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A memoir of the family Blepharostomataceae, II [1]

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TEMNOMA

Temnoma Mitt. in Hooker, Handb. N.Z. Fl. 2 : 753. 1867.

Plants small to rather robust (0.8-3.2 mm wide), suberect and ± caespitose to loosely prostrate, sparingly and irregularly branched, the branches variable in origin: at least predominantly of the Frullania-type, occasionally (or frequently) postical-intercalary, from axils of underleaves; very rarely in part lateral-terminal (of the Microlepidozia-type) or postical-terminal, replacing half of an underleaf (of the Acromastigum-type). *Stems* rather slender and delicate, not paraphyllose, of nearly uniform cells: the cortical in ca. (12)18-64 rows, narrowly and regularly rectangulate, (2-3)4-8 × as long as broad, rather translucent, the walls hardly thickened; medullary cells similar to cortical (or ± larger in diam.), thus without a sharply defined cortex. *Leaves* slightly or moderately to strongly succubously inserted, rarely transverse, at an angle of (5-10)15-65° with axis, equally (rarely ± asymmetrically) quadrifid, the lobes (2)4-10 cells wide at base or more, with margins and sinus not or distinctly reflexed, the margins ± toothed to prominently ciliate (at least on mature plants); cilia of ± elongate cells in uniseriate rows. *Underleaves* quadrifid like lateral leaves, similarly toothed or ciliate, hardly to much smaller than lateral leaves, inserted by a slightly to distinctly arched line. *Rhizoids* not abundant, but often at base of nearly every underleaf, confined to underleaf bases. *Cells* non-collenchymatous, trigones (if any) small and ill-defined, slightly to distinctly and equally thick-walled, the median and basal cells tending to be elongated and regularly rectangulate (1.5-3 × as long as wide); oil-bodies present, colorless, granulate, (3)4-10(12) per cell; cuticle usually distinctly to sometimes strongly verrucose to verrucose-striolate (rarely smooth). *Asexual reproduction* lacking. Dioecious [2]. *Androecia*

[1] Publication of this memoir was aided by a subsidy from Graduate School, University of Massachusetts. A summary, together with a bibliographical index, will follow in the third and final instalment of this paper.

[2] The statement that *T. quadripartitum* is monoecious (Hodgson & Allison 1962) is based on erroneous observations.

initially terminal on leading axes or ± elongate, postical branches; bracts nearly leaflike, quadrifid like the leaves (usually less deeply so), shallowly to deeply ventricose at base, the entire discus ± concave; 1-2-androus. *Antheridia* short-ovoid, the body with cells numerous, irregularly oriented and irregular in shape; antheridial stalk biseriate, rather long (to 10 cells long); no paraphyses. *Bracteoles* like small underleaves, flat, without antheridia. *Gynoecia* terminal on leading axes, without subfloral innovations (if fertilized; if not, often with one innovation). *Bracts* similar to leaves, usually somewhat larger, usually narrower, ± obtrapezoidal, the lobes always sharply toothed or ciliate with opposed teeth. *Bracteole* similar to bracts, free. *Perianth* large, becoming ± stipitate, obtusely trigonous above, occasionally with weak accessory plicae, normally wide at mouth; mouth freely, copiously ciliate-dentate, dentate or ciliate, the teeth 20-50 to 50-70 in number. *Sporophyte* with seta penetrating ± deeply into shoot-apex; seta of ca. 12-17 to 18-20 epidermal rows, often slightly larger (ca. 23-27 to 32-40 μ) and somewhat thicker-walled than the collenchymatous, numerous rows of interior cells (which are ca. 16-20 to 25-32 μ in diam.). *Capsule* narrowly ovoid-ellipsoid, quite firm, the wall 3-5-stratose; epidermal layer of large, polygonal or rectangulate, hyaline cells (only 2-3 rows adjacent to suture of valves with coarse nodular thickenings), averaging (14)16-20(23) μ thick ×(25) 35-50 μ wide or wider. Inner 2-4 layers much smaller, reddish-brown, the interior layers each only 5-7 to 7-9 μ thick (on an average), the hypodermal layer 7-10 μ thick, the internal 1-3 strata with numerous nodular (radial) thickenings, the innermost layer with weak, transverse to oblique, incomplete to complete semiannular bands, locally reduced to nodular thickenings. Hypodermal cells regularly rectangulate, ca. 14-16 μ wide ×(24-30)35-60 μ long; innermost layer very irregular, the cells irregular in size and shape. Epidermal hyaline cells ± oblong, 40-60 μ long. *Elaters* short, contorted, narrowly bispiral, blunt on the attenuated ends, 6.5-8 to 9-10 μ in diam. *Spores* yellow-brown, nearly smooth, 9-10 to 15-18.5 μ in diam. (their diam. 1-2× that of elaters).

TYPE. *Temnoma pulchellum* (Hook.) Mitt., lectotype by designation (Schuster 1959).

Temnoma consists of approximately 10 species, almost exclusively Antipodal in range. Although the majority of these occur in the " Antarctic " *Nothofagus* zone and range from southeastern Australia and Tasmania to New Zealand and the Auckland Islands and southern South America (Chile, Argentina), one species, *T. setigerum*, occurs from Java to Taiwan, the Philippines and Himalaya. *Lepidozia randii* S. Arn. (1953 : 417, fig. 6) is identical with *Temnoma quadripartitum*, thus extending the genus to Marion Island. Arnell (1958 : 5) actually reports *T. quadripartitum* from Marion Island [1], as well as from Tristan da Cunha and Inaccessible Island, and from Kerguelen Island.

The species constituting *Temnoma* were, until recently, uniformly placed in *Blepharostoma* (Stephani 1909; Müller 1951-58). Fulford (1951 : 252) published an extraordinary map (l.c.: fig. 5) purporting to represent the distribution of " *Ble-*

[1] I would assume from the fact that Arnell (1953) reported no *Temnoma* from Marion Island, but described *Lepidozia randii*—whereas in 1958 he recorded *Temnoma quadripartitum*—that he now regards the former as a synonym of the latter.

pharostoma ". She states that this is a genus of " about 13 species ", which would correspond to the 12 species cited under *Blepharostoma* by Stephani (1909), plus *Blepharostoma vaginatum* (Herzog 1935) [1]. Of these 13 species, *Blepharostoma dusenii* was placed in *Vetaforma* (Fulford 1962; Schuster 1963), a genus considered by Fulford and Taylor (1960) to represent a distinct family ! *Blepharostoma whiteleggei* and *B. vaginatum* were placed by Schuster (1961*a*) in, respectively, *Chaetophyllopsis* and *Herzogianthus*, constituting the family *Chaetophyllopsidaceae: B. antillarum* belongs to the genus *Telaranea* of the *Lepidoziaceae*. Thus, until the papers of Schuster (1959, 1961, 1963) *Temnoma* was confused with a series of unrelated elements under the genus name *Blepharostoma*.

From data presented earlier (Schuster 1959), it was shown that consideration of *Temnoma* as a synonym of *Blepharostoma* is untenable. Equally erroneous is the disposition of *Temnoma* as a genus of *Lophoziaceae*, as in Buch (1933), followed by Buch, Evans and Verdoorn (1938), Evans (1939), Schuster (1951) and Müller (1951-58). All of these efforts to place *Temnoma* in the *Lophoziaceae* were predicated on *Temnoma setiforme* being correctly referred to *Temnoma*, an assumption based on Howe (1901). However, Howe was incorrect in this disposition of the common arctic-alpine *Jungermannia setiformis* Hook., as Müller (1951-58) and Schuster (1961) pointed out. *Jungermannia setiformis* differs from *Temnoma* in (1) the strongly pluriplicate perianth; (2) stem anatomy; (3) scattered rhizoids; (4) strong dimorphism between leaves and underleaves; (5) branching, which is preponderantly intercalary in all cases. As shown elsewhere *Jungermannia setiformis* cannot be referred to *Temnoma*; it is much more closely allied to *Chandonanthus*. It therefore must be referred to the *Lophoziaceae*.

RELATIONSHIPS. Detailed studies of sporophyte-bearing plants bring out a series of important generic criteria (first pointed out in Schuster 1959). Among them are the following: (1) capsule-wall 3-5-stratose, with the epidermal cells forming a large hyalodermal stratum, only those adjoining the dehiscence lines of the valves having pigmented thickenings; (2) perianth normally wide at the orifice, trigonous; (3) rhizoids sharply restricted to the basal portions of the underleaves, lacking from the stem; (4) seta of numerous cell rows; (5) stem with narrowly rectangulate cortical cells not differentiated as a thick-walled, short-celled cortex; the cortical cells not larger than medullary; (6) underleaves somewhat smaller than the lateral leaves to subequal; (7) spore-elater diameter ratio 1:1 to 2:1; (8) branching sporadic, in part at least lateral and terminal, of the Frullania-type, but usually not exclusively so; (9) leaves and underleaves both quadrifid, usually symmetrical; (10) leaf cells non-collenchymatous, strongly elongated and rectangulate, tending to develop equally thickened walls, much like the cortical stem cells (although broader); (11) leaves slightly to distinctly succubously inserted; (12) leaves with margins generally sharply

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[1] Fulford (1951 : 250-251) speaks also of a species of *Blepharostoma* " endemic in Sikkim ". This represents *Lophochaete trollii*—a seventh generic element confused by her under " *Blepharostoma* ".

The statement in Fulford that the 13 species of " *Blepharostoma* " represent a " type of distribution pattern, where a genus of southern origin has become very widespread in the Northern Hemisphere, in part since glaciation " is extraordinary in drawing sweeping phytogeographic conclusions based on a taxonomic artifact !

spinescent or ciliate-setigerous; (13) antheridial stalk biseriate, and the body formed of numerous, irregularly oriented cells.

In criteria Nos. 2, 3, 5, 7, 8 and 9, above, *Temnoma* agrees with, or approaches *Blepharostoma*, hence can logically be placed in the *Blepharostomataceae*, if that family is emended as in Schuster (1957, 1959, 1961).

Temnoma differs from *Blepharostoma* (and the diagnosis of the *Blepharostomataceae* in Müller, (1951-58) in a series of criteria, including Nos. 1, 4, 6, 11, 12 and 13, above [1]. In addition, the species of *Temnoma* are much more robust, lack gemmae and bear leaves that are normally at least somewhat succubously inserted. I believe capsule-wall anatomy alone precludes considering *Blepharostoma* and *Temnoma* as congeneric, the thin capsule wall of *Blepharostoma*, with two subequally thick cell layers (ca. 10 μ each), both bearing thickenings, serving effectively to separate *Blepharostoma* from *Temnoma*.

Temnoma and *Blepharostoma* appear widely separated phylogenetically. However, *Archeophylla* (Schuster 1963, 1965) almost connects the two groups. This genus has the collenchymatous cells and uniseriate, attenuate lobe apices reminiscent of *Blepharostoma* and the variability in leaf-lobe number typical of *Blepharostoma*. However, the retention of a distinct disc of the leaf and underleaf bases, the massive seta, the lack of gemmae, the antheridia and their stalk are all as in *Temnoma*. Significantly, the capsule wall in *Archeophylla* has three or four strata, thus approaching *Temnoma*, but differs from the latter in that most epidermal cell walls usually bear nodular thickenings.

Considerable fundamental similarities exist between *Temnoma* and *Trichocolea* (Schuster 1959), among them: hyaline epidermal cells of the capsule wall; succubously inserted, ciliate and 4-lobed leaves; narrow cortical stem cells; low spore-elater diameter ratio; quadrifid and ciliate underleaves that are smaller than the lateral leaves, with the rhizoids restricted to their bases. In spite of these similarities, *Temnoma* is more closely related to *Blepharostoma*, with which it shares a similar perianth (Schuster 1959). There is also a suggestive affinity to certain *Trichocoleaceae* (such as *Trichocolea lanata*) in that the sporophyte of *Temnoma* seemingly " bores " deeply into the axis, with correlated evident proliferation of axial tissue, the bracts and bracteole becoming widely separated [2]. One can readily visualize the Trichocolea lanata-like coelocaule, with vestigial perianth, arising from a Temnoma-like gynoecium by a gradual reduction in size of the bracts and perianth, associated with an increase in mass and complexity of the coelocaule. Certainly, *Temnoma* develops a coelocaule precursor. In this conjunction, the highly dissected leaves of such taxa as *Temnoma pilosum* and the exclusively lateral, Frullania-type

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[1] It should be noted, however, that certain weak phases of *T. paucisetigerum* may have leaves with the lamina only 1-1.5 cells high, and the " lobes " reduced to four uniseriate cilia; underleaves are similar and may have the lamina even more extremely reduced. Such plants form an effective model from which the reduced Blepharostoma-type organization of the gametophyte may be derived.

[2] As is pointed out elsewhere, this " seeming boring " of the sporophyte into the gametophyte axis apex is a precursor of coelocaule formation. The penetration of the sporophyte is probably a false penetration, a secretion from the embryo inducing axial proliferation of the entire shoot-apex, which grows up and elongates in a cylinder around the developing sporophyte; this cylinder stretches, so to speak, to accommodate the sporophyte.

branching of certain species (such as *T. pilosum* and *T. pulchellum*) are possibly suggestive. My original suggestion (Schuster 1959) of some remote phylogenetic connection between *Trichocolea* and Temnoma-like *Blepharostomataceae*, I think, merits further consideration [1].

The preceding data suggest that *Temnoma*, although sharply separable from *Blepharostoma*, is assignable to the *Blepharostomataceae*. This automatically precludes the genus being allied to *Chandonanthus* Mitt. whose features suggest very different affinities: the underleaves, which are bifid and much smaller than the lateral leaves, do not have a rhizoid-initial field at their bases, the rhizoids being inserted in a haphazard manner on the stem; the stem has a distinct cortex of shortly rectangulate, very thick-walled cells. These features suggest the *Lophoziaceae*, a primitive family of the *Jungermanniinae* (Schuster 1953, 1963). In this instance, the previously uninvestigated rhizoid-distribution pattern, which I first emphasized as a family criterion (Schuster 1949, 1953) gives a clue as to the correct position of these plants. This, of course, effectively demonstrates that the position of Horikawa who has placed *Chandonanthus hirtellus* and *C. birmensis* in *Temnoma*, is untenable.

The treatment of Evans (1939), who places *Temnoma* in the *Lophoziaceae* (*Jungermanniaceae*), *Blepharostoma* in the *Ptilidiaceae*, also cannot be followed. An affinity between *Temnoma* and *Blepharostoma* is most obviously demonstrated by study of such species as *Temnoma pilosum*. This species has nearly transverse, distant leaves and underleaves, equal in size; both are divided virtually to the base into four lobes, each of which is 6-9 cells wide at base; the lobes, in turn, are fringed with uniseriate cilia that almost exactly match the ciliary leaf lobes of *Blepharostoma*. In other words, *Blepharostoma* may be regarded as an extreme, reduced derivative of Temnoma-like ancestors. If only gametophytes were under consideration, I would be tempted to consider *Temnoma* a mere subgenus of *Blepharostoma*. The salient differences in the anatomy of the seta and the capsule prohibit such a conservative treatment, with today's generic concepts as a frame of reference [2].

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[1] Since the preceding account was completed, Fulford (1963) arbitrarily placed *Temnoma* in the *Trichocoleaceae*. She defines that family as with exclusively lateral, Frullania-type terminal branching—which holds for *Trichocolea*, but not for *Temnoma*. Her disposition of *Temnoma* in the *Trichocoleaceae* appears based on study of only *Temnoma* pilosum-like taxa, in which there are normally only terminal, Frullania-type branches; if she had studied the other taxa, such an erroneous disposition would not have been proposed.

It is clear, if we study taxa such as *Archeochaete* and *Lophochaete*, in which we find a varying admixture of criteria common to *Blepharostoma* and *Temnoma*, that the *Blepharostoma-Archeochaete-Lophochaete-Temnoma* complex cannot be subdivided into families, and that these genera form a natural and interrelated whole. It is not impossible that the *Trichocoleaceae* evolved from the *Blepharostomataceae;* almost all characters of *Trichocolea* represent an evolutionary advance over those of Temnoma-like *Blepharostomataceae*.

In placing *Temnoma*, study of the most primitive taxa such as *T. quadrifidum*, in which transverse leaves and bisbifid lobing are linked with perfect isophylly, is necessary. Such taxa show a decided approach in vegetative features—and in their polymorphous branching—to *Lophochaete;* they differ strikingly from the *Trichocoleaceae* in almost all respects.

[2] Pearson (1887) states that " Dr. Spruce merges Mr. Mitten's genus *Temnoma* into *Blepharostoma* of Dumortier. I was for a time inclined to dissent from this view, having in mind the succubous insertion of the leaves of several of the species referred to this genus by Mr. Mitten; but a study of the perianths of *B. quadripartitum* (Hook.) shows that the character relied upon by Mr. Mitten (the wide mouth of the perianth) does not obtain, for they are more or less constricted by the plication of the mouth, so linking them with those of *B. trichophyllum* ". Pearson goes on to

Temnoma is also remotely allied to *Lophochaete*. The latter genus consists of species with bisbifid leaves and underleaves that are entire-margined, a perianth that is 4- or 5(6)-plicate, nearly perfectly transversely inserted leaves and a bistratose capsule wall. Since *Temnoma quadripartitum* and *T. quadrifidum* produce forms with virtually entire leaf lobes, the absence of teeth of the leaves cannot be regarded as of primary importance, even though the teeth are always produced at least on perichaetial bracts in *Temnoma*, while they are absent even there in *Lophochaete*. More significant is the basically trigonous perianth of *Temnoma* vs. the 4-5(6)-plicate perianth of *Lophochaete*, and the very different sporophyte anatomy.

BRANCHING. The diversity of branching types in *Temnoma* is so great that little weight can be placed on differences in branching between *Temnoma* and *Lophochaete*. Collectively all types of branching, except the Lejeunea- and the Radula-type, have been found [1]. As developed under *Temnoma palmatum*, this species has largely lateral, terminal, Frullania-type branches, although an occasional terminal, postical, Acromastigum-type branch is found, while isolated postical-intercalary branches arising from the underleaf axils are also demonstrable. In the primitive *T. quadrifidum*, terminal branching of the Frullania-, the Acromastigum- and the Microlepidozia-type occurs, as well as intercalary lateral and postical branching. In other species of which adequate materials have been available (*T. pulchellum*, *T. setigerum*), I have seen only terminal, lateral, Frullania-type branching. By contrast, I have found to date only lateral (rarely postical), terminal branches in *Lophochaete* [2]. It would be foolhardy to predict, on the basis of the proved ability of *Temnoma* to produce such a wide diversity of branching, that lateral-intercalary branches cannot be found in this genus, except in *T. quadrifidum*. Indeed, the diversity of branching patterns in *Temnoma* demonstrates one significant fact: a polymorphism that suggests *Temnoma* is an old and plastic genus, rather than a modern and specialized, rigid one.

GYNOECIUM AND SPOROPHYTE ANATOMY. The capsule wall of *Temnoma* is similar to that of *Trichocolea*, although the latter may have as many as 5-7 strata of cells bearing thickenings, within a large, pellucid layer of nearly or quite unpigmented, epidermal cells. In *Temnoma* there are only 2-4 such strata of cells bearing thickenings within the layer of much larger hyaline epidermal cells. This difference is of minor significance, and its significance is further reduced by *Eotrichocolea* (Schuster 1963). The capsule shape in these genera is identical; they also possess a relatively complex seta, although that of *Trichocolea* consists of a much larger

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quote Lindberg, to the effect that he agrees with merging *Temnoma* with *Blepharostoma*. Admittedly the basis for setting up *Temnoma* was superficial, but no more superficial than much of Mitten's other work which is accepted today. The only valid basis for judging the merits of *Temnoma* must reside in the overall differentiating features of that genus " vis à vis " *Blepharostoma*, and not whether the sole character used by Mitten has merit.

[1] Fulford (1963) erroneously states that only terminal, Frullania-type branching occurs in *Temnoma*. The accompanying plates clearly show this is not so.

[2] I cannot substantiate, with the limited material at hand, the claim of Fulford & Taylor (1960) that *Lophochaete* subgen. *Pseudolepicolea* develops intercalary branches, other than as a rare exception.

number of small epidermal cells (65-80, approximately) surrounding numerous inner cell rows, of which the innermost disintegrate with maturation, resulting in a hollow seta. Both *Trichocolea* and *Temnoma* constantly appear to have small spores, no more than twice the diameter of the elaters [1].

Temnoma, in some respects, also approaches *Trichocolea* in the pronounced manner in which the developing sporophyte seems to " bore " into the axial tissue. Knapp (1930 : 105-110) discusses " coelocauly " in *Trichocolea tomentella*; in this the nearly mature sporophyte, before elongation of the seta, may be totally surrounded by axial tissue. The manner in which this takes place is clear from the fact that the unfertilized archegonia remain near the summit of the swollen shoot-tip enclosing the sporophyte. Furthermore, this results not from tubular proliferation of axial tissue peripheral to the receptacle, i.e. not by formation of an Isotachis- or Marsupella-type stem perigynium s. str., but by the activity of a receptacular meristem directly peripheral to (and under) the archegonia with the result that superficially the sporophyte literally " seems " to eat its way backward into the stem. In actuality, copious secondary cell division and elongation take place in the axis apex, which forms a receptacle to hold the developing sporophyte; associated we find that no calyptra or shoot-calyptra forms. This situation also holds, to a lesser extent, in *Trichocolea lanata* and *T. tomentosa*, but here there is also strong axial proliferation, or intercalary growth, of the receptacular stem tissue at the foot and in the lower part of the venter of the fertilized archegonium and in the region of the sterile archegonia (which, as a consequence, come to lie scattered over the surface of a distinct " shoot-calyptra "). This latter condition also obtains in *Temnoma*, where the embryo seemingly " bores " into the axis to a depth of 4-5 leaf cycles (including the floral leaves); in addition, the apical axial tissue under the sterile archegonia proliferates to some extent, the archegonia becoming elevated for some distance on the " calyptra " s. lat.—actually, calyptra s. str. plus " shoot-calyptra " situated below it. The major differences between *Temnoma* and *Trichocolea* lie in the retention of a delicate calyptra in *Temnoma vs.* the reduction or loss of the calyptra, associated with elaboration of a fleshy coelocaule in *Trichocolea*; in the retention of a distinct perianth in *Temnoma vs.* its obsolescence or total loss in *Trichocolea.* These characters of *Trichocolea* are of an obviously derivative nature. As a consequence, the superficially very different gynoecial systems of *Temnoma* and *Trichocolea* appear to be related to each other, and a derivation of the *Trichocoleaceae* from Temnoma-like ancestral types, involving perianth and bract reduction, is not contradicted by the reproductive features.

The paragynoecial and gynoecial complex in *Temnoma* is thus much more complicated than Fulford (1963) states, since it involves the development of a perianth (formed from foliar tissue) and of a coelocaule-precursor and a shoot-calyptra (both derived from axial tissue).

TAXA EXCLUDED FROM TEMNOMA. I have been impressed by the uniformity of the species of *Temnoma* in the following respects: (*a*) the leaves, at least near

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[1] Statements in Hatcher (1958) that the spores are 3× the elaters in diameter in *Trichocolea* are apparently based on error.

gynoecia, armed with paired, opposed cilia or teeth that are always pluricellular; (*b*) plants sparingly, irregularly branched; (*c*) the ± thick-walled leaf cells lacking trigones; (*d*) the nearly or quite symmetrically quadrifid leaves—even " weak " leaves of small or juvenile stems generally showing a retention of the quadrifid form, even if possessing a tendency for the reduction of the cilia or teeth; only *T. quadripartitum* may produce trifid leaves [1].

On the basis of the lack of this ensemble of features, the following are excluded:

1. Two species, originally referred to *Blepharostoma*, depart very significantly from *Temnoma* and *Blepharostoma* in the preceding features; these are " *Blepharostoma* " *whiteleggei* Steph., and " *Blepharostoma* " *vaginatum* Herz., placed (Schuster 1961*a*) into, respectively, *Chaetophyllopsis* Schust. and *Herzogianthus* Schust. These species agree in the following ensemble of features, separating them from *Temnoma* s. str.: (*a*) leaves armed with unicellular, acuminate, thick-walled, often falcate or curved cilia; (*b*) plants sparingly and irregularly to freely and very regularly pinnately branched, the branches uniformly lateral, abbreviated, more or less determinate, often subequal in length; (*c*) leaf cells thin-walled, with distinct to slightly bulging trigones; (*d*) leaves fundamentally trifid, typically somewhat asymmetrically so; (*e*) perianths 3-5-stratose, polystratose, strongly narrowed to the mouth. As amply documented (Schuster 1961), these genera share some features with the *Blepharostomataceae* (such as succubous leaves, lack of a sharply defined cortex, a distinct perianth, lack of perigynium or coelocaule), while leaf form, development of collenchyma, and the exclusively lateral, sometimes plumose branching suggest the *Ptilidiaceae*. The constellation of features shared by these two genera seems sufficiently impressive that their segregation as a distinct family, the *Chaetophyllopsidaceae*, is warranted (Schuster, 1961*a*). The extraordinary, unique, tetrahedral, pluricellular gemmae of *Chaetophyllopsis* support this conclusion.

2. *Temnoma schusteri*, recently described by Hodgson and Allison (1962), exhibits a large-celled cortex, thin-walled cells with coarse, trigones and a variable number of leaf and underleaf lobes, ranging from 2-4; it also has a contracted perianth mouth and mostly postical-intercalary branches. In my opinion, the extraordinarily different leaf cells alone serve to exclude this species from *Temnoma*. For that reason it is described as the genus *Archeophylla* Schust. (Schuster 1963*a*, 1965). *Temnoma pungens* (Herz.) Fulf., placed by Fulford (1963) in *Temnoma*, exhibits the same ensemble of features and also falls in *Archeophylla*.

3. A final complex of species needs to be considered in conjunction with the redefinition of the genera *Blepharostoma* and *Temnoma*. These species are *Lepicolea trollii* Herz., from the Sikkim-Himalaya; *Lepicolea fryei* Perss., from Arctic America; and *Lepicolea* or *Blepharostoma quadrilaciniatum*, from Patagonia. These taxa all possess the sparing branching of the *Blepharostomataceae* and have symmetrically bisbifid leaves and underleaves. There is no question about the position of these species in the *Blepharostomataceae*. The presence of a simple, unistratose perianth in " *Lepicolea* " *fryei* and in " *Lepicolea* " *quadrilaciniata* removes these species

[1] Juvenile phases of *T. paucisetigerum* may produce 2-3- to 3-4-fid leaves and underleaves; such plants are also divergent in showing a reduced disc 1-2 cells high.

from the vicinity of *Lepicolea*, a genus not further considered here. Schiffner (1911) clearly demonstrated that *Lepicolea quadrilaciniata* could not, on this basis, be retained in *Lepicolea*, a genus which I refer (Schuster 1957, 1963) to a unigeneric family, the *Lepicoleaceae*. He placed the species in the portmanteau genus *Blepharostoma*, then also taken to include *Temnoma*. The 4-5-6-plicate perianth, contracted to a small mouth, and the total lack of any tendency towards development of teeth or cilia of the leaf lobes (even of the bracts), suggest these species cannot go into *Temnoma* s. str.; for these species the genus *Lophochaete* was proposed (Schuster, 1957). The relatively slightly elongated cells of the perianth, the stipitate perianth and only slight ability of the sporophyte to bore into the axial tissue, the bistratose capsule wall, and the less massive seta all serve to separate *Lophochaete* further from *Temnoma*.

4. Gola (Ann. Bot. 6 : 274, 1906; Il Ruwenzori, Relazioni scient. I : 523, 1909) described a *Blepharostoma cavallii* Gola; this plant, as Arnell has shown, is a species of *Chandonanthus*.

In addition to this *Blepharostoma*, Gola (1922) published two others from Tierra del Fuego, *B. acanthifolium* Gola (: 169) and *B. pigafettoanum* Gola (: 169). These are so imperfectly described and miserably figured that it is impossible to gain any understanding of the generic position of the plants from his paper. The first may be a form of *Temnoma quadripartitum*; the latter is a *Lophochaete*, and may be *L.* "*georgica*". (I have attempted to locate the specimens on which these "species" were based, and have been informed by Dr. Sebastiano Filipello, of the Universita di Torino, that after the death of Prof. Sappa (1956), "le collezioni... in gran parte disperse" and that the specimens could not be located.)

5. *Blepharostoma corrugatum* Steph., although transferred to *Temnoma* by Schuster (1959) because of the Temnomoid features of the sterile gametophyte, has been shown to diverge in the small, spicate, postical-intercalary androecial branches and distinct leaf collenchyma; for this reason it has been made the type of the monotypic genus *Trichotemnoma* Schust. (Schuster 1964).

CLASSIFICATION. I cited seven species under *Temnoma* (Schuster 1959), of which one (*T. dusenii*) is admittedly sufficiently divergent to need segregation, as the genus *Vetaforma* (Fulford 1962; Schuster 1963). One species, *T. pinnatisetum* (Steph.) Schust., appears identical with *T. pilosum* (Evs.) Schust., leaving five species. *Blepharostoma setigerum* was transferred to *Temnoma* (Schuster 1963), and, nearly simultaneously, Hodgson and Allison (1962) and I (Schuster 1963) transferred *Isotachis palmatiloba* to *Temnoma*, a species here synonymized with *T. quadrifidum*. On the following pages I describe four others as new, *T. paucisetigerum*, *T. angustifolium*, *T. townrowii*, and *T. patagonicum*, and transfer the relatively recently described *Lophozia pilifera* Horik. to *Temnoma setigerum* thus totalling 10 species for the genus. One other species, *T. corrugatum* has been transferred (Schuster 1964) to *Trichotemnoma* [1].

[1] Since the above account was completed, Fulford (1963) has published two supposed new species. One, *T. chilense*, is at best a luxuriant form of *T. pilosum*. The other, *T. subintegrum*, is in my opinion one of the numerous extremes of *T. quadripartitum*. The species total hence remains at 10.

In my opinion, two large groups are represented. One consists of primitive species, with more nearly transversely inserted and oriented, deeply parted leaves; in these, spores are (at least in part) twice the diameter of the elaters and branching patterns remain fluid and unstable. Furthermore, some species retain almost isophyllous, bisbifid leaves. For this group the subgeneric name *Eotemnoma* was proposed (Schuster 1963); it includes 6 of the species. The other group, subgenus *Temnoma*, includes 4 species with obviously succubously inserted, less deeply divided leaves with highly differentiated, smooth cilia or setae; spores are equal in diameter to the elaters; branching has become fixed to one or two modes (lateral, Frullania-type branches and/or postical-intercalary branches); the underleaves have become relatively smaller.

Species recognition within each of these subgenera is complicated by the great malleability and plasticity of the species. As a consequence, there is room for subjective opinion as to what constitutes a species and where specific lines are to be drawn. For example, there appears to be almost a continuum from *T. quadripartitum* var. *randii* (with basal accessory lobes, without reflexed cilia of sinus bases) to *T. quadripartitum* var. *quadripartitum* (with basal accessory cilia sometimes present, but these are rarely lobelike, usually with reflexed spines of the leaf sinuses) to *T. palmatum* (always without basal accessory large cilia, with or without displaced cilia or spines of the sinus bases of the leaves; with leaf lobes becoming broader, shorter and more gradually tapering) to *T. quadrifidum* (with relatively broad, entire lobes; with dentition usually absent or only sporadically present, never reflexed). For these reasons, a simple and straightforward key is difficult to devise. Indeed, the first key I constructed, which was simple and uncomplicated, worked perfectly while only a limited suite of specimens was at hand; with study of longer series, transitions—seeming or real—have come to hand.

These transitions, I am convinced, do not represent intergradations from one basic genotype (species) to the next. In other words, I doubt whether there is active hybridization between species. I have collected, several times, two species growing admixed without evident intergradation between them. Rather, any intergradations seen are owing to poor development of certain plants, which retain persistently juvenile facies. To cite one example only, the extraordinarily distinctive abaxially displaced spines which are a normal complement of the *T. quadripartitum* leaf may, under certain conditions, fail to develop on sterile, mesophytic plants, which can then be easily misidentified. Yet the ability to produce such displaced spines is, perhaps, the single most important criterion of this species, serving to separate it from others with deeply quadrifid leaves. Equally variable may be the degree to which the disc is elaborated. Within this same species—or what I prefer to regard as a single species—weak plants may have a lamina only 2-4 cells high; robust, fertile phenotypes have it 7-9 cells high.

Thus a certain latitude must be allowed in both keys and descriptions—which may result in both longer and more complex key couplets and diagnoses—in order to include all but the most deviant phases of the various species. This, I trust, will not seriously impair the utility of this paper.

The present work was done largely in 1956-57; it was revised, with addition of data derived from personally collected material and from study of the collections

in the herbarium of K. W. Allison, in August, 1961-December, 1962, again in September, 1963-December, 1964, and June, 1965-April, 1966. During this interval, a review of the New Zealand species (Hodgson and Allison 1962) appeared, which in many cases diverges from that given here, especially as regards nomenclature. The Hodgson and Allison paper, unfortunately, includes a high level of both taxonomic and nomenclatural confusion. The following significant differences in taxonomy (and especially nomenclature) between the Hodgson and Allison and my treatment should be noted, otherwise confusion will ensue. Insofar as is feasible, I have given reasons why my treatment differs from that of Hodgson and Allison. Since my concepts are based on study of the types of the species, the nomenclature used here for the species is the only tenable one.

Nomenclature of *Temnoma* species

Schuster [1]	Hogdson & Allison (1962)
*Temnoma quadrifidum**	*Temnoma palmatilobum* (at least in large part, incl. type)
*Temnoma palmatum**	*Temnoma quadrifidum*
*Temnoma quadripartitum**	*Temnoma quadripartitum* *Temnoma palmatum*, in part
*Temnoma pulchellum**	*Temnoma pulchellum*
Temnoma paucisetigerum sp. n.* *Temnoma angustifolium* sp. n.*	*Temnoma palmatum*, in largest part
Temnoma setigerum	(not treated)
*Trichotemnoma corrugatum**	*Temnoma corrugatum*
*Archeophylla schusteri**	*Temnoma schusteri*

Synopsis of subgenera and species of *Temnoma*

1. Leaves (0.4)0.45-0.85 quadrilobed: the narrow lobes ± gradually tapered into the uniseriate distal portions (or lobes uniseriate to base), the apical cilia (if any) usually delicately to conspicuously striolate (like laminar cells), dull when dry; cells of cilia, if differentiated, not normally exceeding 3-5 × as long as wide (under 85[95] μ long). Branching variable: with some Frullania-type branching, but usually some (or many) branches intercalary, postical (and sometimes lateral); occasionally with Microlepidozia- or Acromastigum-type branches. Spore-elater ratio 1.5-2.5 : 1 (where known). Leaf insertion nearly or quite transverse (usually no more than 5-20[25]°, succubous), the orientation subtransverse; underleaves (0.5)0.6-0.9(1.0) the leaves in area, symmetrically quadrifid (rarely in part trifid) for (0.4) 0.5-0.85 their length . . . . . Subgen. *Eotemnoma* Schust. 2

1*. Leaves 0.2-0.4 quadrilobed: the lobes ± broadly triangular, abruptly narrowed into highly differentiated, elongated, setose cilia (which are usually formed of smooth cells, ± glistening when dry), the cells strongly elongated (to 100-135 μ long), thick-walled. Branching rigid: either all or

[1] I have seen type specimens of all species which are cited with an asterisk.

most branches terminal, lateral, of the Frullania-type, or some postical-intercalary (never with Microlepidozia- or Acromastigum-type branches, or lateral-intercalary ones). Spore-elater ratio 1 : 1 (where known). Leaf insertion usually distinctly succubous (25° to 45-60° usually; rarely subtransverse), the orientation usually oblique; underleaves 0.35-0.7 the leaves in area; leaves often ± asymmetrical . . . . Subgen. *Temnoma* 8

2. Mature leaves of sterile stems with cilia (or teeth), if present at all, usually lying in plane of leaf [1]; mature leaves less deeply quadrifid, 0.4-0.65(-0.75) their length, the disc usually (5)6-9 or more cells high; juvenile (and sometimes mature) leaves often lacking cilia or marginal teeth (cells of any teeth present often only 1.5-4× as long as broad); each leaf lobe with at most 1-2(3) pairs of cilia or teeth, each formed of 1-3(-4) cells. Lobes of ♀ bracts (and subfloral leaves) each with 1-2 to 3-5 pairs of stiff teeth or cilia, the lobe apices formed of cells up to 2-4(5-6)× as long as broad. . . 3

2*. Mature leaves of ♂ and sterile axes (not gynoecial plants alone) at least in large part with cilia or teeth well-developed at and near sinus-bases and along margins of disc, the lower teeth of disc margins occasionally reflexed (occasionally enlarged to simulate accessory lobes), the cilia or teeth near sinus-bases sharply reflexed or displaced, abaxially projecting, not lying in leaf plane; leaves usually (0.65)0.7-0.85 quadrifid (rarely trifid), the disc (2)3-5 cells high to (large forms of *T. quadripartitum*) 5-6(7-8) cells high [2]. Lobes of ♀ bracts slenderly lanceolate, long-acuminate with numerous (to 7-8 pairs) cilia or spines; lobe apices of ♀ bracts formed of cilia or setae 350 μ long or more (5-6 superimposed cells or longer) 6

3. Leaves (and some underleaves) in large part appearing palmately 5-6-lobed, tending to produce a large, lobe-like tooth at one or both disc bases, the margins otherwise ± edentate, the lobes usually entire; leaves squarrose, remote. [Leaf lobes usually (2-3)4-(7)8 cells broad basally, acuminate, ending in tips of (2-3)4-6(7-8) subisodiametric or elongated cells; disc 5-8 cells high]. South America—Marion Island—New Zealand
T. quadripartitum (Hook.) Mitt.

3*. Leaves simply (3)4-lobed, never with large, lobe-like teeth or appendages of leaf bases (margins of disc, if with cilia, with them suprabasal and never lobe-like); leaves suberect to obliquely or widely patent, never squarrose. (New Zealand-Tasmania-Australia) 4

4. Leaves with disc margins edentate (except occasionally, below gynoecia); leaves frequently bisbifid, with median sinus clearly deeper; leaf lobes blunt to acute but not acuminate, normally ending in 1-3 superimposed single cells that are but little elongated (1-2.5 : 1). Bracts with lobes with 1-2(3) pairs of teeth at most, the teeth usually short and disc margin on each

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[1] In ♀ plants of *T. townrowii* and *T. palmatum*, short, stiff, displaced spinose teeth may occur at the sinus bases—even on leaves far below the gynoecia. The disc, in most populations, is relatively high (6 cells high or more).

[2] If disc 6-7 cells high or more, see also var. *pseudospiniferum* of *T. palmatum*; this has the longer cells of cilia 3-5× as long as wide.

side with 0-2(3) teeth. Underleaves usually almost identical in size to lateral leaves. Branching mostly postical-intercalary; never with Acromastigum-type branches . . . . . *T. quadrifidum* (Mitt.) Mitt.

4*. Mature leaves with disc margins often or usually bearing 1-2 to 3-4 slender, sharp, suprabasal cilia or teeth; leaves not bisbifid, the sinuses equal; leaf lobes acuminate, ending in cilia of 3-5 to 7-8 superimposed single cells that are, in part, greatly elongated (ca. 2.5-8 : 1). Bracts variable, often with 3-5 pairs of cilia per lobe, the cilia usually longer, the disc margins usually each with 2-5(6) sharp, spinose teeth or cilia. Underleaves clearly smaller than lateral leaves 5

5. Plants strongly spinescent-ciliate, the cilia with longer cells 14-16 × 90 μ up to 16-18 × 100-135 μ, sharply, abruptly contrasted to the subquadrate cells within the leaf lobes. ♀ Plants with leaf lobes to 8-11 cells wide; perianth mouth with longer cilia 4-6 cells long (350-400 μ long), the longer cells to 100-150 μ long. Only with Frullania-type branches. Tasmania *T. townrowii* Schust.

5*. Plants slightly to rather conspicuously spinescent-ciliate (in var. *pseudo-spiniferum*), the cilia with longer cells to 14-18 × 60-78 μ, less sharply differentiated from the usually oblong cells of the lobes. ♀ Plants with leaf lobes usually 3-9 cells wide; perianth mouth with longer cilia 2-5 cells long, the longer cells to 65-90 μ long. With Frullania-(rarely also Acromastigum-) type terminal and ventral-intercalary branches. Australia-New Zealand. . . . . *T. palmatum* (Lindb. ex Pears.) Schust.[1]

6. Teeth of leaf lobes short, rigid, spine-like, abruptly tapering, not ciliiform, of (1)2-4(5) superimposed cells, the cells subisodiametric to 1.5-2.5(3) × as long as wide, 18-30 μ long; lobes (3)4-5 to 5-6(8) cells wide at base, armed with few stiff, rigid, spinescent teeth (each lobe with (0)1-2(3-4) pairs of rigid teeth 1-3 cells long); underleaves smaller, merely quadrifid (or lobes armed with 0-1(2) short, basal spines). ♀ Bracts with lobes bearing pairs of opposed, stiff teeth. Stem (5)6-8 cells high, the cortical cells in part larger than medullary . . . . . *T. quadripartitum* (Hook.) Mitt.

6*. Leaf lobes with long and slender cilia, to 4-6 or 5-7 cells long and uniseriate, the constituent cells to 4-7 × as long as wide, 40-50 to 50-100 μ long; lobes (4-)5-9 cells wide at base; lobes copiously ciliate with 3-7(-8) pairs of opposed cilia; underleaves similar, copiously ciliate. Stem 8-9 to 12-15 cells high, with 25 or more rows of cortical cells, 0.6-1.0 diam. of medullary cells 7

7. Leaves longly ciliate, with capillary segments; mature leaf with 50-85 cilia; cilium cells to 4-7 × as long as wide, the longer to 60-90 μ long or more; each lobe with (4-)5-8 pairs of cilia, the longer cilia to 350-525 μ long; stem with ca. 40 or more rows of cortical cells, the cortical cells smaller than medullary, strongly elongated, narrowly rectangulate ca. (16)18-20(22) × 72-130 μ long (length-width ratio ca. 4-7 : 1) *T. pilosum* (Evans) Schust.

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[1] A typus polymorphus, extremes of which are distinguished (: 330) as distinct varieties.

7*. Leaves spinose-ciliate, each mature leaf with 28-42 cilia; cells of cilia to 3-4 × as long as wide, the longer cells 40-52(60) μ long; each leaf lobe usually with 3-4 pairs of lateral cilia, the longer to 250 μ long; terminal cilia of lobes formed of 3-6 superimposed cells, 130-250 μ long; stem ca. 8-9 cells in vertical diam., with ca. 24-26 cortical rows of cells that are ± equal to medullary in diam., short-oblong to oblong-hexagonal, dorsally ca. (22)24-28(30) × 48-65(75) μ long (length-width ratio 1.5-3.2 : 1) *T. patagonicum* Schust.

8. Lamina of leaf 20-27 cells high, the mature leaves ± symmetric, only 0.2-0.25 quadrilobed (exclusive of cilia). Median cells ca. (13)15-19(20-22) × (16)18-30(35) μ, thick-walled, strongly verrucose. Cilia of leaves ± stiff and straight, dimorphic (the terminal 2-3.5 × as long as the lateral). [Leaves very oblique or subhorizontal]. (Java-Formosa-Philippines-Himalaya) *T. setigerum* (Lindenb.) Schust.

8*. Undivided (laminar) portion of leaf (5-)6-16 cells high, the mature leaves 0.25-0.4 quadrilobed (cilia omitted). Median cells of lamina ca. (17)19-28 × (32)40-75(90) μ or larger (except *T. townrowii*), 2-4 × as long as broad, slightly or moderately verrucose. Cilia usually not clearly dimorphic (except *T. townrowii*). (Australasia) 9

9. Plants vigorous, 2.2-3.5 mm wide on sterile stems, the stem 250-350 μ wide or more; leaves imbricate, ± asymmetrically 4-lobed (antical lobe ± shorter), bearing (30)35-55 cilia or more; each lobe of leaf usually with (2)3-4(5-6) pairs of cilia. Disc, to sinuses, 12-16 cells high, much broader than long; cilia stiff, straight, those of disc sides never reflexed. Perianth mouth with 60-70 cilia, each to 550-700 μ long. Branches all lateral-terminal . . . . . *T. pulchellum* (Hook.) Mitt.

9*. Plants small or medium in size, 1.15-1.8(1.9) mm wide, the stems 130-180 (200) μ wide; leaves distant or contiguous, with (6-8)10-24 cilia, near gynoecia to 24-35(45) cilia; each lobe of sterile leaves with 0-2 pairs of cilia. Disc usually (5)6-12 cells high; cilia in part tortuous or recurved, at least the lowermost. Perianth mouth with 35-40 cilia, 175-450 μ long. Some (or most) branches postical-intercalary 10

10. Leaf lamina strongly asymmetric, oblique, longer than wide, very unequally 4-fid (dorsal lobe small or obsolete, only 2-5 cells wide × 1-2 cells long 7, the other lobes also often small; lamina 17-25(28) cells broad on mature leaves × (5)6-8(9) cells high; cilia very long (to 800-835 μ) in relation to lamina, particularly on juvenile leaves, even on mature leaves longer cillia exceeding lamina in length; leaves rather concave adaxially, the setose and rather stiff cilia obliquely erect or ascending *T. angustifolium* Schust.

10*. Leaf lamina essentially symmetrically obdeltoid to reniform-obtrapezoidal in outline, wider than long (to apex of longest lobe), ± symmetrically 4-fid; lobes (mature leaves) triangular, (7)8-13 cells broad at base; lamina 28-35 cells wide (mature leaves) or more × (8)9-11(12-13) cells high; cilia moder-

ately long, the terminal of mature leaves not longer than length of lamina (to lobe tip); leaves nearly flat, both lamina and cilia widely patent 11

11. Cilia smooth and glistening, the basal 1-2 cells occasionally excepted, contrasted to the verrucose-striolate laminar cells; usually remote-leaved; mature leaves ± reniform, usually strongly succubous; with some postical branches; lobes broadly triangular; lateral disc margins with long, ± tortuous cilia; (4)5-9(10) oil-bodies per cell *T. paucisetigerum* Schust.

11*. Cilia dull, their cells striolate, roughened as are adjacent laminar cells; dense-leaved; mature leaves ± obtrapezoidal, subtransversely oriented; only lateral branches; lobes triangular, their lamina longer than broad; lateral disc margins with short, stiff, setose cilia 3-5 cells long usually; oil-bodies (2)3-6(7-8) per cell. . . . . *T. townrowii* Schust.

Artificial key to species of *Temnoma*

1. Leaf lobes gradually tapered into uniseriate distal portions (formed by 1-5[7] superimposed cells, usually only gradually differentiated from cells in lobes); apical cilia, if at all distinguishable, usually dull when dry, verruculose (if smooth, remainder of lamina smooth) their longest cells to 50-85[95] μ long [to 2.5-5(7) : 1]; lobes lanceolate or triangular-lanceolate to linear-lanceolate, at least 2 × as long as wide. Branching variable: in most species 2-3 branching types present 2

1*. Leaves ± copiously armed with highly differentiated, long, slender cilia, the longer terminal ones formed of 5-8 or more superimposed, strongly elongate (4-8 × as long as wide, up to 90-135 μ long) cells 7

2. Leaves highly reduced, the lobes uniseriate to base, inserted on a disc 2-3(-4) cells high × ca. 8 cells broad . . . . See *Archeophylla pungens*

2*. Lobes not uniseriate throughout (or, if so, rarely, at base with insertion 2-3 cells wide, and there with 1-2 smaller teeth) 3

3. Mature leaves of non-gynoecial regions with disc and lobes normally both edentate; isophyllous; leaves ± bisbifid, the median sinus usually deeper; lobes lanceolate-triangular, never acuminate, usually edentate; disc usually (7-8)9-12(14-17) cells high; lateral sinuses descending 0.35-0.55(0.6) leaf length . . . . . *T. quadrifidum* (Mitt.) Mitt.

3*. Mature sterile leaves all or in large part with teeth or cilia or laciniae of the disc margins (in extreme cases superficially 5-6-lobed); leaves equally quadrifid, usually for (0.5)0.6-0.85 of their length 4

4. Leaves of sterile stems with lobes edentate or towards base with 1-3(-4) pairs of short, stiff cilia or teeth; cuticle mostly ± distinctly roughened; anisophyllous, the underleaves ca. 0.5-0.75 size of lateral leaves; sometimes with Microlepidozia-type and/or Acromastigum-type and postical, intercalary branching. [Plants, if with leaves other than just 4-lobed, often spinescent in aspect] 5

4*. Leaves appearing dissolved into innumerable (28-85 per leaf) long cilia, each lobe with (3)4-5 to 7-8 pairs of slender, long cilia; cuticle (virtually) smooth;

nearly isophyllous; only with Frullania-type branching. [Perianth mouth with numerous, crowded cilia, often 3-5 cells long] 6

5. Lateral disc margins of some (rarely few) mature leaves with 1-2 slender, usually uniseriate teeth or cilia, arising well above base, the leaves never 5-6-lobed in aspect; leaves 0.5-0.65(0.7) quadrilobed, the lobes to 6-9 or to 9-14 cells wide, lanceolate but often acuminate; disc usually (5)6-9, occasionally to 9-14 cells high; perianth mouth wide open, with irregular, remote, few cilia, the longer 3-5 cells long; ♀ bracts 0.25-0.55 quadrilobed, ciliate . . . . . *T. palmatum* (Lindb. ex Pears.) Schust.

5*. Lateral disc margins at or near base, on one or both sides of disc, frequently with a large, lobelike tooth or lacinium, often reflexed, the leaves often incipiently 5-6-lobed; leaves (0.65)0.7-0.85 lobed, the lobes (2)3-7 cells wide at base usually, linear-lanceolate to setaceous-lanceolate; disc usually 2-6(7) cells high; perianth mouth ± contracted, with numerous, crowded, 1-3(4)-celled stiff teeth at mouth; ♀ bracts 0.65-0.75 quadrilobed, spinose-dentate . . . . . *T. quadripartitum* (Hook.) Mitt.

6. Leaves spinose-ciliate, each with (24)28-42 cilia, the longest of 3-6 superimposed cells, 130-250 μ long; cells within cilia to 40-52(60) μ long (length: width, 3-4 : 1); stem with cortical cells short-oblong (24-30 × 48-75; 1.5-3.5 : 1) . . . . . *T. patagonicum* Schust.

6*. Leaves copiously, longly ciliate, with 50-85 cilia each, the longest of 6-8 superimposed cells, 350-525 μ long; cells of cilia to 70-90 μ long or more (length: width, 4-7 : 1); stem with cortical cells narrowly oblong (18-20 × 72-130 μ; 4-7 : 1) . . . . . *T. pilosum* (Evans) Schust.

7. Plants whitish, without brownish pigment, hardly chlorophyllose, soft-textured; cells collenchymatous; leaves crispate, strongly concave, with erect lobes with recurved sides and sinuses
See *Trichotemnoma corrugatum* (Steph.) Schust.

7*. Plants chlorophyllose, usually ± brownish, firm; cells without trigones; sinuses not or weakly reflexed, the leaves not strongly crispate, flat to little concave, the lobes ± spreading 8

8. Leaf lamina 20-28 cells high. Leaves symmetrically 0.2-0.25 quadrilobed. Java-Formosa-Philippines . . . . . *T. setigerum* (Lindenb.) Schust.

8*. Leaf lamina, measured to sinuses, (5)6-16 cells high. Leaves symmetric to asymmetric. New Zealand-Tasmania-Australia 9

9. Disc of leaf 12-16 cells high, 40 cell rows broad or more; sterile leaves densely setigerous with 30-56 cilia. Plants 2.2-3.5 mm wide
T. pulchellum (Hook.) Mitt.

9*. Disc of leaf (5)6-12 cells high, 17-35 cells wide; leaves with (7-8)10-12 to 20-24 cilia on leaves of sterile stems. Plants smaller, under 2 mm wide 10

10. Leaves strongly asymmetrical, lamina 17-25(28) cells wide; terminal cilia of lobes conspicuously longer than lamina lying proxima of them. New Zealand . . . . . *T. angustifolium* Schust.

10*. Leaves symmetrical, lamina 28-35 cells wide on mature leaves; terminal cilia normally shorter than length of lamina from lobe apex to base of leaf 11

11. Cilia smooth and glistening, the basal 1-2 cells occasionally excepted, contrasted to the verrucose-striolate laminar cells; usually remote-leaved; mature leaves ± reniform, usually strongly succubous; with some postical branches; lobes broadly triangular; lateral disc margins with long, ± tortuous cilia; (4)5-9(10) oil-bodies per cell. New Zealand *T. paucisetigerum* Schust.

11*. Cilia dull, their cells striolate, roughened as are adjacent laminar cells; dense-leaved; mature leaves ± obtrapezoidal, subtransversely oriented; only lateral branches; lobes triangular, their lamina longer than broad; lateral disc margins with short, stiff, setose cilia 3-5 cells long usually; oil-bodies (2)3-6(7-8) per cell. Tasmania . . . . . *T. townrowii* Schust.

Subgenus **Temnoma** Mitt.

Plants usually vigorous, often to 3-3.5(4) mm wide, most often creeping to loosely prostrate in growth. *Branching* sparing, largely or exclusively lateral and of the Frullania-type, accompanied in some species by rare or sparing postical-intercalary (axillary) branching. *Leaves* moderately to conspicuously, succubously inserted, usually at an angle of 25-45°; when crowded, owing to development of short internodes, rarely subtransversely oriented; reniform-obtrapezoidal, broad, always shallowly quadrilobed, the sinuses extending down for only 0.2-0.4 of the length of the lamina, often asymmetrically lobed (antical lobe shorter, postical longer), showing an abrupt and conspicuous differentiation between the lamina and long, stiff, slender cilia; cells of lamina ± oblong, not more than 2-3.5× as long as wide (and in lobes mostly 1-2× as long as wide), distinctly verrucose to papillose-striolate, sharply contrasted to cells of the cilia; cells of cilia smooth (very rarely with vestigial ornamentation extending on to cilium bases), more thick-walled, strongly elongated (mostly 3.5-6× as long as wide, in part 90-110 μ long), when dry usually nitid; lobes rather broadly to very broadly triangular to ovate-triangular, abruptly going over into the uniseriate apices (formed usually by 5-8 elongated cells in a row, inserted on a base 2-4 cells wide); disc high, 9-25 cells high, often ± asymmetric. *Underleaves* usually relatively small : generally ca. 0.35-0.45 to 0.5-0.6 the area of the leaves, quadrilobed and ciliate like the leaves, always symmetric. Dioecious. *Bracts* copiously ciliate, like the ordinary leaves. *Perianth* usually relatively long and slender, obtusely prismatic-trigonous, very wide at mouth, with long and slender cilia at the mouth. *Spores* and *elaters* both small, subequal in diam.

TYPE. *Temnoma pulchellum* (Hook.) Mitt.

I have segregated a series of derivative species into the subg. *Temnoma*, as contrasted to another series of less specialized taxa which are placed in the subg. *Eotemnoma* (type: *T. quadrifidum*). The species of the subg. *Temnoma* differ from those of *Eotemnoma* chiefly in (*a*) the more restricted modes of branching, involving only lateral, Frullania-type branching, supplemented in some species by postical-

intercalary branching; (*b*) the highly differentiated cilia of the leaf margins, the leaf lobes ending in similar, sharply differentiated cilia, which are formed of narrow, usually thick-walled, elongated, smooth cells, as contrasted to the thinner-walled, much less or hardly elongated, papillose to striolate cells of the adjoining portions of the lamina [1]; (*c*) leaves tend to be more conspicuously succubously inserted and oriented, although in some forms of *T. paucisetigerum* and *T. townrowii* with shortened internodes, the leaves may appear almost transversely oriented; (*d*) leaves are much less deeply quadrilobed, if we consider the uniseriate differentiated distal cilia of the lobes to be marginal cilia rather than a portion of the lobe, per se; (*e*) spores are small, averaging subequal in diameter to the elaters.

By and large these distinctions sharply separate the species of the genus into two isolated complexes. However, with both *T. townrowii* and *T. pilosum* difficulties may be encountered.

The first, with the differentiated cilia of *Temnoma* s. str., has the cilia roughened as is true of the distal parts of the lobes of *Eotemnoma*; the latter species is an *Eotemnoma* in which the cilia have become relatively well differentiated, but the leaf lobes remain lanceolate and the leaf is more than 0.7 quadrilobed; the leaves remain subtransverse.

Associated with the more restricted branching patterns (lateral-intercalary branches, and terminal branches of the Acromastigum- and Microlepidozia-types do not occur in subg. *Temnoma*), subg. *Temnoma* also exhibits another notable and advanced feature : the leaves tend to become asymmetric. In all but *T. paucisetigerum* and *T. setigerum*, where a symmetric, obtrapezoidal-reniform disc is the rule, the other species all exhibit leaves which are slightly to strongly oblique, with the antical lobe shortest, the postical lobe longest. Such tendencies towards development of asymmetric leaves have also been noted (Schuster, 1961*a*) for the remotely allied Chaetophyllopsidaceae; in this group, however, asymmetry involves enlarged antical and reduced postical lobes.

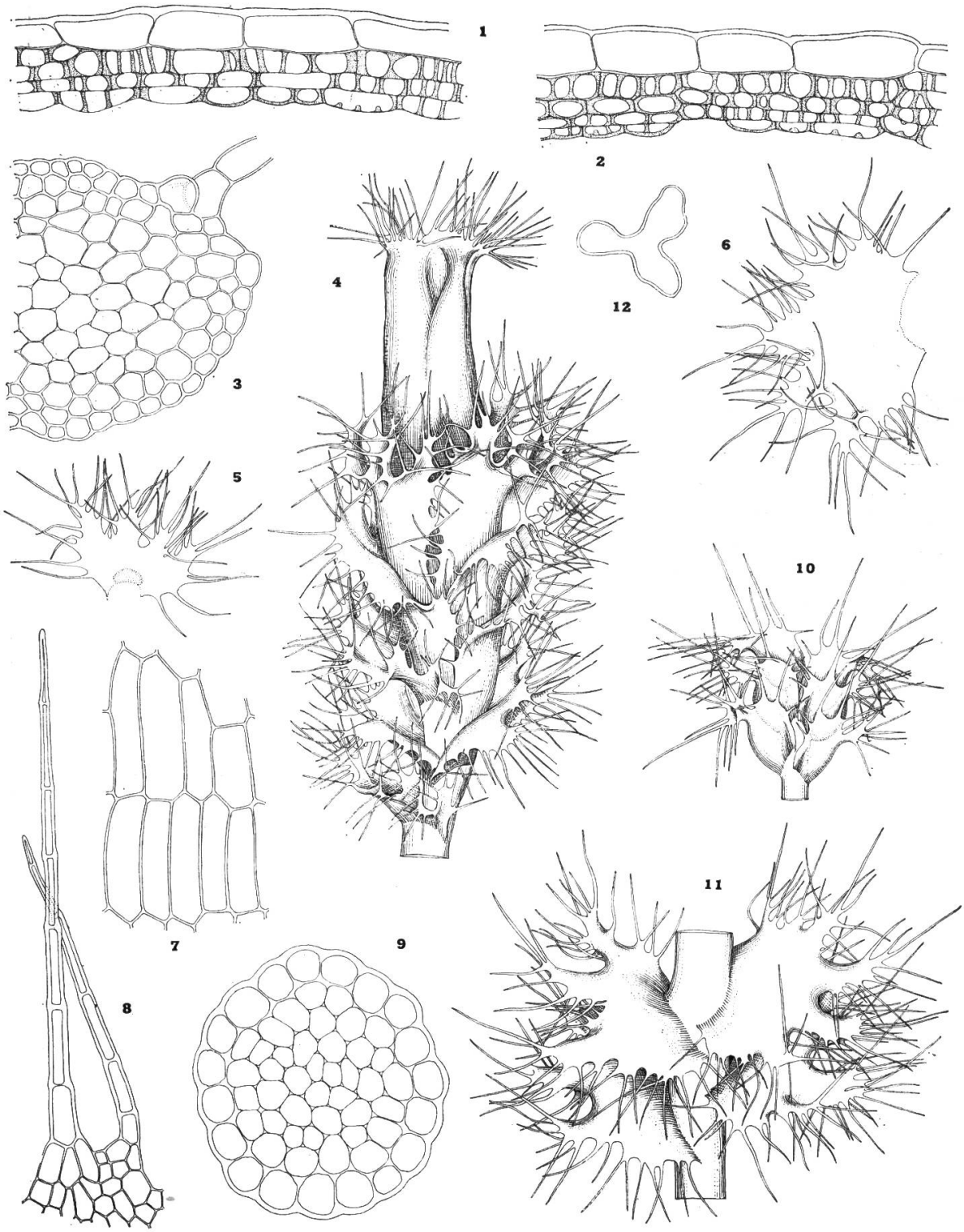
Temnoma pulchellum (Hook.) Mitt. [Figs. 22-24, 27 : 13].

Jungermannia pulchella Hook. Musci Exotici, pl. 94. 1818-20.
Temnoma pulchellum Mitt. in Hooker, Handb., N.Z. Fl. 2 : 753. 1867.
Blepharostoma pulchellum Carrington & Pearson, Proc. Roy. Soc. Tasm. 1887 : 50. 1888 (but erroneously attributed to Spruce).
Temnoma pulchellum Schust. The Bryologist 62 : 234. 1959.

[1] A slight transition is formed by *Temnoma townrowii* Schust., in which we find the highly differentiated cilia of *Temnoma* s. str., but the cilia are distinctly roughened, much like adjoining laminar cells.

FIG. 22. *Temnoma pulchellum* (Hook.) Mitt.

1-2. Cross-sections, capsule wall (×290). – 3. Stem cross-section (×120). – 4. Perianth-bearing shoot (×12). – 5. Underleaf (×18). – 6. Leaf (×18). – 7. Laminar cells above leaf base (×200). – 8. Setose cilia of leaf margin (×100). – 9. Seta cross-section (×212). – 10. Male bracts, in situ, from intercalary androecium (×12). – 11. Antical aspect of sector of sterile shoot (×18). – 12. Perianth cross-section (×18).
All from *Allison H 707*, Waipoua Ravine forest, North Island, N.Z.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Plants robust, 2.2-2.5 to 3.2-3.5 mm wide, to 4 mm near apices of fertile shoots, loosely creeping to suberect to loosely caespitose in growth, green to yellowish-brown, sparingly branched, branches almost exclusively lateral and terminal, of the Frullania-type, replacing the ventral half of a lateral leaf, very rarely and very sporadically with isolated postical, axillary branches. *Stems* ca. 250-300 μ high ×320-360 μ broad, brownish, somewhat translucent, relatively soft; cortical cells in 1-2 layers somewhat smaller in diam. than medullary, ca. 17-23 μ in diam., only slightly thick-walled, quadrangular to polygonal in cross-section, not tangentially flattened, strongly elongated and rectangulate, ca. 16-18(23)×(54)65-100 μ long (length 4-7[8]× width); medullary cells in 8-10 tiers, leptodermous, with angles slightly thickened, 25-36 μ in diam.; without fungal infection of the stem. *Leaves* ca. 925-1550 μ wide (without cilia; with cilia 1980-2650 μ) ×880-1000 μ long (with cilia 1450-1600 μ), somewhat larger on fertile shoots; leaves of sterile shoots moderately imbricate, distinctly succubously inserted (angle 35-45° from transverse), on upper parts of fertile shoots denser and subtransverse, transversely obtrapezoidal to reniform in outline, usually slightly oblique and somewhat but not strongly asymmetrical, somewhat narrowed to the base, quadrilobed for 0.35-0.40 their length (cilia omitted; with a weak tendency for elaboration of an accessory lobe of the antical and postical margins); disc usually somewhat asymmetric, shorter at antical sinus than postical sinus, usually 12-14(-16) cells high (from base to sinuses); sinus bases ± reflexed, carrying basal cilia with them, which become abaxially recurved; each margin of disc with (2)3-5(6) long, stiff, straight, uniseriate cilia which are never recurved; leaf as a whole (lobes and disc) with from 30-38 up to 50 cilia, depending on vigor of the plant, thus copiously ciliate. *Lobes* ± broadly triangular, sharply and conspicuously longly setose-ciliate (lobes each with [2]3-5[6] pairs of opposed cilia), with stiff, smooth, glossy setiform cilia 360-650 μ long, formed of generally 5-8 strongly elongated, thick-walled, rigid, smooth cells; cells of cilia smooth, 75-100 μ long ×10-12 μ wide (in upper, tapering portions of cilia) to 22-25 μ wide (in lower portions of cilia); sinuses somewhat rounded at base and narrowly but sharply reflexed. Lobes and undivided portions of leaves formed of slightly or hardly thick-walled, strongly elongated cells, partially aligned in regular tiers, the cells in the lobes and leaf middle averaging 18-23(26) μ wide ×(43-55)60-80(90) μ long; cuticle nearly smooth to moderately verrucose. *Oil-bodies* relatively small and numerous: median cells with (5)6-9 to (7)8-12(14-18) per cell, usually spherical or subspherical to short-ellipsoid, ca. 3.5-4.8×5.5-6.5 to 5-6×6-7 μ, sporadic ones to 6-7×7-7.5 μ, colorless, formed of minute spherules (externally faintly papillose),

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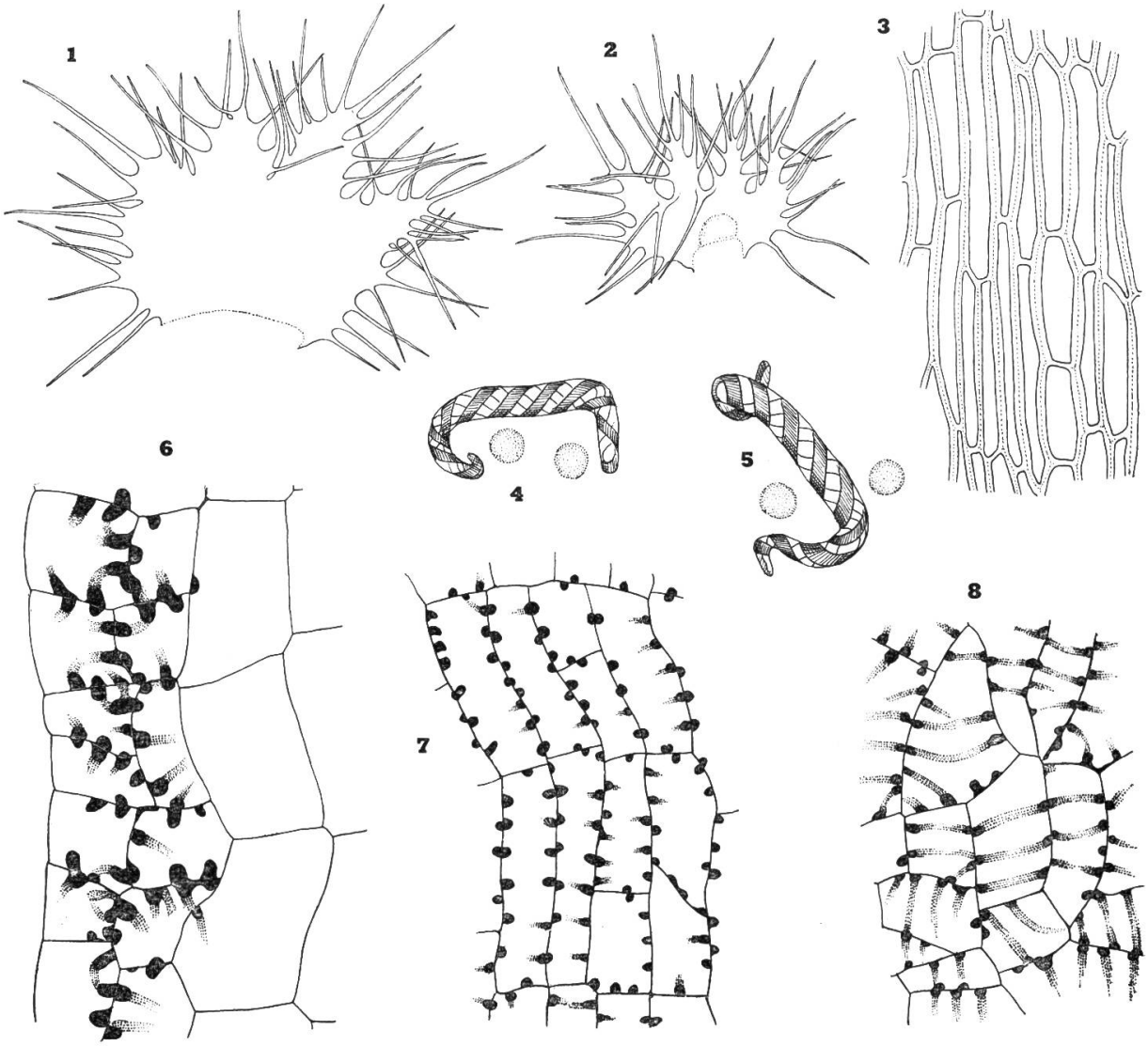
FIG. 23. *Temnoma pulchellum* (Hook.) Mitt.

1. Leaf of phase with nearly symmetric leaves (×24). – 2. Underleaf, same scale (×24). – 3. Cells of perianth middle (×182). – 4-5. Spores and elaters (×400). – 6. Cells of epidermal layer, capsule wall, along suture, showing radial thickening, somewhat tangentially extended, of 2-3 rows of cells peripheral to sutures, hyaline cells elsewhere (×400). – 7. Hypodermal cell layer, showing conspicuous nodular (radial) thickenings (×400). – 8. Cells of inner layer of cells of capsule, showing semiannular thickenings and relatively irregular cell form (×400).

All from *Allison H 707*, Waipoua Ravine forest, North Island, N.Z.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much larger than the minute chloroplasts. *Underleaves* moderately large, but averaging only one-half the size of the lateral leaves, similar in shape to lateral leaves and quadrifid like them, the margins similarly spinescent; underleaf size ca. 950 μ wide (without cilia; 1850 μ with cilia) and ca. 500 μ long (with cilia; with cilia 1000 μ). *Rhizoids* in distinct fascicles at the bases of the majority (sometimes all) of underleaves, absent from the stem, long and brownish, irregularly palmate or dendroid at the apices. Asexual reproduction lacking. Dioecious. *Androecia* becoming intercalary on leading, leafy shoots, of 6-10 or more pairs of rather closely imbricate bracts, somewhat more slender than vegetative portions of shoots (600-700 μ wide, without spines; 1900-2000 μ wide, with spines); *bracts* ventricose, somewhat spreading at base and the undivided portions then erect, only the 3-4 short lobes spreading to squarrose; lobes and margins near them strongly spinous-ciliate with setose cilia similar to those of the leaves. *Antheridia* (largely absent in material available) apparently 1-2 per bract; stalk apparently 2-seriate. *Gynoecia* terminal on leading shoots, without innovations (if fertilization occurs). *Bracts* erect and sheathing, narrowly obtrapezoidal, 1050-1200 μ wide (minus teeth) ×2100-2200 μ long (with cilia), quadrifid (or 5-6-lobed) for 0.2 their length like the leaves, the sinuses more strongly reflexed, the margins of the lobes and undivided leaf bases setigerous or spinescent like the leaf margins; lateral bract margins with 5-6 long cilia. *Bracteole* virtually like bracts. *Perianth* cylindrical, only weakly narrowed distally, to ca. 4 mm long, rather delicate, the mouth rather broad and truncate, densely setigerous and spinescent, similar to the leaf and bract margins; setose cilia and spines 60-70 per perianth mouth usually, polymorphous, the longer 550-700 μ long; perianth relatively elongated, terete below, strongly 3-plicate above, the plicae rounded; perianth composed of somewhat thick-walled, strongly elongated cells, the median cells averaging (13)15-18(20-24) μ wide ×(60)80-110(135-170) μ long (length ca. 4-12× the width); longer cells of cilia of mouth up to 65-75×15.5-17 μ.

Sporophyte with seta 150-165 μ in diam., formed of 19-20 rows of slightly larger epidermal cells that are distinctly collenchymatous, with thin interior walls but obviously thickened angles; inner cells in numerous rows; in 3-4 concentric tiers (seta thus 9-10 cells across); epidermal cells 23-27 μ in diam.; inner cells 16-20 μ in diam. *Capsule* very firm, ovoid-cylindrical, about 2-2.5× as long as broad, reddish-brown; valves straight, firm. Capsule wall 4-5 stratose, ca. 40-50 μ thick; epidermal cells very large, pellucid, colorless and devoid of thickenings (except in 2[3] rows adjacent to sutures, where with strong nodular to incomplete semiannular thickenings), irregularly rectangulate, 16-20(23) μ thick ×(25)35-40(60) μ wide, as thick or thicker than the two layers within combined; hypodermal layer of regularly

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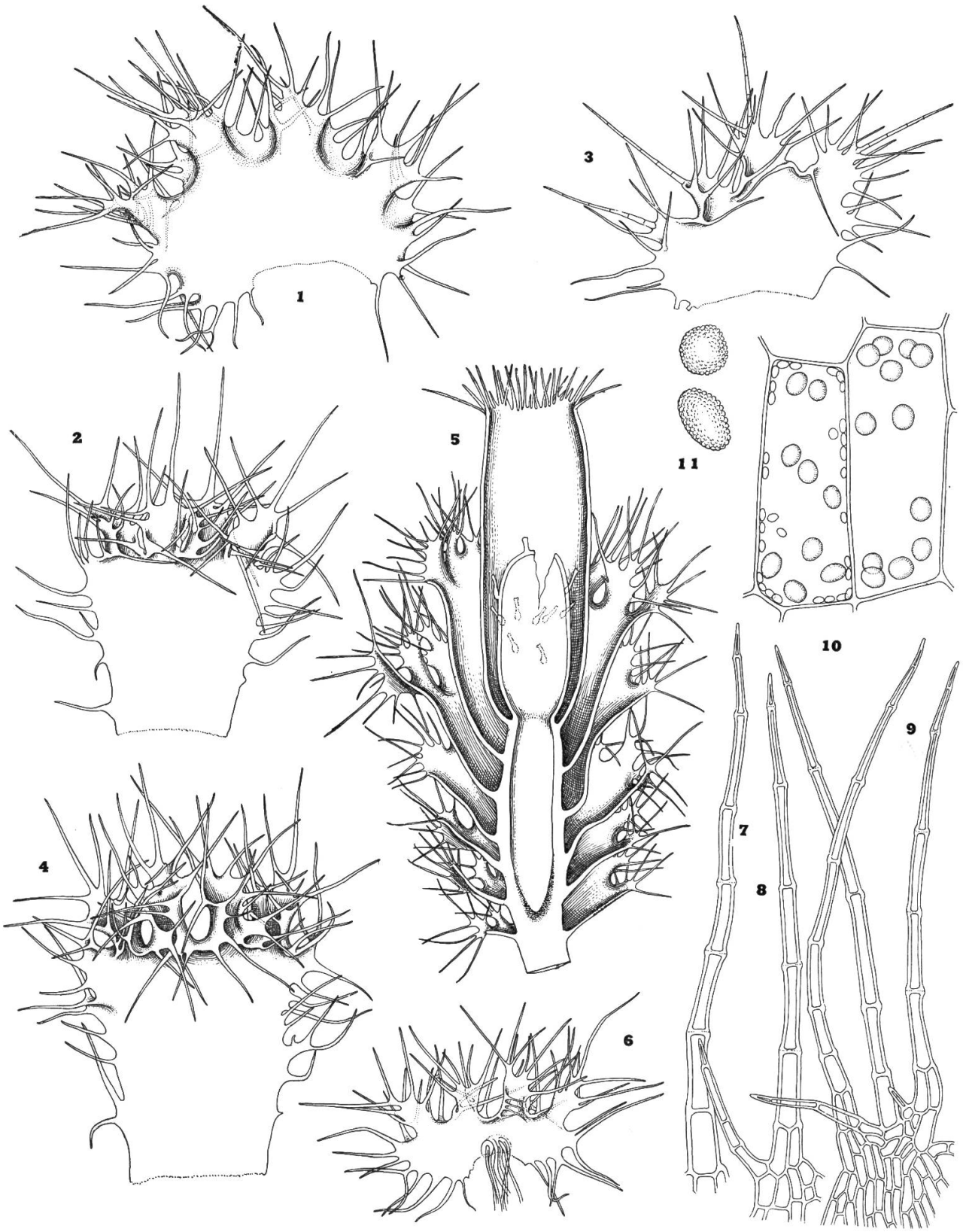
FIG. 24. *Temnoma pulchellum* (Hook.) Mitt.

1. Leaf, showing weak asymmetry (×22.5). – 2. Female bract (×22.5). – 3. Leaf of asymmetric extreme (×28). – 4. Female bract (×22.5). – 5. Longisection of perianth-bearing shoot, with sporophyte excised; apices of perianth mouth cilia partly cut off (×ca. 15). – 6. Underleaf and rhizoids (×22.5). – 7-8. Cilia of perianth mouth (×100). – 9. Perianth-mouth sector (×100). – 10. Cells of disc of leaf with oil-bodies and (at left) chloroplasts (×480). – 11. Two oil-bodies (×1460).

1, 4-8, from type, *leg. Hooker*, NY; 2,9, *Allison H 1580*, Waipoua, North Island, N.Z.; 3, *RMS 49451*, Hutt R., Wellington, N.Z.; 10-11, *RMS 52551*, Elizabeth I., Doubtful Sd., N.Z.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rectangulate, narrower cells, ca. 10 μ thick × 50-60 μ long (or 25-35 μ when subdivided) × 15 μ wide, with numerous reddish-brown nodular (radial) thickenings, but no, or vestigial, tangential extensions; innermost 2-3 layers somewhat variable in thickness : when with only 2 inner layers, these respectively 5-6 and 7 μ thick; when with 3 inner layers, the outer ca. 7 μ thick, and the inner two 4-5 or 5-6 μ thick; inner layers of very irregular cells, bearing numerous nodular to semiannular bands. *Elaters* rather sparingly produced, short and rather thick, bluntly pointed at the weakly tapering ends, 7.5-8.5 μ in diam. × 80-100 μ long, somewhat contorted, closely bispiral, the reddish spirals ca. 3 μ wide. *Spores* translucent, pale brown, weakly verruculose, 8.5-9.5 μ in diam., their diam. subequal to that of elaters.

TYPE. Dusky Sound, Fiordland Natl. Park, New Zealand, *D. Menzies, 1791.*

DISTRIBUTION. Found nearly throughout New Zealand, but—in spite of having been first collected in the southwest portion of the South Island—rare and sporadic in distribution in almost all of the South Island. The species is common in damp forests in the North Island, and can, in proper sites, usually be found in abundance and at will. NORTH ISLAND: Waipoua Forest, N Auckland Prov. *K. W. Allison H 1581, H 1583, H 1582, H 1580, H 660, H 707*; Waipoua Forest, between Dargaville and Opononi, *Lindauer H 1952*; Coromandel Peninsula, *L. J. Mathews H 1442*; base of Coromandel Peninsula, *J. M. Mitchell H 5218*; Hutt R., S Tararua Range, ca. 500 ft., ca. 10 mi. NE of Upper Hutt, *RMS 49451, 57380, 60252*; Little Barrier Island, on sharp ridge between Mt. Hauturu and Mt. Herekohu, in Quintinia-Ixerba-Meterosideros umbellata forest, 2100 ft., *RMS 51531, 51532*; S of Erua, along S facing slopes of Makatote R., Podocarp-Hardwood Forest, ca. 2200 ft., National Park-Wanganui Hwy. *RMS 50978*; Waitakere Mts., track through valley E of Piha, Auckland Prov. *RMS 51635*; Great Barrier Island, *Kirk 38, 43, 44, 207, 189*!, all at G; Auckland, inter Mniadelphum rotundifolium, *Cheeseman 361*, G; Waipoua Kauri Forest Preserve, near Cathedral Kauri Grove, in mature Kauri-Hardwood Forest, Hokianga Co. *RMS 51914*; Waipoua Kauri Forest, S of Opononi, in old, moist manuka scrub, *RMS 51906, 51908*; with Trichocolea lanata; N slope of Mt. Hauturu, Waima Forest, SE of Opononi, 1600-2000 ft., in disturbed Podocarp-Hardwood Forest, *RMS 51713, 51728*. SOUTH ISLAND: Bluff Hill, in bush among Chiloscyphus billardieri, *Allison H 5146* [1]; Secretary Island, Doubtful Sound, Fiordland Natl. Park, *Murray, s.n.*; Elizabeth Island, Doubtful Sound, Fiordland Natl. Park, *RMS 52851*; Westland, inter Blake's et Arahua, *Berggren 2814*; Taieri R. mouth, S of Dunedin, Otago Co., in shade amongst grass-forest remnant, *W. Martin H 558*. STEWART ISLAND: Pegasus, *Murray 2242*; along Pegasus Creek, and along small tributary of Pegasus Creek, ca. 50-250 ft. *RMS 59655, 50000a, 50001*; Port Adventure, E coast, near sea level, mixed Podocarp-Hardwood Forest, *RMS 49990, 49991.*

VARIATION AND DIFFERENTIATION. A " very elegant plant " which is " at once distinguished... by its beautifully ciliated leaves and stipules, which give

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[1] A specimen cited by Hodgson and Allison, from " Bush at head of Leith Stream, Dunedin, *Allison H 5582* " as *T. pulchellum*, consisting of a single plant, is *Trichocolea*, presumably *T. lanata*.

the whole plant, even when seen by the naked eye, a peculiarly tomentose appearance ". (Hooker 1818).

T. pulchellum is, surely, the most handsome species of the genus, and one of the most beautiful of the Jungermanniales. Although bearing close affinities to *T. paucisetigerum*, it is usually readily identified by the extraordinarily copious development of the cilia of leaves and underleaves—as Hooker noted so many years ago. In addition to immediate affinities to *T. paucisetigerum*, there are close relationships to *T. setigerum* and to the rare and local *T. angustifolium*. Affinities to other species hardly exist. In general, the extreme abundance of cilia—with mature vegetative leaves bearing 35-40 cilia or more—separates the species from all other *Temnomae*. Occasional weak phases of *T. pulchellum*, however, can make for difficulties.

The diagnosis (modified from Schuster, 1959; based on the type) was drawn largely from optimal phases of the species seen. Such plants show maximal development of cilia of the leaves and underleaves. Leaves, in such plants, generally possess 3-5 cilia per disc margin and 3-4 pairs of opposed cilia per lobe, in addition to the terminal cilium of each lobe. Thus a total of 36-45 cilia per leaf commonly occurs. Such phenotypes are easily separated by their more copious ciliation from the closely related *T. setigerum*, and from the smaller *T. paucisetigerum*, which always occurs with less copiously ciliate leaves. For example, in fertile plants of *T. paucisetigerum*—e.g., *RMS 48020* [Leith Valley] and *RMS 48103* [Moraine Cr., Hollyford Valley] each leaf lobe bears a maximum of 1-2 pairs of cilia, in addition to the terminal cilia of each lobe and 2-5 cilia of each leaf margin; thus a total of ca. 24-30 cilia per leaf may occur. On weaker (sterile) shoots there may be further reduction in cilium number; each lobe may possess merely the terminal cilium, with an occasional cilium of the sides of the lobe, and 1-3 cilia along each lateral leaf margin. Thus such leaves may bear a total of only 7-10 cilia.

The pauciciliate *T. paucisetigerum* closely approaches and may superficially match plants of *T. setigerum*. Nevertheless, both it and *T. pulchellum* have less extensive, undivided basal portions of the leaf, only 9-11 or 12-16 cells high to the sinuses (in *T. setigerum* 20-25 cells high usually), and the leaf cells are larger and tend to be more elongated (see Key). In addition, cells in *T. paucisetigerum* and *T. pulchellum* are provided with more numerous, smaller papillae, while *T. setigerum* bears fewer, coarser, closer papillae. On the basis of material seen, three closely allied but clearly distinct species are at hand, usually readily separable by the criteria used in the Key.

In all collections of *T. pulchellum* studied lateral, terminal, Frullania-type branching is frequent; this is, indeed, usually the only mode of branching to be found, exclusive of the subfloral innovations. However, in *T. paucisetigerum (RMS 48103)* I have found fertile and sterile plants which produce postical-intercalary branches!

T. pulchellum approaches *Trichotemnoma corrugatum* in that there is a tendency (quite lacking in *T. paucisetigerum*!) for leaves to become asymmetrical, the antical lobe being reduced in size " vis à vis " the ventral lobe. However, the degree of asymmetry is usually slight, and evident generally only on leaves dissected free, flattened under the cover glass. In its other characters (non-collenchymatous

cells, with more numerous, smaller oil-bodies; green to olive-green to somewhat brownish, rather deep coloration; the less reflexed sinuses of the leaves; the longer, more spinescent and setose cilia; the silkier appearance; the basically nearly flat, rather than concave leaves) *T. pulchellum* is very distinct from *Trichotemnoma corrugatum*. The degree of asymmetry of the leaves varies somewhat; it is at times hardly perceptible (as in the type), but may be quite notable (as in *RMS 49451*, Hutt R., North Island).

Although the distinctions separating *T. pulchellum* from *T. paucisetigerum* are largely quantitative (see Table 1 : 273, under *T. paucisetigerum*), the two species are very different in general appearance, the *T. pulchellum* being a much more vigorous, silky-appearing plant. Some of the significant characters of *T. pulchellum*, not previously alluded to, emerge clearly in this table.

Temnoma paucisetigerum Schust., spec. nov. [Figs. 25-27].

Folia remota ad contigua, succuba; *lamina folii* symmetrica, reniformia, 9-12 cellularum alt.; *folia* (7-8)10-12 ad 20-24 cilia habentia, cilium longissimum brevius quam lamina folii; *cilia* levia lucentiaque; *cellulae* ciliorum longiores ad 14-18 × 75-92 μ; nonnulli *rami* ventrali-intercalarii visi; *os perianthii* 35-40 cilia habens, cilia longiora 175-265 μ long.

TYPE. New Zealand: South Island: Moraine Creek, Hollyford Valley, *RMS 48103*. Type in herbarium of author, with schizotype in herb. G.

Similar in general aspect to a small, remote-leaved, lax *T. pulchellum*, but smaller in all its parts. *Shoots* (1100)1250-1400(1500-1900) μ wide with leaves, sporadically branched, with terminal, Frullania-type branches and relatively frequent postical-intercalary branches. *Stems* ca. 150-170(200) μ in diam.; cortical cells usually relatively short-oblong, averaging ca. 2.5-3.5(4.5) × as long as wide, only slightly thick-walled (16)17-20(21) × 52-78 μ to (13)15-17 × 65-80(100) μ, then up to 4-6 × as long as wide. *Leaves* remote or subcontiguous to weakly imbricate (less so than in *T. pulchellum*), somewhat succubously inserted, ± flat, regularly quadrilobed for 0.25-0.3 their length (cilia excluded), with a reniform-obtrapezoidal disc 9-12(13) cells high, quite perfectly symmetrical, ca. 30-35 cells wide (mature leaves), much wider than long, each lobe ending in a long cilium formed of (5)6-8(9) superimposed, highly elongated cells, the cilium ca. 375-400(520) μ long, its length approximately the length of the lobe and disc below it, but never conspicuously exceeding it on mature leaves; each lobe, in addition, with 0-1-2 pairs of cilia (the lowest situated near sinus bases and often abaxially displaced); lateral margins below lobes with 1-3(4-5) cilia, varying in length, the cilia in part ± tortuous or sinuous, the lowest sometimes recurved; leaf as a whole with (7-8)10-22 up to

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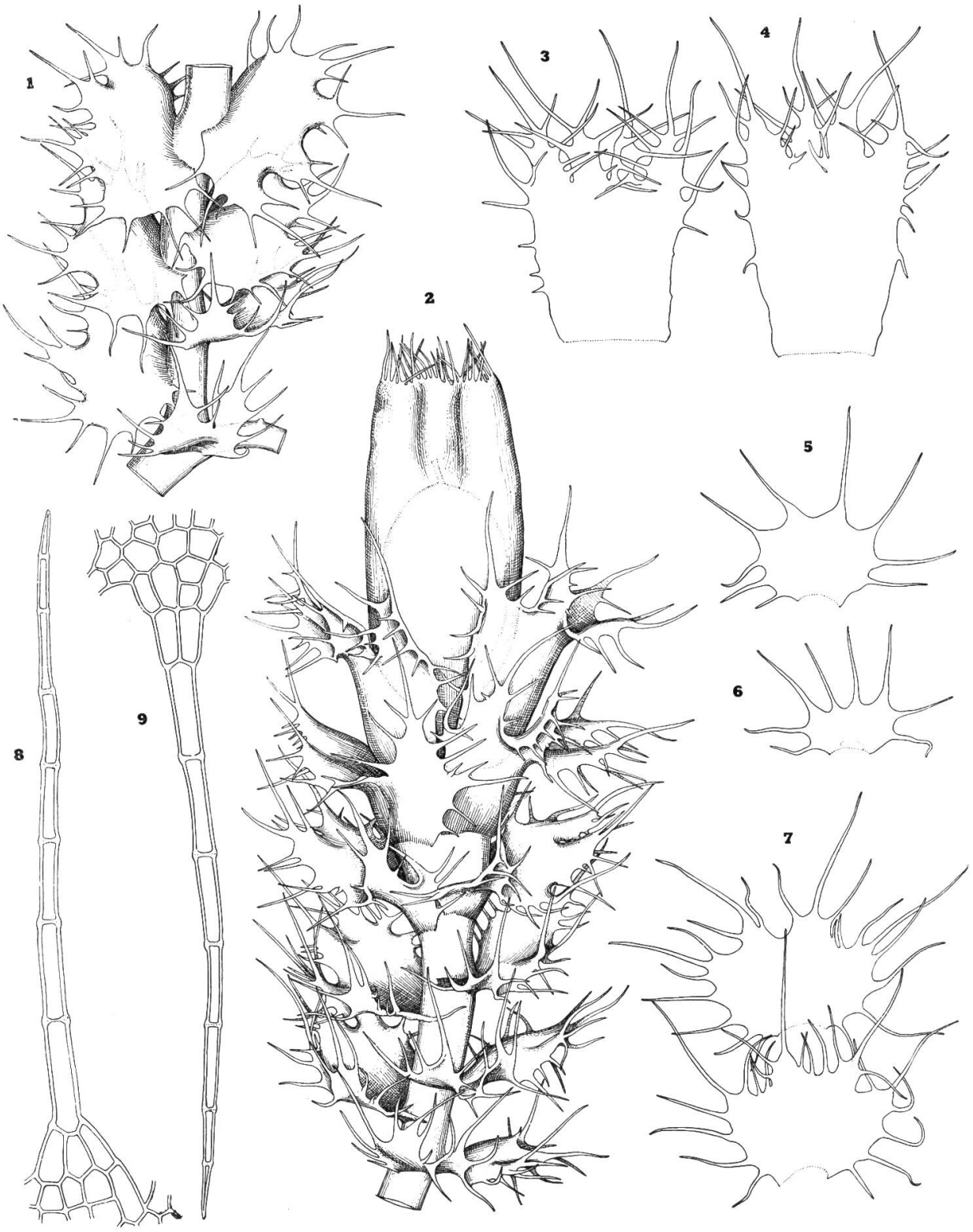
FIG. 25. *Temnoma paucisetigerum* Schust.

1. Shoot-sector with Frullania-type branch (×27). – 2. Fertile plant with mature perianth (×27). – 3. Female bract (×27). – 4. Bracteole (×27). – 5-6. Leaf and underleaf from sterile shoot (×27). – 7. Two leaves of optimal size with optimal cilium development (×27). – 8-9. Cilia of apices of leaf lobes (×144).

All from type, *RMS 48103*, Moraine Creek, Fiordland, N.Z.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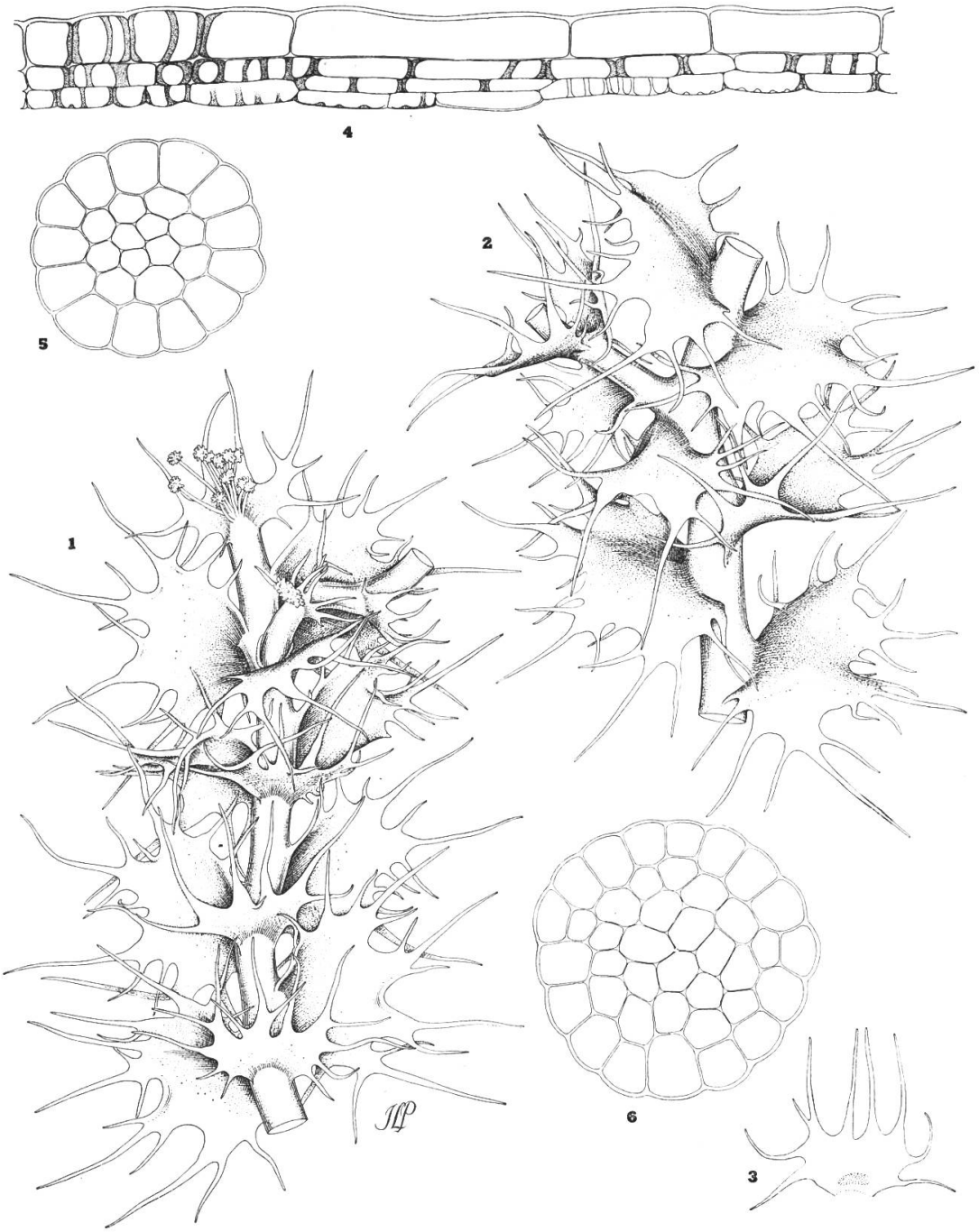
(gynoecial plants) 24-30 cilia; leaves of sterile stems ranging from (475)650-860 μ wide (disc only; with cilia (1050)1300-1450 μ wide) ×(875)1000-1150 μ long, occasionally slightly larger on ♀ plants near their apices; sinuses descending 0.25-0.3 disc length (measured from base of uniseriate cilia down), their bases not or obscurely reflexed, not carrying cilia with them (thus usually without cilia lying at a sharp angle to the leaf planes); lobes 9-13 cells wide at base. *Juvenile leaves* with a reniform-obtrapezoidal disc which is shallowly quadrilobed and ends in 4 long, setose, terminal cilia, with occasional accessory ones developed, quite symmetrical. *Cells* variable, on weaker leaves only short-oblong (in disc middle ca. [20-]25-30×40-65 μ to [16-17] 18-26×36-52 μ), slightly thick-walled; longer cells of cilia 14-16.5(18)×75-92 μ (4.5-6× as long as wide), thick-walled, usually smooth and glistening; cuticle distinctly to strongly and closely verruculose-striolate, except on cilia. *Oil-bodies* (4)5-8(9-10) per cell, smooth, faintly granulate in appearance, colorless, mostly spherical to short-ovoid, ca. 5-7 μ to 6.5-7×7-9.5 μ, a few to 6-7.5×11 μ, much larger than chloroplasts (which are ca. 2.8-3.3 μ). *Underleaves* ciliate like leaves, smaller, disc shorter and broader, more or less reniform to transversely oblong, the disc from 530 μ wide (with cilia 1050 μ) ×800 μ long (incl. cilia) to somewhat larger, usually quadrifid, sometimes trifid, each lobe ending in a long cilium. Dioecious. ♂ Plants more slender (ca. 1100-1250 μ wide) and with less freely ciliate leaves, the vegetative leaves reduced in size, the disc only obsoletely lobed, each of the 4 reduced lobes ending in a long, setaceous, rigid cilium; cilia otherwise absent or sometimes 1-2 per leaf lobe and, occasionally to often, 1-2 on each side of the disc (thus with a total of ca. 4-10 cilia only). *Androecia* intercalary, slender, ca. 750-900 μ wide (with cilia), usually of 4-5 pairs of contiguo-imbricate bracts; *bracts* closely appressed to the stem, subequal to leaves in size, the base ventricose, the antical margin of the disc incurved, the apices shallowly lobed and ciliate like vegetative leaves; *lobes* (and cilia) nearly erect to suberect, the lobes setaceous, slender. *Gynoecia*, if fertilized, lacking subfloral innovation, if unfertilized, with 1(2) subfloral innovations. *Bracts* erect, rather closely applied to perianth, narrowly obtrapezoidal in basic outline, ca. 725-815 μ wide distally (without cilia; apex of lamina) ×1625-1750 μ long (with cilia); quadrilobed for ca. 0.2 its length, the sinus bases and sides weakly or moderately reflexed; *lobes* pluriciliate, like leaf margins; margins of bracts, below lobes, each bearing 1-5 stiff, short teeth or short cilia, partly recurved and uncinate. *Perianth* about 0.5 emergent, bluntly trigonous, weakly contracted to the ciliate mouth; mouth bearing ca. 35-40 setose cilia of varying lengths, the longer 175-265 μ long, of ca. 5 superimposed cells; longer cells of cilia to 65-75×15.5-17 μ; *cells* in distal one-fourth of perianth somewhat thick-walled, oblong, but never sigmoid, ca. 14-18×55-88 μ. *Spores* 9-10 μ in diameter; *elaters* 8-10 μ in diameter ×70-90 μ long.

FIG. 26. *Temnoma paucisetigerum* Schust. (1-3) and *T. palmatum* var. *pseudospiniferum* Schust. (4-6).

1. Shoot-sector with ventral-intercalary branch (×30). – 2. Same, antical aspect, with Frullania-type terminal branch (×30). – 3. Underleaf (×22). – 4. Capsule-wall cross-section, at left margin the edge of the valve (×380). – 5. Small seta (×190). – 6. Large seta (×165). Figs. 1-3 from *RMS 48558*, Morrisons Cr., Dunedin, N.Z.; figs. 4-6, from *Berggren 2812*, Maungaroa, N.Z.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TYPE. New Zealand: South Island: Moraine Creek, Hollyford Valley, Fiordland Natl. Park, 400-650 ft. *RMS 48103*, c. capsules.

DISTRIBUTION. Widespread in New Zealand, although apparently most common in the South Island and southern part of the North Island.

PARATYPES. NORTH ISLAND: Mt. Egmont, E side, above treeline, 4500-5000 ft., *RMS 48802, 48804, 48807a*; E of Taupo, ca. 2000 ft. *K. W. Allison H 1598*; in " bush " beyond Rotorua, edge of Urewera Co. *K. W. Allison H 1957*; Old Mangaiti Rd. near Atiamuri, *K. W. Allison H 340*; bush near top of Tauhara Mt. near Taupo, ca. 3000 ft. *K. W. Allison H 1954*; Little Akatarawa Valley near Wellington, *H. M. Hodgson H 1953*; Puaiti Bush near Rotorua, *K. W. Allison H 1955*; Pukerimu Bush, ca. 2500 ft., E of Taupo, *K. W. Allison 559*; with fruit, Oct. 3, 1934; NW Ruahine Mts., ENE of Taihape, dissected limestone plateau W of Mt. Makiriki, 3500 ft. *RMS 54450, 52450a*, with T. palmatum. SOUTH ISLAND: Route Burn Track, Fiordland, *RMS 49471*; Moraine Creek, Hollyford Valley, Fiordland Natl. Park, 400-650 ft., *RMS 48103*, type; Morrisons Greek, Leith Valley, Dunedin, 350-450 ft. *RMS 48020, 48009a 48558*; head of Lake Tekapo, at edge of small creek, 4000 ft. *D. Scott 129*; Haast Pass, Otago Prov., ca. 1800 ft., in beech forest, *RMS 49723; RMS 53430; K. W. Allison H 5948*; Bealey R. near Arthurs Pass, *S. Berggren*, 1874; head of Lake Manapouri, Fiordland Natl. Park, *G. Simpson*, Jan. 8, 1947; Arthurs Pass, on floor of beech forest, *H. H. Allan H 381*; Akatone, S of Dunedin, *K. W. Allison H 5654*; Doubtful Sound, Deep Cove, on steep wet wooded slope near Helena Falls, 100-200 ft., Fiordland Natl. Park, *RMS 52766*, with Lejeunea, on moist rocks; ca. 1.5-2 mi. S of Wilmot Pass, between Lake Manapouri and Doubtful Sound, N of Spey R., ca. 1500 ft. *RMS 52661*, among type of T. palmatum var. cuneatum; Valley of the Waiho R., at Callery R. juncture, 3-4 mi. below mouth of Franz Josef Glacier, 400-700 ft. *RMS 59061*; Black Birch Brook, near The Hermitage, 2500 ft., Mt. Cook Natl. Park, *RMS 49664, 49658*; Steep cliffs ca. 0.6 mi. N of Haast Pass, Westland Prov., ca. 1700 ft. *RMS 59617b*, with Blepharidophyllum xiphophyllum; Otiro R. gorge, W of Arthurs Pass, ca. 1000-1200 ft. *RMS 48491a*.

ECOLOGY. Concurrent with its wide dispersal, this species occurs under a considerable ensemble of environmental conditions, usually on soil, or thin soil over rocks, often where partly or wholly shaded. Here often with *Isotachis lyallii*,

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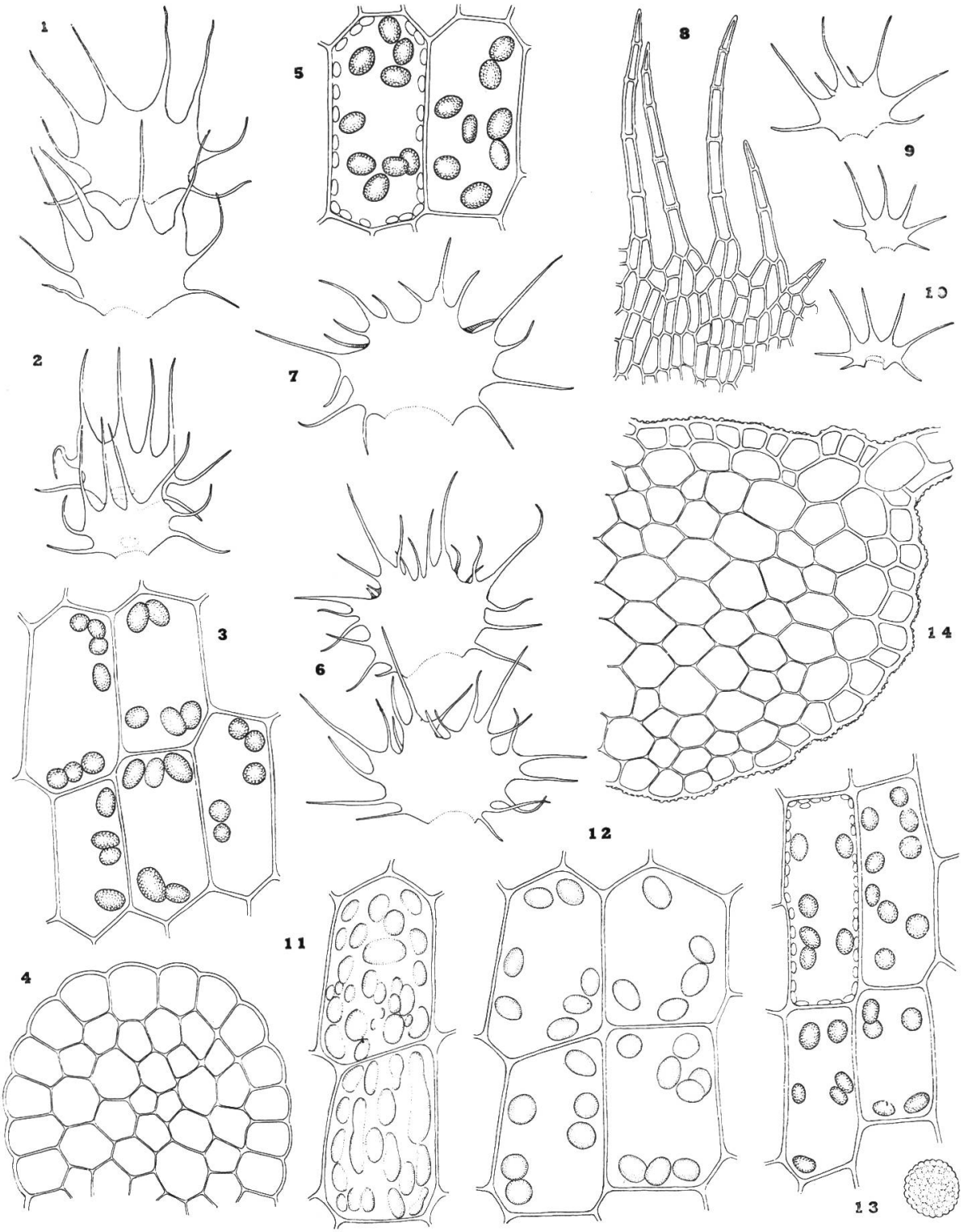
FIG. 27. *Temnoma paucisetigerum* (1-12); *T. pulchellum* (13); *T. setigerum* (14).

1-2. Leaves and underleaves (×22.5). – 3. Cells of disc, with oil-bodies (×442). – 4. Seta cross-section (×120). – 5. Two cells with oil-bodies and, at left, chloroplasts (×465). – 6-7. Three leaves, drawn to scale of *T. angustifolium* leaves in fig. 29: 3-7 (×25). – 8. Perianth-mouth sector (×126). – 9-10. Two branch leaves and a branch underleaf (×25). – 11. Two cells of disc, showing surface papillae (×612). – Cells with oil-bodies (×612). – 13. Cells of disc, with oil-bodies and (upper left) chloroplasts (×400) and a single oil-body drawn to larger scale (×1080). – 14. Stem cross-section (× ca. 175).

1-3, *RMS 49471*, Route Burn Track, Fiordland, N.Z.; 4, Moraine Creek, N.Z., *RMS 48103*; 5, *RMS 48558*, Leith Valley, Dunedin, N.Z.; 6-10, *RMS 48802*; 11-12, *RMS 48007a*, Mt. Egmont, N.Z.; 13, *RMS 49451*, Hutt R., Wellington, N.Z.; 14, Java, *Nyman*.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Trichocolea mollissima, *Haplomitrium gibbsiae*, etc. (Leith Valley, below 500 ft.) or with *Trichocolea mollissima*, *Lophocolea* sp., *Temnoma palmatum* (NW Ruahines, 3500 ft.). Occasionally growing subject to submersion in the mountains, in the Danthonia Zone (Mt. Egmont. 4500-5000 ft.), along rills, and around pools in such places, associated with *Temnoma quadrifidum*. Also (Humboldt Mts.) occasionally at or above treeline and associated with *Temnoma quadripartitum*.

VARIATION AND DIFFERENTIATION. One of the most malleable and difficult of the species in the genus, showing a tremendous range of variability. On one hand the ♀ plants may approach *T. pulchellum*, with which some phases agree in the shallowly lobed and broadly reniform leaves, developing 20-24 cilia (rarely more) which are highly differentiated. On the other hand, ♂ plants may be much more slender, with the leaf lobes reduced and each ending in a rigid cilium, but other cilia suppressed, or very few. Such plants bear no similarity to either ♂ or ♀ plants of *T. pulchellum*. *T. paucisetigerum* also develops compact forms with subtransverse leaves, and short internodes, which are habitually very different. Such forms may develop more deeply quadrifid leaves, with distinct leaf lobes. There is, equally, variation from plants with the nitid, glistening, smooth cilia of *T. pulchellum* to phases (such as *RMS 48807a*); where faint striolations extend on to the cilia. The leaves also show variation from a pauciciliate phase with the cilia all lying in the plane of the lamina, to extremes where the shorter cilia of the sinus bases are reflexed or displaced abaxially.

At the opposite point of the spectrum of variation lie small phases, which appear juvenile (such as *RMS 49724*, just S of Haast Pass, and *RMS 52766*, Doubtful Sound) but may produce scattered androecia. Smaller plants of such phases may have the disc reduced to a height of 1-1.5 cells, producing only 2-3 or 3-4 lobes which are, in effect, the uniseriate cilia produced at the tips of " normal " leaf lobes of more copiously developed phenotypes. Such small plants form a perfect model from which one can derive the Blepharostoma-type of organization ! Needless to say, identification of such phases hinges on finding an occasional stem which shows an approach to the more normal development of the species.

In spite of the development of such miniature extremes, *T. paucisetigerum* is closely allied to *T. pulchellum*, the generitype, and, for some time I was of the opinion that it simply represented a small phase of this species. However, the type (and some cotype) material freely bears perianths and capsules, so is quite mature. Furthermore, I have seen no material of typical *T. pulchellum* with the reduced, pauciciliate leaves of weaker shoots of *T. paucisetigerum*. Robust sterile plants of *T. paucisetigerum* are only 1150-1300 to 1200-1500 μ wide; in *T. pulchellum* 2200-2500 μ wide or more. Leaves of the former are 1.5-2 mm wide; in the latter 2.5-3 mm wide (cilia included). Stems of *T. paucisetigerum* are ca. 150-180 μ thick; in *T. pulchellum* ca. 250 μ thick or more. Cortical cells are often less elongated in *T. paucisetigerum*, averaging 17-20 × 52-78 μ; in *T. pulchellum* they average 16-18 × (54)65-100 μ. The whole plant in *T. paucisetigerum* gives a less tomentose, silky impression than that of *T. pulchellum*—thus has a quite different aspect. In all phases of *T. pulchellum* seen there is a vague to marked tendency for the leaves to be asymmetrical, while in *T. paucisetigerum* the leaves are always provided with

a symmetric disc and lobes. The cilia, per leaf, in *T. paucisetigerum* range from 7-10 per leaf (apical cilia included) to at most 12-18 or 20-24, on gynoecial plants rarely 24-30. In *T. pulchellum*, sterile plants have a minimum of 30-38 cilia each, more usually 35-45 per leaf. Associated with a sharp tendency for the leaves to have reflexed sinus bases, the cilia, in part, in *T. pulchellum*, are reflexed to the abaxial leaf surface; associated with this, the lobes spread widely, lying in the plane of the undivided disc of the leaf. By contrast, in typical *T. paucisetigerum* the sinuses are not or hardly reflexed, carrying no or few cilia with them (thus the cilia, with rare exceptions, all lie in the plane of the leaf); leaves are usually rather concave, with somewhat ascending lobes.

In the reduced number of cilia per leaf, and in general aspect, *T. paucisetigerum* closely agrees with *T. setigerum*. It differs from this species in (1) the larger leaf cells, with generally a more faintly verruculose cuticle; (2) the much shorter disc of the leaves, usually only 9-11 cells high from leaf base to sinuses. *T. paucisetigerum* and *T. pulchellum* are sufficiently similar so that the following comparison may prove useful in extreme cases. I am particularly impressed with the differences in the perianth mouth, that of *T. paucisetigerum* being armed with much shorter and fewer setose cilia.

Table 1. — A comparison of *Temnoma paucisetigerum* with *T. pulchellum*.

Character	*T. paucisetigerum* (Type material; ♀)	*T. pulchellum*
Width of shoot (mature sterile stem)	1150-1300(1500) μ	2200-2500 to 3200-3500 μ.
Branching	Terminal and postical intercalary	Usually all terminal
Stem diameter	150-160 to 160-200 μ	250 to 320-360 μ
Cortical cells	17-20 × 52-78 μ to (13) 15-17 × 65-80(100) μ	16-18(23) × (54)65-100 μ
Leaf shape	Perfectly symmetric	Somewhat to noticeably asymmetric
Leaf size (cilia incl.)	1.5-2 mm wide, or usually less	to 2.5-3 mm wide
Cilia per lobe	0-1(-2) pairs	2-3(-4) to 3-5 pairs
Cilia per leaf	7-10 up to 20-24, on ♀ shoots to 24-30(40-45 below ♀ bracts), some ± tortuous	30-38 up to 35-45 per leaf of sterile shoots, normally straight

Character	*T. paucisetigerum* (Type material: ♀)	*T. pulchellum*
Sinus bases of leaves	Hardly or not recurved	Strongly reflexed
♀ Bracts	Narrowly obtrapezoidal, 0.2 quadrilobed, 725-815 μ wide (without teeth) ×1625-1750 μ long (cum cilia); lateral margins with 1-5 sharp, short, partly recurved spines	Narrowly obtrapezoidal, 0.2 quadrilobed, 1050-1200 μ wide (without teeth) ×2100-2200 μ long (cum cilia); lateral margins with 5-6 long cilia
♀ Bract sinuses	Weakly reflexed	Strongly reflexed
Cilia, perianth mouth	35-40 per perianth, polymorphous; longer, 175-265 μ long, occasionally to 375 μ	60-70 per perianth, polymorphous; longer, 550-700 μ long
Longer cells of cilia of perianth mouth	Up to 150-170×15-18 (20) μ	Up to 65-75×15.5-17 μ
Cells below apex (distal ¼) of perianth	17-19×45-75 μ	14-18×55-88(110) μ

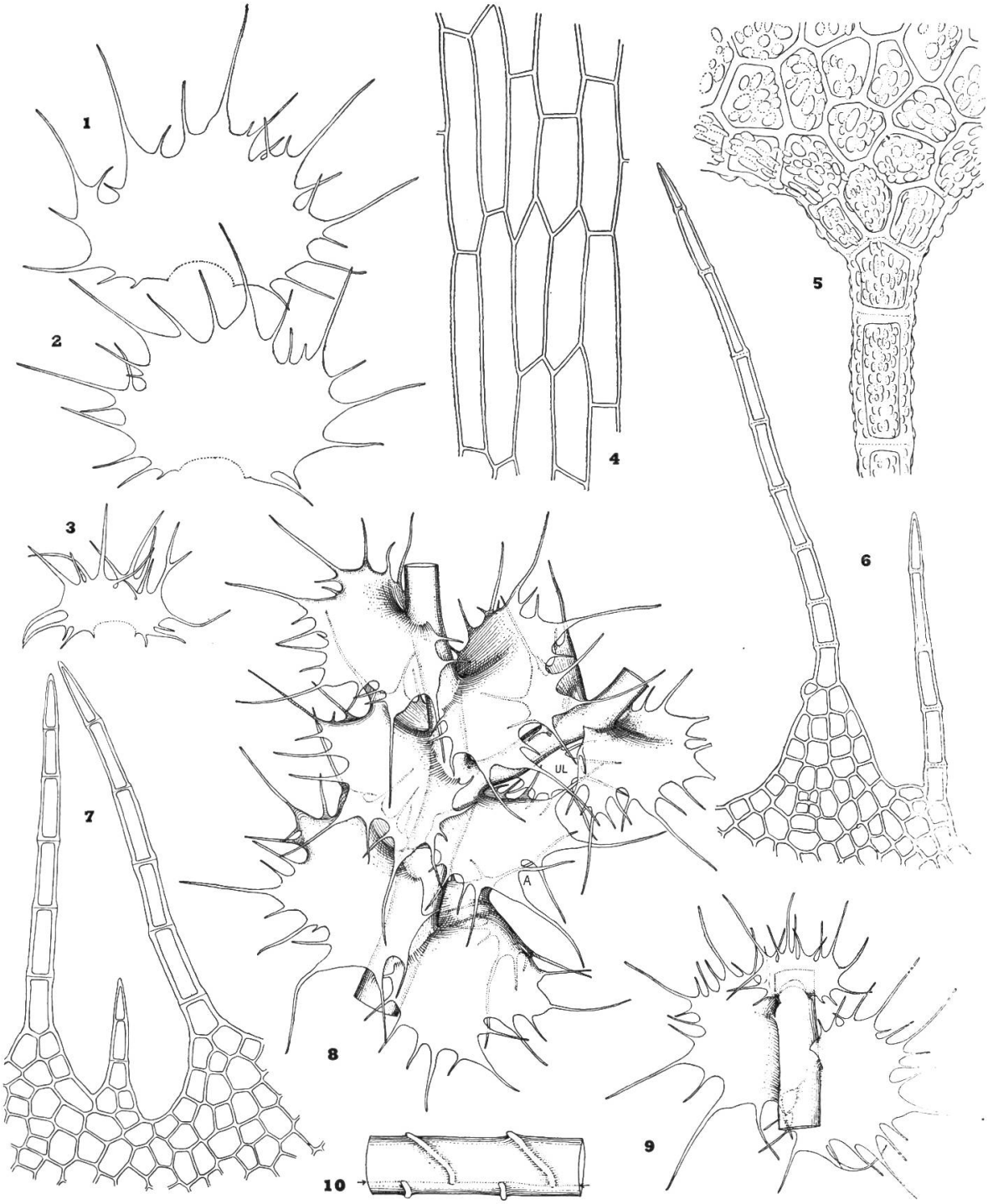
Temnoma setigerum (Lindenb.) Schust. [Figs. 27 : 14, 28].

Jungermannia setigera Lindenb., in G. L. & N., Syn. Hep. 131. 1844.
Blepharostoma setigerum Steph., Spec. Hep. 3 : 637. 1909.
Lophozia pilifera Horik., J. Jap. Bot. 12(1) : 20, fig. 9. 1936.
Temnoma setigerum Schust., Nova Hedwigia 5(1-2) : 35. 1963.

Plants rather slender, intricately interwoven, loosely prostrate, to 4 cm long ×(1.6)2.2-3.0 mm wide, sparingly branched; branches all of the Frullania-type, subtended by a reduced, bilobed leaf [1]. *Stem* (210)225-300 μ in diam., rather firm, slender and nearly terete; cortical cells strongly elongated, rectangulate, their radial

[1] Stephani (1909, : 638) misinterpreted the branching, stating it is axillary and from the postical portion of a leaf axil. All of the many lateral branches I have seen are definitely terminal, arising from near the lower angle of insertion of a bifid rather than quadrifid leaf; I have seen no postical branches.

FIG. 28. *Temnoma setigerum* (Lindenb.) Schust.
1-2. Stem leaves (×22.5). – 3. Underleaf (×22.5). – 4 Lateral cortical stem cells (×263). – 5. Leaf lobe apex with base of terminal cilium, showing cuticular ornamentation (×340). – 6. Leaf lobe apex with terminal and marginal cilium (×125). – 7. Cilia from sinus between two leaf lobes (×170). – 8. Shoot-sector with Frullania-type branch at right, a dorsal half-leaf at A, the first branch appendage an underleaf at UL (×20). – 9. Two leaves and an underleaf, in situ (×20). – 10. Shoot-sector, apex towards right, lateral aspect, showing oblique leaf insertion; boundary between lateral and ventral merophyte series indicated by stippled line and arrow (× ca. 25).
All from plants from Java, leg. *Nyman.*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walls slightly and evenly thickened, the free walls striolate (14)16-20(22) μ wide ×70-95(100-120) μ long (averaging 4-8× as long as broad). *Leaves* contiguous, nearly plane, very widely spreading, obtrapezoidal-reniform in outline, averaging (1000)1250-1350 μ wide ×(680)800-850 μ long without cilia ([2000]2100-2200 μ wide ×[1200]1275-1400 μ wide with cilia), very strongly succubously inserted and oriented, shallowly and obscurely but ± symmetrically 4-lobed or 5-lobed (divided for 0.2-0.25, rarely 0.35 the length of the leaf, without cilia; basal undivided portion 20-27 cells high to the sinuses), nearly plane, the sinuses not reflexed or gibbose; lobes broadly triangular, each beset with a long, stiff terminal cilium usually 8-10 cells long (length ca. 450-600 μ), and usually with a pair of nearly opposed, much shorter (100-220 μ) cilia along their sides, occasionally with 3 or 4 cilia per lobe; antical and postical leaf margins below the lobes with (1)2-3 additional cilia (the leaf as a whole usually with 18-25 cilia). *Cells* small, thick-walled: the apical cells 18-21 μ, subquadrate, the median ca. 17-22(23) μ wide ×23-30(35) μ long, averaging only 1.2-1.8× as long as wide, short-rectangulate, rather opaque because of the close, coarse, cuticular papillae; basal cells hardly larger, ca. 19-24×(26)32-45 μ; cells of cilia thick-walled, the intervening septae swollen externally, the cells averaging 60-80 μ long (occasional cells to 110 μ) ×13-17 μ wide. *Underleaves* averaging 0.3-0.4 the size of the leaves, reniform, similar in shape to the leaves, inserted by an arcuate line, with a poorly defined, reniform, rhizoid-initial region of small cells at the base (which may freely develop rhizoids); underleaves to 550-580 μ wide ×300-325 μ long without cilia (ca. 1100×650 μ with cilia), very obscurely and shallowly 4-lobed, each of the shallow lobes with (2)3-4 cilia, the underleaf as a whole with 14-20 stiff, setose cilia. Dioecious. Young (unfertilized) *gynoecia* terminal on main shoots, with 1-2(-3) subfloral innovations.

Known only from material with young *gynoecia*.

DISTRIBUTION. Java (Junghuhn, Haskarl; type material); the preceding diagnosis and the following discussion based on a study of the Nyman material [Java; without specific locality] in the Stephani herbarium (G; Farlow Herbarium). I have also seen a specimen from Java (Pangerango), July 16, 1897, *Nyman*; V).

Also reported from several localities in the Philippines (Grolle, 1964), from Formosa (see under f. *piliferum*), and supposedly occurring in the Himalayas (according to a communication from Dr. H. Inoue).

Temnoma setigerum is a distinctive species; it possesses the most shallowly lobed leaves of any member of the genus and, indeed, of the family.

Leaves are shaped basically as in *T. pulchellum* and show the same, sharp differentiation of long-celled, stiff, setose cilia which are very clearly distinct from the much more nearly isodiametric, smaller cells at their bases. In both species the longer cells of the seta may average up to 80-110 μ long × only 12-17 μ wide (near the bases of the cilia to 24 μ wide). *T. setigerum* also agrees with *T. pulchellum* in the strongly succubous leaf insertion and in the strong anisophylly (underleaves averaging hardly half the area of the leaves). Indeed, the two species are closely allied and deserve to be placed into a single section. Diagnostic of this group, as well, is the exclusively terminal, Frullania-type branching (although unfertilized gynoecia may possess innovations).

T. setigerum differs from *T. pulchellum* in several not wholly reliable vegetative features, among the more important are the following: (1) *Leaves* are more shallowly lobed, with the undivided leaf base 20-27 cells high, up to the sinuses; indeed, at first glance, the leaves look basically reniform in shape, with margins beset with stiff, bristly cilia of varying length. Closer inspection reveals that the leaves are basically symmetrically 4-5-lobed for up to a maximum of 0.25-0.3 of their length, each of the broadly triangular lobes ending in a long cilium and bearing on each side, often nearly opposed to each other, a single, shorter cilium. Not infrequently one or rarely two additional cilia of the lobes are developed, but the normal number is a single pair, in addition to the longer terminal cilium; the margins of the leaf, below the lobes, bear an additional 2-3 cilia each; the total number of cilia does not exceed 20-25 per leaf. (2) *Cells* are more opaque, owing to their smaller size, often thicker walls, and particularly because of the coarse, prominent papillae which their free faces develop. In *T. pulchellum*, leaf cells below the lobes are more elongate, thin-walled, larger and delicately to moderately papillose; they vary from about (18)20-28 μ wide × (40)48-75, occasionally 100 μ long, with the surface area averaging at least 1200-1500 μ². By contrast, *T. setigerum* has thick-walled, subquadrate to short-rectangulate cells that vary from ca. 17-22, rarely 22-23 μ wide × 23-30(35) μ long, the surface area averaging about 500-650 μ² (or only $^1/_3$-$^1/_2$ that in *T. pulchellum*). (3) *Cilia* of the leaves are clearly dimorphic, as to length; the leading lobes end in cilia which average 2-3 × as long as the remaining cilia of the lobe bases and disc margins.

In several respects, *T. setigerum* is closely allied to the new species *T. paucisetigerum* (: 226). For example, both taxa possess leaves with fewer cilia than are formed in *T. pulchellum*—the number ranging usually below 25 per leaf. Furthermore, almost all phases of *T. pulchellum*, from all environmental niches in which I have seen it, have distinctly imbricate leaves; in both *T. paucisetigerum* and *T. setigerum* the leaves are distant to contiguous, and hardly ever perceptibly imbricate. Two obvious distinctions separate *T. setigerum* from *T. paucisetigerum*: (1) the disc of the leaves is much higher (it is usually no more than 10-12 cells high in *T. paucisetigerum*); branching would appear to be almost exclusively of the Frullania-type, as in *T. pulchellum* (in *T. paucisetigerum* postical-intercalary branches are always to be found). Furthermore, *T. paucisetigerum*, like *T. pulchellum*, has the setose cilia of the leaves, although variable in length, not belonging to two discernible size groups.

The relationships of *T. setigerum*, as a whole, are thus complex, and although the species has clear affinites to both of those alluded to above (*T. pulchellum*, *T. paucisetigerum*), it is adequately distinct from them.

Temnoma setigerum f. **piliferum** (Horik.) Schust., comb. n.

Lophozia pilifera Horik., J. Jap. Bot. 12(1) : 20, fig. 9. 1936.

Plants rather robust, rigid, yellow-green (when dead), 2.4 mm wide with leaves, to ca. 3.5 cm long, epiphyllous on leaves of ferns. Stem ca. 220 μ in diam., simple or subsimple, brownish. *Leaves* remote to subcontiguous, strongly succubous and very obliquely inserted, distichous, broadly reniform-semicordate, 1.6 mm wide × 1.2 mm long, 4-lobed, with occasionally a secondary fifth lobe

produced, divided for ca. 0.25-0.3 their length (cilia omitted), lobes broadly triangular, each bearing from (3)5-8 lateral, short cilia, usually 3-5 cells long, which are distinctly shorter (usually 0.3-0.5 as long only) than the long, terminal, setaceous cilia crowning each lobe. Terminal *cilia* of ca. 8-9 superimposed cells, the longest cells 4-5× as long as wide. In addition, lateral disc margins with ca. 6-9 cilia of varying length on each margin, thus the leaf as a whole with ca. 42-56 cilia. Apical *cells* of lobes only ca. 15×18 μ; median cells ca. 18×33 μ, ranging basally to ca. 18×45 μ; walls distinctly, evenly thick-walled; cuticle densely covered with conspicuous, elongated, elliptical to linear-elliptical papillae. *Underleaves* large, ca. 600 μ wide ×700 μ long, shallowly 2-4-lobed and bearing (as a whole) ca. 30-35 cilia and ciliiform teeth, the cilia of the lobe apices markedly longer. *Rhizoids* frequent from underleaf bases.

Otherwise unknown.

TYPE. Formosa: Mt. Taihazan, Taihoku Province (*S. Matsuura*, Oct. 10. 1934); herb. Hiroshima Univ.

The type, the only specimen known, was collected from the fronds of a *Hymenophyllum*—a habitat paralleled by the occurrence, in New Zealand, of the related *T. paucisetigerum* on fern fronds.

This plant was overlooked for some years, during the early stages of preparation of this monograph. The reasons for this are two-fold: I did not think the genus occurred well into the Northern Hemisphere, and hence was not prepared to search the literature of Northern Hemisphere Hepaticae; secondly, I hardly expected that a species of *Temnoma* would have been described by anyone conversant with the Hepaticae under the wholly unallied genus *Lophozia*!

Horikawa states his " new species is most easily distinguished by the ciliated leaves and epiphyllous habit ". If the plant is erroneously referred to *Lophozia*, it is surely distinct from that genus in these criteria; in *Temnoma* these are no distinctions at all.

Working from the brief diagnosis and the somewhat more meaningful figures, it is clear that a *Temnoma* of the *T. pulchellum* complex is at hand. *T. setigerum* fo. *piliferum* differs, judging from the illustrations, from the Australasian members of the complex (*T. pulchellum*, *paucisetigerum* and *angustifolium*) in the rather strong dimorphism in cilium length. Thus, the leaf lobes end in cilia ca. 8-9 cells long, while the cilia arising from the margins of the lobes are only 3-5-celled (and formed of shorter cells, so that the lateral cilia are only 0.3-0.5 the length of the terminal cilia). A rather similar but apparently hardly as strongly marked discrepancy in cilium length occurs in typical *T. setigerum* (see Fig. 28 : 1-2, 6-9), and it is with this taxon that " *L. pilifera* " bears the most immediate affinity. The two agree in the symmetric, rather reniform-obtrapezoidal leaves, their shallow lobing, the dimorphic cilia of the leaves, the small, rather rigid, coarsely verrucose leaf cells and in the high disc of the leaves.

Whether the Formosan *T. setigerum* fo. *piliferum* will prove to be distinguishable from typical Javan *T. setigerum* remains an open question, in the absence of adequate material. The few collections I have seen of the *T. setigerum-piliferum* complex fall into two recognizable units: the fewer-ciliated Javanese *T. setigerum* and the

pluriciliate Formosan *T. setigerum* fo. *piliferum*. Studies of the abundant New Zealand members of the complex suggest this distinction may not prove adequate.

Temnoma angustifolium, Schust. spec. nov. [Fig. 29].

Lamina folii valde asymmetrica, obliqua, longior quam lata, impariter 4-fida (lobis dorsalibus parvis obsoletisve, 2-5 cellularum lat. ×1-2 cellularum long., cilio apicali excepto); lamina 17-28 cellularum lat. ×(5)6-8(9) cellularum alt., cilia levia lucentiaque, longissima (usque ad 800-835 μ), longiora quam lamina folii; cellulae in ciliis usque ad 18×130-160 μ. Typus: Otupae, Taihape, NW Ruahine Mts., New Zealand (*Hodgson 666*).

Plants brownish, loosely prostrate to ascending to suberect in growth, moderate in size; shoots, including the extraordinarily long, setigerous cilia, (1000)1100-1800 (2000) μ wide × ca. 2-4 cm long, sparingly, irregularly branched; branches terminal, of the Frullania-type and postical, intercalary only. *Stems* yellow-brown, to 180-220 μ in diam.; dorsal cortical cells strongly elongated, ca. 23-26×125-210 μ (5-8: 1), slightly thick-walled, regularly rectangulate, with yellow-brown walls. *Leaves* quite succubously inserted, weakly to moderately imbricate, rather concave usually, the lobes and the long cilia usually directed forward (the leaf orientation thus at times appearing subtransverse, in contrast to its insertion), normally very strongly asymmetrically quadrilobed, the dorsal distinctly 1-2 lobed, often greatly reduced in size (except, occasionally, on very large leaves), ca. 0.2-0.25(0.3) quadrilobed (omitting the uniseriate cilia), but the antical lobe frequently so reduced that the leaf approaches a trifid condition; disc normally strongly asymmetrical, oblique, ca. 375-475 up to 600-640 μ wide ×500(650) μ long (including lobes but not terminal cilia), posterior margin much longer than the anterior (ca. 600 vs. 440 μ on ordinary leaves), the width of disc (at level of apex of dorsal lobe) usually inferior to the length; disc ca. 17-25(28) cells wide only, its length (5)6-7(8-9) cells to sinuses; lobes asymmetric, the postical two usually larger, ca. 4-6 cells wide at base, the antical often obscure and only 1-2 cells long and 2-3(-5) cells broad at base, the lobes each ending in an extremely long, setose hair (650-835 μ long, thus much longer than the leaf lamina lying below) and with at most 2-3(-4), or 1-2 pairs, of shorter setose cilia per lobe margin; sides of lamina each usually with 1-2 long, setose cilia, often a little tortuous but not usually recurved, usually ca. 330-500 μ long; sinuses V-shaped with rounded bases, normally not or obscurely gibbous, without cilia (and thus without abaxially displaced cilia); leaves of sterile stems ranging from ca. 1650-1800 μ wide (total width, cilia included) to 1200-1300 μ long (cilia included), by far the maximal area covered by the cilia, the disc relatively small. Total number of cilia per leaf ca. 18-21. Juvenile leaves with disc becoming greatly reduced, only 150-160 μ high (2-3 cells long ×6-8 cells wide), but the setose cilia remaining very long, ca. 600 μ long, few (often only terminating the 4 lobes; other 0-4 usually). *Cilia* of lobe apices formed of up to 6-8 cells; cells smooth, highly differentiated, linear, very thick-walled, up to 130-160 μ ×18 μ (7-9: 1), dilated at the septae. *Cells* of lamina large, somewhat, but quite evenly, thick-walled, closely and moderately strongly verrucose-striolate, averaging (25)26-29(30)×(45)55-65(70) μ in middle of disc. *Underleaves* symmetrical, smaller than lateral leaves, with greatly reduced disc, which is broadly reniform-

obtrapezoidal, from ca. 360-420 μ wide ×120-170 μ high, to 775 μ wide, only ca. 3 cells high (to sinuses) and ± symmetrically quadrifid, each short lobe only 2-4 cells wide ×2-3 cells long; each lobe bearing 1-3 long, stiff, setose cilia, the terminal one longest (to 650-775 μ long, thus 4-5× the height of lamina; formed of 6-8 cells); cilia per underleaf as a whole ca. 10-14, occasional ones bifurcate; underleaf as a whole, cilia included, ca. 875-950 μ long ×1150-1325 μ wide.

Otherwise unknown.

TYPE. New Zealand: North Island (" Side of gorge, Otupae, Taihape ", NW Ruahine Mts., *E. A. Hodgson*, March 1932, *No. 666*). Known only from the scanty type material, which was cited in Hodgson and Allison (1962) as part of their " *Temnoma palmatum* ". Type in herb. of author: portions of the type number in herb. K. W. Allison; E. A. Hodgson; Geneva.

T. angustifolium is, in many respects, an extraordinary species. The trifid, smallest leaves, with cilia 300 μ long, have the lamina of 3-6 cells only. Other small leaves, may have cilia fully 600 μ long, even though the rudimentary lamina is only 150-160 μ high (2-3 cells high ×6-8 cells wide). Such leaves show the greatest degree of lamina-reduction I have seen anywhere within the genus. Plants with such leaves have a distinctly Blepharostoma-like aspect, bearing three or four long, setose lobes, often with no accessory lobes. From these there is gradual gradation to the mature leaves, which still show a relatively poorly developed lamina (for the subg. *Temnoma*), consisting of a generally very oblique lamina perhaps 17-25(28) cells wide and only 5-7 up to 7-9 cells long from base to the sinuses. The extraordinary asymmetric form of the leaf is well marked even on most small leaves, and is distinct on all mature leaves—only an occasional leaf having a tolerably well-developed dorsal lobe. I have seen no other species of the genus where, on mature leaves, the dorsal lobe may be only 2-5 cells wide at base ×1-2 cells long—usually ending in a single, abrupt seta (or at most with 1-2 setae arising at the base, at juncture of lobe with the undivided disc). On most leaves the length of the extremely oblique lamina of the leaf, measured from the base to the apex of the longest lobe (i.e., maximal length of leaf) is clearly in excess of the maximal width; average measurements are 500-600 μ long ×375-475 μ wide. The terminal setose cilia of the longer lobes, which attain a length of from 550-600 μ to 650-835 μ, are thus longer than the leaf lamina that bears them—a unique condition in the genus.

Branching in this species is, as in the related *T. paucisetigerum*, by means of intermingled, sparing, terminal branches of the Frullania-type (dorsal half of stem leaf preserved) and by postical-intercalary branches. There are at least as many of the last type produced as terminal branches. In this, and other respects, the

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FIG. 29. *Temnoma angustifolium* Schust.

1. Mature sterile shoot-apex (×33). – 2. Juvenile shoot-sector, lateral aspect, showing the diagnostically setigerous leaves with reduced disc (×29). – 3-5. Medium-sized leaves (×25). – 6-7. Leaves of optimal size, the dorsal lobes towards left (×25). – 8. Leaf from slender branch (×25). – 9. Three larger underleaves (×25). – 10. Cilia from leaf-lobe apices (×110). All drawn from type.


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species diverges very markedly from the also somewhat asymmetrically-leaved *T. pulchellum.*

It is a pity this species is known only from the meager, and apparently uniformly sterile type. Nevertheless, the plant is so distinct under the dissecting microscope—particularly in the rather concave leaves with setose cilia of extraordinary length (for the size of the plant) that its uniqueness was immediately recognized. I have seen numerous specimens of the most nearly allied taxon, *T. paucisetigerum*, and have seen no distinct tendencies towards intergradation. Admittedly, the largest leaves of *T. angustifolium* tend to be less asymmetrically quadrifid, and to have a lamina that becomes as wide or somewhat wider than long; such leaves still retain the extraordinarily long, slender, bristly cilia so diagnostic of this species. Furthermore, I have never seen any leaves of *T. paucisetigerum* with the strongly asymmetric lamina so diagnostic of *T. angustifolium.*

Subgenus **Eotemnoma** Schust.

Temnoma subg. *Eotemnoma* Schust., Nova Hedwigia 5(1-2) : 31. 1963.

Plants very small to medium-sized, rarely vigorous, 0.5-1.5 mm wide usually, often erect or suberect in growth, occasionally creeping, less frequently prostrate. *Branching* irregular, polymorphous (within, and from species to species); in addition to terminal lateral branches of the Frullania-type, there are occasionally terminal branches of the Microlepidozia-type, of the Acromastigum-type (sporadically) and lateral and postical-intercalary (axillary) branches. *Leaves* transverse or subtransverse in insertion and orientation, at most 10-25° oblique, deeply (3)4-lobed, symmetric, the sinuses descending from 0.55-0.85 the leaf length; lobes linear-lanceolate to lanceolate, sometimes setaceous, acute to acuminate, gradually tapering to uniseriate apex, ending in 2-5(5-7) single cells that do not, or only rarely, form a differentiated cilium, the uniseriate apex with the cells striolate, dull (unless all cells are smooth); cells of lamina oblong, usually 2.5-5 × as long as wide, usually verruculose to papillate-striolate, rarely almost smooth; cells of cilia usually roughened, usually weakly or not differentiated in form from those of the lobe below, little to moderately elongated (1.5-4 × as long as wide); disc usually low, usually (2)3-8(9-12) cells high to sinuses, symmetric. *Underleaves* large: ranging from equal in size to lateral leaves to 0.65-0.85 as large, (2-3)4-lobed, ciliate or dentate like leaves (when these are dentate). Dioecious. *Bracts* with lobe margins spinose-dentate to ciliate, disc marginally dentate to ciliate. *Perianth* from short and ovoid to longly prismatic, with cilia of mouth short, tooth-like to moderately long and slender. *Spores* (always?) 1.5-2.5 × the diam. of elaters.

TYPE. *T. palmatilobum* (Hodgs.) Hodgs. & Allis. = *T. quadrifidum* (Mitt.) Mitt.

The subg. *Eotemnoma* was founded initially for the subgeneritype only. However, the other taxa assigned to it appear to be more nearly allied to *Eotemnoma* than to the species in the subg. *Temnoma* s. str. (centered around *T. pulchellum*). They share a high number of primitive characters, such as: subtransverse leaves; little or no differentiation of cilia of the leaves; a closer approach to isophylly; larger

spores (at least in part); uniformly quadrifid underleaves; symmetric leaves; and a much greater polymorphism in branching.

The subgenus is still heterogeneous and includes the following species groups:

Key to sections of *Eotemnoma*

1. Leaves (and underleaves and bracts) at least in large part bisbifid; leaves of vegetative stems with margins of lobes and of disc both unarmed, edentate [only near gynoecia do marginal teeth regularly occur]; isophyllous; lobe apices eciliate; cuticle rough.
   Sectio Quadrifidae sect. n. [*T. quadrifidum*]
1. Leaves (and underleaves and bracts) symmetrically quadrifid, median sinus never distinctly deeper; lobes, or disc bases, or both regularly with teeth or cilia (weak stems excepted); lobe apices with ± distinctly differentiated teeth or cilia, of ± elongated cells 2
2. Leaves not copiously ciliate with strongly elongated cilia: branching polymorphous; ± anisophyllous; often with disc margins bearing conspicuous teeth (the lobes by contrast edentate or with short, rigid, often displaced teeth); cuticle often conspicuously roughened.
   Sectio Palmatae sect. n. [*T. palmatum, T. quadripartitum, T. townrowii*]
2. Leaves largely dissociated into cilia, which are strongly elongated, occasionally branched, often tortuous; only Frullania-type branching; perfectly isophyllous; disc margins not with cilia contrasted to those of lobes; cuticle smooth or almost so.
   Sectio Pilosae sect. n. [*T. pilosum, T. patagonicum*]

Temnoma quadrifidum (Mitt.) Mitt. [Figs. 30-32].

Jungermannia quadrifida Mitt., in Hooker, Flora N.Z. 2 : 128, pl. 94, fig. 1. 1854.
Temnoma quadrifidum Mitt., in Hooker, Hdbk. N.Z. Fl. 2 : 753. 1867.
Blepharostoma quadrifidum Pears., J. Bot. 25 : 193, pl. 275. 1887.
Isotachis palmatiloba Hodgs., Rev. Bryol. et Lichén. 18(1-2) : 20. 1949 (new synonymy).
Temnoma palmatilobum Hodgs. & Allis., Trans. Roy. Soc. N.Z., Bot. 1(12) : 146. 1962 (new synonymy).

Plants erect to suberect, medium-sized or (rarely) small, the shoots (0.8)1.0-1.35 (1.55) mm wide (to 2 mm on perianth-bearing shoots) ×1-2(4) cm long, rather lax, green to yellowish-brown to brownish, in depressed-caespitose interwoven patches. Sparingly to freely branched, particularly from older plants and from ♀ shoots, branching variable, the *branches* in large part intercalary and postical (less often lateral-intercalary), some of them remaining positively geotropic, reduced-leaved and stoloniferous; other branches terminal, usually of the Frullania-, sometimes of the Acromastigum- and Microlepidozia-types. *Stems* slender, brownish, 140-185 μ in diam. except below gynoecia, where becoming stouter, terete; cortical cells ca. (16)18-24(28)×(52)60-110(120) μ, averaging 4-8× as long as broad, regularly

and narrowly rectangulate, nearly leptodermous. *Rhizoids* rather frequent, brownish, at bases of many underleaves. *Leaves* exceptionally variable in form, size and degree of dentition, remote to (above) imbricate, transversely oriented and transversely inserted (less than 10° succubous; exceptionally vaguely incubous), the line of insertion slightly acroscopically arcuate, the antical and postical bases at most weakly decurrent; leaves suberect to obliquely patent, trapezoidal to obdeltoid or obdeltoid-obcuneate in outline, narrow at base and gradually broadened upward, to 1000-1100(1250-1430-1780) μ broad ×850-900(1050-1100-1300-1550) μ long, palmately quadrifid for 0.5-0.6(0.6-0.85 in middle sinus; the leaves often bisbifid) their length, the undivided portion (5-7)9-12 cells high, occasionally on vigorous, lax plants 14-17 cells high, edentate and without development of basal accessory lobes and usually with development of few or no accessory teeth or cilia (1 or 2 lobes, occasionally with 1 [rarely 2] small, short, tapering teeth, situated near or above lobe bases, but usually the lobes edentate); lobes lanceolate-triangular to lanceolate-acuminate (4-5)6-8(9-15) cells wide at base, gradually tapering, usually ending in (1)2-4(5) superimposed cells that are only 1.2-2 up to 2-2.5(-3.5)× as long as wide (20-30, rarely 38-40 μ long ×17-22 μ wide); sinuses acute, V-shaped, not reflexed, without small-celled swollen areas at base. *Underleaves* very similar, transversely inserted, somewhat narrower and more obcuneate, up to 725-840 μ wide ×780-870 μ long to 1100-1350(1400) μ wide ×850-1070(1100) μ long, quadrifid or bisbifid for 0.5-0.6 their length, the narrowly lanceolate segments usually in part entire, in part with 1-2 sharp to spinose marginal teeth; rhizoids restricted to the underleaf bases. *Cells* of the uniseriate apices of the lobes little elongated, usually 17-22(24) μ wide ×20-30 (38-40) μ long, usually in rows of merely 2-4, rarely 5 superimposed cells; cells in lobes ca. (18)20-24×(32)40-65 μ; median cells and cells at bases of lobes from 17-20(24)×35-45(50) μ to (22)24-28×(44)48-75 μ; basal cells averaging 22-25× 38-48(60-72) to (20)28-32×(45)50-90 μ; cells slightly to moderately, evenly thick-walled, moderately, but quite distinctly, closely verruculose-striolate. *Oil-bodies* large and conspicuous, in median cells from (1)2-3(4) to (2)3-5(6-9) per cell, ovoid to circular, from (5)6-7×(7)7.5-10 μ to 8-9×10-13 μ, up to 11-13(14)×12-17(18.5) μ, appearing nearly homogeneous (obscurely granulate), smooth on surface, colorless and translucent. Without asexual reproduction. Dioecious. Androecial plants slenderer than female; *androecia* terminal to intercalary, on main stems or on elongating postical-intercalary branches, 1000-1150(1250) μ broad; *bracts* in (3)5-10 to 8-12 pairs, forming a laxly to compactly spicate androecium; bracts ca. 350-450 μ wide ×440-560 μ long, similar to leaves but usually slightly smaller, transverse, less deeply and often somewhat asymmetrically quadrifid for 0.45-0.55 their length, the lobes erect and

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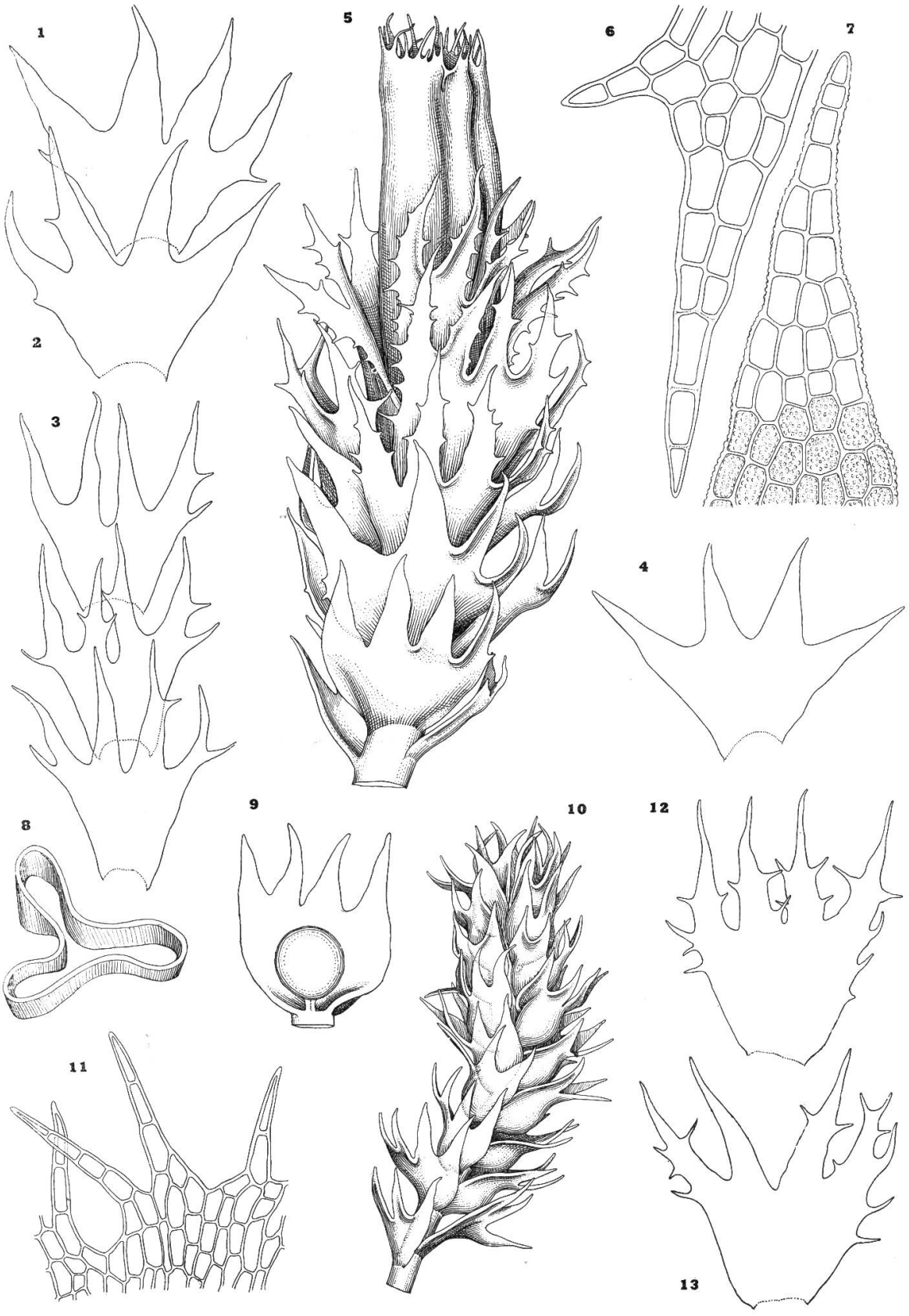
FIG. 30. *Temnoma quadrifidum* (Mitt.) Mitt.

1-2. Leaves from female plant (×35). – 3. Underleaves (×35). – 4. Leaf (×35). – 5. Fertile shoot, lateral aspect (×23). – 6. Lobe of underleaf, without papillae indicated (×205). – 7. Lobe of leaf (×205). – 8. Cross-section, perianth middle (×38). – 9. Small male bract, from slender androecium (×57). – 10. Androecial shoot (×23). – 11. Perianth mouth (×130). – 12-13. Female bracts (×22).

All from type; NYBG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not divergent, lanceolate, acute but not acuminate, entire-margined, the entire basal portion strongly ventricose and suberect, only the lobes suberect to widely spreading. *Antheridia* 1-2 per bract, ovoid to subspherical (ca. 155-210 μ wide ×170-200 μ long), on a ± elongate, biseriate stalk (ca. 18-21 ×90 μ; to 10 cells long); jacket layer with cells irregularly oriented; no paraphyses. *Bracteoles* somewhat patent, smaller than underleaves and bracts, relatively shallowly (0.35-0.45) quadrilobed, the undivided base nearly flat to moderately concave, narrowly obdeltoid. *Gynoecia* terminal on leading shoots, without innovations if perianth develops (older gynoecial shoots with frequent intercalary branches, but these originating some distance below the bracts); ♀ shoots broader above, to 1900-2000 μ wide above. Subinvolucral *leaves* and *bracts* gradually larger upward, progressively with margins bearing more frequent, often opposed, sharp teeth on lobes. *Bracts* erect, loosely sheathing perianth, similar to leaves but larger, somewhat more freely dentate, broadly obcuneate to obdeltoid, 1400-1500 μ wide ×1425-1600 μ long, bisbifid for 0.5-0.6 their length, the lanceolate, long-acute to short-acuminate lobes little divergent, varying from entire to sparingly toothed: the teeth 2-3 per lobe or more rarely 4-5, mostly 2-5-celled, the larger teeth broad-based, never aciculate, relatively short but sharp and formed of cells that are hardly differentiated from leaf cells (1.2-2× as long as broad), the teeth averaging shorter than width of lobes, lying in the plane of the bracts, usually opposite to each other; sinuses often somewhat, if narrowly reflexed, narrowly rounded. *Bracteole* similar to bracts (ca. 1450 μ wide ×1450 μ long), similarly lobed and toothed. Subinvolucral leaves grading in form from that of bracts (i.e., sparingly toothed) to that of leaves (i.e., lobes usually entire). *Perianth* one-half or more emergent, hyaline, pale dull green to light brownish, strongly trigonous-triplicate for its whole length, narrowly oblong-prismatic, slender (ca. 650-700[750] μ wide ×2.2-2.4 mm long; length 3-4× the width), tapering slightly from the basal one-third, where broadest, but the mouth rather wide, armed with remote to contiguous sharp teeth to short cilia (2-5, occasionally 6-8 cells long, the shorter uniseriate throughout, the longer tapering and 2-3 cells broad at base); cells of cilia (35)40-50(70)×12-17(20) μ, occasionally 35-45×20 μ, thus no more than 2-3× as long as wide; cells in distal fourth of perianth rectangulate, 16-18× 25-38 μ; median cells of perianth 20-25×48-72 μ. *Capsule* purplish-brown to reddish-purple, the wall fleshy and rather thick, with nearly opaque valves, 4-5-stratose, from 35-36 μ thick (when 4-layered) to 41-46 μ thick (when 5-layered). Epidermal *cells* hyaline, rather large, devoid of pigmentation or localized thickenings (except near margins of valves, bordering dehiscence lines, and near or along the valve midline, where they are found with vertical bands or nodular thickenings; rarely a few cells elsewhere have a few sporadic thickenings along their longitudinal walls), ca. 12-15(16.5) μ in radial diam. ×25-50(55) μ wide. Internal 2 or 3 strata each with strong vertical thickenings (in superficial view walls with strongly nodular, deep brown thickenings); internal 2-3 cell layers each 7.5-9 μ thick, each averaging little more than half the thickness of epidermal cells. Innermost *layer* of relatively irregular cells, usually less in thickness than internal cell layers, ca. 5-5.5(6) μ thick only, with numerous semiannular bands, complete or subcomplete across free tangential walls. *Spores* 15-18.5 μ in diam., twice to 2.5× the elater diam., brownish, faintly but distinctly sharply papillate-granulate, the papillae not uniformly dispersed. *Elaters*

6.5-8 μ in diam., tortuous, strongly tapering on the ends, ca. 100-150 μ long, bispiral, the reddish-brown spirals ca. 3 μ wide.

TYPE. New Zealand (*Colenso 1177*, in herb. Hooker, K !); a portion of the type in the Mitten Herbarium (NY) has been used for the preparation of part of the associated figures and the preceding diagnosis; the type of *Isotachis palmatiloba* Hodgson corresponds completely [1]. The diagnosis of the sporophyte is based largely on material of *Isotachis palmatiloba* from Mt. Egmont (*Druce*).

DISTRIBUTION. Restricted to New Zealand, as far as known, and, in my experience, usually montane or submontane, ascending to ca. 5000 ft. on Mt. Egmont. NORTH ISLAND: Mt. Egmont, Taranaki Prov. *RMS 48004*, *48007*; stream bank, Kaimanawa Mts., 4500 ft. *A.P. Druce 1329*, type of Isotachis palmatiloba, Hodgson, 1949 !; wet, dripping bank, Mt. Egmont, ca. 4000 ft. *A.P. Druce 1328*, *1330* ! cited by Hodgson, 1949, as Isotachis palmatiloba and by Hodgson and Allison, 1962, as Temnoma palmatilobum !; Soda Springs, head of Mangatepopo Stream, ca. 4500 ft., saddle between Mt. Ngaurhoe and Tongariro, Tongariro Natl. Park, *RMS 51100*, *51101*, *51102*, p.p. among Triandrophyllum subtrifidum. SOUTH ISLAND: Fiordland Natl. Park: along Route Burn Track, between Earland Falls and Lake Howden, ca. 4000 ft. *RMS 48627*, abundant, with capsules !; Homer Tunnel, Fiordland Natl. Park, at head of Hollyford Valley, 3200 ft. *RMS 55598*; Naseby, Central Otago, amidst patch of Bartramia on damp ground in open, ca. 2000 ft. *K. W. Allison, H 5423* ! also thus reported by Hodgson and Allison, 1962 [2]; power line gully, Cass, North Canterbury, Phillipson, cited by Hodgson and Allison as T. palmatilobum; Otira Gorge, Arthurs Pass Natl. Park, *Berggren 2811*, Feb. 1874.

ECOLOGY. Typically a species of wet sites, occasionally growing submerged (then often with *Balantiopsis*), often in large masses on rocks adjoining cascades and waterfalls (then often in immense pure mats, or mixed with *Clasmatocolea paucistipula*, and/or with *Triandrophyllum subtrifidum*). The hygromorphic phases are usually deep green or brownish green, with large and relatively soft-textured, dense leaves. Occasional, more remote- and small-leaved terrestrial forms occur, which are much less diagnostic.

VARIATION. An exceptionally variable species which, initially, is apt to prove taxonomically baffling. The variations appear to me to be entirely environmentally induced and reflect the wide toleration of this species to varying moisture conditions. Large, green, erect or ascending growth forms, forming black-green, soft-textured patches, may grow around waterfalls, and at the margins of pools between rocks,

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[1] I have studied part of the type gathering in the herbarium of A. W. Allison. The type plants are sterile and poorly developed. It is inexplicable to me why the second collection cited by Hodgson, made by Druce: Mt. Egmont, ca. 4000 ft., Dec. 13, 1948, No. 1328 (in herb. Hodgson et herb. Allison) was not designated as the type, since this is of well-developed plants, with perianths, androecia, and at least a single capsule.

[2] This specimen has a single long, slender, trigonous-prismatic perianth, as is typical of *T. quadrifidum*. The perichaetial bracts are also paucidentate, with 1-2 pairs of spinose teeth per lobe. This, together with the leaf form (0.5-0.55 quadrifid, teeth few or none) which approaches or equals that of *T. palmatilobum* (= *T. quadrifidum*) from Mt. Egmont, clearly places this collection in *T. quadrifidum* as that species is circumscribed here.

where they are subject to inundation. Such plants are rarely provided with mature perianths, and must sometimes be determined on the basis of sterile material. Nevertheless, the somewhat concave and suberect, loosely sheathing leaves, and the almost perfect isophylly, are readily evident on all plants. Such subaquatic phases, obviously members of a single population, may produce weak sterile shoots with simply bisbifid, unarmed leaves only 725 μ wide ×615 μ long, while gynoecial shoots may produce relatively enormous leaves, 1560-1780 μ wide ×1450-1550 μ long, which are almost always provided with a sharp, small tooth on the bases of some lobes, or may have 2-3 pairs of opposed, sharp teeth per lobe ! Such variation in leaves is depicted in Fig. 31: 7-13 (*RMS 48007*), Mt. Egmont. Perhaps the most " typical " leaves are those produced on sterile innovations from beneath gynoecia; they are medium-sized, bisbifid for 0.45-0.55 their length, and bear almost without exception edentate lobes and discus margins (Fig. 31: 7-9). The variation in leaf form and size depicted for *RMS 48007* encompasses almost all that is to be found within the species. However, small terrestrial forms occur in which there may be even smaller and less vigorous leaves (Fig. 31: 16; *RMS 48004*), in which the leaves may be merely 415 μ wide ×285 μ long; such plants are almost impossible to reconcile with the vigorous subaquatic phenotypes, yet appear to be genetically similar.

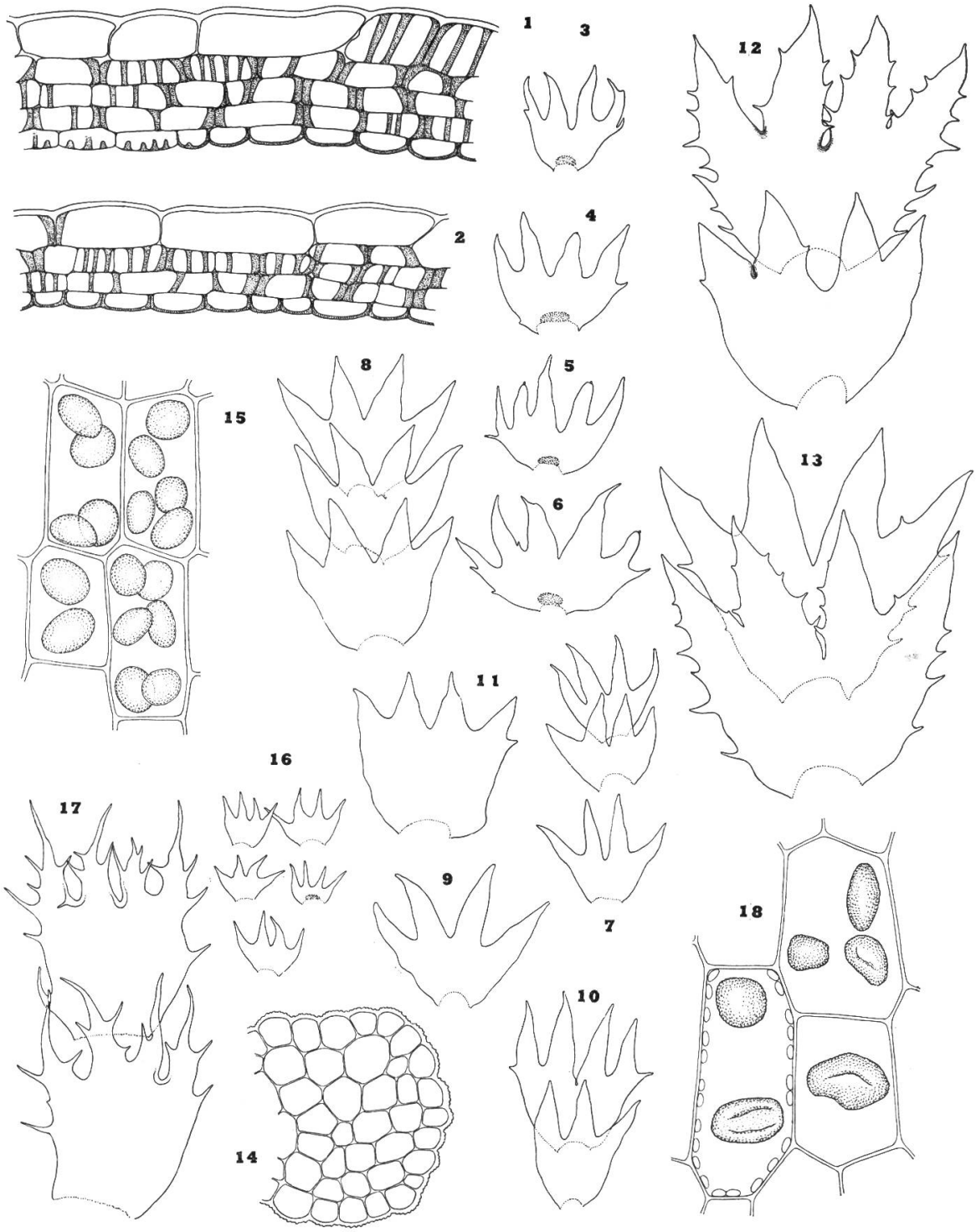
DIFFERENTIATION. The species is sharply isolated and perhaps bears affinities only to *T. palmatum*, a New Zealand species with which it has been confused, and (less so) to *T. quadripartitum* from Patagonia. All three taxa share a common tendency for sterile leaves to become merely quadripartite on at least the slender shoots; i.e., there is a " tendency " for the suppression of cilia or teeth. The three taxa form a polymorphous and troublesome complex. On the basis of available collections, it is clearly necessary to maintain three species.

Of these species, *T. palmatum* can usually be eliminated at once on the basis of the short, terete, obtusely to hardly plicate perianths that are not at all contracted to the mouth. This species agrees in general cell size with *T. quadrifidum*, but *T. quadripartitum* usually has smaller and shorter leaf cells. Both *T. palmatum* and *T. quadrifidum* have a closely if finely verruculose cuticle; in *T. quadripartitum* the cuticle appears to be nearly or quite smooth.

FIG. 31. *Temnoma quadrifidum* (Mitt.) Mitt.

1-2. Capsule-wall cross-section (×400). – 3-6. Four underleaves (×21.5). – 7. Three small leaves, subterrestrial extreme, sterile plant (×21.5). – 8. Three normal leaves, vegetative shoot-sector, from sterile stems (×21.5). – 9. Leaf with atypically deep sinuses, from sterile stem (×21.5). – 10. Atypical leaves, from subaquatic phase, one trifid (×21.5). – 11. Atypical leaf, showing minimal degree of lobing (×21.5). – 12. Two leaves from a female plant (not bracts; not subfloral leaves) (×21.5). – 13. Two leaves from below female bracts (×21.5). – 14. Part of stem cross-section (×142). – 15. Cells, small terrestrial phase, with oil-bodies (×700). – 16. Four leaves and an underleaf (×21.5). – 17. Two female bracts of terrestrial extreme (×21.5). – 18. Median cells of disc, lax, large subaquatic extreme with cuticle strongly striolate (×525).

1-2, *Druce 1328*, Mt. Egmont, cotype of *T. palmatilobum*; 3-14, *RMS 48007*, Mt. Egmont (subaquatic phase); 15-17, *RMS 48804*, Mt. Egmont (small terrestrial extreme); 18, *RMS 55598*, Homer Tunnel, Hollyford Valley head (subaquatic phase).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T. quadrifidum differs from all forms of *T. quadripartitum* in the high disc of the leaves, 9-12 cells high in all but juvenile phases (from a minimum of 3-5 to, usually, 6-7 cells high in *T. quadripartitum*); in the lack of accessory lobes or teeth originating below the lobes, from the disc margin (in *T. quadripartitum* all phases show a marked tendency towards development, even on weaker stems, of leaves with a large, broad, recurved tooth on one or both margins, the tooth inserted only a little above the base of the disc); in the broader leaf lobes, usually 6-8, even 8-10 cells wide at the base (in *T. quadripartitum* usually only [3]4-6 cells wide at the base); in the shallower sinuses, descending ca. 0.5-0.65 the leaf length (ca. 0.65-0.75 or even 0.8 in *T. quadripartitum*). The leaves and bracts below the inflorescence in the two species are also very different, those of *T. quadrifidum* being divided, like the leaves, 0.5-0.6 their length, with the disc margins edentate or with 1-3 teeth per margin, but never with accessory lobes. In *T. quadripartitum*, by contrast, the sinuses descend ca 0.75-0.8 the length, the disc margins often bear on each side a large, strongly divaricate or recurved tooth (which, itself, may bear 1-4 sharp, spinose teeth, often in 1-2 opposed pairs). As a consequence, I am convinced that two well-defined species are at hand.

Utilizing these criteria, all but occasional juvenile forms can be placed. Such a juvenile form is *Hodgson 6321* (" *Temnoma quadripartitum* (Hook.) Schust. approaching *quadrifidum* " on the label of Hodgson's material). These plants, although in some ways deviant, seem to me more like a juvenile phase of *T. quadripartitum*, with which they agree in the occasional development of a sharp, strongly spreading (if not recurved) tooth from the margins of the disc, while the lobes are constantly edentate.

I have spent many hours carefully comparing the type plants of *T. quadrifidum* and " *Isotachis* " *palmatiloba*, and cannot find a single significant criterion that will separate them. Leaf and underleaf form is identical, and, of the utmost significance, there is the same tendency for at least the larger (upper) leaves to produce a single, spur-like tooth of one or two of the lobes (often of outer margins of outer lobes). I originally maintained the two species distinct, partly on the basis of the " tendency " in *T. palmatilobum* for leaf lobes to be merely acute at the tip, in *T. quadrifidum* for weakly differentiated apiculi, formed by up to 4-5 cells, to be developed (Fig. 30: 6-7). However, in plants I collected on Mt. Egmont (one of the two original localities for *T. palmatilobum*) I found phases with leaf lobes ending

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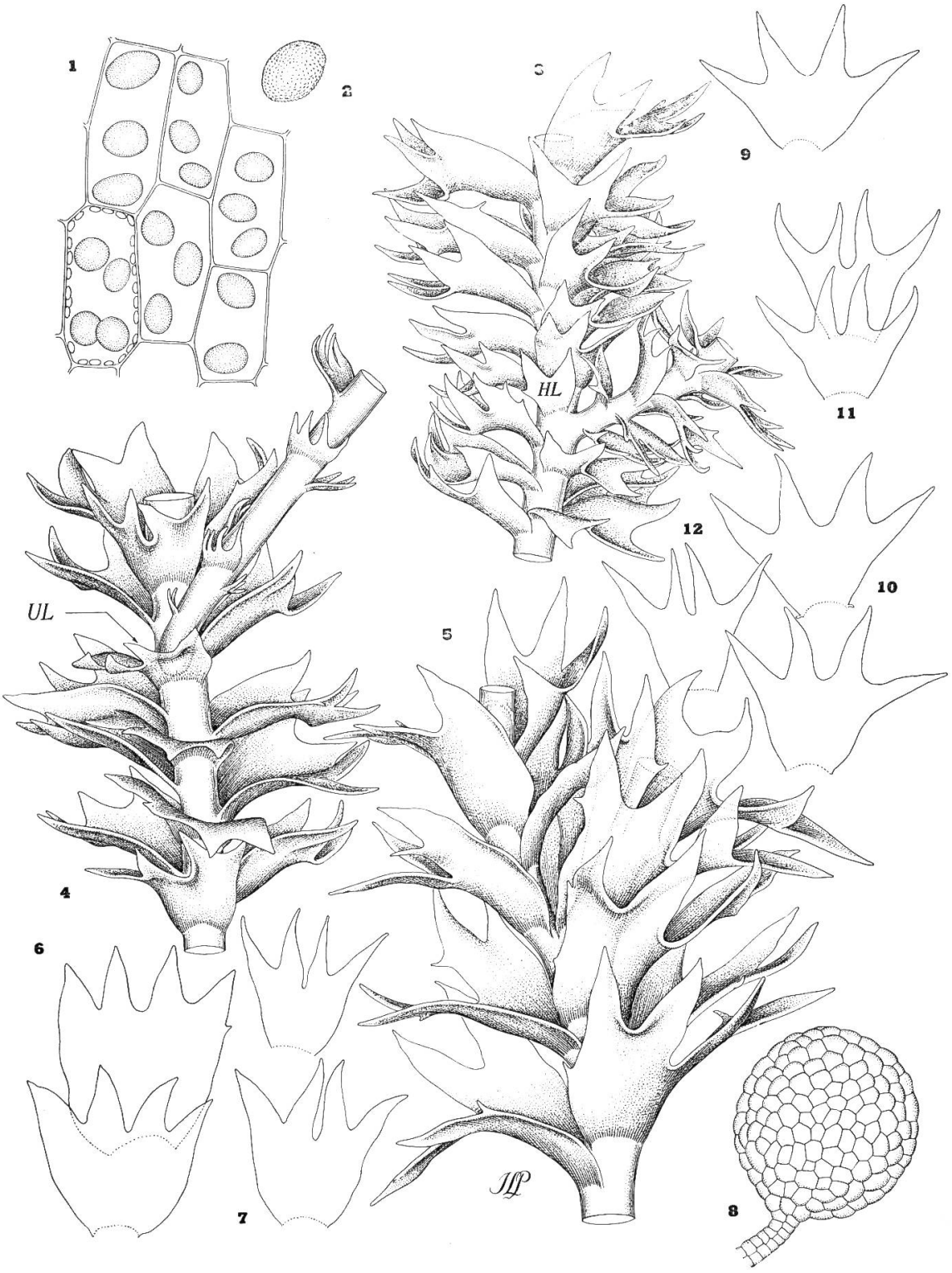
FIG. 32. *Temnoma quadrifidum* (Mitt.) Mitt.

1. Disc cells with oil-bodies (and, lower left, chloroplasts) (×335). – 2. Individual oil-body (×720). – 3. Ventral aspect of shoot, underleaves rather arched to right, the right hand row of leaves largely obscured; at HL a half underleaf associated with an Acromastigum-type ventral-terminal branch (×27). – 4. Ventral aspect of shoot-sector, with ventral-intercalary branch from underleaf (UL) axil (×25). – 5. Shoot-sector, antical aspect, with a terminal (? Microlepidozia-type) branch to left, the half leaf away from observer (×25). – 6. Two leaves from male shoot (×27). – 7. Two underleaves from same shoot (×27). – 8. Antheridium (×125). – 9-10. Leaves of male shoot (×27). – 11-12. Underleaves from same shoot (×27).

Figs. 1-8 from *RMS 48627*, Fiordland, N.Z., a hygromorphic phase with unusually high disc; figs. 9-12 from type, leg. *Colenso*, a less hygromorphic form with lower disc.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in 3-4 cells, the longest cells rather sharply differentiated (ca. 16-17 × 38-40 μ); thus even this supposed distinction " fails ". Oil-bodies of the weak and somewhat deviant, juvenile Mt. Egmont plants (*RMS 48804*) exactly match those of plants from the Humboldt Mts. (*RMS 48627*), which are perfectly typical *T. quadrifidum*. In sparing plants of the type of *T. quadrifidum* I was able to find only postical intercalary branches. This is, I think, not relevant, since the sample examined consisted of no more than 10-12 stems.

There are three intergrading extremes of this species, as is evident from the comparison in table 2.

Table 2. — Comparison between the three intergrading extremes within *T. quadrifidum*.

Criteria	Type of *T. palmatilobum*	Type of *T. quadrifidum*	*RMS 48804* (Mt. Egmont)
Leaf size (length × width)	to 1300 × 1430 μ	850-900 × 1000-1100 μ	275-300 × 450-480 μ
Underleaf size	to 1100 × 1400 μ	725-840 × 780-870 μ	175 × 200 μ
Leaf lobes	to (8)9-15 cells wide	6-8(9-10) cells wide	4-5(6) cells wide
Disc height	to 14-17 cells high	9-12 cells high	5-7 cells high
Cell size (middle of disc)	(22)24-28 × (44)48-75 μ average	17-20(24) × 35-45(50) μ average	(14.5)15-21 × 24-35 μ

BRANCHING. I have devoted much time to the study of branching patterns in this species, dissecting hundreds of individual shoots. The species shows extraordinarily diverse modes of branching, with at least the following types represented: (1) postical-intercalary, axillary branches, from axils of both underleaves and male bracteoles; particularly frequent on male plants; (2) lateral-intercalary, axillary branches (rare: seen only once from a leaf axil of a female shoot, several leaf pairs below the perianth); (3) lateral, terminal branching of the Frullania-type, the branch replacing the ventral half of a leaf, with the associated stem leaf thus bifid rather than quadrifid; (4) lateral, terminal branching of the Microlepidozia-type, the branch seemingly latero-dorsal in origin, replacing the dorsal half of a lateral stem leaf, which is again only bifid. The only other branching type found in the *Blepharostomataceae*, terminal-postical branching (Acromastigum-type), has been found in *Temnoma palmatum*, *Lophochaete quadrilaciniata*; with sufficient investigation, this type might also be found in *T. quadrifidum* [1].

LEAF INSERTION. Many hours have been spent in studying a variety of plants, with the following results: in general, insertion of the leaves is nearly transverse to weakly succubous, but on vigorous, sterile plants it unquestionably is sometimes

[1] Since the above lines were written, a single unquestionable Acromastigum-type branch has been seen (Fig. 32), with a narrow, bilobed underleaf associated with the branch. Thus, in *T. quadrifidum* all types of branches known in the family may be observed.

very slightly incubous, and the rather concave leaves may be slightly incubously oriented, with respect to the dorsal pair of lobes. However, shoot-sectors with almost perfect transverse leaves can be found, and at least on several of the ♂ plants I saw leaves with a distinctly succubous insertion. When the insertion is not transverse, it does not become more than 5-10° oblique.

Capsule Wall and Contents. The capsule wall shows cross-sections which were both 5-layered and 4-layered. The capsule wall closely corresponds to that which I have described (Schuster 1959) and illustrated (Schuster 1961) for *T. pulchellum*. The only deviation—a minor one—is a sporadic tendency for a few epidermal cells away from the margins of the valves to possess radial (nodular) thickenings. However, except for the area peripheral to the valve margins (and sometimes for a line near the valve-midline), epidermal cells are virtually all colorless and without localized thickenings. As in *T. pulchellum*, the larger, thick-walled outer cells are almost equivalent in thickness to the two cell layers lying within.

In the spore size, however, there are significant differences. It has already been emphasized that Müller (1948) artificially delimited the *Blepharostomataceae*, in part on the basis of the virtual identity in diameter of both spores and elaters. To date, this criterion apparently has held, and the generic type of *Temnoma*, *T. pulchellum*, is described (Schuster 1959) as having spores " 8.5-9.5 μ in diameter, their diameter subequal to that of elaters ". In *T. quadrifidum*, however, spores are 15.0-18.5 μ in diameter, averaging more than twice that of the elaters, which are 6.5-8 μ in diameter. Thus another of the criteria previously used to separate the *Blepharostomataceae* has proved inadequate, and the diagnosis of the *Blepharostomataceae* in Schuster (1959, 1961) must be emended on this point.

It is perhaps significant that *T. quadrifidum*, which so closely approaches *Lophochaete* in vegetative structure that confusion with it is readily possible, agrees with *Lophochaete* in the approximately 2 : 1 spore-elater diameter ratio, and in the bisbifid leaves. It is surely the most primitive species of *Temnoma*.

Temnoma quadripartitum (Hook.) Mitt. [Figs. 33-38, 50: 4-10].

Jungermannia quadripartita Hook. Musci Exot., pl. 117. 1820.
Jungermannia podophylla Ångström, Öfversigt Kgl. Vetensk.-Akad. Förhandl. 29(4): 11. 1872 (non *J. podophylla* Thunberg).
Blepharostoma quadripartitum Trev. Mem. Ist. Lomb. III, 4 : 417. 1877 [1].
Temnoma quadripartitum Mitt. J. Linn. Soc. 15 : 68. 1877 [2].
Teinnoma quadripartitum Mitt. Hepaticae, in J. Murray & C. W. Thomson, Rept. Sci. Res. Voy. H. M. S. Challenger, I (2) : 230. 1884 (nom. nudum).
Teinnoma quadripartitum Mitt. in J. D. Hooker, Phil. Trans. Roy. Soc. 168 [extra vol.] : 32, 33. 1879 (nom. nudum).

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[1] In Fulford (1963 : 57) this citation is erroneously given as " 4 : 417. pl. 345, f. 7, 8. 1877 ".

[2] In Fulford (*loc. cit.*) the species combination is accredited to Mitten, 1879; actually it was legitimately formed two years earlier. Furthermore, the combination *Temnoma quadripartita* cannot be accredited to Mitten (1879), since he then formed it under the genus *Teinnoma* Mitt. (not *Teinoma* [sic !] of Fulford). This was not regarded as a variant spelling or error in typography, since Mitten spells it *Teinnoma* consistently, on both pages 32 and 33.

Lepidozia randii S. Arn. Sv. Bot. Tidskr. 47(3) : 417, fig. 6. 1953 (new synonymy).
Temnoma subintegrum Fulf. Mem. N.Y. Bot. Gard. 11 : 57. 1963 (new synonymy).

Plants usually rigid, small to medium-sized, rather wiry-stemmed, brownish to brownish-green, usually scattered, rather rarely in small, nearly pure tufts, creeping to, with crowding, caespitose, ca. 750-1000(1200) μ in width ×(6)8-12(18) mm long usually, the stems flexuous, sparingly and irregularly branched; branches usually terminal, Frullania-type [in type], occasionally of the Microlepidozia-type, rarely postical-intercalary. *Stem* slender (70)80-130(160) to ca. 130-165 μ in width, of only (10-12)15-17(18-22) rows of cortical cells that are feebly to moderately thick-walled (on their external walls at least); cortical cells in cross-section ca. 16-21(23-28)μ wide ×16-23 μ high, averaging equal or slightly greater in diam. than the leptodermous medullary cells (which are [12]14-18[21] μ in diam.), cortical cells short-oblong, 16-21(23-28)×(28)30-55(72) μ. *Rhizoids* frequent, at underleaf bases, long, pale brownish. Moderately anisophyllous. Lateral *leaves* often rigid, small, remote to barely contiguous, the lamina stiffly, widely spreading, with ± suberect to ascending lobes, thus feebly to rather concave, insertion ranging from transverse to somewhat succubous to (rarely) feebly incubous; leaves obtrapezoidal to subquadrate-obtrapezoidal to obdeltoid to reniform-obtrapezoidal in outline, ca. (400)450-600(700) μ wide ×(265)300-425(540) μ long up to (rarely) 1200-1450 μ wide ×850-1100 μ long, including cilia or teeth, symmetrically quadrilobed for (0.6)0.75-0.85 their length (isolated leaves trifid), concave, at the antical and/or postical base with a tooth (widely spreading or reflexed) which is often larger than normal and is often large enough to suggest a 5-6-lobed leaf; lobes slenderly lanceolate-triangular, ± gradually acuminate, only (2)3-5 to 6(7-8) cells wide at base, the tapering apex acute to acuminate and formed by 3-5(6-7) cells in a row; lobe bases often with (0)1-2(3-4) pairs of spinescent, stiff teeth, often the teeth only in part in pairs (the upper frequently solitary), the teeth never bifurcate, short above (and there only 1-2 or 2-3 cells long) and longer below (there sometimes 3-5-celled); teeth of lobes (particularly near the sinuses) sharply reflexed, postically displaced, and lying almost at right angles to the leaf plane, in profile the plants thus appearing to have a stiffly spinose abaxial leaf surface; undivided lamina of leaf only (2)3-5(6-7) cells high, occasionally 6-8 cells high on very vigorous plants. *Underleaves* distinctly smaller than lateral leaves, perhaps 0.55-0.75(0.8) the size; 250-285 μ long ×400(500) μ wide to 800-825 μ long and wide, disc (1)2 or 3-5 cells high, somewhat less widely patent from stem, often some with rhizoids at base, quadrifid 0.65-0.90, like leaves but margins espinose or with mostly only 1(2) sharp, short teeth per lobe; one or both lateral bases often with a larger reflexed tooth. *Cells* of teeth and lobe apices short, rigid, thick-walled

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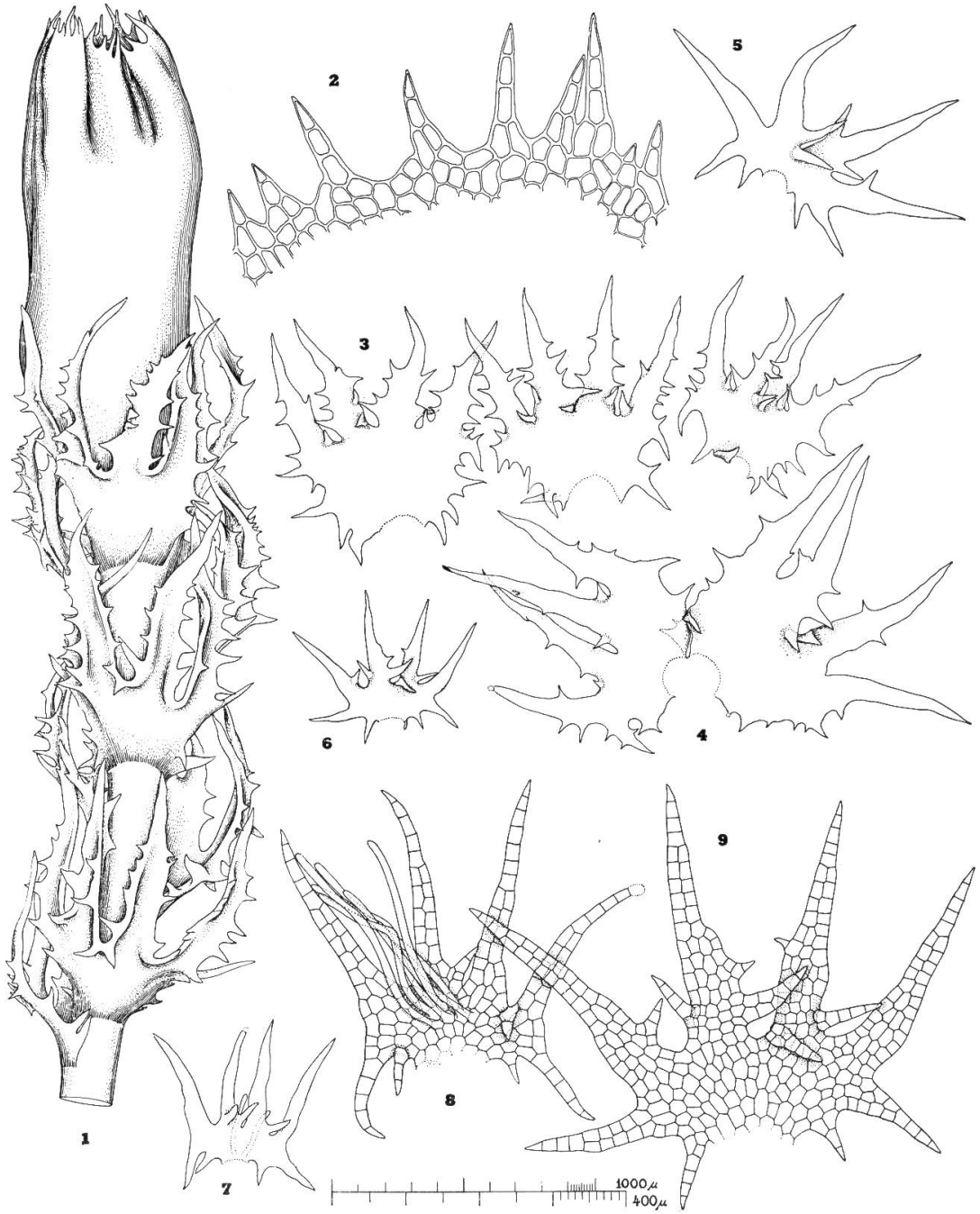
FIG. 33. *Temnoma quadripartitum* (Hook.) Mitt. var. *quadripartitum*.

1. Perianth-bearing shoot-tip (×30). – 2. Cells of perianth mouth (×132). – 3. Three subfloral leaves (×30). – 4. Bract (right) and bracteole (left) (×30). – 5-6. Large and medium-sized leaves (×30). – 7. Underleaf (×30). – 8-9. Underleaf and leaf (×82.5). (Figs. 1, 3-7, drawn to top scale; 8-9, drawn to bottom scale).
All from *RMS 60441*, Mt. Hector, Tararua Mts., N.Z.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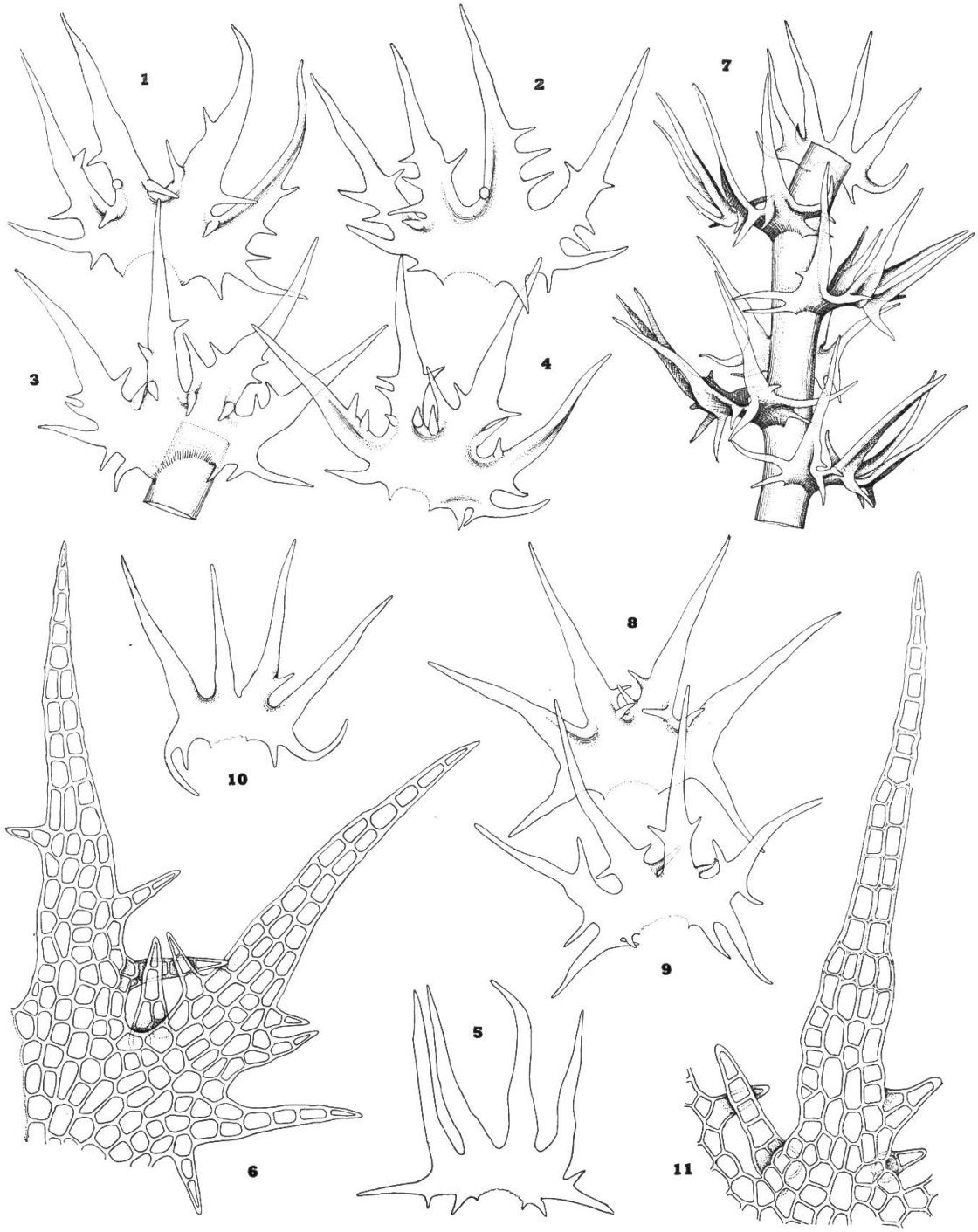
(septae weakly dilated externally), ca. 13-18(21)×(18)20-28 μ (weak phases) to 16-18×36-65(90) μ (vigorous phases), smooth to usually faintly, rarely strongly striolate; cells in lobes thick-walled, ca. 13-16(17-19)×18-30 μ; basal cells moderately larger, 16-20(24)×(28)32-45 μ; cells smooth to faintly verrucose-striolate, rather thick-walled except sometimes for the basal cells which are sometimes almost leptodermous. *Oil-bodies* rather large (except for distal cells of lobes) mostly (3)4-7(8) per cell, spherical to short-ovoid or irregularly ovoid, from 3-3.5×3.5-5 μ to 3.5-4 ×6-7.5 μ to 5.5×7 μ, rather glistening, colorless, translucent, formed of minute spherules in a matrix of nearly identical refractive index, smooth externally. Without asexual reproduction. Dioecious [1]. *Androecia* intercalary (sometimes on rather short lateral branches), strongly differentiated, of only (2)3-5(6) pairs of bracts; *bracts* very strongly concave, transverse, equal to or even slightly larger than leaves, much less deeply lobed than leaves and with shorter, usually erect lobes; margins of lobes spinose like the more spinose leaves, but disc bases without the large teeth of the leaves; 1-2-androus. *Gynoecium* on main stem; bracts narrowly obtrapezoidal, to ca. 800-1150 μ wide (apex; 350-400 μ at disc) ×1000-1100 μ long, gradually larger and longer than leaves, becoming much more spinescent, erect, the linear-lanceolate lobes with 3-8(9) pairs of (generally abaxially reflexed) spinescent teeth per lobe; sinuses descending to ca. 0.6-0.75 bract length; lobes linear-lanceolate, longly acuminate, ending in a filament of (3)4-6(7-8) isodiametric to ± strongly elongated single cells, often somewhat canaliculate; disc margins as well as lobe margins with spinescent teeth formed of (1)2-3 cells, those of the disc margins ca. 4-6 per margin. *Perianth* strongly elongate, ca. 420-450 μ in diam. ×1800-2000 μ long, strongly triplicate for 0.35-0.55 its length, distally with feeble accessory plicae, contracted to the mouth, which bears greatly crowded, juxtaposed, short, stiff teeth and short cilia, strongly tapering to sharp points, the terminal cells ca. 10-12×38-48 μ. *Spores* 12 μ; elaters 2-spiral, 7.2-9×70-85 μ, the spirals narrow, 2.5-3 μ wide [from specimen (BM) from Hermite I., Cape Horn, ex herb. Hampe, as "*Jungerm. antarctica* n. sp."].

TYPE. South America: Staten Island, near Cape Horn (Menzies); K, V!

[1] Hodgson and Allison (1962 : 144) state the species is "monoicous", on the basis of a specimen collected by Santesson in Tierra del Fuego (S-PA); I have also checked this specimen and carefully dissected a large number of fertile plants. Although androecial and gynoecial branches occur admixed, in each case where I have followed the branches carefully, no connection between the two sexes could be demonstrated. I therefore assume, although further proof is required, that this represents a mere admixture of the two sexes and that the species is dioecious; it is so described in Fulford (1963). Most collections I have seen consist of plants of one sex only, e.g., *RMS 60441*, Mt. Hector, N.Z.

FIG. 34. *Temnoma quadripartitum* (Hook.) Mitt. var. *quadripartitum*.

1-4. Leaves; in fig. 3 with the feebly succubous attachment to stem shown (×60). – 5. Underleaf (×60). – 6. Half of a leaf (×140). – 7. Part of shoot of optimal size (×35). – 8-9. Two leaves of optimal size (×44.5). – 10. Underleaf of optimal size (×44.5). – 11. Lobe of mature sterile leaf, 21-23 cells long and 6-7 cells broad (as in "var. *randii*", ×140).
1-6, from Arthurs Pass, N.Z., *Hodgson 5441*; 7-11, from mature stem of the type, Lindenberg Herb., Vienna.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DISTRIBUTION (var. *quadripartitum*). The most widespread species of the genus and the only one with a disjunctly circum-subantarctic range [1]. SOUTH AMERICA: TIERRA DEL FUEGO: Magellan Straits, Port Famine, *Andersson*, type of J. podophylla; Halt Bay, Tierra del Fuego, *Cunningham*, K; Hermite Island, Tierra del Fuego *Hariot 1276*, a form with mostly 3-parted leaves; labelled " = new genus + new species " by M. Fulford; Magellan Straits, West Channel, *H. Rom, 1797*, G, sparing [2]; Isla Clarence, *Hariot*, trace, among Pleurocladopsis simulans (Mass.) Schust., K. ARGENTINA: Sierra Sorondo, above Las Cotorras, ca. 20 km ENE of Ushuaia, Tierra del Fuego, 260 m, in Nothofagus pumilio forest, *Santesson M 23*, ♂ and ♀ plants admixed with Riccardia floribunda. Neuquen Prov.: Parque Nacional de Nahuelhuapi, at El Tronador, Filo Bariloche, *A. Donat 188 ex p.*; Cerro Garibaldi, SE of Lago Escondido near route from Ushuaia to Rio Grande, *RMS 58303*, optimal form, approaching f. spiniferum. CHILE: Rio Aysen, *Dusén G-1796*. MARION ISLAND: *Arnell, 1958*. KERGUELEN ISLAND: no loc.; *Moseley, Jan. 1874*, Challenger Exped., K; *Mitten, 1877, 1884*. TRISTAN DA CUNHA: *Arnell, 1958*. INACCESSIBLE ISLAND; *Arnell, 1958*. NEW ZEALAND: South Island: Over peaty soil and amidst other Hepaticae, wet, peat-covered insolated ledges just S of Haast Pass, Otago Prov., ca. 1700-1800 ft. *R. M. & O. M. Schuster, 48740a, 49740a*; Milford Sound, Fiordland Natl. Park, on track to foot of Bowen Falls, near sea level, *RMS 48601e*; track from Lake Howden to Lake Mackenzie, W slope of Humboldt Mts., ca. 4200-4500 ft., within 2 mi. of Lake Mackenzie, just above treeline, Upper Hollyford Valley, Fiordland Natl. Park, *RMS 49471*; Arthurs Pass. 3000 ft., " amongst Conostomum, Lepidozia, etc." *M. Hollsworth, Sept. 8, 1950*; Bealey [Arthurs Pass Natl. Park], *Berggren, 1874*; Lund. North Island: Mokai Patea Spur, Ruahine Mts., ca. 5000 ft., by tarn, *A. P. Druce 5950*; West Peak of Mt. Hector, Wellington Prov., 4400-4700 ft., along water course near Hut; a form with disc to 7-8 cells high, lobes to 6-7-8 cells broad at base, *RMS 60440, 60443*; same loc., a vigorous but typical form with perianths, *RMS 60441*; E slope of Mt. Egmont, Taranaki Prov., 5400-5500 ft. *RMS 48890a*, a form superficially like a small T. palmatum, but with often recurved lobes of disc; Otupae, NW Ruahine Mts. *Hodgson 6321*.

ECOLOGY. In New Zealand a species often found in exposed, insolated but moist sites in the mountains. Occurring from sea level to at least 5000 ft.; at lower altitudes found in Nothofagus menziesii forest, in openings over peaty, Sphagnum-covered ledges; at higher elevations on wet ground in the Tussock Grassland region.

The first New Zealand material cited (Haast Pass) occurred, in large part, amidst other Bryophyta, over Sphagnum and moss-covered, insolated, steeply sloping ledges; associated were *Calyptrocolea gemmipara*, *Lepidolaena menziesii*, *Tetracymbaliella cymbalifera*, etc. The Milford Sound plants occurred on wet, peaty, insolated, see page-moist cliff faces, admixed with a wide array of other Hepaticae, among them: *Trichotemnoma corrugatum*, *Anastrophyllum schismoides*, *Herberta alpina*, *Clasmatocolea turgescens*, *Chiloscyphus notophyllus*, *Tetracymbaliella decipiens*,

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[1] The report from Tristan da Cunha (Arnell, 1958) is based (at least in part) on plants of *Archeochaete temnomoides*.

[2] Labelled (G) by Fulford, 1960, as " *Trichocolea* or something close to it ".

Cheilolejeunea sp., *Cryptochila pseudocclusa*, *Lepidolaena magellanica*, *Calyptrocolea falcata*, *Acromastigum brachyphyllum*, *Eotrichocolea polyacantha*, *Telaranea herzogii*, *Jamesoniella sonderi*, etc. (*RMS 49471*) occurred amidst *Allisonia cockaynii*, *Temnoma pauciseti gerum*, *Balantiopsis*, *Dendroceros* sp. and *Cryptochila pseudocclusa*, in a wet, steeply sloping snow-tussock covered slope, just above tree line.

DIFFERENTIATION. A tremendously variable species, yet with a distinctive facies, induced by (*a*) stiff, remote, wide-spreading, transversely oriented leaves; (*b*) deeply quadripartite leaves, with narrowly lanceolate-triangular to linear-lanceolate segments; (*c*) development, at least locally, of stiff, short, sharp-pointed, 1-3-celled marginal teeth of the lobe bases, which are diagnostically abaxially displaced; (*d*) frequent elaboration of the basal—and often only—marginal tooth of one or both sides of the disc into an accessory lobe, the leaves and underleaves then incipiently 5-6-lobed; (*e*) long perianths, contracted at the mouth, with short, stiff, crowded teeth; (*f*) ♀ bracts and bracteole mostly 0.6-0.75 quadrifid, with narrowly lanceolate, longly tapered lobes bearing only short, spinescent teeth—never well developed cilia.

This polymorphous species is best characterized by the marked tendency towards production of a sharply recurved, lobe-like, tooth of the antical and/or postical underleaf and leaf bases, originating from low on the discus margin (and not the bases of the leaf lobes). As a result, underleaves, less often leaves, appear to be palmately 5-6-lobed. This is not entirely clear from Hooker's illustrations, but even these show (as is evident from Hooker's figures of the whole plant), some 6-lobed, palmatifid leaves. Associated with the development of such accessory lobes is, often a lack of other marginal teeth of the leaf lobes, even though (1)2-3(4) such teeth may be developed along the lower portions of the lobes, particularly on fertile plants. Leaf lobes are typically very slender, only (2-3)4-6 cells broad at the base, are long-acuminate or even subulate-acuminate in form usually, with the apices formed by (3)4-6 or even 7-8 superimposed single cells. The discus is very short and at most only 6-8 cells high normally, with cells that are only short-oblong (ca. 18-22 × 24-32 μ in the type of " var. *subintegra* "); the cuticle is often apparently nearly or quite smooth, but some nearly typical phenotypes are perceptibly papillose-striolate.

The species is allied to *T. pilosum* Evs. and *T. patagonicum* Schust., from Patagonia and Tierra del Fuego, and less so to *T. palmatum* of New Zealand. It agrees with the former two taxa in the deeply quadripartite leaves with linear-lanceolate to lanceolate lobes; in the very predominantly Frullania-type branching; in the subtransverse leaf insertion, and particularly in the somewhat reflexed bases of the leaf sinuses (and the reflexed or postically displaced teeth or cilia of the sinus bases). The last character separates it from all other New Zealand species, except for extreme forms of *T. palmatum* (which, however, lack the basal large teeth of the disc) and of the otherwise very different *T. pulchellum*.

Temnoma quadripartitum is in many ways a stiffer edition of *T. patagonicum* and *T. pilosum*. It is more slender, but more rigid, and has fewer teeth or cilia of the leaves; the teeth are never bifurcate and are usually much shorter and more spinose—never slender and capillary as in *T. patagonicum* and *T. pilosum*. The

characters employed in the preceding diagnosis will readily separate *T. quadripartitum* from *T. patagonicum* and *T. pilosum*. The aspect of these species is very different: *T. quadripartitum* is spinose-dentate to spinose-ciliate on the leaf margins and the armature of the leaves is quite rigid in appearance, more suggestive of *T. palmatum*; by contrast, the long, more numerous, slender, more capillary cilia of *T. patagonicum* and *pilosum* consist of highly differentiated cells, which are more elongated than the cells within the lobes proper and the plants resemble a *Trichocolea*. Such a differentiation between the cells of the lobes and of the cilia is lacking in small, sterile forms of *T. quadripartitum* (such as *RMS 48601e*), as well as in many vigorous fertile phases (such as *RMS 60441*). In these, for example, the narrow lobes, only 4-5 cells broad at base, gradually " go over " into the uniseriate apex, which consists of cells with the same basic length-width ratio (ca. 1-2 : 1) as the cells within the lobes. By contrast, certain (but by no means all) vigorous forms of *T. quadripartitum* may show highly differentiated terminal, almost setose cilia of the leaves, formed of 4-6 superimposed, elongated cells (cells to 16-18 × 50-60 μ, often to 3.5 × as long as wide).

I have made only a limited study of branching patterns in *T. quadripartitum*; insofar as material suffices, the generalization can be hazarded that branching is predominantly lateral, of the Frullania-type, with the dorsal half of the subtending leaf preserved. The type has branches of this kind only. I have seen almost only Frullania-type branches, a few postical-intercalary branches, and one Microlepidozia-type branch. Insofar as the material allows, therefore, one can conclude that branching is somewhat less restricted in this species than in *T. pilosum* and *T. patagonicum*. Unfertilized gynoecia (which may produce perianths) may bear 2-3 subfloral innovations, often very slender in form.

As is noted under var. *randii*, Microlepidozia-type branches occur occasionally in this variant; they also occur in typical var. *quadripartitum*. In the very spiny extreme of var. *quadripartitum* (type of *J. podophylla* Ångstr.) I have seen highly ramified ♂ plants, with branches normally of the Frullania-type, but in one case the highly unusual situation occurs where an entire lateral leaf is replaced by two branches, one dorsal to the other (the branches are fused at the base, and diverge shortly after their common origin). Here, then, we find both a Frullania- and a Microlepidozia-type branch originating from a single merophyte !

Material from the Humboldt Mts., N.Z. (*RMS 49471*) is more slender than, e.g., the type of *J. podophylla*, and on many leaves the sharp but short reflexed teeth at the bases of the leaf sinuses are absent or only sporadically developed; sinuses descend slightly more deeply, usually to within two cells of the base. These plants

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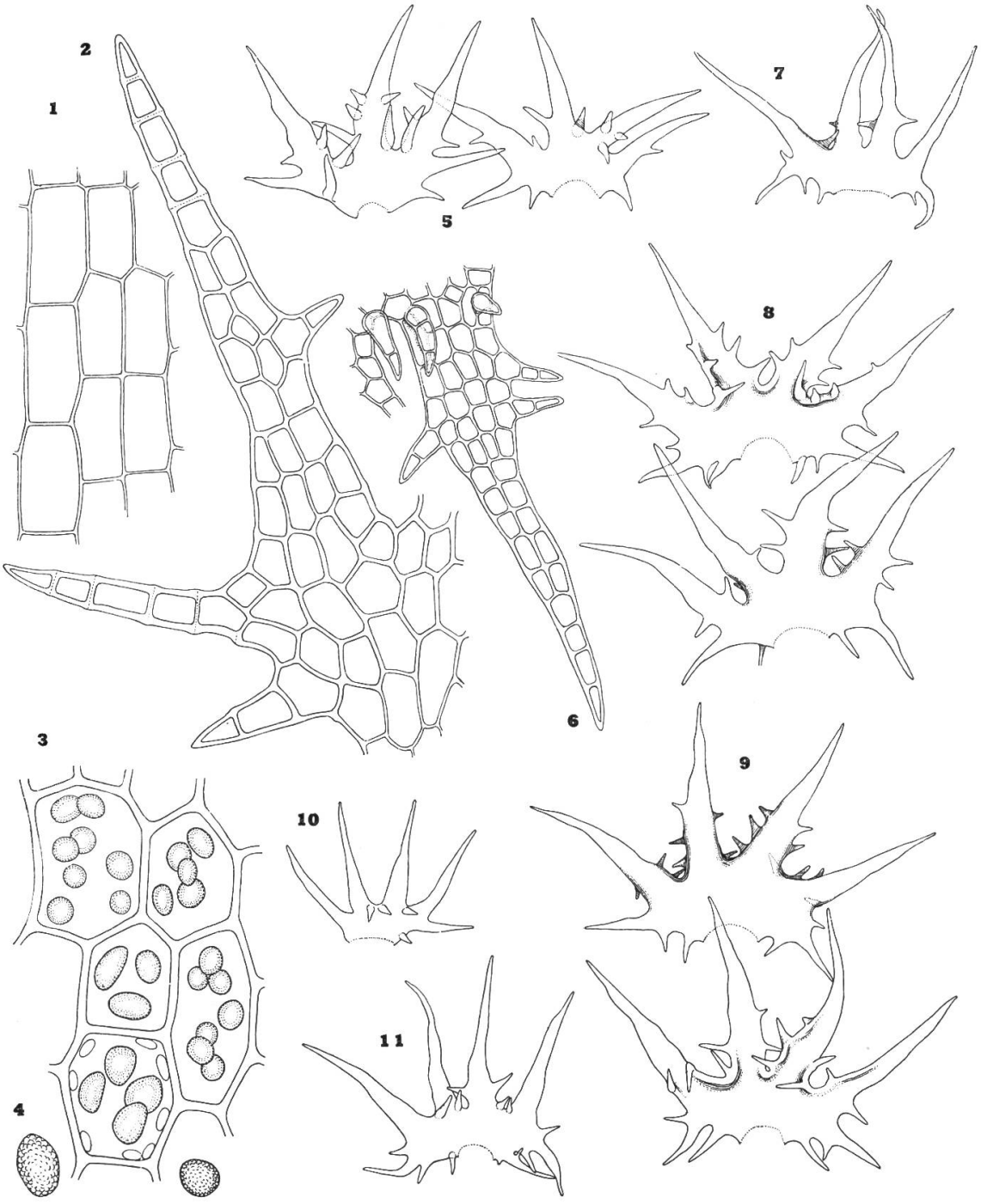
FIG. 35. *Temnoma quadripartitum* (Hook.) Mitt. var. *quadripartitum*.

1. Dorsal cortical cells (×335). – 2. Leaf lobe and adjoining disc (×270). – 3. Cells of disc with oil-bodies and (lower cell) chloroplasts (×680). – 4. Two oil-bodies (×1070). – 5. Trifid and quadrifid leaves (×43). – 6. Lobe of leaf with abaxially displaced spines near sinus bases (×152). – 7. Large underleaf (×43). – 8-9. Mature leaves (×43). – 10. Leaf of minimal size (×43). – 11. Large underleaf (×43).
1-5, from *RMS 48601e*, Bowen Falls, Milford Sound, N.Z.; 6, Arthurs Pass, N.Z., *Hodgson 5441*; 7-11, *RMS 48740a*, Haast R., 1750 ft., South Island, N.Z.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have a very high incidence of trifid leaves and underleaves. However, at least occasional leaves in the plants of *RMS 48601e* are also trifid.

T. quadripartitum has a simple axial anatomy, as contrasted to most other species of the genus. The cortical cells, as in other *Temnomae*, are only weakly incrassate; they are relatively few in number and fully as large in diameter, on the average, as the medullary cells. In this the species diverges from *T. pilosum*, in which the numerous cortical cells are, on the average, clearly smaller than the cells of the medulla. In fact, *T. quadripartitum* somewhat approaches *Archeophylla* in its axial anatomy, without developing the clearly differentiated cortex of that genus. The relatively abbreviated cortical cells of the stem in *T. quadripartitum*, only 2-2.5(3-3.5)× as long as wide, also closely recall *Archeophylla*, and stand in contrast to the sublinear, narrowly rectangulate cortical cells of *T. pilosum*.

There are also similarities in leaf form between *T. quadripartitum* and *Archeophylla*. Both taxa have the ability, apparently absent in other *Temnomae*, of producing intermixed trifid and quadrifid leaves and underleaves.

In addition to the preceding similarities, *T. quadripartitum* may bear a very close resemblance to certain forms of *T. palmatum* (especially var. *pseudospiniferum*). From *T. palmatum* we may distinguish *T. quadripartitum* by the more deeply lobed leaves, with the disc generally less elaborated, and the leaf lobes longer and usually narrower and more attenuate. Transitional collections occasionally occur (e.g. *RMS 60443*, Mt. Hector, N. Z.) with the sinuses less pronounced, the lobes to 7-8 cells broad and less slender. However, such forms of *T. quadripartitum* differ from *T. palmatum* in the spinelike, stiff, recurved teeth of the leaf bases. The two species also differ fundamentally in the perianth mouth: that of *T. quadripartitum* is conspicuously narrowed and armed at the apex with crowded, short, stiff, 1-4-celled teeth; that of *T. palmatum* is very wide at the mouth, with irregular, remote teeth of greatly variable size, the longer always 3-5 cells long. The ♀ bracts of *T. quadripartitum* are also much more deeply quadrifid.

VARIATION. The type of this species, judging from the diagnosis and figures in Hooker (1820, pl. 117 and facing page), was a slender plant with deeply (" ad basin ") quadrifid leaves; the disc is 3-4 cells high and the setaceous lobes only two cells broad at the base, running out in capillary and attenuate segments uniseriate for most of their length. The lateral bases of the leaves bear, on each side, a slender, horizontally recurved lacinium. In general aspect, fig. 3 in Hooker strongly suggests typical var. *quadripartitum*, particularly in that each lobe may bear one or even 2-3 small, sharp teeth. Type fragments (Vienna) are of a more vigorous extreme (suggesting a juvenile plant was used for Hooker's plate and diagnosis), with the disc 6-7 cells high. The diagnosis of fo. *quadripartitum* is based on the type fragments seen.

The extraordinary polymorphism of *T. quadripartitum* has already been alluded to; this has led to the description, within recent years, of two synonyms, *Lepidozia randii* (Arnell 1953) and *T. subintegrum* (Fulford 1963); these two synonyms, furthermore, belong to a single phenotype.

The variation, aside from robustness, is chiefly along two lines: (*a*) the degree to which the basal teeth of the disc margins are elaborated to form incipient accessory

lobes; (*b*) the degree to which the abaxially displaced, short, rigid spinose teeth of the lobe margins (often only lobe bases) are developed. One, but almost never both of these features may be nearly or quite suppressed.

There also tends to be a correlation between the development of numerous spinose teeth on the lobe margins and of several spinose teeth of each margin of the discus, and suppression of accessory lobe formation (as in the type of *J. podophylla* Ångstr.; here 30-40 spinose teeth per leaf may occur and occasionally leaves are provided with broad, lobelike, lateral teeth which may themselves bear spinose secondary teeth). Inversely, there is a tendency towards formation of a strong basal lobe on each side of the leaf, correlated with which the number of short, spinose, marginal teeth of the leaves tends to be reduced; an extreme is formed by the various New Zealand phenotypes, which usually bear 0-1(2) pairs of spinose teeth per lobe, with at most 4-18 spinose teeth per leaf. Even more extreme is the situation with the rather large phases with long lobes (var. *randii*), in which isolated teeth of the lobes may be present (type, var. *randii*) or may be virtually suppressed (" *Temnoma subintegrum* " Fulf.).

With robustness, apparently induced by growth under mesic conditions with adequate nutrition, we find that the leaf lobes become 6 or even 7-8 cells broad at the base and become more attenuated, and to 20-25 cells long or more. [These are the extremes described by Arnell (1953) as *L. randii* and by Fulford (1963) as *Temnoma subintegrum*] [1]. Inversely, under some conditions which I do not yet understand, the plants show reduction of the leaf and underleaf lobes to a nearly or quite uniseriate condition (Fig. 36 : 9), and the gynoecial bracts lose their more narrowly trapezoidal form and develop caudate apices to the lobes, similar to the leaf lobes. Such plants (var. *pseudopungens*) are very distinct in the strongly elongated cells of the uniseriate leaf and bract lobes.

These variations, and various transitions between them, are almost innumerable. There is, furthermore, an evidently feebly defined geographical correlation, at least to this extent: (*a*) typical var. *randii* is very rarely found in New Zealand; the New Zealand phenotypes seen have generally shown lobes to 16-18 cells long ×4-5(6-7) cells broad. (*b*) The very copiously spinose phenotypes (fo. *spinifera*) with 30-40 spines per leaf, appear restricted to southern South America; they include the type of *J. podophylla* Ångstr. (nec Thunberg). (*c*) The phenotype with lobes reduced to the point where they are almost completely uniseriate seems restricted to New Zealand. (*d*) The majority of New Zealand phenotypes are paucispinose, with from 6-20 spines per leaf, and are smaller, more rigid plants than the most nearly allied South American plants of fo. *spinifera*.

I have been tempted to segregate some of these extremes; there have been past attempts at segregation, with three synonyms at the species level (*podophylla* Ångstr., *randii* Arn., *subintegrum* Fulf.). Yet, if species distinctions are to be attempted, I am quite unable to see where they are to be drawn. If there is more than one

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[1] Fulford (*loc. cit.* 23 : 54) attempts to restrict the name *T. quadripartitum* to phenotypes with the " segments mostly two or four cells broad at the base, to twelve cells long..." The type of the species (Vienna), however, has mature leaves of the sterile axes with lobes 5-7 cells wide at base and 16 cells long ! In this respect the type of *T. quadripartitum* more nearly keys out to her " *T. subintegrum*."

species in *T. quadripartitum*, as I broadly circumscribe it here, phenotypic variation is so great as to obscure completely any hypothetical major genotypic differences. Owing to the extraordinary amplitude of variation, some of which is seemingly geographically correlated (e.g., the *randii* phenotypes and forms approaching them almost fail to occur in New Zealand: *pseudopungens* phenotypes seemingly occur only in New Zealand), I have attempted to recognize several varieties and forms. These remain unestablished hypotheses in the absence of good biological data to support them—but are almost necessary to give us some concept of the variation within this extraordinary species [1].

I have checked the type of *Lepidozia randii* S. Arnell; it is definitely a *Temnoma* —the facies, brownish coloration, stem anatomy, sparing branching, etc.—all clearly proclaim this fact. Within *Temnoma*, the longly quadripartite leaves, divided to within 0.25 of their base, with the discus to a maximum of 6-8 cells high and with a large, almost lobe-like lacinium, often reflexed, of both dorsal and ventral discus margins—all of these speak clearly for *T. quadripartitum* s. lat. Equally indicative of this identity is the occurrence on most mature leaves of a few short marginal spines near the lobe bases that are abaxially displaced. Except for this last feature, the plants are identical to *Temnoma subintegrum* Fulf. Leaf lobes of mature leaves are 5-6 to 6-8 cells broad, lanceolate-acuminate, and 17-20 cells long. The plants thus correspond to the large, mesophytic phase of the species, recently described as " *Temnoma subintegrum* " by Fulford (1963). I have compared the types of the two and find no differences of any significance, even on the varietal level.

Key to the major phenotypes (putative varieties and forms) of *Temnoma quadripartitum*

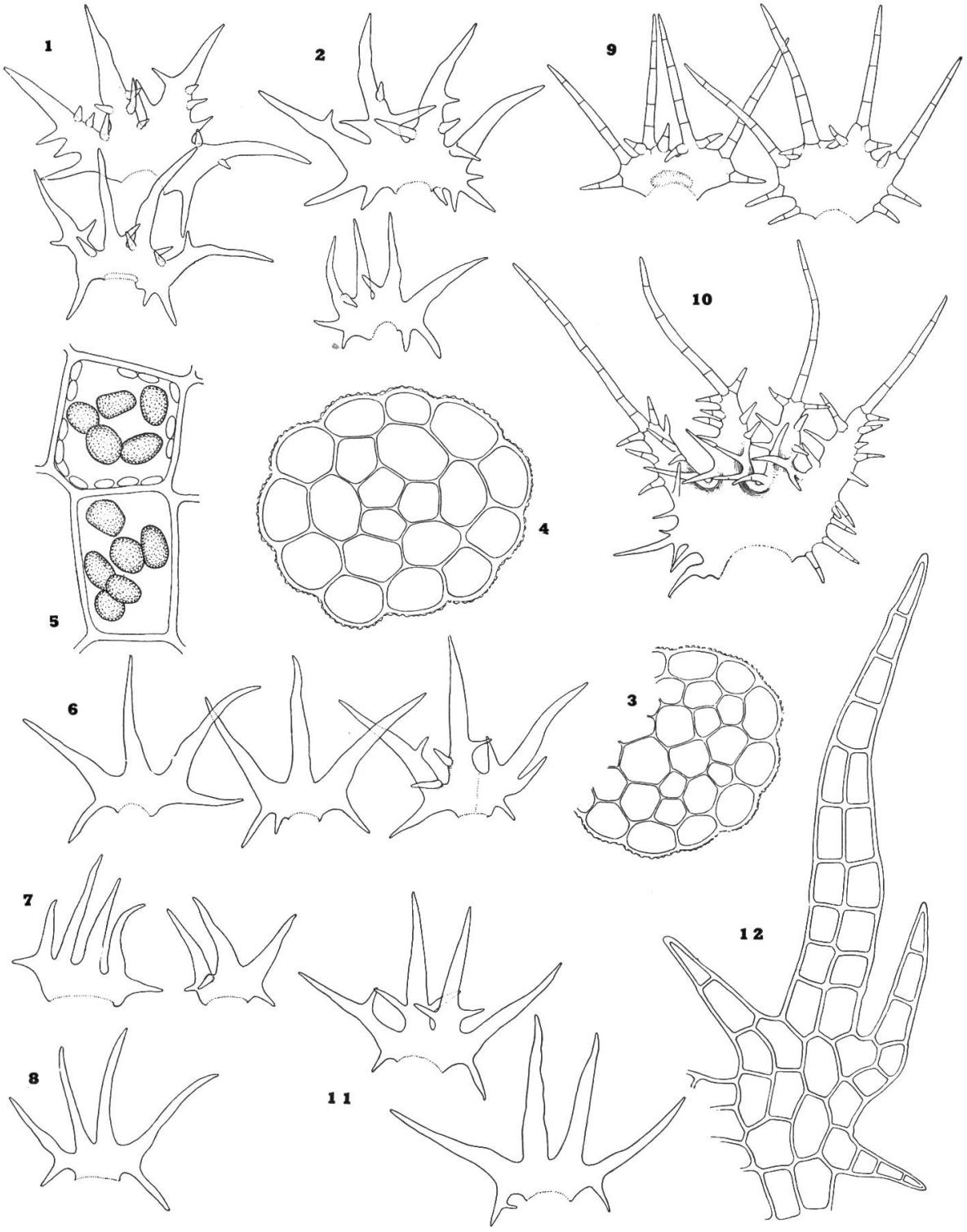
1. Leaves with lobes rigidly setaceous, of thick-walled cells 14.5-16 × 65-90 μ, uniseriate except at the very base (there with vestigial bases 2-3 cells broad); disc margins with 2-3-celled cilia, but lacking accessory lobes at base; bracts obtrapezoidal, the disc much wider than long, the lobes with 4-6 pairs of opposed, stiff teeth, abruptly ending in uniseriate terminal cilia longer than lobes below them . . . . . var. *pseudopungens* Schust.

1*. Leaves with lobes gradually tapering, 2 or more cells wide for most of their length (even on weak, juvenile stems); perichaetial bracts narrowly

[1] The collections from Mt. Hector, N. Z. (*RMS 60440-60444*) may prove critical. All but *RMS 60444* consist of nearly typical phenotypes, with optimal spine formation of the sinus- and lobe bases. The last, however, is, in part, of a softer form, with the abaxial spines suppressed in large part, and lobes (as in var. *randii*) to 30 cells long × 8 cells wide.

FIG. 36. *Temnoma quadripartitum* (Hook.) Mitt. var. *quadripartitum*; reduced extremes (1-8, 11-12) and *T. quadripartitum* var. *pseudopungens* Schust. (9-10).

1-2. Leaves, and below them, underleaves (×64). – 3. Stem cross-section (×245). – 4. Stem cross-section (×490). – 5. Two discal cells, with oil-bodies (and, upper cell, chloroplasts; ×705). – 6. Three trifid leaves (×64). – 7-8. Underleaves (×64). – 9. Extreme with leaf lobes uniseriate to base, underleaf and leaf (×36). – 10. Female bract of phenotype in fig. 9 (×56). – 11. Two leaves (×64). – 12. Lobe of leaf in fig. 6, at right (×262).
1-3, from *RMS 48601e*, Bowen Falls, N.Z.; 4-8, 11-12, from *RMS 49471*, Route Burn Track, Fiordland, N.Z.; 9-10, from *RMS 49649a*, Haast Pass, N.Z.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obtrapezoidal—cuneiform, disc no wider than long, the long-acuminate lobes with 5-9 pairs of spinose teeth each, the apical uniseriate cilium shorter than the remainder of lobe below 2

2. Lobes (3)4-5(6) cells wide at base [1], relatively abruptly narrowed distally, 12-16(17) cells long usually; disc margins rarely with accessory teeth so conspicuously lobelike that the leaf is seemingly 5-6-lobed; margins of lobes usually freely spinose-dentate towards base (miniature juvenile leaves excepted); cuticle feebly to distinctly roughened . . var. *quadripartitum* 3

2*. Lobes either 3-4(5) or 6-8 (rarely to 9-11) cells wide at the base, longly acuminate, gradually tapering, 16-22(23-30) cells long (on stem leaves); disc margins near or at base commonly with an enlarged spine that is lobelike, often reflexed, the leaf seemingly palmately 5-6-lobed; lobe margins entire or with isolated, usually small (1-2[3]-celled) abaxially displaced teeth near sinus bases; cuticle smooth or nearly imperceptibly roughened var. *randii* (Arn.) Schust. 4

3. Leaves quite rigid, paucispinose: each lobe with (0)1-4(5-6) abaxially displaced teeth that are usually 1-4(5)-celled; leaf as a whole with usually to (5-6)8-20 teeth, lobe apices excepted . . . . . f. *quadripartitum*

3*. Leaves relatively pellucid, less rigid, strongly spinose: each lobe with 4-8 abaxially displaced teeth, the longer at sinus bases often 4-6 cells long; leaf as a whole with usually (24-28)30-48 spinose teeth, lobe apices excepted f. *spiniferum* Schust.

4. Lobes (5)6-8 or even 9-11 cells wide at base, acuminate, terminated in a tip formed of 4-7(8) superimposed cells which are not or moderately elongated (1-3[4] : 1); sinus bases with spinose teeth rare, infrequent or lacking, short and 1-3-celled; disc usually 6-8(9) cells high. [Postical-intercalary branches frequent] . . . . . f. *randii*

4*. Lobes 3-4 cells wide at base, distally filiform-setaceous, rigid, terminated by a tip formed of (5)6-9 superimposed, differentiated, highly elongated cells (3-5 : 1); sinus bases with several longly spinose, abaxially displaced teeth, the longer 4-5(6) cells long, very conspicuous; disc only 4-5 cells high f. *setacea* Schust.

Temnoma quadripartitum (Hook.) Mitt. var. **quadripartitum**

The species dignosis has been constructed to describe basically the " normal " phase of the species. The specimens cited after the diagnosis all pertain to typical var. *quadripartitum.*

Var. *quadripartitum* is circumscribed by a variable series of criteria: medium-sized leaf lobes, usually 3-5(6), rarely 6-8 cells broad at the base and 12-16(17-19) cells long; the regular occurrence of some abaxially displaced, spinose, conspicuous,

[1] In occasional vigorous ♂ plants (e.g., *RMS 60443;* see under fo. *quadripartitum*) the lobes may be 6-8 cells broad, but remain 15-16 cells long; such plants belong here because the lobe bases are freely armed with abaxially displaced stiff, short teeth.

if short, usually 1-3(4-5)-celled teeth on the basal portions of the lobes and on the sinus bases; the narrow, cuneate-obtrapezoidal, strongly plurispinose gynoecial bracts.

Two extremes of the species, which appear to intergrade, occur:

f. *quadripartitum*, [Figs. 33-35, 36 : 1-8, 11-12].

Shoot to 1200 μ wide; stem ca. 140-160 μ in width; cortical cells ca. 20-28 ×50-72 μ, ± thin-walled. Leaves distally 1000-1200(1400) μ wide ×700-800(850) μ long (type) or often much smaller; relatively rigid, concave, paucispinose: each lobe 4-5(6) cells wide at base ×12-16(17-19) cells long near base with 1-4(5-6) abaxially displaced teeth, which are normally 1-3(4-5)-celled; leaves as a whole with (5-6)8-20 spinose teeth, one of which, on each side of disc, near base, is commonly several cells wide at base, enlarged to form an incipient accessory lobe, and may bear 1-2 small basal spines.

f. *spiniferum* f. nov. [Fig. 38 : 9-10].

Forma *T. quadripartito* typico similis, differens foliis subpellucidis, minus rigidis, valde spinoso-ciliatis (omnis lobus 4-8 dentes abaxialiter dispositos habens, dentibus longioribus ad 4-6 cellularum long.), folia 36-48 dentibus spinosis plerumque praedita. Typus: Port Famine, Magellan Strait, *H. J. Andersson* S-PA.

Leaves rather large, to 975-1050 μ wide distally ×560-675 μ long, rather pellucid, extremely spiny, strongly to moderately concave: each lobe with 4-8 abaxially displaced teeth, which are often 3-5-celled (and to 125-150 μ long); leaves as a whole with 24-32, on large sterile leaves to 36-48, spinose teeth, of which 1-2 on each side may be larger, several cells wide, and may themselves bear 1-3 small spinose teeth, forming ill-defined incipient accessory lobes. *Cells* rather hyaline, almost smooth, in disc middle (18)20-23(24)×25-36 μ, relatively pellucid.

TYPE. Port Famine, Magellan Strait, *H. J. Andersson* S-PA.

The f. *spiniferum* approaches most closely to *T. patagonicum*, and may, indeed, prove more closely allied to this. The extremely spiny aspect of the leaves closely recalls *T. patagonicum*, and the marked tendency for the very numerous cilia of the leaf lobes to become pluricellular and elongated also suggests *T. patagonicum*. Indeed, the plant is almost intermediate between *T. patagonicum* and "normal" *T. quadripartitum*. Yet, in *T. patagonicum* the longer cilia of the sinus bases and disc margins are to 5-7 cells (and to 250 μ) long, whereas in *T. quadripartitum* f. *spiniferum* the cilia are only to 3-5 cells long (and to 125-150 μ long). There is a broad intergradation in cilium number in *T. quadripartitum* f. *spiniferum* and in *T. patagonicum*: both taxa usually have ca. 28-42 cilia per mature leaf.

Temnoma quadripartitum var. **randii** (S. Arn.) Schust., comb. n. [Figs. 37; 38 : 1, 4-8].

Lepidozia randii S. Arn. Sv. Bot. Tidskr. 47(3) : 417, fig. 6. 1953.
Blepharostoma quadripartitum var. *subintegrum* Steph. MS.
Temnoma subintegrum Fulf. Mem. N. Y. Bot. Gard. 11 : 57, fig. 4 (: 58). 1963 (new synonymy).

Leaves to ca. 1200-1300 μ wide ×850-900 μ long, ± squarrose. Similar to var. *quadripartitum* in the deeply (0.65-0.75) quadrifid leaves, with the disc ca. (5)6-7(8-9)

cells high. With one or both sides of disc base with a large (often tortuous or reflexed) tooth. Differing from var. *quadripartitum* in the more linear-lanceolate lobes which are 17-22(23-25) cells long or more on mature leaves and (5)6-8(9-11) cells wide at the base; margins of vegetative leaves with lobes entire or with an occasional tooth (rarely 2) per lobe, the teeth short, stiff, only occasionally abaxially displaced when present; disc bases usually or often with a long, curved lobe-like lacinium. *Cuticle* ± smooth. *Leaf lobes* ending in (3)5-7 superimposed single cells that are little elongated.

TYPE. Marion Island, *W. Rand 3276*; S-PA, type of *T. subintegrum*, Puerto Bueno, Patagonia, *Dusén 46*; G, H.

In the initial version of this manuscript I treated *Lepidozia randii* as a straightforward synonym of *T. quadripartitum*, and recognized its identity with the MS name *Blepharostoma quadripartitum* var. *subintegrum* Steph. (as typified by a small specimen in the Stephani microherbarium at the Farlow Herb.). In the meantime, Fulford (1963) published the new " species " *Temnoma subintegrum* Fulf. If this taxon deserves species status, it must, however, be known by the name *Temnoma randii*, the name *subintegrum* not being validated until 1963.

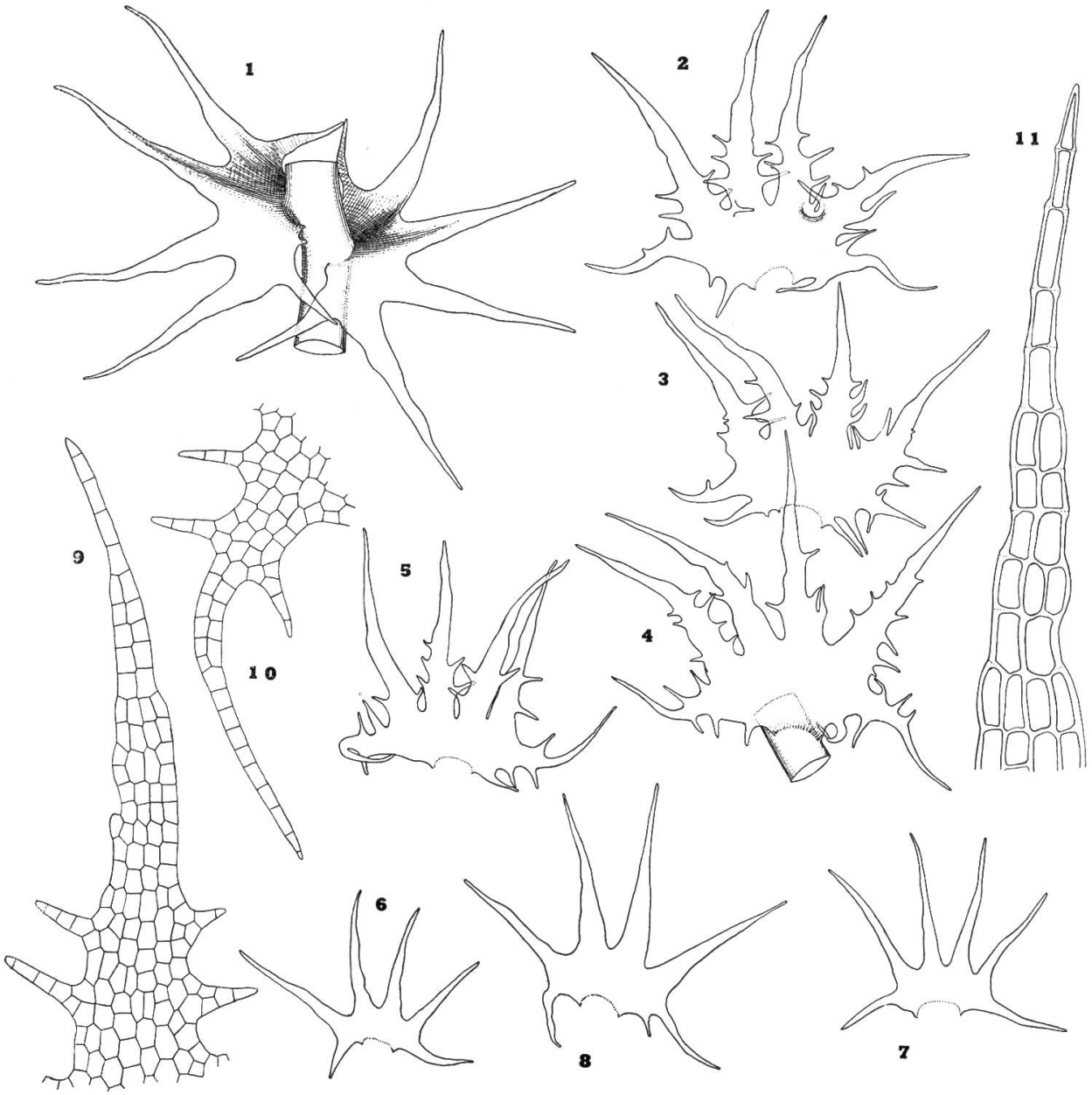
I am of the opinion, however, thar *T. randii* possibly represents nothing more than the meso-hygrophytic extreme of *T. quadripartitum*, and may possibly not even deserve varietal recognition. For this reason, I do not append a detailed diagnosis and treatment of this questionable taxon. The New Zealand plants of *RMS 60444*, which key here, are from a more mesic niche than *RMS 60440-60441*, which key to var. *quadripartitum*, and strongly suggest that the " *randii* " phenotype can be produced from the " *quadripartitum* " phenotype under unduly moist conditions. Grolle (1964) suggested that the " simpler " ♀ bracts of " *subintegrum* " warranted retaining the latter as an autonomous species. However, the range of variation in the bracts is relatively slight (compare Figs. 33: 3-4, 36: 10, 38: 6). Also, the tendency towards a weaker formation of teeth on the bract margins seems to reflect the moister habitat (associated with which sterile leaves are also much more sporadically armed with teeth).

The plant tends to be larger and longer than var. *quadripartitum*, perhaps the result of growth under very wet (or even submerged) conditions, with the shoot width to ca. 900-1050 μ, the stem 150 μ or more in diameter (and ca. 9-10 cells high). At times the teeth near the leaf sinus bases are virtually absent, except on leaves near the gynoecia (as in the type of *T.* " *subintegrum* "), but they are usually present on scattered leaves, at least on gynoecial plants (type of " *Lepidozia* " *randii*) [1].

[1] The specimen from Fuegia (*Halle, 1908*), cited as *Temnoma* " *subintegrum* " by Fulford (*loc. cit.*) has many leaves with 1-3 postically displaced, spinose teeth near the sinus bases, and, in all its characters, agrees perfectly with the type of *Lepidozia randii*.

FIG. 37. *Temnoma quadripartitum* var. *randii* (S. Arn.) Schust.

1. Mature shoot-sector in antical aspect, showing somewhat succubous leaf insertion (×37). – 2-4. Optimally-sized upper leaves of female shoot (×29). – 5. Underleaf from same sector of shoot as in 2-4 (×29). – 6-7. Smaller underleaves of sterile shoot-sector (×29). – 8. Leaf of branch (×29). – 9. Lobe of subfloral leaf from female plant (×100). – 10. Basal accessory lobe of such a leaf (×100). – 11. Cells of apical part of lobes from leaf in fig. 1 (×165). All drawn from type of *Temnoma subintegrum* (Steph.) Fulf.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The cuticle in this variant is usually smooth or with the leaf tips almost imperceptibly roughened. In presumably aquatic or subaquatic extremes (such as *Halle and Skottsberg*, Port Gomez, Tierra del Fuego) the leaves may become large, to 950-1025 μ wide ×650-700 μ long. Then the leaf lobes may be 6-11 cells wide at the base and (17)18-22 cells long; the disc may become rather higher and 7-9 cells high.

Perhaps associated with caespitose growth under very wet conditions, the laxer larger forms (such as the Halle & Skottsberg specimen) occasionally produce *Microlepidozia*-type branches, as well as the ordinary, Frullania-type branches.

DISTRIBUTION. Known principally from South America and Marion Island. MARION ISLAND: *W. Rand 3410* (S-PA). SOUTH AMERICA: Patagonia: Puerto Bueno, *Dusén 46*; Patagonia, s. d. *Hariot*, Munich; Tierra del Fuego: Fuegia, *Halle, 1908*; Port Gomez, in silva primaeva, Feb. 26, 1908, *Halle & Skottsberg*; Staten Island (1837?; in herb. Lehmann, Stockholm, two plants only: a rather weaker form, with lobes only 16-19 cells long and 4-6 cells wide at base, but otherwise typical; a second specimen, also of two stems, from the Lehmann herbarium, seems to be the same; it is labelled as collected by Menzies, and is dated 1836); Straits of Magellan, July, 1885, com. *Warnstorf 11*, p.p., G. INDIAN OCEAN: St. Paul Island, *de l'Isle*, inter Symphyogyna, G, only a few slender stems, but typical. NEW ZEALAND: Slopes of West Peak of Mt. Hector, 4400-4700 ft., S. Tararua Mts., N. Island, *RMS 60444*; a soft form, in part, from along a water course, with lobes rarely 25-30 cells long ×7-9 cells wide at base.

The New Zealand plant has leaves to 725 μ long ×1150 μ broad. Except for the deeper sinuses and longer lobes they closely approach the phenotype figured in Fig. 50: 4-7, which shows superficial similarities to *T. palmatum.*

Temnoma quadripartitum var. **randii** f. **setaceum** f. nov. [Fig. 38: 2-3].

Forma *T. quadripartito* v. *randii* similis, lobi, autem, 3-4 cellularum lat. ad basim, distaliter setacei, rigidi, in setase 6-9 cellulis superimpositis valde elongatis (long.: lat. ca. 2.5-5 : 1) compositas, terminantes; bases sinus aliquot dentes abaxialiter dispositos, ad 4-6 cellularum long., praebentes; discus solum 4-5 cellularum alt. Typus: Halt Bay, Fretum Magellanicum, *Cunningham*, G, K.

Plants, when mature, with rigid, widely spreading leaves (ca. 650-700 μ long ×1050-1150 μ wide distally), divided for ca. 0.8-0.85 their length; disc only 4-5(6) cells high; lobes hardly lanceolate, setaceous to needle-like, at base 3-4 cells wide, distal 0.4-0.55 uniseriate, rigid, formed by (5)6-9 superimposed, elongated, smooth,

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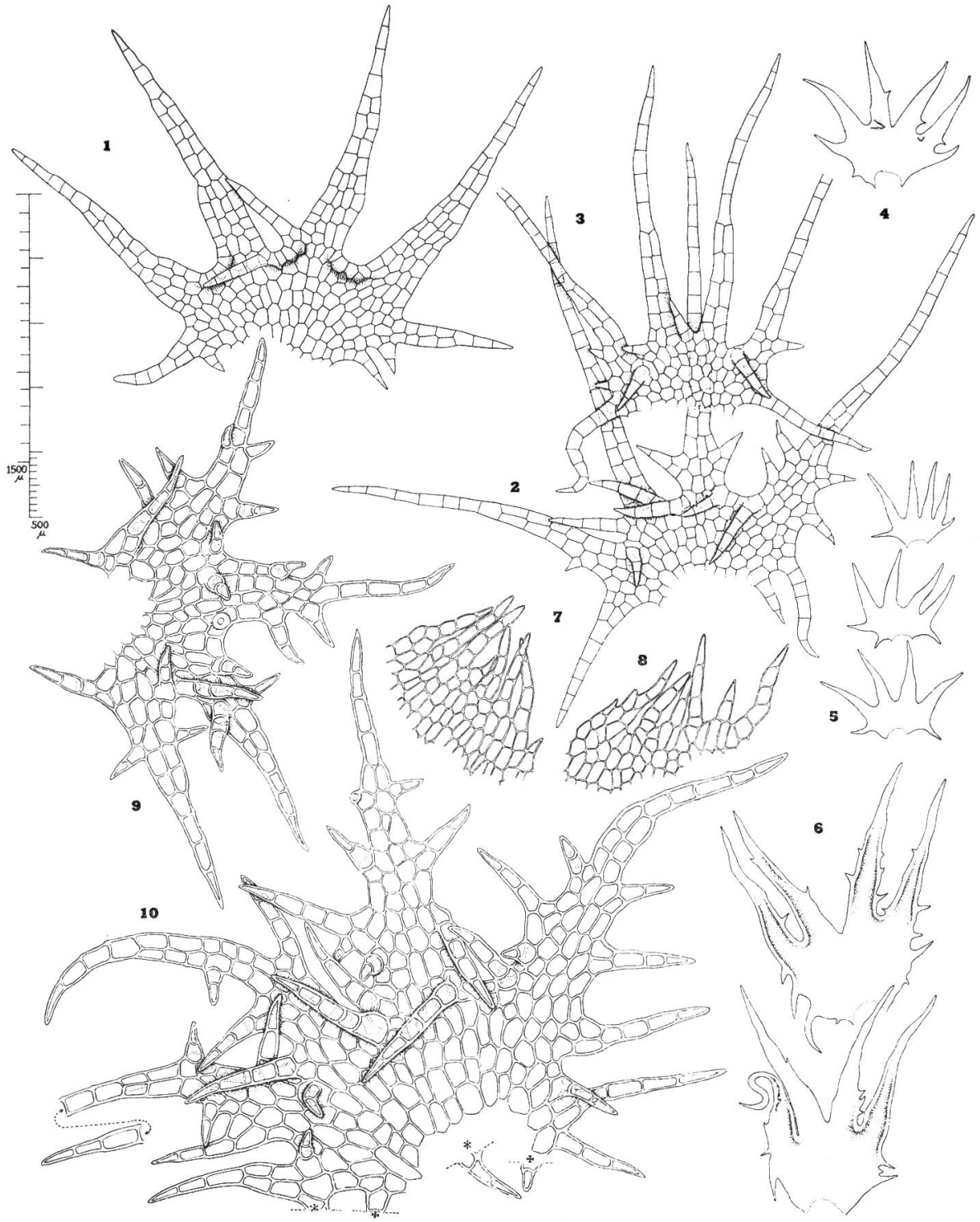
FIG. 38. *Temnoma quadripartitum* (Hook.) Mitt. (1, 4-8, var. *randii*; 2-3, var. *randii* f. *setaceum*; 9-10, var. *quadripartitum* f. *spiniferum*, a form grading towards *T. patagonicum*). 1. Mature leaf (×80). – 2-3. Underleaf, above, and leaf, below (×80). – 4. Leaf from female shoot (×22). – 5. Three leaves from male shoot (×22). – 6. Two female bracts (×25). – 7-8. Sectors of perianth mouth (×115). – 9-10. Small and large leaves (×62). (1-3, drawn to scale at right; 4-5, drawn to scale at left).
1, Staten I., South America, *Lehmann* herb.; 2-3, from type, from Halt Bay; 4-8, from Pucón, towards Volcano Villarica, Chile, *Hosseus 221*, p.p.; reported by Grolle, 1964 as " *T. subintegrum* "; 9-10. from type, Port Famine, S.A.; see also Fig. 50.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1500 μ
500 μ

thick-walled cells (the longer ca. 10-12×45-48 μ to 10-13×58 μ; thus the length: width ratio 4-5 : 1); terminal cells of lobes elongated, to 9-12×36-52 μ, stiffly pointed and slenderly acute; lobes as whole usually 16-20 cells long on mature leaves.

TYPE. Halt Bay, Fretum Magellanicum, *Cunningham*; G; K.

PARATYPE. Isla Desolacion, Puerto Angusto, Tierra del Fuego, *Dusén 148*, 26-3-96, with *Schistochila pachyla*.

The type specimen is labelled " new genus, new species " by M. Fulford; in Fulford (1963) it is cited simply as *T. quadripartitum*! It consists, unfortunately (portion at Geneva), of only 2-3 mature axes, the others are juvenile.

This plant is of very special interest in that it combines some of the features of var. *quadripartitum* (e.g., the lobes are narrow and only 3-4 cells wide at base; the sinus bases are very conspicuously armed with spinose, abaxially displaced teeth) and features characteristic of var. *randii* (e.g., the longly attenuated lobes, to 20 cells long [1], which are edentate except at base). The existence of such plants wholly invalidates a separation of *T. quadripartitum* s. lat. into two or more species. Yet the plants fail to fit well into either var. *quadripartitum* or var. *randii*. I place them as a forma of the latter because of the diagnostically attenuated, long-acuminate leaf lobes up to 20 cells long, and the inability of the lobes to produce marginal, displaced spines except at the very base.

Temnoma quadripartitum var. **pseudopungens**, var. n. [Fig. 36: 9-10].

Folia lobos uniseriatos nisi ad basim ipsam (ibi 2-3 cellularum lat.) habentia; margines disci cilia 2-3 cellularum habentes; bracteae femineae obtrapezoideae, disco multo latiore quam longus, lobis ciliatis in cilia longa terminalia abrupte terminantibus. Typus: S of Haast Pass, Otago Prov., 1780-1810 ft., South Island, New Zealand, *RMS 49649a*.

Small, brownish, rigid (leaves to 500-575 μ long ×568-800 μ wide). Similar to var. *quadripartitum* in developing, on both leaves and underleaves, and bracts, short stiff, 1-2-3-celled, sharp, abaxially displaced, conical teeth. Differing from var. *quadripartitum* as follows: leaves with stiff, setaceous vestigial lobes, except for the uniseriate apex which is usually 4-6 cells long (and is inserted on a lobe proper, that may consist of only 2-3 cells, side-by-side); all or some of the vestigial rigid, erect or suberect lobes producing, at the base, 1-2 sharp, stiff, 1-2-celled teeth that are stiffly abaxially displaced; disc stiffly spreading, relatively well preserved, producing 1-2, 2(3)-celled marginal teeth which are never lobe-like (the leaf thus never incipiently 5-6-lobed). *Underleaves* very similar, also with lobes reduced to uniseriate segments 4-6 cells long, inserted on vestigial lobes formed of 2-3(4-6) cells, also with 1-2 sharp, short, displaced teeth at lobe bases; disc lower (5-7 cells high) and broader, producing (at least at times) a single 2-3-celled spinose tooth on each margin, thus never 5-6-lobed. ♀ *Bracts* with disc rather low, divided for ca. 0.65-0.75 their length, the lobes spinose-ciliate or spinose-dentate with 4-5 pairs of stiff, displaced (1)2-3(4)-celled teeth that are usually opposed, the lobes ending in long, setaceous

[1] In the paratype only to 16 cells long; this is largely a ± juvenile, slighter phenotype.

apices formed of 5-8 superimposed cells, which are 1.2-1.8× as long as the lobes themselves, the lobes thus caudate in aspect. *Cells* (leaves; ♀ bracts) ca. 17-24×28-35 μ in disc; cells of uniseriate lobe apices to 14.5-16×65-86 μ up to 15×90 μ.

TYPE. New Zealand: South Island: Just S of Haast Pass, Otago Prov., 1780-1810 ft., on damp ledges along small rill, in Nothofagus menziesii forest, *RMS 49649a*, in herb. auct. Occurring with *Calyptrocolea gemmipara* and *Tetracymbaliella cymbalifera*.

This plant, known only from the type, represents a close approximation to *Archeophylla pungens* of South America, differing in that there are somewhat more distinctly preserved lobes, developing the small, spinose, abaxially displaced, stiff teeth so diagnostic of *T. quadripartitum* as a whole. Diagnostic is the sharp contrast between the widely patent leaf disc, the stiff, small, abaxially recurved teeth of the lobes, and the erect setaceous lobes. The development of linear, uniseriate lobes in var. *pseudopungens* does not represent a mere juvenile condition of typical var. *quadripartitum*. In any event, juvenile stems of the last always have leaf lobes that are gradually, rather than abruptly, tapering and are 2-seriate for much of their length.

Similarities also occur to *T. palmatum* var. *pseudospiniferum* and *T. townrowii* (which see).

Temnoma patagonicum Schust., spec. nov. [Fig. 39].

Folia amphigasteriaque subaequalia, spinoso-ciliata, 28-42 cilia habentia (cilia loborum terminalia 130-250 μ long., e 3-6 cellulis superimpositis constantia; stipes diametro 8-9 cellularum, ca. 24-26 ordines cellularum corticalium 1.5-3.2× longiorum quam latae habens. Typus: Patagonia, *Dusén 312*, G.

Plants caespitose, erect in growth, light greenish-brown to yellow-brown, copiously spinose-ciliate, but not with capillary segments; shoots ca. 850-1100 μ wide with leaves ×8-15 mm high, sparingly, irregularly branched, the branches apparently all of the Frullania-type. *Stem* subterete, rather stout, straight, ca. 180-240 μ in diam.; cortical cells leptodermous or nearly so, brownish-walled, in ca. 25-26 rows, similar in diam. to medullary cells, in surface view short-oblong to oblong-hexagonal, (22)24-28(30)×48-65(75) μ (length-width ratio 1.5-3.2: 1). *Rhizoids* rare or almost absent. *Leaves* spinose-ciliate in appearance, abaxially hispid, distant to barely contiguous, although distally imbricate to form a copiously spinose-ciliate apical " head ", almost transversely inserted, widely, stiffly patent, subvertical or vertical, obtrapezoidal-reniform in outline, ca. 580-600 μ wide ×400 μ long to 750-925 μ wide ×500-600 μ long (including cilia), quadrifid for 0.65-0.75 their length, the antical and/or postical bases often with an accessory lobe that may be large enough for the leaves to appear 5-6-lobed; disc usually (3)4-5 cells high; sinuses strongly reflexed; chief lobes narrowly lanceolate, 4-6 cells wide at base, ending in a terminal cilium (130-250 μ long) formed by 3-6 superimposed cells, the margins with 3-4 pairs of opposed, rigid, spinose-ciliiform teeth (formed of up to 5-7 cells in a row, at base sometimes 2 cells wide; up to 250 μ long), the cilia progressively longer towards lobe bases and there strongly abaxially reflexed (the leaves, in profile,

hispid-ciliate abaxially); leaves as a whole with 28-42 cilia or teeth. *Underleaves* only slightly smaller, to ca. 600-800 μ wide ×355-425 μ long, otherwise essentially similar to leaves, somewhat less strongly spreading from stem, similarly hispid-ciliate. *Cells* of cilia much less elongated than in *T. pilosum*: the terminal cells acutely triangular, from 10-13(14)×30-42 μ, the longer cells within the cilia only 12-15×36-45 μ up to 14-18(20)×36-52(60) μ (length-width ratio ca. 2-4 : 1); cells in disc middle ca. 20-24×32-38 to 15-20×35-40 μ; basal cells little or not larger, 20-24×36-48 μ to 18-21×40-55 μ, slightly or hardly thick-walled; cuticle very faintly roughened. Without asexual reproduction.

TYPE. Patagonia (no other locality data), *Dusén 312*, G. The type was confused by Fulford (1963) with *T. pilosum* and is cited under this by her.

DISTRIBUTION. Known, to date, from the type specimen; this is unfortunately sterile, and from one other (paratype). ARGENTINA: Tierra del Fuego, just E of Lapataia, ca. 18 mi. W of Ushuaia; damp soil in rich Nothofagus (Lenga) Forest along small stream, *RMS 58830a*, with *Triandrophyllum subtrifidum*, *Vetaforma*, etc.).

ECOLOGY. The type specimen is mixed with numerous fine sand particles, shoot-apices excepted. Hence I suspect that ecologically this species will prove similar to *T. pilosum*, being a plant of areas subject to flooding, where silt or sand are carried in. The paratype was sparse, growing in deeply shaded silty ground along a stream, in Nothofagus-Drimys forest.

DIFFERENTIATION. A distinctive plant, which occupies in some ways the midground between *T. quadripartitum* and *T. pilosum*—two drastically different-appearing species—and warrants our treating these three as a single phylogenetically allied complex. The three species are allied in a number of ways. They share deeply quadrilobed leaves with, in each case, a marked tendency for the development of accessory lobes of the disc margins; all three have the cilia or teeth near the sinus bases abaxially displaced and have transverse or virtually transverse leaves with lanceolate lobes.

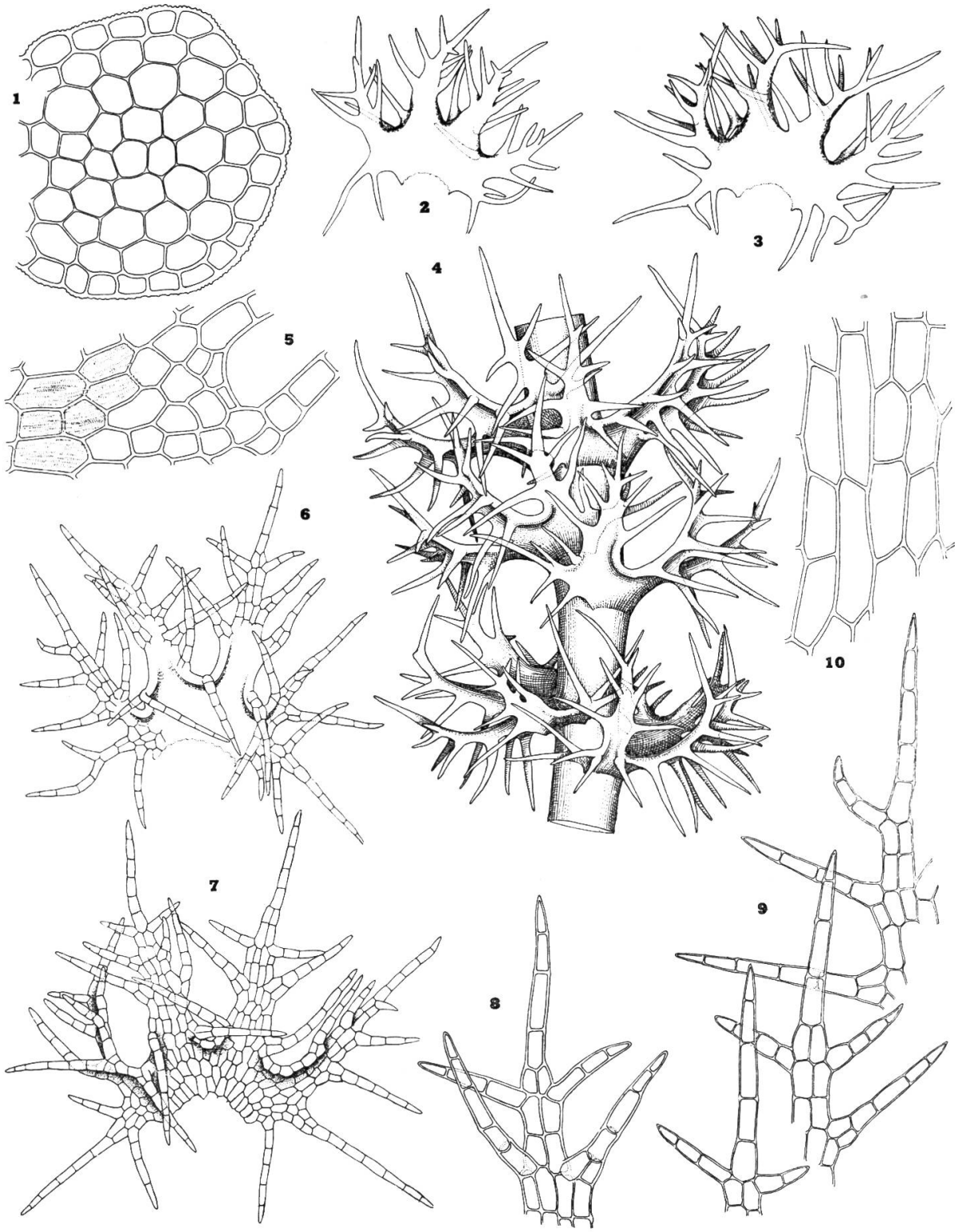
T. patagonicum has more numerous cilia of the leaves than does *T. quadripartitum*; the cilia are longer and less sharply and abruptly pointed, but they are strongly abaxially displaced, particularly near the reflexed sinus bases, exactly as in *T. quadripartitum*—hence in profile the plants look as if the backs of the leaves are strongly hispid. In this hispid aspect they clearly approach *T. quadripartitum*, rather than *T. pilosum*. The latter, as the species name implies, has the leaves largely dissociated into slender, often branched, capillary segments or cilia.

In degree of differentiation of the cilia, *T. patagonicum* stands almost midway between the most spinose extremes of *T. quadripartitum* and " normal " *T. pilosum*.

FIG. 39. *Temnoma patagonicum* Schust.

1. Stem cross-section (×210). – 2-3. Underleaf, left, and leaf, right (×46). – 4. Antical aspect, shoot-sector (×46). – 5. Leaf base, at right two cilium bases, cuticular papillae drawn in (×165). – 6-7. Two leaves, abaxial aspect (×65). – 8-9. Leaf lobe apices (×137). – 10. Cortical cells of stem (×275).

All drawn from type.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I cannot visualize a species able to undergo a range of variability so broad as to include both the *T. patagonicum* and *T. pilosum* extremes. None of the juvenile stems of *T. pilosum* ever show an approach to *T. patagonicum*—hence the only conclusion I can arrive at is that *T. patagonicum* forms a separate taxonomic entity.

The cilia of the leaf margins in *T. patagonicum* are much less highly differentiated than in *T. pilosum*. Admitting that there is much variability in this feature (I regard, for example, *T. chilense* Fulf. as simply a minor form of *T. pilosum* with somewhat atypically elongated cells of the cilia), the degree of difference between all of the specimens of *T. pilosum* and of *T. patagonicum* I have seen is such that I cannot believe the two extremes are merely environmentally induced. Certainly, the available material shows no real overlap in cell measurements. Indeed, in the dimensions of the cells of the spines or cilia, *T. patagonicum* more closely approaches some forms of *T. quadripartitum*.

In axial anatomy, *T. patagonicum* is also intermediate between *T. quadripartitum* and *T. pilosum*. *T. quadripartitum* has only 11-12 rows of short-oblong (1.5-2.5 : 1) cortical cells which average somewhat larger than the medullary cells; *T. pilosum* has 40-50 or more rows of small, elongated (4-7 : 1) cortical cells, averaging clearly less than the medullary in diameter. *T. patagonicum* has about 25 rows of short-oblong (ca. 1.5-3.5 : 1) cortical cells that are equal in diameter to the medullary cells.

I have seen only terminal, Frullania-type branches in *T. patagonicum*—exactly as in *T. pilosum*. By contrast, *T. quadripartitum* sporadically forms Microlepidozia-type branches and postical-intercalary branches (as well as more numerous Frullania-type branches).

Temnoma pilosum (Evans) Schust. [Figs. 40, 41].

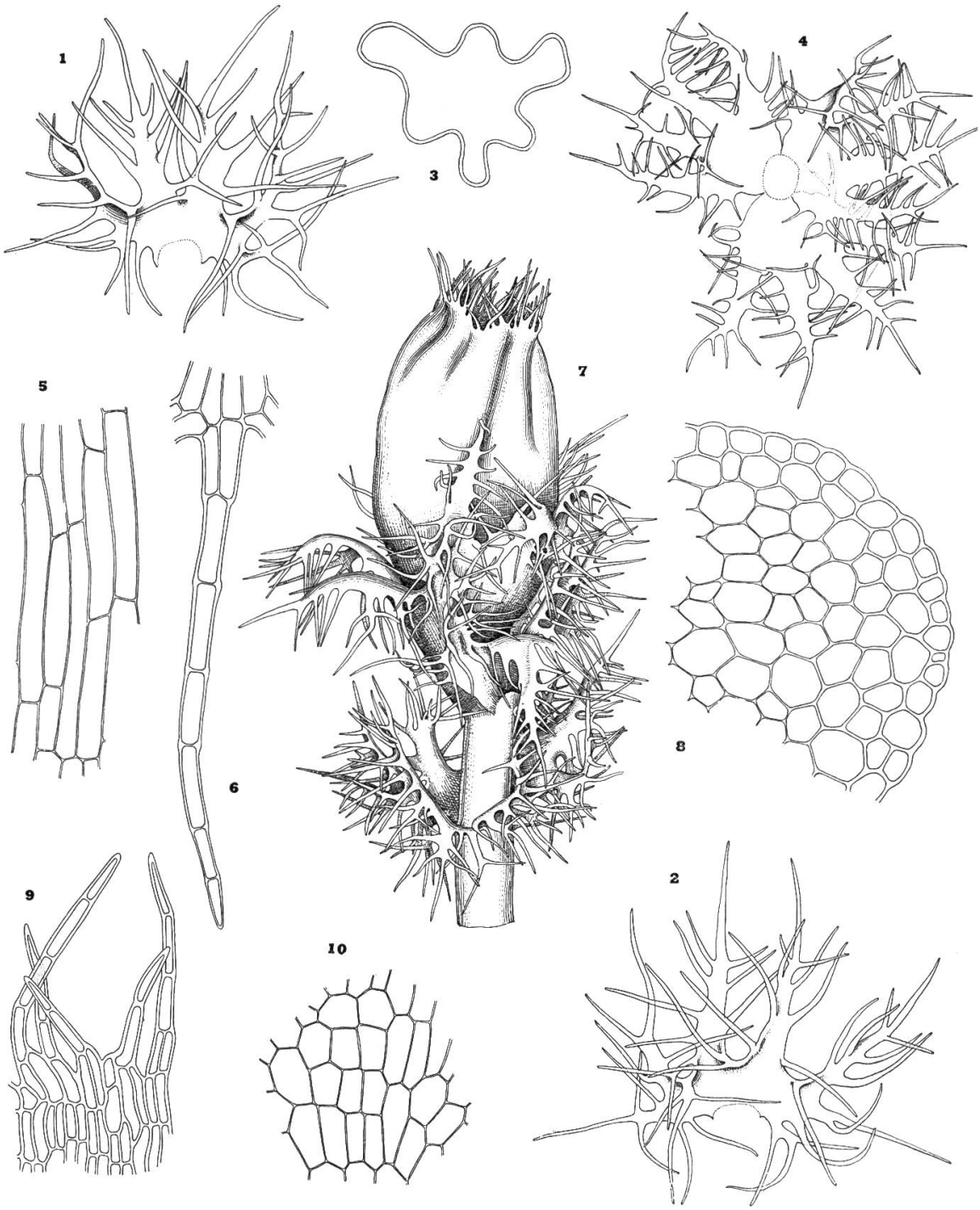
Blepharostoma pilosum Evans, Bull. Torrey Bot. Club 25: 413, pl. 345, figs. 1-6. 1898.
Blepharostoma pinnatisetum Steph. Spec. Hep. 3: 639. 1909.
Temnoma pilosum Schust. Bryologist 62 : 240. 1959.
Temnoma pinnatisetum Schust. *ibid.* 62 : 240. 1959.
Temnoma chilense Fulf. Mem. N. Y. Bot. Gard. 11 : 56. 1963 (new synonymy).

Plants ± caespitose, soft-textured, seemingly formed of numerous capillary segments, light yellow-brown to brownish-green, the shoots ca. 1.5-1.7(2.0) mm in diam. [1], erect, julaceous, simple or with very sparing lateral branches; branches seemingly only terminal, of the Frullania-type, replacing the ventral half of a leaf;

[1] Width of stem " with leaves to 0.2 mm wide " according to Fulford (1963 : 56); this is obviously an error, since the naked stem is to 230 μ in diam.

FIG. 40. *Temnoma pilosum* (Evs.) Schust.

1-2. Underleaf, above, leaf, below (×38). – 3. Perianth cross-section, above middle (×50). – 4. Bracts and bracteole (×29.5). – 5. Lateral cortical cells of stem (×170). – 6. Terminal cilium of leaf (×170). – 7. Apex of shoot with perianth (×50). – 8. Stem cross-section, in part (×230). – 9. Perianth-mouth cells (×62). – 10. Basal cells of leaf disc (×170).
All drawn from type of *Blepharostoma pinnatisetum* Steph.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stem terete, straight, slender and rather firm, 200-300 μ in diam. Cortical *cells* in 40-50 or more rows, narrowly rectangulate, averaging perceptibly smaller in diameter than the medullary cells, slight or hardly thick-walled, the wall thickenings evenly laid down, 16-19(22)μ wide ×72-125μ long (length-width ratio ca. [3]4-7[8]:1); cortical cells delicately striolate; medullary cells thin-walled and with slight thickenings at the angles, pellucid, varying from 19-22 to 22-25μ in diam. *Rhizoids* virtually absent, a few occasionally developed at the bases of the underleaves. *Leaves* distant, almost transversely inserted (less than 15° succubous), rather stiffly, widely, almost transversely spreading, vertically oriented, slightly concave, broadly quadrate-rotund to reniform-rotundate in outline, ca. 1250-1300μ wide ×850μ long [including cilia], quadrifid for 0.75-0.85 their length, with the antical and postical bases commonly with a smaller accessory lobe (thus becoming incipiently 5-6-lobed); chief lobes slenderly lanceolate (4)5-8(9) cells wide at base, ending in capillary or ciliary divisions formed by 5-7(8) superimposed cells, margins of lobes with 4-7(8) pairs of ± opposed, widely spreading similar cilia, which become progressively longer from apices to bases of lobes, the basal cilia occasionally furcate, cilia more or less abaxially reflexed with respect to plane of leaf; undivided basal portion of leaf ca. 4-6 cells high; leaves as a whole with 50-85 cilia. *Underleaves* almost identical and hardly distinguishable from the leaves, similar in size or imperceptibly smaller, similarly widely spreading from the transverse base, usually without rhizoids. *Cells* of cilia very slender, slightly thick-walled (the septae prominently thickened externally), from ca. 11-15(20)×48-72 μ to ca. 12-17×48-85(100) μ long, except for the smaller, tapering terminal cells; terminal cells usually ca. (9)10-11(12)×28-54 μ to 10-12× (36-42)45-65(72-75) μ long; cells in lobes ca. (12)13-20×36-50 μ; basal cells ca. 17-24×30-40(48) μ; cells very delicately striolate, often hardly perceptibly so, thin-walled to somewhat thick-walled, but devoid of trigones. Without asexual reproduction. Dioecious. Androecial plants with *androecia* intercalary on the main stems; bracts remote to hardly contiguous, in 3-8 pairs, similar to the leaves, but with the entire base rather strongly concave, four-lobed but less deeply so than the leaves (ca. 0.55-0.65 their length), the narrow lobes similarly armed as the leaf lobes. Young *gynoecia* forming bristly, somewhat clavate-globose " heads ". *Gynoecia* terminal, without any subfloral innovation; *bracts* similar to the leaves, moderately or little larger, 1650-1750 μ wide, including cilia, × ca. 1200μ long, less deeply (to 0.6-0.65), quadrifid, the narrowly lanceolate and acuminate lobes armed with 5-6(7-8) largely opposed pairs of stiff, bristly, uniseriate cilia the lower and longer of which are reflexed; distal portions of the lobes spreading to squarrose, the basal portions of the bracts sheathing. *Perianth* oblong-ovoid, 550-650 μ wide, in the distal two-thirds deeply 3-plicate, the plicae rounded and with normally three weaker supple-

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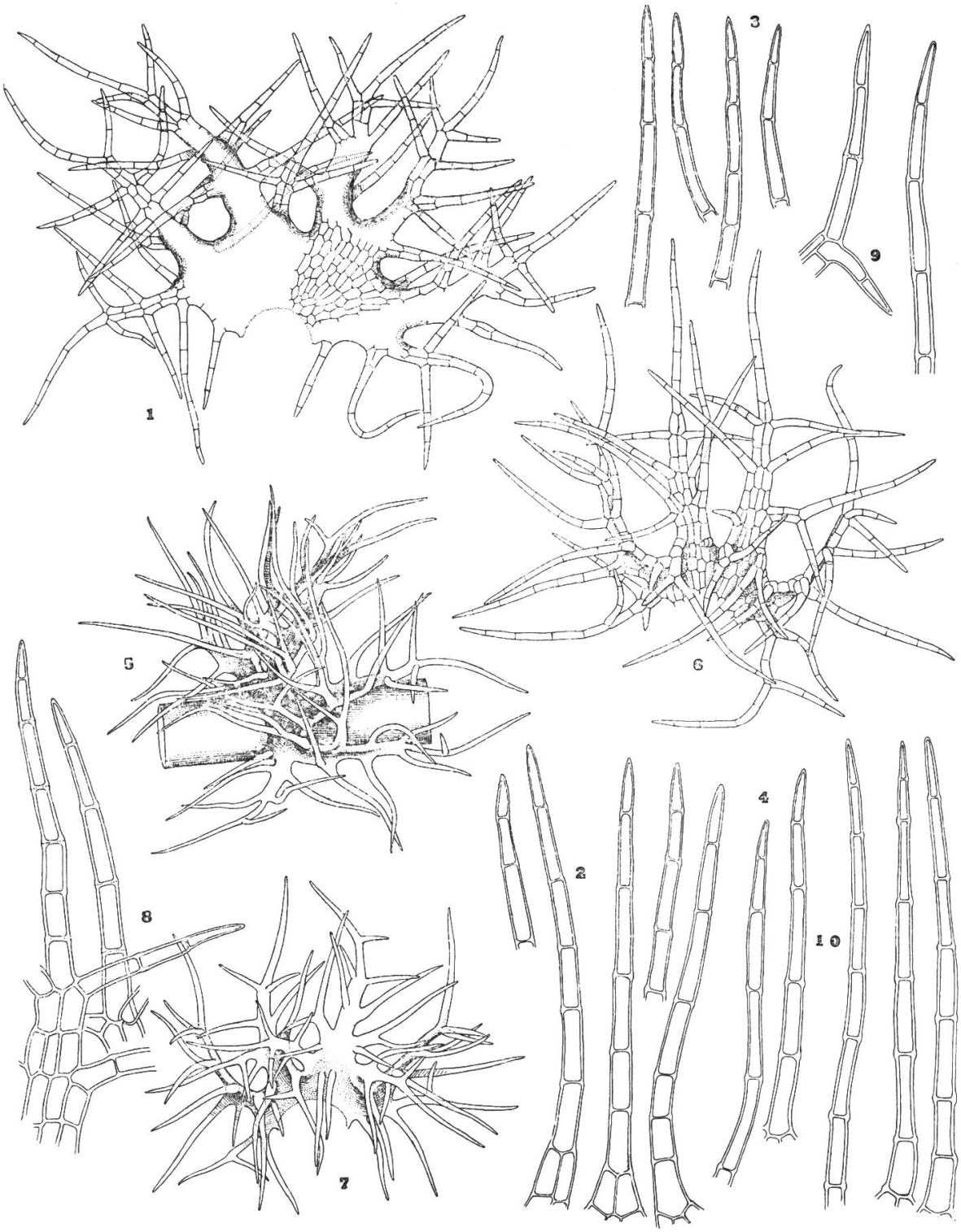
FIG. 41. *Temnoma pilosum* (Evs.) Schust.

1. Large leaf (×55). – 2. Five apices of longer cilia of the leaves (×140). – 3-4. Cilium apices (×140). – 5. Leaf, lateral aspect, showing feebly succubous insertion (×52). – 6. Leaf, somewhat flattened (×70). – 7. Underleaf (×50). – 8. Two apices of leading segments (×140). – 9. Two cilia (×140). – 10. Three cilia (×140).

1-2, " *Temnoma chilense* Fulf.", *Halle 1396*; 3-4, Rio Aysen, *Dusén*; 5-10, Valle Carbajal, Tierra del Fuego, *RMS 48731*.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mentary plicae developed; perianth formed of somewhat thick-walled, narrow, regularly rectangulate cells; mouth ciliate with cilia 2-5(6) cells long, the distal 2-4(5) cells in a uniseriate row, the cells narrow and elongate, thick-walled, ca. 95-120 μ long.

TYPE. Villarina Bay, Tierra del Fuego, *Hatcher*; Y, NY.

The above diagnosis is largely derived from the types of "*Blepharostoma*" *pinnatisetum* and of *T. pilosum;* the two plants are essentially identical.

DISTRIBUTION. Endemic to southermost South America, in essence, to the Nothofagetum of the Andes and Chile, and of southernmost Tierra del Fuego. TIERRA DEL FUEGO: Villarina Bay, *Hatcher*, Y, NY (type). CHILE: Chiloe, *Halle*, BM, G-1793; Rio Aysen Valley, *Dusén 515*, type of T. pinnatisetum, G-515; *Dusén*, "m. Januario a. 1897" as "Blepharostoma quadripartitum", c. per., Munich, Lund, Stockholm, *Dusén 290*, Jan. 29, 1897, G; Puerto Varas, Lago Llanquihue, *Fulford & Hatcher*, type of T. chilense [1]; Chiloe I., Quincan, in barranca, *Halle 92*, Lund. ARGENTINA: Lago Verde, Los Alerces Natl. Park, *Schuster*, s.n.; Ventisquero Torrecillas, Lago Menendez, Los Alerces Natl. Park, *Schuster*, s.n.; along stream margin, near large peat bog, Valle Carbajal, ca. 20-25 km NE of Ushuaia, Tierra del Fuego, *RMS 48731.*

ECOLOGY. I have collected this species many more times than my few reports indicate; the bulk of my collections are not yet worked up. In the field, this species stands out because it looks like a small, caespitose, rather brownish-tinged *Trichocolea*—owing to the strongly capillary-like appearance. Particularly where the leaves are crowded on the stem tips, dense capillary "heads" result that are not at all Temnomoid in facies.

In my experience, the plants usually occur on sandy substrates, along streams, between rocks, along steep rocky slopes between rocks, wherever silt or fine sand accumulates. The ecology is unique, among the species of *Temnoma* with which I am familiar—only *T. patagonicum* seemingly has a similar ecology. Species of *Balantiopsis* and *Triandrophyllum subtrifidum* may be associated.

DIFFERENTIATION. *T. pilosum* is a distinctive species, representing a considerably different type from the generitype, *T. pulchellum.* The more deeply quadrifid leaves, their nearly transverse insertion, the more slender axis, the form of the cilia of the leaves and the rather short, somewhat ovoid perianth, suggest, in part, *Trichocolea* or *Blepharostoma* s. str. Nevertheless, the plant bears much more affinity to *Temnoma* s. str. Most distinctive are the cilia of the leaves. The narrowly lanceolate and acuminate leaf lobes bear 4-7, rarely up to 8 pairs of opposed slender, uniseriate cilia which are soft and capillary rather than stiff and setose in nature. These cilia do not lie in the plane of the leaf, but are more or less reflexed, especially the lower and longer cilia. As a consequence the plant has a rather "hairy" appearance.

Although the purely Frullania-type branching, the copiously cilliate leaves and the smooth cilia, formed of elongate cells, of *T. pilosum* suggest the generitype, *T. pulchellum* and its relatives (subg. *Temnoma*), the affinities of the species are

[1] Cited as from "Patagonia-Tierra del Fuego: Puerto Varis" in Fulford (1963 : 56). I have been unable to obtain this specimen for study.

actually with *Eotemnoma*. This is clear from the following points: (1) the very deeply quadrifid leaves with a very short discus and with narrow, tapering lobes; (2) the subtransverse insertion and transverse orientation of the leaves. Within *Eotemnoma* the species is isolated, by virtue of the highly differentiated, narrow, thick-walled cells of which the cilia of the leaves and underleaves are composed. In this respect the species, however, approaches *T. townrowii*, a plant which also tends to have the cilia lying in the basal portions of the sinuses abaxially reflexed. However, *T. townrowii* has much more stiffly spinose leaves, and the cells of the cilia are clearly striolate and roughened. This species also has a higher discus (thus less deeply quadrifid leaves). The gynoecial bracts and bracteoles of the two species are very different, those of *T. townrowii* closely approaching those of *T. paucisetigerum* in their narrow, obcuneiform-obtrapezoidal form and high discus. In *T. pilosum* the discus is less well developed, the lobe length far exceeding the discus height.

In the deeply quadrifid leaves and abaxial displacement of the cilia situated near the sinus bases *T. pilosum* approaches *T. quadripartitum*. As discussed under this last species, these two taxa are widely separated by their other characters, as is evident on comparing the illustrations of the two taxa given (Figs. 33-38 and 40-41). However, the still poorly understood species, *T. patagonicum* (Fig. 39), which stands almost midway between *T. pilosum* and *T. quadripartitum* serves, to some extent, to connect these two species. Thus there is a probable evolutionary series from *T. quadripartitum* → *T. patagonicum* → *T. pilosum*, with the last the most highly advanced species [1]. The first species is still able to develop Microlepidozia-type branches and postical-intercalary ones; the last two seemingly produce only Frullania-type branches.

The facies of *T. pilosum* recalls that of *Trichocolea*, rather than of *Temnoma* s. str.—perhaps leading to the untenable treatment of *Temnoma* as a genus of *Trichocoleaceae* (Fulford 1963). In the field *T. pilosum* often resembles an erect-growing, usually light brownish *Trichocolea*.

VARIATION. A species with a limited suite of phenotypes, if the rather sparse collections are any basis for judgement. I have collected this species a number of times, in both Argentina and Chile—and have never had any difficulty in determining it, even in the field.

There is variation in degree of vigor and in size and length of the cells of the cilia. An extreme with rather large cells of the cilia was the basis for " *Temnoma chilense* " of Fulford (1963)—a species which was admitted to be " very similar to *T. pilosum*, except for the larger size, and the longer cells of the lamina and the

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[1] *T. pilosum* is usually distinct at a glance from *T. patagonicum* in (*a*) the longer cilia of the leaves, formed of longer cells; (*b*) the more numerous cilia per leaf; (*c*) the stem anatomy. However, occasional lax, poorly developed plants of *T. pilosum* can be found (e.g., plants from " Patagonia occidentalis ", in vale fluminis Aysen, *Dusén 290*) in which the cilia are rather reduced in length, and are considerably fewer. Such plants at times show a superficial approach to *T. patagonicum*, but retain longer cells within the cilia, the strongly elongated cells of the cortex, and the more capillary aspect. Furthermore, a comparison between such plants of *T. pilosum*, which are reduced to a rather juvenile aspect, and *T. patagonicum*, is not altogether germane, since the type of the latter consists of fully mature plants, with relatively dense leaves.

cilia of the leaves and underleaves ". With the demonstrated variability in cell size and degree of development of the cilia (and length of their cells) in taxa such as *T. palmatum*, the trivial differences used to separate " *T. chilense* " from *T. pilosum* become meaningless—warranting not even a forma,—representing perhaps only a simple gene difference from the " typical " species.

T. pilosum and " *T. chilense* " according to Fulford (1963 : 54) supposedly differ as follows: " Cells of the cilia mostly 40-54(72) μ long, the tip cell mostly 36 μ long... *T. pilosum* " vs. " Cells of the cilia mostly more than 72 μ, the tip cells 54-72 μ, mostly 72 μ long... *T. chilense* ".

The following measurements are pertinent: (1) In typical *T. pilosum*, such as the type specimen of *T. pinnatisetum*, the tip cells of the cilia vary from (28)33-54(60) μ long; the cells within the cilia range (typical measurements) from ca. 48-50-60-71-70 μ (one cilium) or 50-66-68-70-74 μ (another cilium). (2) In my material from Valle Carbajal, the terminal cells range (average measurements) from 32-40-45-46-54-56 μ long; the cells within the cilia range from 62-75 μ (one cilium) to 44-50-58 μ (second cilium) to 57-62-70 μ (third cilium) up to 68-73-80 μ (fourth cilium). Taking a series of cilia on another leaf, cells average (including terminal cells) 52-60 μ long. (3) In a specimen from the Rio Aysen Valley, Chile (*Dusén*; Stockholm, as " *Blepharostoma quadripartitum* ") [1] the measurements are even more intermediate between " *T. pilosum* " and " *T. chilense* " in Fulford's sense: terminal cells of the cilia average from 9-11 × 30-34-38-41-43-48-50-52-53 μ (12 isolated measurements); median cells within the cilia average from (12)13-16(18) × 60-64-74-75-85-87-90-92-95 μ (12 isolated measurements). Where is one to place these plants? If the tip cell of the cilia is used as a criterion, they " key " (in Fulford 1963 : 54) most nearly to *T. pilosum* (since the tip cells are certainly not " 54-74 μ, mostly 72 μ long "; if the other cells are used as a criterion, they key to *T. chilense* ! (4) In the specimen from Chiloe Island (*Halle, 1908*; *G 1793*), determined by Fulford as *T. pilosum*, the terminal cells of the cilia range from 9-12 × 35-38-45-47-48-51-52-56-58-59-60-61-62-70-72-73-74-75 μ (20 measurements !). Of these 20 terminal cells, only the first would fall within the diagnosis of *T. pilosum* in Fulford (" tip cells mostly 36 μ long "). The other cells of the cilia range from 12-16 × 56-47-65-66-68-70-78-80-84-85-86 μ long (12 measurements). Of these measurements, all but the last five are " intermediate " in length—using Fulford's key (: 54).

Obviously the four preceding examples show there is no basis whatsoever for continued recognition of a taxon " *chilense* " at any taxonomic level.

The perianth mouth in the several fertile examples of *T. pilosum* I have seen has been uniformly ciliate, with conspicuous cilia (Fig. 40: 7, 9). Fulford (1963 : 56) states the perianth mouth of this species is " spinose to short-ciliate " and she illustrates it (figs. 1*h*, 1*j* : 55) as with short, rigid, spinose teeth mostly two cells long. Particularly the fig. 1*h* in Fulford cannot be reconciled with any perianth of any species of *Temnoma* I have seen. Either an unresolved taxonomic problem (and a much greater amplitude in variation in perianth mouth in *T. pilosum* than I am willing to admit) is at hand, or the figures and account of Fulford are in error.

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[1] A duplicate, evidently of this collection, is at Geneva (*No. 1796*); it is labelled " *Trichocolea* or something close to it, M. Fulford, 1960 ".

The postmature perianths and shoot-apices of this species, in longisection show the identical conditions figured for *T. pulchellum* and *T. palmatum*: the sporophyte " penetrates " deeply into the shoot-tip, the lower half of the mature sporophyte lying technically below the point of origin of the perianth. It is obvious that in this species, as in the others, there has been cell proliferation, stimulated by sporophyte development and that the " penetration " is largely an artifact: the stem apex, which remains meristematic after fertilization, undergoes rapid cell division in the region of the receptacle around the young sporophyte, thus growing up to form a tube on which the perianth, and to a lesser extent, the bracts, are elevated. In addition to this coelocaule precursor, there is also formation of a shoot-calyptra, the sterile archegonia being elevated on the functional calyptra.

Temnoma palmatum (Lindb. ex Pears.) Schust. [Figs. 26: 4-6, 42-47, 48: 8-12, 50: 3].

Blepharostoma palmatum Lindb. ex Pears., Jour. Bot. 25 : 193, pl. 276. 1887; Stephani, Spec. Hep. 3 : 638. 1909.
Temnoma palmatum Schust., The Bryologist 62 : 240. 1959.
Temnoma quadrifidum Hodgs. & Allis., Trans. Roy. Soc. N. Z., Bot. 1 (12) : 142. 1962 p. p. (not of Mitten).

Plants small, delicate, shoots 650-800 μ to 1-1.5 mm wide, to 1-1.5(-2) cm long, often rather lax and flaccid, bright green to somewhat pale yellowish-brown, erect to depressed-caespitose, rather sparingly branched; branching variable, usually terminal, of the Frullania-type, less often of the Acromastigum-type, occasionally postical (terminal or intercalary). *Stems* slender, somewhat brownish, (130)150-220 (275) μ in diam.; cortical cells in only ca. 12-16 to 20-24 rows, slightly or hardly thick-walled, regularly rectangulate, ca. 16-23(24)×50-60 to 90-120 μ, delicately striolate; stems only 7×8 to 8×9, occasionally 6×6-7 cells in diam. *Rhizoids* occasionally frequent, at the bases of the underleaves, colorless or pale brownish. *Leaves* distant to at most contiguous, sometimes weakly imbricate above, mostly appearing nearly transversely oriented, but the insertion is 20-30° succubous, suberect to rather patent and with the undivided basal portion often slightly concave, semi-amplexicaul, obtrapezoidal in outline, narrow at the base and broadened upward, ca. (790)825-875(1050) μ wide ×(660)700-750 μ long, including cilia, equally palmately quadrifid for (0.5)0.55-0.65(0.75) their length, the undivided portion of the leaf (5)6-9 cells high, occasionally higher in subaquatic phases, on small leaves of weak stems sometimes quadrifid for 0.65-0.75 their length, without development of accessory basal lobes; lobes lanceolate-acuminate (3-4)6-9 cells wide at base, or 9-12(-14) cells broad (aquatic phases), tapering gradually, ending in (2)3-5(-6-7) superimposed cells; lateral lobes at base and/or upper margins of disc usually with (0)1(2-3) additional, shorter, tapering teeth, at least on ♀ plants, the teeth hardly cilium-like, usually (1-)2-3(-4) cells long, the cilia usually lying in the plane of the leaf and not reflexed (exc. on ♀ plants); sterile shoots with leaf lobes often eciliate. *Underleaves* similar to the leaves but smaller, to ca. 775-825 μ wide ×530-550 μ long (without cilia only 555×400 μ), 0.5-0.65 the area of the leaves, often more deeply quadrifid than leaves, with narrower lobes, frequently with rhizoids at base. *Cells* of the cilia and of

the lobe apices differentiated, averaging shorter than in *T. pilosum*: usually 36-56 (60-70)μ long ×14-18(20)μ wide [ca. 2.5-3.5 : 1, rarely 4-5 : 1], except for the terminal, shorter, tapering cells; cells relatively large and pellucid, firm, the cells in the lobes ca. 16-18 up to 20-22×24-36 μ; basal and median cells ca. (16)18-24(26)×(28-35) 45-60(72) μ, averaging somewhat larger than in *T. pilosum*, generally somewhat thick-walled, delicately to strongly verrucose to striolate, although closely so, even on the cilia (except in aquatic phases). *Oil-bodies* colorless, faintly granulate, smooth externally, ca. 4.5-5.0×4.5-6.5 to 6-6.5×7.5-9 μ, spherical to irregularly ovoid, usually 2-4(-5) per cell, up to (leptodermous phenotypes) 6-10(-11) per cell. Dioecious. ♀ *Bracts* polymorphic, often somewhat similar to the upper leaves, moderately larger (800)1000-1250(1600) μ wide ×1260-1400(1550-2050) μ long, slightly to much longer than broad, to, often, slightly broader than long, cuneate to obtrapezoidal to subquadrate, quadrifid for 0.2-0.35 to 0.5-0.65 their length, the narrowly lanceolate lobes with (1)2-4(5-6) pairs of more or less opposed sharp, slenderly spinose teeth or cilia, those of the lobe bases usually ± reflexed. *Bracteole* almost identical in shape and size, ca. 925-950 μ wide ×1150-1200 (to 2000) μ long. *Perianth* (xeromorphic forms) rather short, at maturity distinctly, often longly stipitate, about half-emergent, ovoid to obconical to short-tubular, ca. 925-950(1100) μ broad ×1600-1900(2000) μ long (length ca. twice the width), slightly and irregularly crispate and plicate in the distal one-fifth to one-fourth, at times obtusely and obscurely trigonous above, the mouth ± wide open, subtruncate, irregularly lobulate and laciniate-ciliate; hygric forms with perianth prismatic, long, not stipitate. *Teeth* of perianth mouth relatively few and often distant, to 20-30, similar to the teeth of the leaves: variable, irregular in size and orientation, usually formed of 2-3 to 3-5 solitary, superimposed cells (which may arise directly from small lobes), the small and numerous lobes usually ending in a larger tooth of 2-4(5) superimposed cells, arising from a tapering base formed by 2-3 tiers of 2-3 cells lying side by side; uniseriate teeth of elongate cells, 40-50(62) μ long ×15-18(20) μ wide to 75-90×13-18 μ. *Seta* varying according to the vigor of the plants (within one clone): in weak plants only 140 μ in diam. and with only 13-15 rows of epidermal cells that are considerably larger in diam. (28-36 μ) than the 12-13 rows of medullary cells (which are 15-22 μ in diam.); in larger plants seta 200 μ in diam., with 16-18 rows of epidermal cells which average only slightly larger (32-40 μ in diam.) than the ca. 22 rows of medullary

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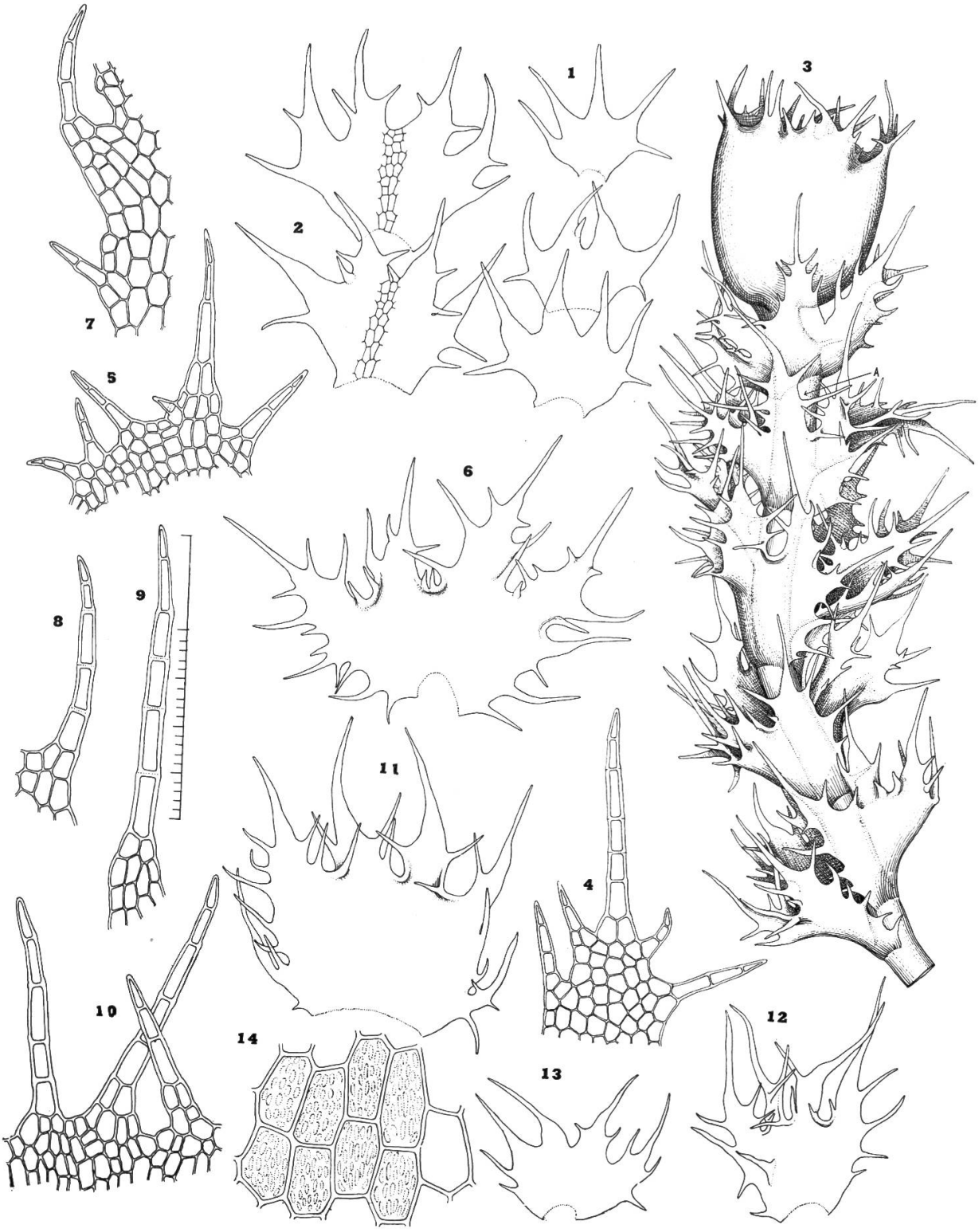
FIG. 42. *Temnoma palmatum* (Lindb. ex Pears.) Schust. var. *palmatum*.

1. Three leaves, of a small sterile shoot (lacking displaced teeth, exc. middle leaf with one such tooth (×48). – 2. Two leaves from middle of female plant, with cells drawn in along median strip (×48). – 3. Fertile shoot (×40); note stipitate perianth, with foot of sporophyte located at A; note only a few displaced teeth of sinus bases. – 4. Lobe of subfloral leaf (×122). – 5. Sector of perianth mouth (×122). – 6. Subfloral bract (×48); note several spinose displaced teeth of sinus bases. – 7. Lateral teeth, disc of female bract (×122). – 8. Lateral tooth, disc of female bract (×122). – 9. Tip of lobe of female bract (×122); to scale at right (= total of 300 μ). – 10. Sector per perianth mouth (×122). – 11. Female bract from vigorous gynoecium (×33). – 12. Bracteole from same inflorescence as bract in fig. 11; note surface lamella (×33). – 13. Leaf, female plant, some distance below bracts (×33). – 14. Cells of disc (×300).

1-6, type material, ex herb. Lindberg (S), Otago, N.Z., *Hector*; 7-14, paratype material, ex herb. Pearson (Manchester), Cambewarra, Australia.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cells (which are 25-35 μ in diam.). *Capsule* short-ellipsoidal, ca. 480 μ in diam. ×650 μ long; wall 3-4-stratose (26-29 μ thick; epidermal cells ca. 13-15 μ high; the 2-3 internal strata 6-7 μ high each, usually—collectively not or little thicker than the epidermal cells are high). *Epidermal cells*, except in 2 cell rows adjoining dehiscence lines (where with strong radial, nodular thickenings) colorless and hyaline, very large, forming a large-celled epithelial layer, the cells from 24×48 to 48×60 μ and larger, irregularly polygonal to oblong. Internal 1-2 cell strata with well-defined, strong, nodular thickenings. The innermost layer very irregular, the cells from 18-22 μ and subquadrate to 12-15×24-28 μ and oblong, to irregular in shape, with ± sharply defined nodular thickenings (of all longer walls, longitudinal and transverse), which are often tangentially extended to varying degrees (but are only locally and often sporadically complete to form semiannular bands). *Elaters* strongly contorted, with, curved to hooked, narrowed apices, small, ca. 6.5-7.2×60-85(100) μ, bispiral (exceptional elaters unispiral), the spirals closely twisted, ca. 2.5 μ wide. *Spores* yellow-brown, 9.4-11.2 μ in diam., feebly punctate-granulate. [Diagnosis of sporophyte from *Berggren 2812*, of var. *pseudospiniferum*]. ♂ Plants more slender; androecia intercalary on the main stem or basal on the lateral, intercalary branches; perigonal leaves 4-8(10) to 20-24 or more, smaller than the leaves, erect, clasping the stem, 1 to (1)2-androus; antheridia globose, shortly stipitate; perigonal bracts with a ventricose, narrowly erect to obtrapezoidal disc from a broadly cuneate base, quadrifid to the middle with erect-spreading, entire or 1-2-dentate subulate-lanceolate lobes 2-4(5) cells wide at base, ending in cilia 2-4 cells long.

TYPE. Two specimens are cited by Pearson (1887 : 194) with his diagnosis of *Blepharostoma palmatum*. The first is in the Lindberg herbarium, from Otago, New Zealand, inter *Hypnum rutabulum* (leg. *Hector 13*, 1863); of this I have seen a portion (or all?) in the herbarium of the Riksmuseum, Stockholm, labeled " ex herbario S. O. Lindberg ". This specimen is considered to be the type by Hodgson and Allison (1962). The second specimen cited by Pearson, from Cambewarra Mts., N.S.W., Australia (*Whitelegge, 1885*) is in the Pearson herbarium at Manchester, labelled the type; this I have also seen.

The Hodgson and Allison typification is ill-advised, in view of the following facts: (1) Pearson (1887 : 193-194, pl. 275) illustrates and describes his " *Blepharostoma palmatum* " from the specimen from " Cambewarra, near Moss Vale, New South Wales ". (2) Pearson states he had " intended publishing this species as new ", and as such forwarded it to Prof. Lindberg, who wrote... to the effect that the

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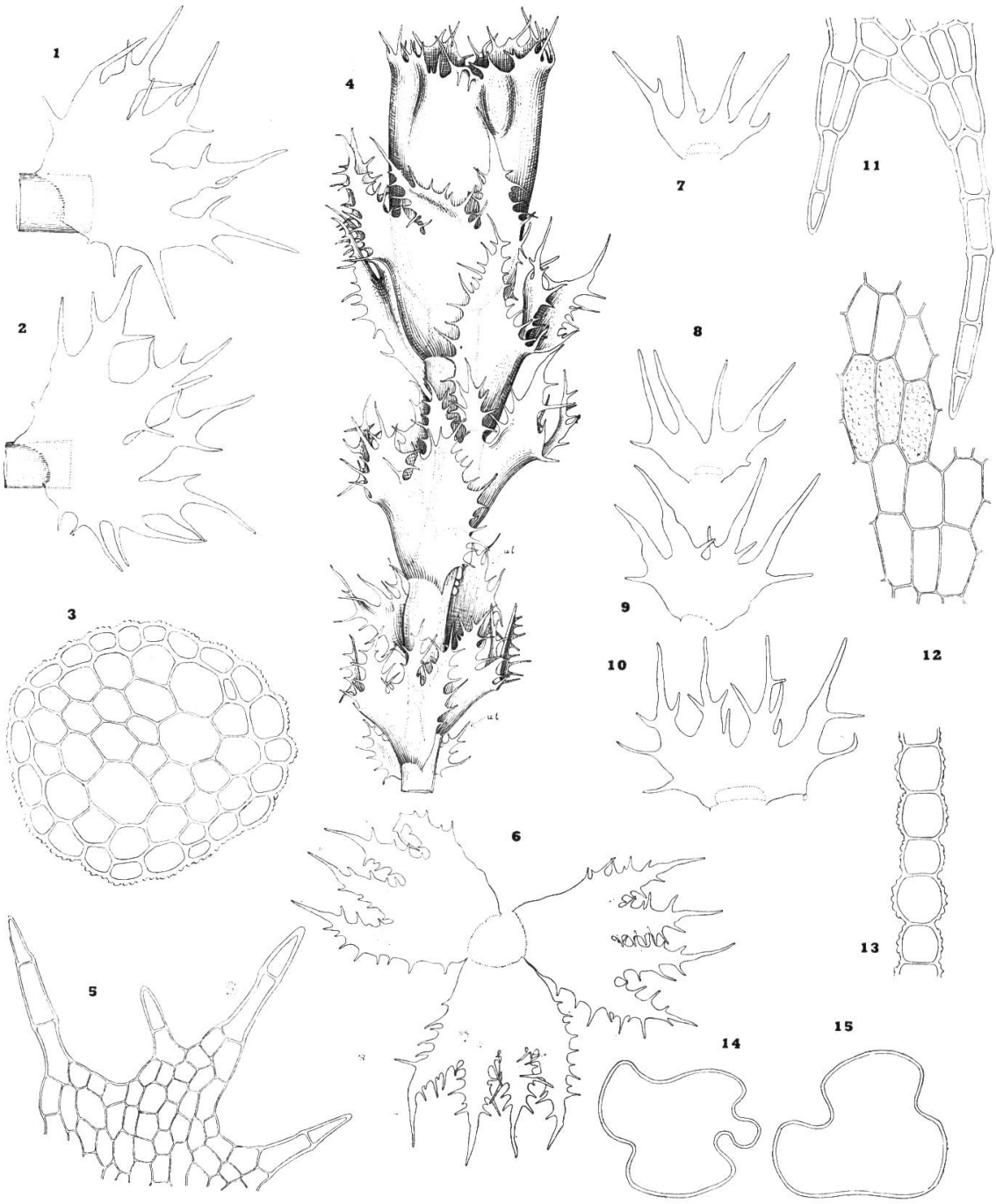
FIG. 43. *Temnoma palmatum* (Lindb. ex Pears.) Schust. var. *palmatum*.

1-2. Leaves of gynoecial stem, somewhat flattened, showing angle of insertion (×18). – 3. Section of mature stem (×213). – 4. Perianth-bearing shoot-apex (×18). – 5. Cells and cilia of perianth mouth (×165). – 6. Bracts and bracteole (×18). – 7-8. Small underleaves with reduced cilium development (×18). – 9. Small leaf from same shoot-sector from which figs. 7-8 were taken (×18). – 10. Normal underleaf from main axis (×18). – 11. Apex of leaf lobe (×165). – 12. Median cells (×165). – 13. Section through part of perianth middle (×250). – 14-15. Cross-sections through, respectively, upper 1/6 and upper 2/5 of perianth (×22).
All from K. W. Allison, Feb. 6, 1932, near Atiamuri, N.Z., reported by Hodgson and Allison as " *Temnoma quadrifida* ".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New South Wales plant " appears to be the same as my *Temnoma palmatum* (Mss. Oct. 10, 1876), which I picked out from a tuft of *Hypnum rutabulum*, from Otago, New Zealand ". (3) It is clear that Pearson never saw the Lindberg material, but simply adopted the Lindberg name for his Australian plant. He cited, in deference to Lindberg, the Otago specimen (" *N. 13; Hector* [Herb. Lindb.] ") first, but designated no type. (4) It is further clear that Hodgson and Allison (1962) never saw Lindberg's original, but arbitrarily regarded this as the type—in spite of the fact that both diagnosis and illustrations of *B. palmatum* in Pearson's paper are derived from the New South Wales plant, which specimen had been annotated as the type in the Manchester herbarium.

Not only is the typification proposed by Hodgson and Allison ill-advised, but the Pearson diagnosis clearly proves that the Hodgson and Allison delimitation of their " *T. palmatum* " is based on a misunderstanding of this plant. Pearson states that his *B. palmatum* differs from *B. pulchellum* in the " leaves not so broad... segments more rigidly spinose, not so long or finely ciliate, and the shorter, broader perianth with 20-30 spines, not 50-60 ". The last statement serves to eliminate both *T. pulchellum* and *T. paucisetigerum* (=*T. palmatum* sensu Hodgson and Allison, 1962) from consideration.

The typification of *T. palmatum* is a relatively unimportant matter, in view of the fact that the two types, which I have carefully compared, agree in all essentials, belonging to the same phase of the species, subsequently described. These plants, furthermore, agree with most other material seen from Otago, and from the Ruahine Mts., N. Z. (*RMS 52450*), they are all referred to on the following pages as " Phase A", of the species.

The type material closely agrees, except in the somewhat shorter, broader perichaetial bracts, with the plants on which Fig. 43 is based (near Atiamuri, Rotorua Prov., Feb. 6, 1932, *K. W. Allison*), sent to me by Hodgson as " *Blepharostoma quadrifidum* " [1].

VARIATION. *T. palmatum* is a small species, often found on soil (but sometimes on peaty ground or decaying wood), usually growing rather closely adnate, at least basally, but with the profuse, short and inflated-looking, perianths erect. The small size is diagnostic, together with the usually rather copiously ciliate appearance —owing to the occurrence of ciliiform apices of the lobes, as well as to the development of marginal cilia. On the uppermost leaves of ♀ plants, and the ♀ bracts (and elsewhere in var. *pseudospiniferum*) the more or less reflexed sinuses bear several to many shorter, stiffer spinescent teeth that are reflexed—so that they project abaxially away from the leaf. Such teeth are almost always produced, except in rare aquatic and subaquatic phenotypes (var. *laxifolium*)—thus are a diagnostic feature. Also

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[1] It must be re-emphasized that *T. palmatum* of Hodgson and Allison (1962) corresponds largely with *T. paucisetigerum* Schust. By contrast, true *T. palmatum* is identical in large part to *T. quadrifidum* sensu Hodgson and Allison (1962), while *T. quadrifidum* Mitt., as determined by examination of the type, is identical to *T. palmatilobum* (Hodgson) Hodgson and Allison (1962).

I have repeatedly studied my material, and that studied by Hodgson and Allison (1962), as well as the types: there is no doubt but that Hodgson and Alison (1962) have misinterpreted the type of *T. quadrifidum*; I do not know if they saw either type of *T. palmatum*. In any event, the names used for three species (*T. palmatilobum, T. quadrifidum, T. palmatum*) are incorrect.

diagnostic is the marked anisophylly: the underleaves always clearly smaller than the lateral leaves, very often bearing rhizoids at their base.

In general, the markedly spinescent-ciliate or bristly appearance of the plants, together with their small stature, is diagnostic. The plants, in the field, are almost always green—brown pigments are rarely formed (but old herbarium specimens turn brown artificially).

T. palmatum, like most species of the genus, is a variable and difficult species, showing, with differences in vigor, an amazing plasticity. It is one of our smaller and more gracile species. The basic constellation of characters circumscribing it are: (1) The deeply quadrifid leaves, with lateral disc margins at a level well above the leaf base but slightly below the origin of the lobes tending to bear 1-2(-3) slender spinose teeth which are primarily uniseriate and not lobe-like [1]. (2) Leaves with lobes mostly (4-)5-9 cells wide at base, and, although gradually tapering into an apical cilium, the cells of the cilium are distinctly differentiated, thick-walled, usually roughened and strongly elongated. (3) The cilia or teeth of vegetative leaves, which are displaced abaxially, usually lacking—the cilia of the leaf, when present, lying in the plane of the leaf [2]. (4) Predominantly, lateral-terminal branching, although, with prolonged search, Acromastigum-type postical branches can be found. (5) Leaves never bisbifid, the median sinus not deeper than the lateral ones.

T. palmatum, as diagnosed above, is perhaps the most difficult and malleable species of the genus. The preceding diagnosis represents the end-product of numerous modifications and emendations made to include one extreme after another, as these have come to light. I am not sure that a single species is involved; after a consideration of the accompanying plates, the reader may be equally uncertain. However, it seems clear that an enormously plastic species is at hand, which reacts radically to differences in the moisture content of its environment. (Fortunately, both type plants belong to very similar phenotypes). Before the species can be understood, the implications of this must be made clear. Unfortunately, experimental data are lacking; the following observations and conclusions are based solely on field experience—hence subject to revision. The species badly needs experimental study to determine what is genetic variation and what is environmentally induced variation.

As I circumscribe this species, it shows the following general variability, as one goes from dry to wet environments: (1) The leaves, which are quadrifid for 0.6-0.7 their length in xeromorphic forms, become only about 0.5 quadrifid. (2) The leaf lobes, which are 4-5 to 6-9 cells broad, become up to 8-12(14) cells broad. (3) The

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[1] Such lateral spinose teeth of the disc margin may be more copiously developed on leaves of ♀ plants, even far from the gynoecium. On such plants, also, the lobes tend to have 1-2 pairs of shorter, stiffer, spinose teeth (those lying in the sinus bases often somewhat abaxially recurved, owing to the margin becoming slightly reflexed). Such leaves simply do not occur on ♂ plants. Parallel sexual dimorphism occurs in the related *T. quadrifidum* (see above) and may lead to errors in identification. Apparently, in these two species, long before gynoecia develop, the ♀ plants tend to produce a whole series of leaves that grade into ♀ bracts. The upper leaves of ♀ shoots, which are transitional to bracts, cannot be used to key plants in the conspectus or keys given.

[2] A variable tendency occurs for ♀ plants, even far below gynoecia, to have leaves with spinous teeth of sinus bases abaxially displaced. Such plants must be separated with care (by, i.a., the higher disc and more elongated cells of the cilia) from *T. quadripartitum*.

apical cilia of the leaf lobes, which are 3-6 cells long, become more setose and up to 7-8 cells long. (4) The disc of sterile leaves, which is low and 5-9 cells high, becomes 9-12 or even to 14 cells high. (5) The elongation of the disc, and the less deep lobing of the leaves are additionally accompanied by an increase in cell length, which is perhaps linked with an increase in oil-body number. (6) The oil-bodies increase in number from 2-4(5-6) per disc cell up to (6)7-10(11) per cell. (7) The ♀ bracts change drastically in shape and form, from subquadrate and as wide or slightly broader than long (length 0.9-1.0× the width) in xeromorphic extremes, to, eventually, narrowly wedge-shaped and 2.1-2.5× as long as broad; associated with elongation, the sinuses decrease in depth from 0.5-0.6 the bract length to as low as 0.2-0.25 the bract length. (8) The perianth, which remains rather low and ovoid, with the mouth not or hardly contracted, becomes situated at the extremity of a tubular extension of the stem—thus elevated above the bracts, in xeromorphic extremes; in hygric extremes it is long, prismatic (as in *T. quadrifidum*), and not clearly stipitate.

These, and other variations, make the circumscription, and the recognition of its extremes most difficult. Since I am not convinced that all extremes are purely environmental in origin—particularly the linkage of a larger oil-body number with less deeply quadrifid leaves seems notable—I present the following key to recognized extremes within the species. For the time being, the phase with shallowly quadrifid leaves, narrow, wedge-shaped perichaetial bracts and prismatic perianths is retained as a distinct variety; it may prove specifically distinct.

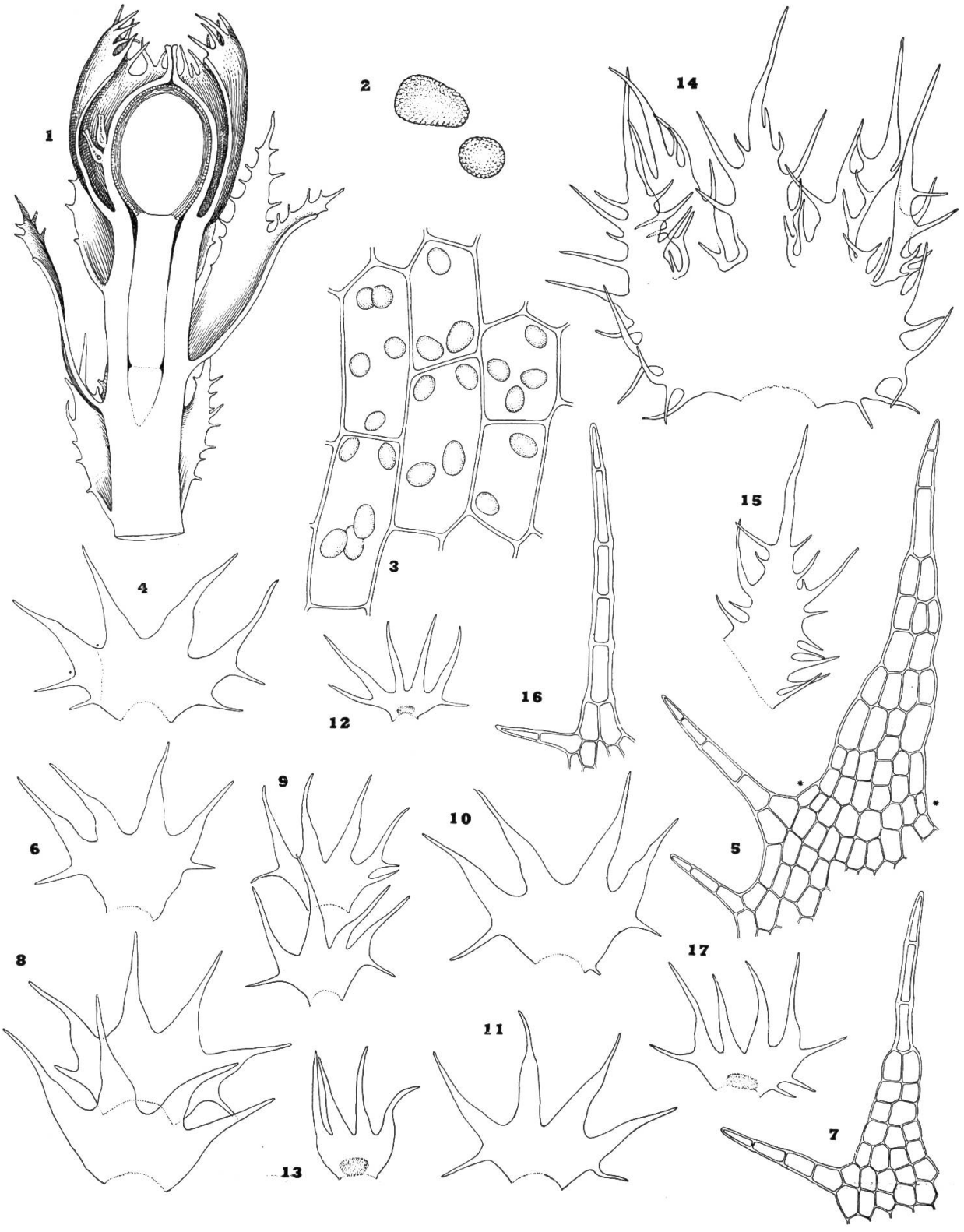
The ecology of the species, and the citation of specimens are given under the extremes here recognized as varietally distinct.

Key to extreme phenotypes of *T. palmatum*

1. Oil-bodies from 6-9 to 7-11 per cell; leaves divided for 0.5-0.55(0.6) their length, the lobes not or little longer than disc; cuticle smooth or verrucose. Perianth (where known) prismatic, long and ± slender, somewhat contracted to mouth, with long cilia (to 400-410 μ long, formed of 5-6 elongated cells, to 100 μ long ×15 μ wide) at mouth, not stipitate and elevated above the bracts. ♀ Bracts (where known) divided 0.2-0.35(0.4)

FIG. 44. *Temnoma palmatum* (Lindb. ex Pears.) Schust. var. *palmatum*.

1. Longisection of sporophyte-bearing plant, showing deep penetration of sporophyte (and/or elaboration of axial tissues) with wide spaced bracts and bracteole; uppermost appendage bracteole (×45). – 2. Individual oil-bodies (×1150). – 3. Cells with oil-bodies (×540). – 4. Leaf from female stem (×33); from same shoot-sector as leaf in fig. 11 and underleaf in fig. 17; crosses indicate lobe bases, dotted line shows sector above drawn in detail in fig. 5. – 5. Lobe of leaf in fig. 4 (×130). – 6. Leaf from male plant (×33). – 7. Detail from leaf in fig. 6 (×130). – 8. Two leaves from large sterile shoot (×48). – 9-11. Four leaves, from smaller sterile and larger female plants, respectively (×33). – 12-13. Two underleaves from sterile stems (×33). – 14. Optimally sized female bract (×33). – 15. Single lobe of female bract, flattened (×33). – 16. Lateral tooth from fig. 15, lobe of female bract (×130). 17. Underleaf from female plant, showing optimal degree of cilium formation (×33).
1, from *Allison 5383*, near Clarendon, N.Z., reported as *T. quadrifidum* by Hodgson and Allison (1962); 2-17, all from *RMS 52460*, N.W. Ruahine Mts., N.Z.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their length, with a high, narrow disc, oblong cuneate to cuneiform-obtrapezoidal in shape, 2.1-2.5× as long as wide; lobes of ♀ bracts small, with usually 2-3 pairs of short, stiff teeth or cilia 2

1*. Oil-bodies 2-6(7) per cell ; leaves and underleaves divided for (0.6) 0.65-0.75(0.8) their length, the lobes (including cilia) normally much longer than disc; cuticle always strongly papillose. Perianth normally short, longly stalked and seemingly elevated above bracts, wide and ± crispulate at the mouth, armed with teeth or short cilia (to 200-240 μ long) formed by 2-3 to 3-5 superimposed cells. Bracts divided for 0.45-0.6 their length, ± narrowly obtrapezoidal to subquadrate. (Leaves with lobes 2-4 to 4-9 cells wide at base, their apices formed by 3-5[6-7] superimposed cells only; disc 5-9[10] cells high) 3

2. Leaves (♂ plants) with disc 9-12(14) cells high, with lobes long-acuminate, ending in 7-8 elongated cells; lobe bases 8-12(14) cells broad; cuticle nearly smooth. Leaves of sterile axes with 1-2(-3) slender cilia per lateral margin of disc . . . . . var. *laxifolium* Schust.

2*. Leaves (♂ and ♀ plants) with disc 7-9 cells high, lobes short-acuminate, ending in 3-5(6) elongated cells; lobe bases 7-9 cells wide (only on leaves below gynoecia to 10-12 cells wide); cuticle closely verrucose. Leaves of sterile axes with 0-1(2) slender cilia per lateral margin
var. *cuneatum* Schust.

3. Leaves (sterile plants) with lobes narrow, ± reduced, only 2-4(5-6) cells broad at base, rather swiftly narrowed into the differentiated terminal setae formed of usually 5-6(-7) very elongated (ca. 3-5 : 1), superimposed cells; ♀ plants, even on smaller leaves, with 1-several abaxially displaced spinose teeth of the sinus bases. Perianth mouth longly, stiffly ciliate (cells ca. 4-8 : 1), and (in part) with reflexed cilia or teeth, with to usually 30-48 teeth. ♀ Bracts narrowly obtrapezoidal. Cells with (2)3-6(7) oil-bodies each . . . . . var. *pseudospiniferum* Schust.

3*. Leaves with lobes well-developed, the larger usually 5-9 cells broad at base, gradually narrowed into ill-defined terminal cilia; all plants, ♂ and ♀, with sinus bases lacking displaced, short, rigid spinescent teeth (except in the actual vicinity of gynoecia). Perianth mouth with fewer short to moder-

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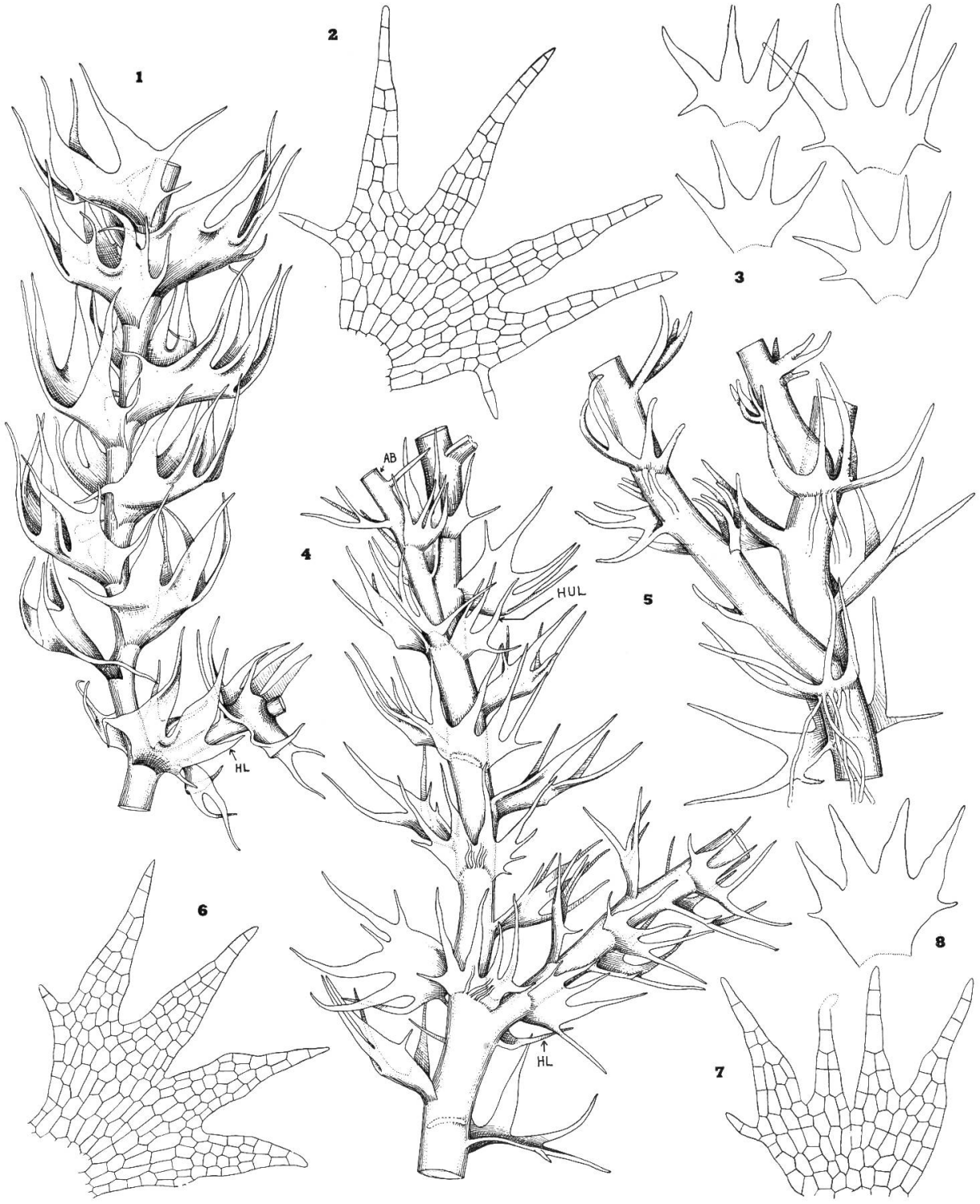
FIG. 45. *Temnoma palmatum* (Lindb. ex Pears.) Schust. (1, var. *laxifolium* Schust.; 2-8, var. *palmatum*).

1. Shoot-sector, antical view, with Frullania-type branch, at HL a dorsal half leaf (×22). – 2. Leaf (×83). – 3. Four leaves (×41). – 4. Shoot-sector, postical aspect, with Frullania-type branch below(HL = dorsal half leaf) and an Acromastigum-type branch (AB) above (at HUL the half underleaf) (×31.5). – 5. Shoot-sector, postical aspect, with two ventral-intercalary branches (×37.5). – 6-7. Medium-sized leaf and underleaf (×83). – 8. Large leaf (×48).
1, from type of var. *laxifolium*, *RMS 49981*, Stewart I.: 2-3, from *Hodgson 6312*, a small form cited in Hodgson and Allison as " *T. quadripartitum* trans. ad *T. quadrifidum* "; 4-5, *RMS 52450*, Ruahine Mts., N.Z.; 6-8, *Allison H 5383*, Clarendon near Dunedin, N.Z.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ately well-developed cilia. ♀ Bracts broader, often broadly obtrapezoidal to subquadrate. Cells with 2-4(5-6) oil-bodies each. . . var. *palmatum* 4

4. ♀ Bracts ciliate-laciniate, subquadrate to broadly obtrapezoidal, sligthly to distinctly wider than long, each lobe with (1)2-4(5) pairs of opposed cilia, the longer of which exceed the lobe base in width
Form. A. (*T. palmatum*)

4*. ♀ Bracts obtrapezoidal, distinctly longer than wide, 0.5 quadrilobed, each lobe with 4-5(6) pairs of opposed short cilia, the maximal cilium length not exceeding lobe width . . . . . Form B. (*T. palmatum*)

DIFFERENTIATION AND RELATIONSHIPS OF THE SPECIES (s. lat.). *T. palmatum* is most immediately allied to *T. quadripartitum* and *T. quadrifidum* [1]. The three taxa share in common basically similar leaves, with usually subtransverse orientation, and with gradually attenuated leaf lobes. In all three species, weaker plants (especially ♂ plants) tend to produce simply quadripartite leaves often lacking accessory teeth or cilia.

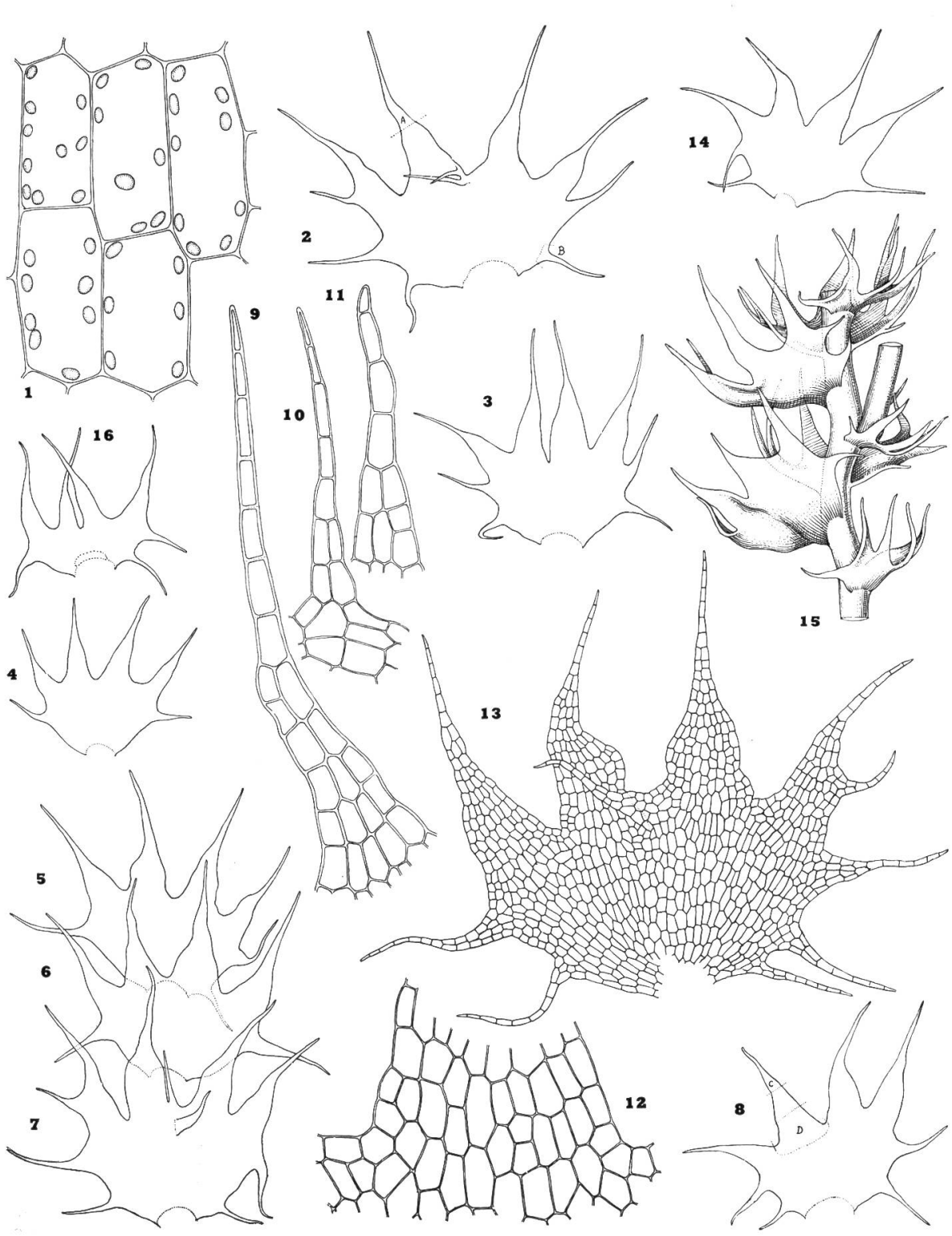
The leaves of the sterile stems of *T. palmatum* normally lack spinescent teeth on the sinus bases, although ♀ plants may produce them on leaves in the vicinity of the gynoecia (an extreme is reached in *T. palmatum* var. *pseudospiniferum*, in which gynoecial plants bear such postically displaced spinescent teeth even on leaves far from gynoecia). The lack of such spinescent, abaxially displaced teeth on the vegetative leaves of sterile stems serves to separate *T. palmatum* s. lat. from *T. quadripartitum*. In difficult cases, such as that offered by *T. palmatum* var. *pseudospiniferum*, the form of the disc (and, correlated, depth of sinus) must be employed to discriminate between these two species.

In some respects, *T. palmatum* occupies a mid-ground between *T. quadrifidum* and *T. quadripartitum*. The lack of lobe-like appendages on the leaf disc allies the first two taxa, and separates them from the last. Yet, the proclivity, never wholly suppressed in *T. palmatum*, to develop marginal cilia or teeth on the upper margins of the disc foreshadows the elaborated, lobe-like teeth commonly developed in *T. quadripartitum*. In *T. palmatum* the leaf is not or exceptionally over 0.7

[1] Indeed, the nomenclature of this complex in Hodgson and Allison (1962) is confused. Their *T. palmatilobum* = *T. quadrifidum* (as determined by comparison of the types of the two), while the plant they call *T. quadrifidum* = *T. palmatum*. *T. paucisetigerum* sp. n. plus *T. angustifolium* sp. n. are equivalent to what they call *T. palmatum*.

FIG. 46. *Temnoma palmatum* var. *laxifolium* Schust.

1. Median cells of disc (×375). – 2. Large leaf (×22). – 3. Bisbifid, exceptional leaf (×22). – 4. Small leaf (×22). – 5-7. Three large leaves, in fig. 7 with abaxial lamella (abnormal) (×22). – 8. A typical, slightly asymmetric leaf; at C and D, respectively, sectors drawn to larger scale in figs. 11-12 (×22). – 9. Lobe of leaf in fig. 2, at A (×115). – 10. Lateral cilium from disc, of fig. 2 at B (×115). – 11. Lobe of leaf, fig. 8,C (×115). – 12. Base of lobe of leaf, in fig. 8,D (×115). – 13. Large leaf (×37.5). – 14. Leaf (×22). – 15. Shoot-sector, lateral aspect, showing postical branch from axil of underleaf (×22). – 16. Underleaf (×22).
All from type, Tin Range, N.Z., *RMS 49981*.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quadrifid, and the disc is 5-6 or more cells high; in *T. quadripartitum* the leaf is normally 0.7-0.85 quadrifid, and the disc is commonly only 3-5 cells high.

Thus although there are obvious similarities between *T. palmatum* and *T. quadripartitum* their separation is usually a simple matter. Isolated extremes are separated only with difficulty. For example, the plants from which I have illustrated *T. palmatum* may possess leaves whose form approaches Patagonian material illustrated as " *Blepharostoma* " *quadripartitum* by Evans (1898, pl. 345, fig. 7). Evidently a troublesome complex of plants is at hand, presumably best separated by the characters of the fertile plant. The perianth of *T. palmatum* is normally stipitate, ovoid-subglobose to, at most, rather short-cylindrical, obscurely and irregularly pluriplicate near the wide, crisped, and often truncate mouth. By contrast, that of *T. quadripartitum* is exactly as described by Stephani: " magna linearia superno obtuse triplicata, ore parum contracto spinuloso ".

The type material of *T. quadrifidum*, from the New York Botanical Garden (Mitten herbarium) has been compared point by point with *T. palmatum* [1]; the following points of distinction should be emphasized:

(1) The perianths of *T. quadrifidum* are sharply, smoothly trigonous, and about 4-5× as long as broad, even when young (at time of maturation of archegonia); they are somewhat narrowed to the ciliate, but hardly lobulate mouth. In typical *T. palmatum* perianths are short and ± subterete, often subovoid, at most about twice as long as broad, little or not narrowed to the mouth, not or indistinctly and obtusely trigonous at the crisped and lobulate mouth, which is very irregularly ciliate-laciniate. Perianths of both species tend to be somewhat stipitate, i.e., their bases arise some distance above the insertion of the sheathing bracts, but in *T. palmatum* this is usually more marked.

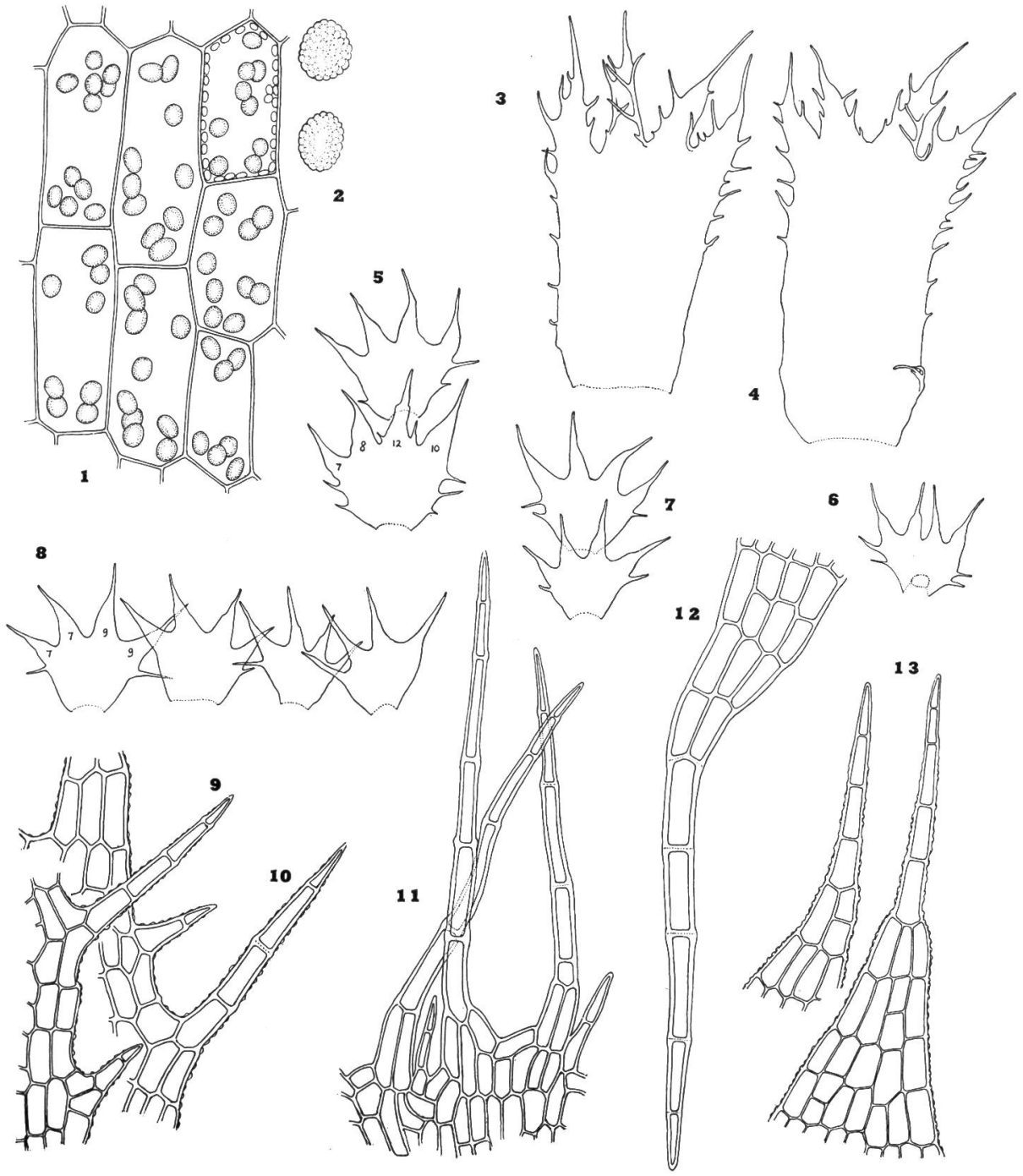
(2) Mature sterile leaves in *T. quadrifidum* are usually edentate; bracts in *T. quadrifidum* are sparingly toothed, with relatively short teeth. The leaves exceptionally bear, in addition to the four lobes, 1-2 small accessory teeth of the lobes, but no teeth of the disc margin. The bracts bear on each lobe (0)1-2 pairs of small teeth of inferior length. By contrast, comparable plants in *T. palmatum* have both leaves and bracts relatively freely toothed. The leaves each have 1-2 or even 2-4 sharp and often long marginal teeth at or near the lobe bases (from upper parts of disc). The bracts commonly bear 4-5 pairs of sharp, ciliiform teeth on each of the four

[1] Including the material from Australia.

FIG. 47. *Temnoma palmatum* var. *cuneatum* Schust.

1. Cells of disc, with oil-bodies and (upper right-hand cell) chloroplasts (×465). – 2. Two oil-bodies, larger scale (×1250). – 3-4. Two female bracts (×24.5). – 5. Two leaves, lower portion of female stem (lobe width indicated in cells on lower leaf (×24.5). – 6. Underleaf, same shoot-sector as leaves, fig. 5. – 7. Two leaves of male plant (×24.5). – 8. Four leaves of male plant (left leaf with width of lobes indicated in cells (×24.5). – 9. Cells and marginal spines from side of disc of leaf (×168). – 10. Same, lateral margin of lobe of female bract (×168). – 11. Cilia of perianth mouth (×140). – 12. Apex of female bract lobe (×168). – 13. Two optimal leaf lobe apices (×168).

All from type, *RMS 52661*, New Zealand.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lobes [1]. Only on juvenile plants is there a sharp tendency for the leaves to become totally edentate or paucidentate in *T. palmatum*.

(3) Mature leaves of typical *T. palmatum*, as well as immature edentate ones, are more deeply quadrifid, with the undivided basal portion of the leaf usually only 5-9 cells high. *T. quadrifidum* has mature leaves with an obtrapezoidal basal undivided portion usually 9-12 cells high, or more, from base to the sinuses. Associated with this, the leaf lobes of typical *T. palmatum* are narrower (4-5)6-9 cells broad at base vs. normally 9-12 cells broad in *T. quadrifidum*. The leaves are divided for ca. 0.55-0.75 their length in *T. palmatum*, for 0.5-0.6 their length in *T. quadrifidum*. Weak extremes of *T. quadrifidum* (such as *RMS 48804*, Mt. Egmont) are apt to have leaves with the discus no higher, and the lobes no wider than in *T. palmatum*. Such plants may remain nearly impossible to place, when sterile. Inversely, the hygric extremes of *T. palmatum* may have the disc 9-12 cells high and the lobes 8-12 cells broad. There thus exists a broad overlap between these two species—yet, by and large, leaf characters will adequately separate them.

(4) The leaf lobes of *T. palmatum* end in well-differentiated cilia formed of (2)3-5 or more superimposed cells, each of which is usually 2.5-4(5)× as long as broad. In *T. quadrifidum* the lobes taper gradually and end in a series of 1-2 to 2-4 superimposed cells that are hardly differentiated from the other leaf cells, i.e., merely 1.2-2.5× as long as broad.

(5) Branching in *T. palmatum* is largely or almost exclusively terminal. The majority of branches are lateral and of the Frullania-type, i.e., they replace the ventral half of a quadrifid leaf. Several Acromastigum-type branches were seen; these replace the lateral half of an underleaf. On older axes intercalary postical innovations may be found. By contrast, in *T. quadrifidum* postical-intercalary branches are common, and these, together with lateral-terminal (Frullania-type) branches are the normal modes of branching. Exceptionally, lateral Microlepidozia-type branches occur. Thus, in spite of a high degree of variability in branching

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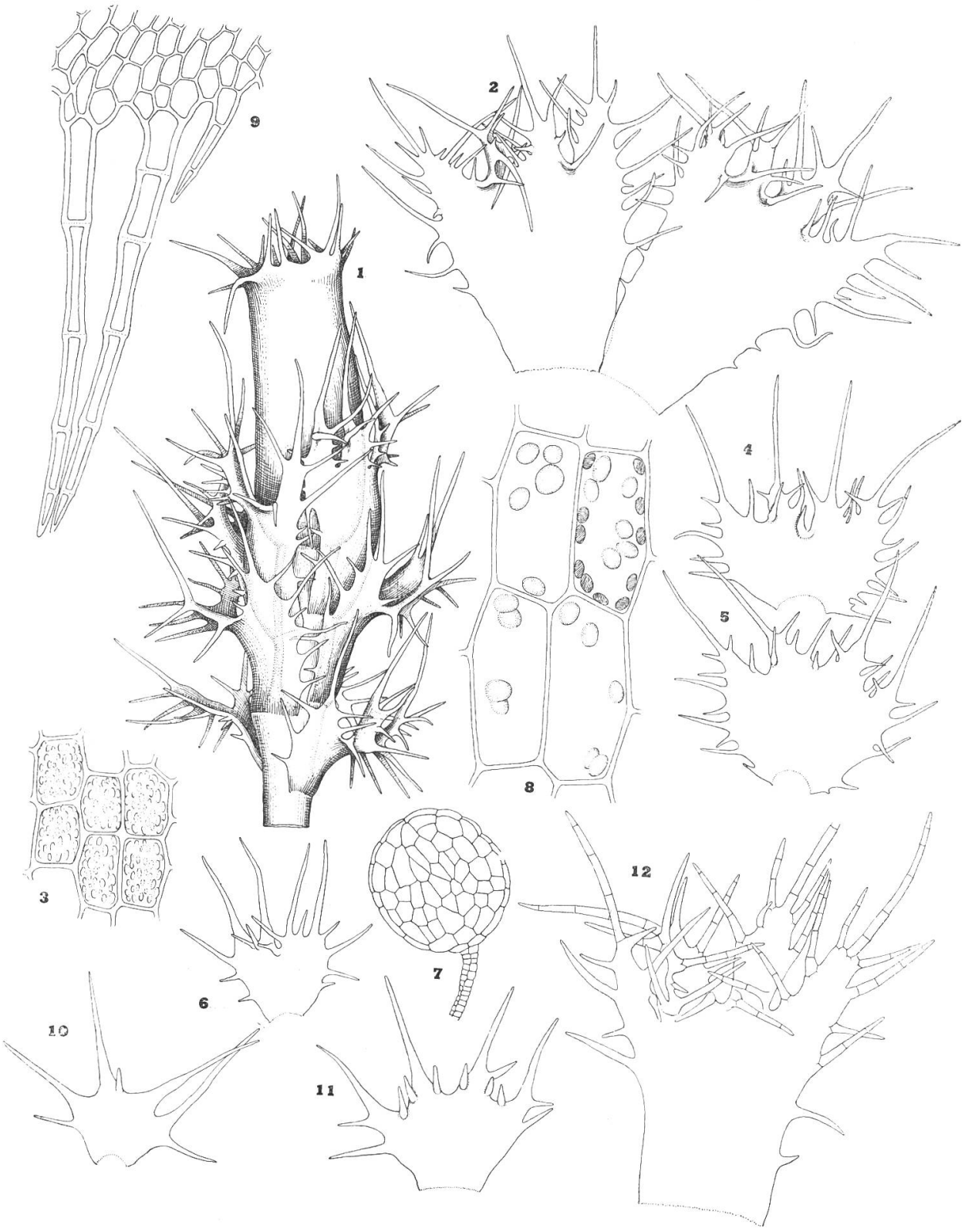
[1] Although, in general, the bracts in *T. palmatum* bear 2-4 pairs of slender, opposed spinose teeth per lobe, the Australian material seen had the lobes with only 1-4(5) spinose teeth per lobe, approaching *T. quadrifidum*. However, even in this material, the teeth of the lobes were narrow, slender and often ciliiform. On the other hand, the plants from the NW Ruahines had copiously ciliate lobes of the ♀ bracts, with long, conspicuous cilia. Thus a certain latitude of variation has to be admitted for these species.

In general, the 2-4 pairs of subfloral leaves in *T. palmatum* are copiously ciliate, approaching the bracts in aspect; in *T. quadrifidum* these subfloral bracts bear few, short, stiff teeth.

FIG. 48. *Temnoma townrowii* Schust. (1-7), and *T. palmatum* var. *pseudospiniferum* Schust. (8-12).

1. Apex of perianth-bearing shoot, antical aspect (×26.3). – 2. Two bracts (×34). – 3. Laminar cells, with cuticular papillae (×285). – 4-5. Leaves of female plant, but far from gynoecium (×34). – 6. Male bract (×44). – 7. Antheridium (×115). – 8. Disc cells with oil-bodies and (upper right) chloroplasts (×610). – 9. Perianth-mouth cells (×175). – 10. Small leaf, male plant (×56). – 11. Larger leaf, female plant (×56). – 12. Female bract (×56).
1-7, *RMS 50421*, type of *T. townrowii*; 8, *RMS 55487*, Cascade Cr., N.Z.; 9-12, from type of var. *pseudospiniferum*, *Allison H 5262*, NW Ruahine Mts., N.Z.; see also Figs. 49, 50 for *T. townrowii*.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modes in these two species, minor differences remain: the ability of *T. palmatum* to form Acromastigum-type branches, coupled with an apparent lack of Microlepidozia-type branches; the ability of *T. quadrifidum* to produce occasional Microlepidozia-type branches, linked with a near inability to form Acromastigum-type branches.

Some of the postical-intercalary branches in the type of *T. quadrifidum* remain slender and quite microphyllous, but freely develop rhizoids. These branches appear to remain geotropic and function as stolons or flagella. Such branches have also been observed in Lindberg's type of *T. palmatum.*

(6) The subinvolucral leaves in *T. palmatum* are rather remote; these leaves are strongly and freely ciliate to spinose-dentate. In *T. quadrifidum*, the subinvolucral leaves grade swiftly into the normal " vegetative " leaves, i.e., have few or no accessory teeth; they are also imbricate.

Temnoma palmatum var. **palmatum** (Lindb. ex. Pears.) Schust. [Figs. 42-44, 45: 2-8].

Leaves to ca. (615)770-1050 μ wide ×(460)550-700 μ long, usually quadrifid for 0.6-0.65(0.75) their length, the lobes slenderly lanceolate, (4-5)6-9 cells wide at the base, usually lacking cilia, on larger leaves occasionally with 1(2) teeth of the lobe bases; disc relatively low (height always inferior to length of lobes), up to a maximum of 7-9(10) cells high; lobe apices short-acuminate, formed of 3-5(6) superimposed cells, the cells to (2)2.5-4(5)× as long as wide. *Underleaves* similar but considerably smaller, more deeply quadrilobed, with usually a cilium on one or both margins of the low disc, with more cilia usually only on underleaves near gynoecia. *Cells* firm, rather small, ± thick-walled, distinctly verrucose or papillose, ca. 17-22 to 20-25×(28)32-48(55) μ, occasionally to 45-60 μ long; oil-bodies rather large for cell size (4.5-5×4.5-6.5 to 6-6.5×7.5-9 μ), (2)3-5(6) per cell.

♀ *Bracts* variable, ± subquadrate, varying from 0.9-1.3× as long as wide, 4(5)-fid for 0.5-0.6(0.65) their length, the disc width (at level of sinuses) greater than length, often much greater; bracts up to 1550 μ long ×1600 μ broad (incl. cilia); lobes with cilia unequal, from 1-2 to 4-5(6) pairs per lobe. *Perianth* normally ± reduced, slenderly ovoid to ovoid-campanulate, 550 μ broad ×1100 μ long up to (725)925-1100 μ broad ×1600-2000 μ long, wide and ± crispulate-lobulate at mouth, the mouth armed with short, spinose teeth or cilia to 2-3 to 3-4 cells long usually; with maturation a long neck usually develops, formed from elaboration of recept-

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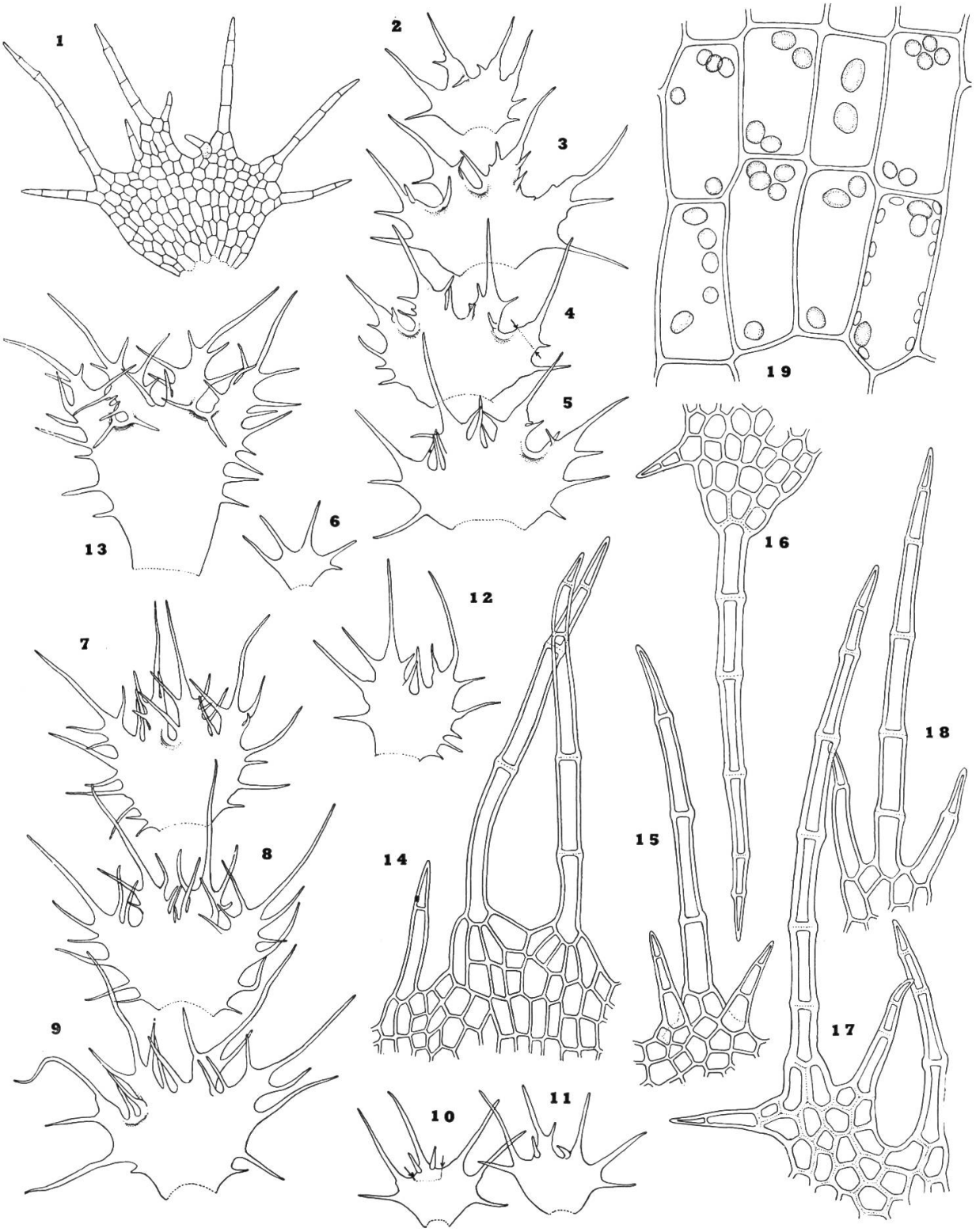
FIG. 49. *Temnoma townrowii* Schust.

1. Small leaf, sterile shoot (×63). – 2. Small leaf (×35). – 3-5. Larger leaves (×35). – 6. Juvenile leaf (×35). – 7. Large underleaf, from gynoecial shoot (×35). – 8-9. Leaves from gynoecial shoot (×35). – 10-11. Two small leaves; 11 drawn to larger scale in fig. 1 (×35). – 12. Bifid supporting stem leaf at base of Frullania-type branch (×35). – 13. Female bract (×35). – 14. Part of perianth mouth (×145). – 15. Cells of lobe of small leaf in fig. 10 (×145). – 16. Distal part of large lobe in leaf in fig. 4 (×145). – 17. Cells of leaf lobe, subgynoecial leaf (×145). – 18. Lobe apex of female bract (×145). – 19. Median discal cells with oil-bodies, and in lower right, chloroplasts (×585).

All from type, *RMS 50421*, Camp Cr., Tasmania; see also Figs. 48, 50.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acular tissue, elevating the perianth on a stipe often equal in length to the perianth proper; the three bracts, widely separated, occur on this stipe.

TYPE. Otago, New Zealand (*Hector 13, 1863*; among *Hypnum rutabulum*); part of type (Stockholm) examined and compared with the Paratype: Cambewarra, N.S.W., Australia (1885); University of Manchester herbarium; BM.

The unfortunate typification of this taxon by the Otago plant—which Pearson (who published the species) evidently never saw, has been alluded to earlier (: 326). Fortunately, the two original plants agree in almost every detail (Fig. 42), so that it does not really matter which is regarded as the type. Both original specimens are characterized by the stipitate, reduced, abbreviated perianths which appear to occur regularly throughout all material of var. *palmatum*.

DISTRIBUTION. Apparently the most widespread phase of the species; known from both islands of New Zealand and southeastern Australia. I have seen the following specimens: AUSTRALIA: New South Wales: Cambewarra, near Moss Vale, *C. Harris*, 1885, Manchester herb., BM. NEW ZEALAND: NORTH ISLAND: Kiwi Hills, Wairoa, Hawkes Bay, *Hodgson 210, 211 = H 379*, reported by Hodgson and Allison, 1962, as *Temnoma quadrifidum*; near Atiamuri, Rotorua, on damp, shady clay bank, *K. W. Allison, 6312*, Feb. 6, 1932, reported by Hodgson and Allison, 1962, as *Temnoma quadrifidum*; Maungaroa, *Berggren 2812*, 1874, as " *T. velutina* sp. n."; N-W Ruahine Mts., along streams, ravines in Limestone Plateau, W of Mt. Makirikiri, N-W of Mt. Te Rakaunuiakura, 3500 ft., *RMS 52450, 52496, 52476*; Wellington, *Berggren*, Aug. 1874, Lund, very typical, det. and rept. by Hodgson as *T. quadrifidum*! SOUTH ISLAND: Otago, no other data, *Hector 13*, type, among *Hypnum rutabulum*; Otago, near Clarendon, south of Dunedin, on low ridge in open, ca. 200 ft., *K. W. Allison H 5383*, reported by Hodgson and Allison, 1962 as *T. quadrifidum*; above Quartz Reef Hill, ca. 2300 ft., near Naseby, Central Otago; on earth with *Meesia*, damp ground in gully, *K. W. Allison H 5721*, reported by Hodgson and Allison, 1962 as *T. quadrifidum*, but the single gynoecium seen had freely spinose-dentate bracts, each bract lobe with 4-5 pairs of teeth; W side of Lake Waihola, S of Dunedin, Otago, on earth among mosses, short growth on hillside facing south, sheltered by sparse Manuka (*Leptospermum scoparium*) growth, ca. 200 ft. *K. W. Allison H 5369*, reported by Hodgson and Allison, 1962, as *T. quadrifidum*.

ECOLOGY. Often occurring as a small phase in open, insolated areas where it is subject to drying out ; here found occasionally associated with Manuka

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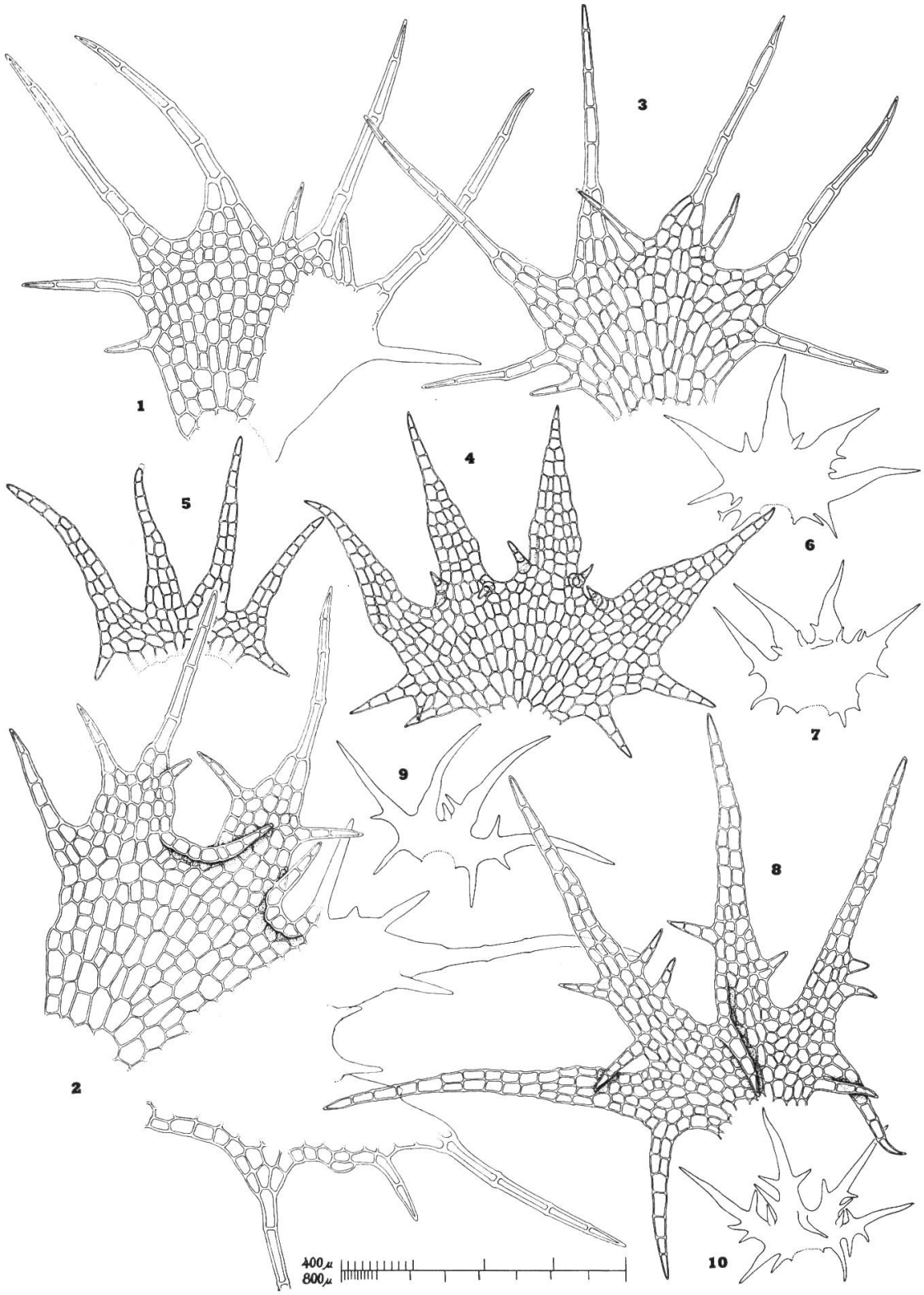
FIG. 50. *Temnoma townrowii* Schust. (1-2), *T. palmatum* var. *pseudospiniferum* Schust. (3), and *T. quadripartitum* (Hook.) Mitt. (4-10).

1. Leaf from ♂ plant (×87.5). – 2. Leaf from sterile sector of ♀ plant (×87.5). – 3. Leaf (×87.5). – 4. Mature sterile leaf (×87.5). – 5. Underleaf (×87.5). – 6-7. Leaves (×44). – 8. Leaf (×87.5). – 9-10. Leaves (×44).

Figs. 1-5, 8, drawn to top scale ; 6-7, 9-10, drawn to bottom scale. Figs. 1-2 from type, *T. townrowii, RMS 50421*; 3, from *RMS 55765*, Maungatua near Dunedin, N.Z.; 4-7 from a phenotype with high disc, superficially with an approach to *T. palmatum* s. lat., *RMS 60433*, Mt. Hector, N.Z.; 8-10, from *Donat 188*, Nahuel Huapi, Argentina, a phenotype approaching var. *randii*.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800 μ

(*Leptospermum scoparium*). Such phases from dry sites are sometimes slightly brownish and more compact than the phases from moist places; they have less attenuated leaf lobes, and on sterile shoots show the marginal spines of the lateral leaf margins to a much lesser extent.

In moist sites occurring on thin soil over limestone, associated with *Temnoma paucisetigerum*, *Lophocolea* sp., *Trichocolea mollissima*, *Aneura* sp., *Riccardia* sp. (Ruahine Mts.).

DIFFERENTIATION. *T. palmatum* var. *palmatum* includes a series of phenotypes which, typically, are characterized by small size; by the relatively non-spinose aspect—even ♀ bracts having relatively short cilia in most cases; the broader ♀ bracts, with the disc usually wider than long, at most broadly obtrapezoidal; by leaves with slender lobes and deep sinuses, with sinus bases normally lacking teeth or cilia (and particularly abaxially displaced cilia or teeth). Leaf lobes are well developed but are relatively narrow at base, gradually tapered, but do not normally end in very strongly elongated cilia. However, there may be a tip of 3-4, occasionally five thicker-walled and rather differentiated, elongated cells (Fig. 44 : 5, 7). The plant is usually habitually distinct from var. *pseudospiniferum* by the non-spinous aspect of the whole plant. Displaced spines, giving the abaxial surface of the leaf, in profile, a " hedge-hog aspect " are lacking, or are few and confined to the ♀ bracts and immediately subjoined leaves. Also, leaf lobes consist mostly of lamina—much less of the apical cilium. In var. *pseudospiniferum* the most striking aspect of the leaf lobes are the reduced lamina and the predominant, strongly elongated distal cilium.

GYNOECIA. I have studied a number of gynoecia of typical *T. palmatum* and find that the protection of the sporophyte is effected to a large extent by the shoot-apex, the sporophyte penetrating rather deeply into the gametophyte apex, which undergoes considerable elongation. In any case, the bracts and the bracteole are widely spaced, forming part of a lax spiral, with the insertions separated by a distance fully equivalent to that between the leaves and underleaves on sterile shoot-sectors. The entire seta, which is rather elongate even when the capsule is still soft, green and very immature, lies within the hollowed-out shoot-apex, below the point at which the perianth is inserted (Fig. 44 : 1) [1]. There is, therefore, no question of a stem perigynium s. str.—the axial tissue in which the seta lies not representing a secondary proliferation of cells lying solely below the perianth; rather, a coelocaule precursor is formed. The perianth itself, in this variety, seems much less highly developed as a consequence, being often ovoid with its length not exceeding the length of the bracts. There is at least weak formation of a shoot-calyptra in *T. palmatum* var. *palmatum* with unfertilized archeogonia being elevated well above the " calyptra " base. The structure of the gynoecium thus closely corresponds to that in *Lophochaete fryei*, as previously shown (Schuster 1961).

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[1] The figure is based on *Allison 5383;* the material in question was reported by Hodgson and Allison (1962) as *Temnoma quadrifidum*. The Otago type and the Cambewarra, N.S.W. plants of *T. palmatum* show an identical degree of " penetration " of the sporophyte into the axis.

In lax plants from moist, shaded sites, sporophyte penetration may be much less, and then axial tissue in the region of the foot is less affected, elongating less. For example, in spiny, light green, leptodermous extremes seen (Kiwi Hills, Wairoa, *Hodgson 210, 211*) the perianth is only obscurely stipitate. Associated with a more mesophytic growth form, the perianth is thin and elongated, and approaches that of *T. quadrifidum* in form, even though it is less strongly trigonous. The few mature perianths seen in this extreme are clearly, if not strongly contracted distally. Thus the distinction in perianth form between *T. palmatum* and *T. quadrifidum* appears to depend in part on external factors. Nevertheless, in such lax extremes with larger perianths, these still appear more inflated, and are only obscurely plicate-trigonous distally. Also the bracts are very copiously spinose-ciliate, each lobe bearing 4-5 pairs of spinose, spreading teeth.

Temnoma palmatum var. **laxifolium,** var. nov. [Figs. 45: 1, 46].

Folia discum 9-12(14) cellularum alt. habentia; lobi longo-acuminati 8-12(14) cellularum lat. ad basim, omni lobo in cilium terminale e 7-8 cellulis elongatis formatum, attenuato; cuticula fere levis. Typus: Tin Range, Stewart I., New Zealand, *RMS & G. A. M. Scott 49981*, in herb. auct., G, S-PA, NY. Schizotype material is widely scattered.

Plants very soft-textured, lax, aquatic to subaquatic. *Stems* 1-2 cm tall, ca. 180-240 μ in diam., rather soft-textured. Branching of two types: lateral, terminal, Frullania-type, and postical-axillary. *Leaves* usually larger, as a whole, than in var. *palmatum*: from 910 μ wide ×825 μ long (cilia included) to 1325-1650(1925) μ wide ×1400-1525 μ long (cilia included; without cilia, to 1300-1450 μ wide ×600-650 μ long), virtually transverse, usually quadrifid 0.5-0.6 their length, rather concave, distant to subcontiguous, soft-textured, lax, not at all spinescent; lobes lanceolate, broad-based (8-12, occasionally 14 cells wide), gradually long-acuminate, ending in a slender, setiform cilium formed of up to 7-8 elongated cells lying in a single row; leaf lobes usually quite free of cilia, the sinus bases occasionally to exceptionally with a cilium, which is rarely abaxially displaced; disc high, (8)9-12(14) cells high, obtrapezoidal, lateral margins bearing 1-2(-3) slender, often long, tapering cilia on each side. *Underleaves* similar to leaves but smaller, more deeply (to 0.65-0.8) quadrifid, lobes without cilia, lateral margins of disc with 1-2 long, often recurved cilia on each side. *Leaves* and *underleaves* near *androecia* more copiously ciliate-dentate but hardly spinescent. *Cells* quite leptodermous, delicate, without perceptible surface papillae, ca. (24)25-30×(40)45-60(65) μ; oil-bodies small for size of cell, (6)7-9(10) per cell, 4.4-4.8 μ and spherical to ellipsoidal and 3.8×7.5 to 3.5-5.5 ×4.5-6 μ. *Cells* in cilia to ca. 22×55 μ to 18-20×70 μ, strongly elongated (2.8-5 : 1). Dioecious. ♂ *Plants* with *androecial* region more spinous-dentate, otherwise similar to vegetative leaves. ♀ Plants unknown.

TYPE. Stewart Island, New Zealand: " Tin Range ", N of Pegasus, ca. 1000 ft., in a shallow, flowing rivulet in an open, peaty valley, *R. M. Schuster & G. A. M. Scott 49981*; the type with *Riccardia* sp. and *Cephalozia* cf. *bicuspidata.*

In addition known from South Island: Boggy wet draw, near summit of Mt. Maungatua, near Dunedin, Otago Prov., 2800 ft. (*RMS 55783a*, with *Cryptochila pseudocclusa* (Hodgs.) Schust.).

This plant, known unfortunately only from ♂ plants, cannot be satisfactorily placed elsewhere. It is most closely allied to typical *T. palmatum* and to *T. quadrifidum*, as I have delimited these taxa. From *T. quadrifidum* it differs in free development of marginal, long, often tortuous cilia of the disc of the leaves, and in the smaller and more numerous oil-bodies per cell (6-9 per cell usually vs. 2-5[6] per cell in *T. quadrifidum*).

The resemblances to "normal" *T. palmatum*, however, are more marked and the two often agree in the frequent, terminal, Frullania-type branching, in orientation of the leaves, in their basic form, and in the proclivity for developing a few marginal cilia of the disc margins of the leaves. *T. palmatum* var. *laxifolium* is perhaps merely an aquatic to subaquatic extreme of typical *T. palmatum*, from which it differs as follows: (1) disc 9-12(14) cells high vs. 7-9 cells high in *T. palmatum*; (2) lobes to 8-12(13-14) cells broad at base vs. 6-9 cells broad; (3) lobes terminating in up to 7-8 single cells in a row, rather than in (2)3-5(6) cells; (4) leaf insertion varying from essentially transverse to 5-10° succubous on one hand, to 5-10° incubous on the other, on larger sterile stems the orientation often slightly incubous; (5) cells leptodermous, smooth, or nearly so, large, the median ca. 25-30×(40)45-60 μ vs. firm and somewhat thick-walled, delicately verruculose in *T. palmatum*, and smaller in size (ca. 17-22 to 20-25×40-55 μ); (6) cells with 6-9 oil-bodies per cell, rather than 2-4(5) oil-bodies. These distinctions are slightly less impressive when the gathering from Maungatua is examined, in which the disc is rarely over ten cells high, and the lobes rarely over nine cells broad. However, even in this rather small phase, the cilia of the leaf discs are long, often tortuous and often recurved, exactly as in the type of var. *laxifolium*.

It is notable that the degree to which the disc of the leaf produces cilia (and the degree to which the leaf lobes are attenuated into terminal cilia, in ♂ plants of *T. palmatum* var. *laxifolium*) approaches that of *T. palmatum* var. *palmatum*, ♀ plants. Confusion might thus arise if these alone are compared. However, the ♂ plants of *T. palmatum* var. *palmatum* have leaves which are radically different, with much less attenuate leaf tips.

The occasional mature shoot-sectors of *T. palmatum* var. *laxifolium* with very slightly incubously inserted leaves are notable; such shoots are unknown in typical *T. palmatum*. Similar shoot-sectors occasionally occur in *T. quadrifidum* (at least in the Mt. Egmont plants). Also notable is the nearly uniformly terminal, lateral, Frullania-type branching. In the related *T. palmatum* var. *palmatum* I have also found, in addition to predominant Frullania-type branching, a few Acromastigum-type terminal branches, and a few postical-intercalary branches. In *T. palmatum* var. *laxifolium* I have seen, besides regularly produced terminal branches of the Frullania-type, only a few, sporadically produced ventral-intercalary branches.

The oil-bodies, in size and number, approach those of typical *T. pulchellum*: they occur mostly 6-9 per median cell and are relatively small (3.5×5 μ to 3.8×7.5 μ, a few to 5.5×6.5 μ, with some spherical and ca. 4.5 μ in diameter); they are virtually

homogeneous in appearance. The oil-bodies are, for the cell size, small and relatively inconspicuous (as contrasted to *T. quadrifidum* and *T. palmatum* var. *palmatum*).

Temnoma palmatum var. **cuneatum**, var. nov. [Fig. 47].

Folia discum 7-9 cellularum alt. habentia, lobis brevi-acuminatis, 7-9 cellularum lat. ad basim, in 3-5(6) cellulas elongatas terminantibus; cuticula crebre verrucosa; bracteae femineae angustae, cuneiformes, 0.2-0.3 quadrilobatae. Typus: S of Wilmot Pass, between Lake Manapouri and Doubtful Sd., New Zealand, *RMS 52661*, in herb. auct.

Plants small, brownish or bright green, sometimes without secondary pigmentation, often relatively soft-textured. *Leaves* occasionally or often weakly asymmetric, usually 0.5-0.55 quadrifid, on sterile shoot-sectors (and on ♂ plants) up to 790-925 μ broad (at tips of lateral lobes) ×660-725 μ long on ♀ plants to 800-850 μ broad ×800-850 μ long, the lobes slenderly lanceolate, usually 5-6 to 7-9 cells broad at base (some lobes of leaves of ♀ plants to 10-12 cells broad), the lobes normally edentate (♂ plants), or on ♀ plants with at most 0-1(2) non-recurved teeth near the base; disc 7-9 cells high, formed of rather elongated cells and appearing as high as the lobes are long, with 0-1(2) spinous teeth on each side; lobes gradually tapered, with apices short-acuminate, formed by usually 3-5 superimposed, elongated cells, each cell 3-5× as long as broad. *Underleaves* similar, distinctly smaller. *Cells* leptodermous but with conspicuous close papillae, quite evidently roughened, the median of disc ca. 18-20×40-55 μ; oil-bodies ca. 7-10(11) per cell, rarely and sporadically 5-6 per cell, ca. 4.5-5 to 5.5-6×6-7.5 μ.

♀ Bracts exceedingly high, narrow, cuneiform to oblong-cuneiform, 1875-2050 μ high ×900-1100 μ total width, 0.2-0.25 to 0.3-0.35 quadrilobed, the lobes each with usually 2-3 pairs of small, spinose uniseriate teeth mostly 2-4 cells long; disc high and very narrow, from 1275 μ high ×900 μ wide distally ×530 μ wide at base to 1580 μ high ×775 μ wide distally ×550 μ wide at base; median disc cells much elongated, ca. 16-24×70-125(150) μ; Perianth long, prismatic, to 2.0-3 mm long ×615-725 μ in diam., sharply trigonous almost throughout, somewhat contracted to the mouth, which is conspicuously, longly, closely ciliate (cilia up to 350-410 μ long, formed of up to 5-6 superimposed cells, the longer of which are ca. 13-17.5×75-90 [100] μ; median perianth cells ca. 16.5-18.5×35-55 μ; perianth not or obscurely stipitate, the bracts and bracteole with their insertions approximated.

TYPE. Ca. 1.5-2 mi. S of Wilmot Pass, between Lake Manapouri and Doubtful Sound, N of Spey R., ca. 1500 ft., *RMS 52661*, April, 1962. The type material includes also admixed *T. paucisetigerum*.

The plants grew over a wet, shaded rock, in a site on a mountain slope where inundation could not occur; associated were several *Lophocolea* species.

PARATYPE. Mt. Egmont, Taranaki Prov., N. I., New Zealand; ca. 5400-5500 ft., on cliff-faces and rocks in herb-field, near "Warwick Castle", in alpine zone, *RMS 48890*.

T. palmatum var. *cuneatum* shows a bewildering constellation of features. The oblong-cuneiform perichaetial bracts are without a known parallel elsewhere in the species as a whole; they have lent the variety its name. An approach to them occasionally occurs in var. *pseudospiniferum* (Fig 48 : 12). In the bracts var. *cuneatum* comes much closer to *T. quadrifidum* than to other populations of *T. palmatum*, and it resembles this species also in the more slender, prismatic perianths, and in the lack of distinct elongation of the shoot-tip below the perianth. Yet the leaves, with their acuminate lobes and their lobe apices formed of strongly differentiated cells strongly suggest *T. palmatum*, as does the widespread occurrence, on both ♂ and ♀ plants, of slender cilia of the upper disc margins. On the basis of these two criteria, and on the basis of the smaller leaves, with narrower lobes, I would venture to place var. *cuneatum* into *T. palmatum* as an extreme deviant. The strongly elongated form of the bracts, in actuality, separates this form from both normal *T. palmatum* and *T. quadrifidum*. *T. palmatum* var. *cuneatum* also has leaves and perichaetial bracts with equal sinuses—the median not being perceptibly deeper; in this it agrees with the other phenotypes of *T. palmatum*, and diverges from *T. quadrifidum*.

An approach to var. *cuneatum*, as regards form of the ♀ bracts, occasionally occurs in var. *pseudospiniferum* (e.g., in *Berggren 3468*, from Castle Hill). In all forms of var. *pseudospiniferum*, however, the ♀ bracts bear more longly spinose lobes (see Fig. 48 : 12), while the leaves bear short, displaced spines of the leaf-sinus bases (see Fig. 48 : 10-11). The lack of such displaced spines in var. *cuneatum* is very distinctive, and separates that variant from var. *pseudospiniferum*, suggesting instead var. *laxifolium* (to which there are clear similarities also in the gradually tapered leaf-lobes; the leptodermous cells; the more numerous, smaller oil-bodies; the shorter and less setaceous-tipped leaf lobes).

The paratype plants show all the essential features of the type, but are of a small mod. colorata. On these plants the leaves also are very often distinctly asymmetrical, and, in a few instances, 5-6-lobed, in isolated cases, 3-lobed. Underleaves are only 0.5-0.6 the leaves in size and may also be asymmetric. The ♀ bracts are a little more oblong and less clearly obcuneiform, but average twice as long as wide at maturity, and are less than 0.3 quadrifid, with rather few, stiff and short cilia and teeth; disc margins bear only a few teeth along their upper portions.

If the type and paratype plants are a fair gauge of the range of variation and if the tendency towards development of asymmetric leaves lacking all cilia is shown to be constant, then the var. *cuneatum* probably should be elevated to the status of an independent species. This, at the moment, seems premature, in view of the extreme malleability of *T. palmatum*.

Temnoma palmatum var. **pseudospiniferum**, var. nov. [Figs. 26 : 4-6, 48 : 8-12, 50 : 3].

Folia lobos reductos habentia, lobis ad basim latitudine solum 2-4(5) cellularum, omni in cilium longum terminale uniseriatum mox angustata, cilium e 5-6(7) cellulis elongatissimis compositum; bracteae femineae anguste trapezoideae; omnis cellula 2(3-6)7 guttis olei praedita. Typus: Otupae, NW Ruahine Mts., North Island, New Zealand (*Druce 3525* = *Allison H 5262*); in herb. E. A. Hodgson et auct.

Plants with an aspect approaching that of *T. quadripartitum*. *Leaves* usually quadrifid for 0.6-0.65 their length, the lobes of mature leaves with lamina reduced, only 3-4(5) cells broad at base, on larger leaves (♀ plants) often with a pair of teeth per lobe that are 1-3 cells long and spinescent, situated at the sinus bases and sharply postically displaced, not lying in leaf plane; lateral disc margins on each side with (0)1-2 short to long, spinose teeth or cilia; disc low (height always slightly to much inferior to lobe length), usually only 6-7 cells high; lobes setaceous, each ending in a well-differentiated apical spine, formed of to 6-7 superimposed cells (the longer cells ca. 14-18 × 60-78[96] μ). Median cells of disc small, ca. 16-18 × (25)30-36(40) μ, each with 4-6(7) oil-bodies, the oil-bodies ca. 4 × 5-6 to 5-6 × 7 μ, or spherical and 4.2-5.5 μ; cuticle rough. *Androecial* branches elongate, the *androecia* rather compactly spicate, terminal (at least initially), of 3-5(6) pairs of imbricate bracts ca. 750-800 μ wide, with setose cilia (500-515 μ wide excluding these). *Bracts* quadrifid ca. 0.5 their length, the lobes with a short triangular base 2 cells long × 3-5 cells broad and a uniseriate, setose apex formed of 3-5 elongated, striolate cells (longer cells 18-10 × 60-70 μ); lobes occasionally at one or both sides with a stiff, 1-2-celled spine; lateral margins of discus, antically, less often postically also with 1-2, 2-3-celled spines, the bracts thus quite spinescent in appearance; bracts (incl. spines) ca. 530-550 μ wide × 550-570 μ long. *Antheridia* one per bract; stalk 2-seriate. *Bracteoles* somewhat smaller than underleaves, quadrifid for 0.55-0.7 their length, with setose-terminated lobes. *Gynoecia* terminal on leading stems, without subfloral innovation (if fertilized). *Bracts* initially forming, with the bracteole, a spinescent, thistle-like capitulum, with development of sporophyte becoming widely separate, the perianth becoming longly stipitate. *Bracts* narrowly obtrapezoidal, 875-1000 μ long, quadrifid ca. 0.3-0.45 their length, the lobes copiously, longly spinescent-ciliate, each lobe with 2-3(4) opposed pairs of setose cilia, formed of 2-3(4) thick-walled, strongly elongated cells (cells to 16-18 × 65-75 μ); apices of lobes setaceous, the seta to 300-400 μ long, formed of 4-5(6) strongly elongated, highly differentiated cells (longer ones ca. 18 × 90-110 μ); sinus bases and some spinescent, rigid cilia originating there, sharply reflexed. *Perianth* relatively abbreviated, strongly stipitate at maturity and elevated above bracts, ca. 440-475 μ in diam. × 1300 μ long (900 μ without apical fringe of setose cilia), ovoid-ellipsoid, subterete and hardly perceptibly trigonous, inflated, the base narrowed, the distal part at best slightly narrowed, but again dilated to mouth, which is ± crispate and armed with ca. 24-28 to 35-48 stiff, setose, variable cilia and spines which in part are curved or reflexed outward or at least spread widely; cilia ranging from mere spines 1-2 cells long (usually under 200 μ long) to long bristles 300-450 μ long, then formed of 4-6 thick-walled, very elongated cells, the longer ca. 17-19 × (75)80-90(100) μ long.

TYPE. New Zealand: Otupae, NW Ruahine Mts., North Island, *A. P. & H. M. Druce, H 5262* in herb. Allison, *3525* in herb. Hodgson. A fragment in the writer's herbarium.

PARATYPES. Cascade Creek, near Lake Gunn, Eglinton Valley, Fiordland Natl. Park, South Island, *RMS 55487, 55490.*

DISTRIBUTION. Known only from the rather sparing, but strikingly distinct, type plants, and the following few collections: NORTH ISLAND: Wellington, *Berggren*

2813 [1874]; as " T. velutina sp. n." ± trans ad. var. palmatum; Pukerino Bush, near Taupo, *K. W. Allison*, no number or date, K; Wellington, *Berggren 2813*, c. per. SOUTH ISLAND: Castle Hill, *Berggren 3468*, Lund; *Berggren 3865*, trans. ad. var. palmatum form B; Maungaroa, *Berggren 2812* [1874], Lund, with capsules !; Just S of Haast Pass, Otago Prov., 1780-1810 ft., on bark of Nothofagus menziesii, *RMS 49722* [a rigid form close to T. townrowii]; *RMS 55460a*.

DIFFERENTIATION. A difficult and problematical taxon, which, superficially at least, seems to connect *T. palmatum* s. lat. to *T. quadripartitum* f., *spiniferum* and var. *pseudopungens*. The fertile plant gives much the appearance of *Temnoma palmatum* var. *palmatum*. The perianth is, as in that species, relatively abbreviated, almost always wide at the mouth; the mature capsule almost fills the perianth, thus the foot and seta are deeply sunken into the shoot-apex (which is correspondingly elongated—the bracts and bracteole being widely separated, the perianth proper appearing stipitate). ♀ Bracts and subfloral leaves are, as in *T. palmatum* var. *palmatum*, copiously ciliate-spinose to spinose-dentate on the margins. But, with this, similarities largely cease and a number of differences emerge, among them: (1) The ♀ bracts bear longer, more spinose teeth on the lobe margins, formed of 2-3 thick-walled, strongly elongated cells (cells to 16-18 × 65-75 μ); apices of the lobes are setaceous, ending in a seta to 300-400 μ long, formed of 4-5 strongly elongated, highly differentiated cells (cells to 18 × 90 μ, but usually somewhat shorter); some lower spines of the lobe margins may be reflexed. (2) The perianth mouth is spinose-ciliate with dimorphic, stiff spines and setae, the shorter of which are stiff spines, in part are widely spreading, if not reflexed (approaching the spines of the leaf sinuses in this respect); setae are longer and more crowded, rigid, at times in part 4-5-6 cells long (to 250-450 μ), formed of thick-walled, elongated cells, the longer of which are ca. 18 × 75-100 μ. (3) The androecia are spicate and rather compact, and bracts bear not only four setaceous lobes, but commonly several shorter, stiff, sometimes in part recurved spines—thus appear conspicuously spinose-ciliate.

As a consequence, with fertile plants, or even mature, sterile plants at hand, there should be no occasion to confuse *T. palmatum* var. *pseudospiniferum* with *T. palmatum* var. *palmatum*. Unlike the last variety, the leaf lobes normally end in sharply defined terminal spinose setae (4)5-6 to 6-7 cells long, formed of (largely) strongly elongated cells which are more strongly thick-walled and ca. 14-18 × up to 65-75(96) μ. Added to this is a definitive difference which, in my opinion, is unmistakable: the leaf lobes usually bear (except on weak ♂ plants) near their bases, a pair of 1-2-3-celled, rigid spines which are often displaced to the abaxial surface of the leaf (the leaf, seen in profile, when a plant as a whole is examined from dorsal or ventral view, is thus spinose on the abaxial surface). In other phases of *T. palmatum* I have examined no such reflexed spines of the sinuses occur, except in the gynoecial region. These spines, it should be noted, are displaced rather than reflexed, being technically not entirely marginal. They occur on leaves in which the sinuses are not or almost imperceptibly reflexed, hence occur independent of whether or not the sinus bases become reflexed. On many weak plants, and even some rather vigorous ones, most leaves are simply quadrifid and lack such accessory spines.

The ensemble of differences cited almost suggests an independent species is at hand [1]. Indeed, the reduction of the leaf lobes (terminal cilia excepted) is extreme in this phenotype, the plants being habitually distinct in this alone. However, in paratype material from Cascades Creek the lobes are less reduced and may be 5-6(7) cells broad at the base, even though the displaced spinose teeth are quite distinct. These last plants serve to bridge the gap between var. *pseudospiniferum* and var. *palmatum*. Equally transitional are plants from Wellington (*S. Berggren 2813*). Thus, although the type itself is strikingly distinct, it seems nonetheless connected by transitional forms to the species proper.

In one postmature gynoecium I found a few spores which had begun to undergo germination; these were to 15-16.5 μ in smaller diameter and finely papillose. Associated were a few elaters which were ca. 11 × 95-110 μ, and which bore a single wide (6.5-7.5 μ wide) red-brown spiral. If, as I assume, these spores and elaters belonged with the *Temnoma*—and there is no reason to assume otherwise—then in *T. palmatum pseudospiniferum* there are unispiral elaters as in *Archeophylla schusteri*. Since *T. quadrifidum* and *T. pulchellum* possess elaters with two slender spirals, it is possible that an excellent criterion may exist here, within *Temnoma*, which has not been as yet exploited to full advantage. These observations could not be substantiated, however, on fertile plants of *Berggren 2812*; see species diagnosis.

T. palmatum var. *pseudospiniferum* is exceedingly similar to (and, with ♂ plants only, often almost inseparable from) the Tasmanian *T. townrowii*. The distinction between the two is discussed under the latter taxon. In particular, the collection from Haast Pass (*RMS 49722*), referred to var. *pseudospiniferum*, is so close to *T. townrowii* that it might well be placed in the last taxon.

Temnoma townrowii Schust., sp. n.[2] [Figs. 48: 1-7, 49, 50: 1-2].

Plantae ramificationem tantummodo typi Frullaniae habentes, valde spinescenti-ciliatae; folia subtransversa, plus quam 0.5 quadrilobata, lobis ad apices lanceolatis acuminato-ciliatis; cilia cellulas longiores 14-16-18 × 90-135 μ habentia; lobi foliorum (in plantis femineis) latitudinem 8-11 cellularum habentes; os perianthii cilia usque ad 350-400 μ long,, ex 4-6 cellulis (omnibus usque ad 100-150 μ long) composita, habens; amphigastria manifeste minora quam folia lateralia. Typus: Camp Creek, Surprise Valley, Tasmania (*RMS 50421*).

Plants usually forming pure, compact turfs, small, erect or suberect, only 8-15 mm tall, 0.9-1.2 mm wide; brownish, rather dull. Plants compact, with short internodes, dense and subtransverse leaves, appearing quite bristly rather than ciliate, infrequently to occasionally branched, the branches uniformly lateral, of the Frullania-type. *Leaves* stiffly spinescent-ciliate, only weakly succubously inserted, transversely oriented, dense, widely patent, rather concave, the lobes and longer cilia often ascending to suberect; leaves basically obtrapezoidal to obdeltoid

[1] The distinctiveness of this taxon also seems to have impressed Berggren, who gave the plant the herbarium name *Blepharostoma velutina*.

[2] Named in honor of Dr. and Mrs. John Townrow, of Hobart, Tasmania. The type was collected while the author was on a joint expedition with Dr. Townrow.

in outline, never reniform, narrower than in *T. paucisetigerum*, ca. 1100 μ wide ×730-850(960) μ long (with cilia; on ♀ plants; smaller and simpler on ♂ plants); disc with nearly straight, only moderately divergent sides, ca. 10-12(14) cells high (to sinuses; ♀ plants), symmetrical, 25-30 cells wide; distinctly quadrifid, the sinuses descending 0.3-0.35(0.4) the leaf length (cilia omitted; to 0.6-0.7, cilia included), the lobes ovate-triangular, longer than wide, to (6-7)8-11 cells broad. *Leaves* with cilia of two types: the lobes ending each in a long, slender cilium 350-400 μ long formed of 5-7 strongly elongated cells (cells to 14-16×90 μ up to 16-18×100-135 μ; the cell length from 4-5 to 5-8× the width), the lateral margins of lobes and the sides of the disc with shorter, stiffer, ± straight and rigid, more abbreviated cilia mostly formed of 3-5 cells which are not tortuous or flexuous; leaf (♀ plant) as a whole with 16-30 cilia; sinuses rounded at their bases, usually ± reflexed, carrying with them the shorter, spinescent cilia, which, in situ, project from the abaxial leaf surface. Occasional *cells* of cilia 16-18×100-135 μ, but usually appreciably shorter (to 14-16×90 μ), distinctly striolate (the distal cells usually almost smooth); cells of lamina oblong, averaging ca. 14-18 μ wide ×(24)26-40(45) μ long, smaller and notably shorter (± isodiametric) within lobes, somewhat thick-walled, each with (2-3)4-6(7-8) oil-bodies which are smooth, almost homogeneous in appearance, spherical to ovoid, ca. 3.5-4.5 μ to 3-4×3.5-4.5 μ to 4.5-5.5×5.5-6.5 (rarely 6-6.5×7-7.5) μ. Dioecious. ♂ Plants more slender than ♀ plants, with much smaller leaves (disc to 10-12 cells high; spines only 2-5, in addition to terminal cilia); ♂ bracts dense, a spiny, compact androecium resulting. ♀ Inflorescence with leaves grading gradually into bracts, becoming narrower and larger. *Bracts* (with cilia) (1150)1350-1540 μ high×(725) 1300-1400 μ wide (without cilia [680]800-950 μ long to sinuses ×[410]740-820 μ wide), obcuneiform, narrow and narrow-based, 0.25-0.4 quadrifid, the lobes spinose-ciliate and ciliate like leaves of ♀ shoots. *Perianth* cylindric-trigonous, ± weakly stipitate, mouth strongly spinose-ciliate (some cilia reflexed), cilia ± dimorphic, short ones (1-3-celled) accompanied by larger ones (4-6 cells long, 350-400 μ long; larger cells 100-150 μ long ×19-21 μ).

TYPE. Tasmania: Near Camp Creek, along road from Derwent Bridge to Queenstown, ca. 1800-2000 ft.; in Surprise R. Valley, ca. 2 mi. W of King Billy Divide (*RMS 50421*); material abundant (isotypes widely distributed). I have seen only one other gathering of this species from Tasmania (*Oldfield*, without loc. or date; K), consisting of a perianth-bearing shoot and several ♂ plants.

DIFFERENTIATION. *T. townrowii* exhibits a character complex which effectively prohibits its disposition under the nearly similar *T. palmatum* var. *pseudospiniferum* and *T. paucisetigerum*, with both of which it shares many features (see below).

The species is relatively small, forming a rather dense, often nearly pure, low turf; it is light brownish-tinged and compact in growth. The extraordinarily stiffly, spinescent-ciliate leaves are rather dense, although since they are rather widely patent they do not appear conspicuously imbricate. They are somewhat succubous, although rather subtransversely oriented, much as in the *T. pilosum-patagonicum* and *T. palmatum* complexes, to which *T. townrowii* is similar, owing to the common possession of displaced cilia or teeth of the leaf sinuses. As in these last species, the leaf sinuses tend to be recurved, often carrying with them several stiff, rigid,

setose cilia, which thus become abaxially displaced. Superficially, therefore, mature leaves appear armed with a series of marginal setose cilia or stiff, bristly hairs, and with a smaller series of stiff, shorter, abaxially displaced cilia, which appear to project stiffly from the convex abaxial leaf surface [1].

Unlike in *T. paucisetigerum* the leaves are armed with two rather distinct types of cilia: long cilia terminating the four lobes, and much shorter, more rigid-appearing cilia or spinose teeth of the lobe bases and the disc margins. The several cilia—usually 2-4 per disc margin on mature sterile leaves—on each margin of the disc are never long and tortuous, not or rarely arcuate or flexuous, and are relatively short. On weak leaves (particularly of the somewhat weaker ♂ plants), only the four terminal cilia of the lobes may be developed, with one or both lateral leaf margins bearing 0-1(2) short cilia or teeth.

I have repeatedly studied branching in this species, and, thus far, have been able to find only lateral, terminal branches of the Frullania-type. The evident inability to produce postical-intercalary branches suggests a genotype is at hand distinct from both *T. paucisetigerum* and *T. palmatum* var. *pseudospiniferum* with which *T. townrowii* otherwise shows close similarities.

This is a difficult and critical plant to evaluate; it bears certain similarities to compact forms of *T. paucisetigerum*, but is more similar to *T. palmatum* and *T. quadripartitum*. The species approaches *T. quadripartitum* and some forms of *T. palmatum* in the displaced or reflexed, stiff and rather short cilia lying near the bases of the sinuses—the leaf appearing stiffly spinose-armed abaxially, and in the subtransverse orientation of the leaves. The much less deeply divided leaves, with a high and well-developed lamina (and short lobes) will at once separate the species from *T. quadripartitum*. In this respect the Tasmanian plant closely approaches *T. palmatum*.

At first glance—perhaps because of the highly specialized cilia—the most direct affinities appear to be with the New Zealand *T. paucisetigerum*. From this plant *T. townrowii* differs as follows: (1) The uniseriate cilia are roughened, rather than being essentially smooth; (2) leaves tend to be more obdeltoid in shape, rather than reniform-obtrapezoidal; (3) leaf lobes, below the uniseriate tips, are narrow and distinctly triangular; (4) cilia of the lobe margins and of the lateral disc margins are shorter and stiffer than is the rule in *T. paucisetigerum*; (5) cells of the lamina have from 3-6 oil-bodies each, rare and exceptional cells having 2 or 7-8 oil-bodies, rather than (4)5-9(10) oil-bodies as in *T. paucisetigerum*; (6) the shorter, stiffer cilia lying in the sinus bases tend to be sharply, stiffly reflexed—the leaf thus being distinctly prickly on the abaxial surface. Occasional extremes of *T. paucisetigerum* also show this tendency towards displacement of the cilia of the sinus bases, but never as conspicuously as in the present plant. My impression is that *T. townrowii* represents a distinct species, altogether separate from *T. paucisetigerum* s. str., allied more to *T. palmatum*. In interpreting material, the following comparison of *T. paucisetigerum*, *T. townrowii* and *T. quadripartitum* may be of use: see table 3.

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[1] This is true only of ♀ plants and the larger leaves (and bracts) of ♂ plants. The ordinary vegetative leaves of ♂ plants tend to be small and simpler in structure, more shallowly 4-lobed, with each lobe ending in a setaceous uniseriate segment, the leaf lobes exceptionally developing cilia (but one or both sides of disc with a rigid, short cilium usually developed).

Table 3. — A comparison of *T. paucisetigerum*, *T. townrowii*, *T. quadripartitum* and *T. palmatum* var. *pseudospiniferum*

Character	*T. paucisetigerum*	*T. townrowii*	*T. quadripartitum*	*T. palmatum* var. *pseudospiniferum*
Setae of leaf lobes very much differentiated	+	+	—	± sharply so
Uniseriate lobe apices: Length: width of cells	to ca. 4.5-6 : 1	to ca. 4.5-8 : 1	ca. 1.5-2 : 1	ca. 2.5-4(5) : 1
Striolations of cilia	—	+	+	+
Length of cilia in cells	to 7-9 cells	5-7 cells	(2)3-5 cells	to 5-7 cells
Leaf shape (mature leaf)	Reniform-obtrapezoidal	Obdeltoid-obtra-pezoidal	Obdeltoid-obtra-pezoidal	Obdeltoid-obtrapezoidal
Leaf lobes (minus cilia)	Very broad, short, to 9-13 cells wide	Triangular, 4-6 to 8-11 cells wide	Linear-lanceolate, 4-5(6-8) cells wide	Triangular, to 3-5(6) cells wide
Lateral cilia or teeth of disc	Slender, uniseriate, ± tortuous, long, supra-basal	Slender, stiff, straight, short, suprabasal	Stout, reflexed, often lobe-like, usually basal	1-2 per side of disc, stiff, slender, suprabasal
Cilia or teeth of sinus bases:				
length	3-6 cells	to 3-5 cells	1-3 cells	1-3 cells usually
displaced	no, rarely yes	yes	yes	yes
Postical branching	+	—(always ?)	+(rare)	+
Oil-bodies	(4)5-8(9-10) per cell, small	(2)3-6(7-8) per cell, ± small	(2)3-6(8) per cell, large	4-6(7) per cell, rather small

Of the preceding taxa, the most immediate affinity is clearly with *T. palmatum* var. *pseudospiniferum*. On weak, ♂ or sterile axes, a distinction may, indeed, be almost impossible to perceive. Yet, *T. townrowii* differs from *T. palmatum pseudospiniferum* in a series of features: (1) the cilia are formed of cells which are generally more sharply and abruptly differentiated, from the notably smaller cells in the lobe; cilium cells are to 90-135 μ long (vs. usually 60-78 μ in *pseudospiniferum*)—as a consequence, cells in the lobes look notably smaller than those of the cilia; (2) the lateral disc margins of leaves of ♀ plants are more freely spinose-ciliate, each disc margin commonly with 3-4 or even 5 spinose teeth, rather than 1-2 per margin; (3) the total lack of intercalary branching; (4) the leaf lobes are broader, to 8-11 cells wide on ♀ plants, rather than mostly 3-5 cells wide. This last distinction fails with ♂ plants, on which the smaller leaves have very greatly reduced lobes in both taxa.

For some time I attempted to place *T. townrowii* in *T. palmatum* s. lat., as a variety or subspecies. Such a treatment seems untenable, chiefly owing to the very highly differentiated cilia of the leaves, which have more abruptly differentiated cells (as contrasted to the cells of the lobes below the cilia) than in any other species of subg. *Eotemnoma*. When these two species are placed side by side they look different: *T. townrowii* is more spinescent than even *T. palmatum* var. *pseudospiniferum*. More significant, perhaps, the rectangulate laminar cells of the leaf middle become notably abbreviated and subquadrate in the lobes in *T. townrowii*—thus we go from rectangular laminar cells to isodiametric, quadrate lobar cells, into abruptly and strongly elongated cells of the cilia. By contrast, in almost all forms of *T. palmatum* the rectangulate cells of the lamina go over into little or hardly shortened cells of the lobes, and the elongate lobar cells " go over " relatively gradually into cells of the cilia; compare Fig. 50: 1-2 with 50: 3. It was these distinctions that led me, ultimately, to maintain the two taxa as autonomous species. Admittedly, isolated transitional specimens (such as *RMS 49722*; referred to *T. palmatum* var. *pseudospiniferum*) occur, which, in part, break down these distinctions.

(The final installment and conclusions will appear in a later volume)