DONOGHUE, AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. Syst. Zool., **33**: 83–103.
- MADDISON, W. P., AND D. R. MADDISON. 1992. MacClade: Analysis of phylogeny and character evolution. Version 3.0. Sinauer Associates, Sunderland, Mass.
- MILLER, H. A. 1985. Pacific bryophytes: 2. *Arachniopsis* in southern Melanesia. Phytologia, **57**: 91–94, f. 1.
- . 1986. Pacific bryophytes: 3. An overview of *Telaranea*, Hepatophyta. J. Bryol., **14**: 231–244, f. 1–4.
- MILLER, H. A., H. O. WHITTIER, AND B. A. WHITTIER. 1983. Prodrum Flora Hepaticarum Polynesiae. With a key to genera. Bryophyt. Biblioth., **25**: 1–423.
- MITTEN, W. 1859. Nat. Ord. VI. Hepaticae, pp. 221–241. In Hooker, J. D., The Botany of the Antarctic Voyage of H. M. Discovery Ships *Erebus* and *Terror* in the Years 1839–1843. III. Flora Tasmaniae, vol. II, Monocotyledones and acotyledones. Reeve Brothers, London.
- MIZUTANI, M. 1974. Lepidoziaceae, subfamily Lepidoziodeae from Sabah (North Borneo). J. Hattori Bot. Lab., **38**: 371–385, f. 1–8.
- . 1976. Lepidoziaceae, subfamily Lepidoziodeae from the Philippines. J. Hattori Bot. Lab., **40**: 447–451, f. 1.
- MONTAGNE, C. 1845. Plantes cellulaires, pp. 210–280. In Hombron, J., and Ch. Jacquinot, Botanique. Voyage au pôle sud et dans l'Océanie, sur les corvettes l'*Astrolabe* et la *Zélée*. Vol. 1.
- . 1856. Septième centurie de plantes cellulaires nouvelles, tant indigènes qu'exotiques. Ann. Sci. Nat. Bot. IV., **5**: 333–374. (Hepaticae, pp. 348–352).
- MÜLLER, K. 1905–1916. Die Lebermoose Deutschlands, Oesterreichs u. d. Schweiz. In Rabenhorst's Kryptogamen-Flora, 2 Aufl., **6**(1): 1–870, f. 1–363; **6**(2): 1–947, f. 1–207. Leipzig.
- . 1951–58. Die Lebermoose Europas. In Rabenhorst's Kryptogamen-Flora, ed. 3, **6**, pp. 1–1365, f. 1–514.
- NELSON, G. J. 1972. Phylogenetic relationship and classification. Syst. Zool., **21**: 227–231.
- NEWTON, A. E., C. J. COX, J. G. DUCKETT, J. A. WHEELER, B. GOFFINET, T. A. J. HEDDERSON, AND B. D. MISHLER. 2000. Evolution of the major moss lineages: Phylogenetic analyses based on multiple gene sequences and morphology. Bryologist, **103**: 187–211.
- PAGÁN, F. M. 1942. Catalogue of the Hepaticae of Guadeloupe. Bryologist, **45**: 76–110.
- PAGE, R. D. M. 1996. TreeView: An application to display phylogenetic trees on personal computers. Computer Applic. Biosci., **12**: 357–358.
- . 2000. TreeView. Tree drawing software for Macintosh and Windows, vers. 1.6.1. University of Glasgow, Scotland.
- PATON, J. A. 1965. *Lophocolea semiteres* (Lehm.) Mitt.

- ana *Telaranea murphyae* sp. nov. established on Tresco. Trans. Brit. Bryol. Soc., **4**: 775–779, f. 1.
- . 1976. Distribution maps of bryophytes in Britain and Ireland: *Riccia nigrella* DC., *R. canaliculata* Hoff., *Telaranea sejuncta* (Ångstr.) S. Arnell, *T. murphyae* Pat., *Solenostoma oblongifolium* (K. Müll.) K. Müll. J. Bryol., **9**: 107–110.
- . 1992. *Telaranea longii* sp. nov. in Britain, and a comparison with *T. murphyae* Paton. J. Bryol., **17**: 289–295, f. 1–2.
- . 2000. The liverwort flora of the British Isles. Harley Books, Colchester, pp. 1–626, f. 1–314.
- PEARSON, W. H. 1886. Hepaticae Natalenses. A clarissima domina Helena Bertelsen missae. Chr. Videns. Selsk. Forh., **1886**(3): 1–19, pl. 1–12.
- . 1922. Hepaticae. In A systematic account of the plants collected in New Caledonia and the Isle of Pines by Mr. R. H. Compton, M. A., in 1914. Part III. Cryptogams (Hepaticae—Fungi). J. Linn. Soc., Bot., **46**: 13–44, pl. 1–3.
- PIIPPO, S. 1984. Bryophyte flora of the Huon Peninsula, Papua New Guinea. VI. Lepidoziaceae subfam. Lepidozioidae, Calypogeiaceae, Adelantheaceae, Cephaloziaceae subfam. Cephalozioidae and subfam. Odontoschismatoideae and Jubulaceae. Ann. Bot. Fenn., **21**: 309–335, f. 1–12.
- . 1985. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XIII. *Arachniopsis* and *Kurzia* (Lepidoziaceae subfam. Lepidozioidae, Hepaticae). Acta Bot. Fenn., **131**: 169–179, f. 1–6.
- . 1986. Bryophytes from Frieda River, East and West Sepik Provinces, Papua New Guinea. II. Hepaticae, (Haplomitriaceae—Frullaniaceae). Ann. Bot. Fenn., **23**: 1–10, f. 1–4.
- PÓCS, T. 1984. Synopsis of the African Lepidozioidae K. Müll., pp. 107–119, f. 1–3. In J. Vána, ed., Proceedings of the Third Meeting of the Bryologists from Central and East Europe. Univerzita Karlova, Praha.
- . 1995. East African bryophytes, XIV. Hepaticae from the Indian Ocean islands. Fragm. Flor. Geobot., **40**: 251–277, f. 1–4.
- PÓCS, T., AND K. A. LYE. 1999. New records and additions to the hepatic flora of Uganda. 2. Trop. Bryol., **17**: 23–33.
- PORLEY, R. D., B. J. O'SHEA, M. J. WIGGINTON, H. W. MATCHAM, N. G. HODGETTS, AND C. R. STEVENSON. Bryophytes of Uganda. 2. New and interesting records. Trop. Bryol., **16**: 179–193.
- RATKOWSKY, D. A. 1987. Check-list of the Tasmanian liverworts. Pap. & Proc. Roy. Soc. Tasmania, **121**: 153–158.
- RODWAY, L. 1916. Tasmanian Bryophyta. Vol. II. Hepatics, pp. i–vii, 1–95 (issued separately on 30 August 1916); appeared as “Tasmanian Bryophyta” in Pap. & Proc. Roy. Soc. Tasmania, **1916**: 51–143 (19 February 1917) but without preface, glossary, and appendix of the separate.
- RONQUIST, H. 1994. Ancestral areas and parsimony. Syst. Biol., **43**: 267–274.
- SCHÄFER-VERWIMP, A. 1999. Some additions to the bryophyte flora of Dominica, West Indies. Haussknechtia Beih., **9**: 317–331.
- SCHIFFNER, V. 1893. Hepaticae (Lebermoose), pp. 3–141, f. 1–73. In Engler, A., and K. Prantl, eds., Die natürlichen Pflanzenfamilien, Teil I (Abt. 3, 1 Hälfte): 1 (3). Leipzig. [Preprint, Sept. 1893].
- . 1900. Hepaticae Massartianae Javanicae. Systematisches Verzeichniss der von Jean Massart im Winter 1894/95 auf Java gessammelten Lebermoose. Hedwigia, **39**: 191–208.
- SCHIFFNER, V., AND S. ARNELL. 1964. Hepaticae (Lebermoose), pp. 1–156, f. 1–158. In Ergebnisse der Botanischen Expedition der Kaiserlichen Akademie der Wissenschaften nach Südbrasilien 1901. II. Band (Thallophyta und Bryophyta) . . . Österr. Akad. Wiss., Math.-Naturwiss. Kl., Denkschr. 111.
- . 1963. Studies on antipodal Hepaticae. I. Annotated keys to the genera of antipodal Hepaticae with special reference to New Zealand and Tasmania. J. Hattori Bot. Lab., **26**: 185–309.
- . 1965. Studies on Hepaticae XXVI. The *Bonneria-Paracromastigum-Pseudocephalozia-Hyalolepidozia-Zoopsis-Pteropsiella* complex and its allies: A phylogenetic study (Part I). Nova Hedwigia, **10**: 19–61.
- . 1966. The Hepaticae and Anthocerotae of North America east of the hundredth meridian. Vol. 1. Columbia University Press, New York, pp. i–xvii, 1–802, f. 1–84.
- . 1968. Studies on Hepaticae, XXIX–XLIV. A miscellany of new taxa and new range extensions. Nova Hedwigia, **15**: 437–529, pl. 49–67.
- . 1969. The Hepaticae and Anthocerotae of North America east of the hundredth meridian. Vol. 2. Columbia University Press, New York, pp. i–xii, 1–1062, f. 85–301.
- . 1973 (1972). Phylogenetic and taxonomic studies on Jungermanniidae. J. Hattori Bot. Lab., **36**: 321–405, f. 1–11.
- . 1978. Studies on Venezuelan Hepaticae, I. Phytologia, **39**: 239–251.
- . 1979. The phylogeny of the Hepaticae, pp. 41–82. In Clarke, G. C., and J. G. Duckett, eds., Bryophyte Systematics. Systematics Assoc. Special Volume no. 14. Academic Press, London and New York.
- . 1980. Studies on Hepaticae, LIV–LVIII. *Kurzia* v. Mart. [*Microlepidozia* (Spr.) Joerg.], *Megalembidium* Schust., *Psiloclada* Mitt., *Drucella* Hodgs. and *Isolembidium* Schust. J. Hattori Bot. Lab., **48**: 337–421, f. 1–19.
- . 1982. Exogenous branching and its phylogenetic significance in Calobryales and Jungermanniales. J. Hattori Bot. Lab., **51**: 1–50, f. 1–6.
- . 1984. Comparative anatomy and morphology of the Hepaticae, pp. 760–891, f. 1–35. In Schuster, R. M., ed., New Manual of Bryology, Vol. 2. Hattori Botanical Laboratory, Nichinan.
- . 1988. Ecology, reproductive biology and dispersal of Hepaticae in the tropics. J. Hattori Bot. Lab., **64**: 237–269, f. 1–4.
- . 1999. Studies on Hepaticae, LXVII–LXVIII. Lepidoziaceae subfamily Zoopsidoideae (4): *Monodactylopsis* and *Pteropsiella*. Nova Hedwigia, **69**: 517–540, f. 31–36.

- . 2000. Austral Hepaticae. Part I. Beih. Nova Hedwigia, **118**: 1–524, f. 1–211.
- SCHIFFNER, V., AND H. L. BLOMQUIST. 1955. A comparative study of *Telaranea nematodes*. Amer. J. Bot., **42**: 588–593, f. 1–23.
- SCHIFFNER, V., AND J. J. ENGEL. 1985. Austral Hepaticae V(2). Temperate and subantarctic Schistochilaceae of Australasia. J. Hattori Bot. Lab., **58**: 255–539, f. 1–76.
- . 1996. Austral Hepaticae. XXI. *Paracromastigum fiordlandiae*, sp. nov. and the delimitation of *Paracromastigum* and *Hyalolepidozia* (Lepidoziaceae). Brittonia, **48**: 165–173, f. 1.
- SCHWAEGRICHEN, C. F. 1814. Historiae muscorum hepaticarum prodromus. Commentatio qua hortum botanicum lipsiensem feliciter instrauratum, renuntiat D. Fridericus Schwaegrichen, . . . Sumtu Joannis Ambrosii Barth, Leipzig, pp. 1–39, pl. 1.
- SCOTT, G. A. M. 1985. Southern Australian Liverworts. Australian Flora and Fauna Series Number 2. Australian Government Publishing Service, Canberra, pp. i–ix, 1–216, f. 1–134.
- SCOTT, G. A. M., AND J. A. BRADSHAW. 1986. Australian liverworts (Hepaticae): Annotated list of binomials and check-list of published species with bibliography. Brunonia, **8**: 1–171.
- SHAW, A. J. 2000. Phylogeny of the Sphagnopsida based on chloroplast and nuclear DNA sequences. Bryologist, **103**: 277–306.
- SIM, T. R. 1926. The Bryophyta of South Africa. Comprising Sphaerocarpaceae, Marchantiales, Jungermanniales, Anthocerotales, Sphagnales, Andreaeales, Polytichales, Bryales. Trans. Roy. Soc. South Africa, **15**: 1–475.
- SOLARI, S. S. 1987. *Lepidozia disticha* vs. *L. fernandezensis* (Hepaticae). Bol. Soc. Argent. Bot., **25**: 143–147, f. 1.
- SPRUCES, R. 1876. On *Anomoclada*, a new genus of Hepaticae, and on its allied genera, *Odontoschisma* and *Adelanthus*. J. Bot., **14**: 129–136, 161–170, 193–203, 230–235, pl. 178, 179.
- . 1882. On *Cephalozia* (a genus of Hepaticae). Its subgenera and some allied genera. Pp. I–IV, 1–99. Walton.
- . 1884–85. Hepaticae Amazonicae et Andinae. Trans. & Proc. Bot. Soc. Edinburgh, **15**: 1–308, pl. 1–4, 1884 (part I); i–xi, 309–589, pl. 5–22, 1885 (part II).
- STEARNS, W. T. 1966. Botanical Latin. Hafner Publishing Co., New York, pp. i–xiv, 1–564.
- STEPHANI, F. 1885. Hepaticarum species novae vel minus cognitae. II. Hedwigia, **24**: 166–168, f. 3, 4.
- . 1889. Hepaticae Australiae. Hedwigia, **28**: 128–135, 155–175, 257–278. 3, 4.
- . 1892. A revision of Colenso's New Zealand Hepaticae, with descriptions of new species collected by him. J. Linn. Soc., Bot., **29**: 263–280, pl. 26–28.
- . 1898–1924. Species Hepaticarum. 6 vols. Geneva.
- . 1911a. Hepaticae. In Mildbraed, J. Wissenschaftliche Ergebnisse der deutschen Zentral-Afrika Expedition, 1907–1908, II (Botany): 111–134, f. 1–46. (Jan.–Mar., 1911)
- . 1911b. II. Die Lebermoose, pp. 1–92, f. 1–35. In Skottsberg, C., ed., Botanische Ergebnisse der Schwedischen Expedition nach Patagonien und dem Feuerland 1907–1909. Kongl. Svenska Vetenskapsakad. Handl. 46 (9). (after 13 Sept. 1911)
- STEPHANI, F., AND W. WATTS. 1914. Hepaticae Australes. J. & Proc. Roy. Soc. New South Wales, **48**: 94–135.
- SWOFFORD, D. L. 1998. PAUP. Phylogenetic Analysis Using Parsimony (and Other Methods). Version 4. Sinauer Associates, Sunderland, Mass.
- TAYLOR, J. 1961. Some morphological characteristics of the female gametophyte of *Lepidozia apiahyna*. Bryologist, **64**: 351–355, f. 1–7.
- . 1962. Intercalary branching in the Lepidoziaceae. J. Hattori Bot. Lab., **25**: 102–106, f. 1–4.
- THIERS, B. M. 1993. A monograph of *Pleurozia* (Hepaticae, Pleuroziaceae). Bryologist, **96**: 517–554.
- VÁNA, J., T. PÓCS, AND J. L. DE SLOOVER. 1979. Hépatiques d'Afrique tropicale. Lejeunea N. S., **98**: 1–23.
- VANDEN BERGHE, C. 1972. Hepaticae and Anthocerotae, pp. 1–202, f. 1–86. In Symoens, J., ed., Hydrobiological survey of the Lake Bangweulu Luapula River Basin 8(1).
- . 1973. Quelques Hépatiques récoltées au Gabon par G. Le Testu. Rev. Bryol. Lichénol., **39**: 365–385, f. 1–6.
- VERDOORN, F. 1932. Classification of hepatics, pp. 413–432. In Verdoorn, F., ed., Manual of Bryology. The Hague.
- VIANNA, E. C. 1974. Ramificações masculinas, femininas e esporogonio de *Telaranea sejuncta* var. *brevisetia* (Herzog) Fulford. (Hepaticopsida). Iheringia, **19**: 3–10, f. 1–5.
- VITAL, D., MOREIRA, AND S. R. VISNADI. 1994. New records and notes on Brazilian Hepaticopsida. Bryologist, **97**: 71–72, f. 1–2.
- WARDLE, P. 1991. Vegetation of New Zealand. Cambridge University Press, Cambridge, pp. i–xx, 1–672.
- WATROUS, L. E., AND Q. D. WHEELER. 1981. The out-group comparison method of character analysis. Syst. Zool., **30**: 1–11.
- WATTS, W. W. 1902 (1901). Notes on some Richmond River hepatics. Proc. Linn. Soc. New South Wales, **26**: 215–216.
- WEYMOUTH, W. A. 1903. Some additions to the bryological flora of Tasmania. Pap. & Proc. Roy. Soc. Tasmania, **1902**: 115–132. (Hepaticae, pp. 121–132).
- WHEELER, J. A. 2000. Molecular phylogenetic reconstructions of the marchantioid liverwort radiation. Bryologist, **103**: 314–333.
- WIGGINTON, M. J., AND R. GROLLE. 1996. Catalogue of the Hepaticae and Anthocerotae Sub-Saharan Africa. Bryophyt. Biblioth., **50**: 1–267.
- WILEY, E. O., D. SIEGEL-CAUSEY, D. R. BROOKS, AND V. A. FUNK. 1991. The complete cladist. A primer of phylogenetic procedures. Univ. Kansas Mus. Nat. Hist. Spec. Pub. 19. 1–158. Lawrence, Kansas.
- YAMAGUCHI, T. 1983. *Telaranea iriomotensis* Yamaguchi et Mizutani (Hepaticae), a new species from Japan. Misc. Bryol. Lichen., **9**: 161–163, f. 1.



## Index to Taxa

Recognized taxa are in roman type; illegitimate or synonymous taxa are in *italics*. New taxa, new combinations and new names are in **boldface**.

- Acrolepidozia* Schust. 5, 11, 112  
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