

A Peculiar New Species of *Trichomanes* sect. *Selenodesmium* and Several of its Probable Hybrids¹

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On December 27, 1965 a peculiar species of *Trichomanes*, first thought to be in the sect. *Davalliopsis*, was collected in New Caledonia. It proved to be the first species of *Trichomanes* sect. *Selenodesmium* that has leaf blades more than one cell thick. The relatively exposed habitat (altitude ca. 300 m along the trail from the Dumbea Dam to Montagne des Sources) which, however, seemed to be supplied with subsurface water, correlates with the nearly sclerophyllous fronds of the new species. Substratum samples unfortunately yielded no hymenophyllaceous gametophytes, only thallose ones identified as *Blechnum* sp. and filamentous ones clearly belonging to *Schizaea fistulosa*. Bierhorst NC460 included two mature specimens, and Bierhorst NC465 included one sterile, half-grown plant with associated substratum. The material was preserved in a chromic acid-acetic acid-formaldehyde solution in the field and was later transferred to glycerine alcohol. Type material will be dried and deposited in the Gray Herbarium, Harvard University.

Freehand sections of all parts of the plant were prepared and stained with 1% Methyl Green for 5 min followed by two rinses in water. The sections illustrated in Figs. 11 and 13–18 were prepared in this manner. The cleared leaf shown in Figs. 4 and 20–22 was bleached in "Clorox" until white (ca. 15 min; monostromatic species generally take 1–3 min), rinsed with three changes of water, dehydrated in 70%, 95%, and 100% ethanol (5 min each). It was then stained with Fast Green (1% in 100% ethanol) for 3–5 min, rinsed in two changes of 100% ethanol (total ca. 5 min), then one change of 1:1 xylene-absolute ethanol, then cleared in xylene (two changes of 5 min each), and finally mounted in synthetic resin "HSR." The new species is designated:

***Trichomanes polystromaticum* Bierhorst, sp. nov.**

Planta terrestris. Rhizoma crassum adscendens, trichomata numerosa fuscata attenuata articulata plerumque 2 mm longa ferens. Stipites tenaces fasciculati asperi fuscati, trichomata decidua sparsim ferentes. Stipites penitus alati vestigialiter, ala decidua basi. Lamina bipinnata, segmentis ultimis incis, stratis 2 vel 3 cellularum composita, coriacea, cellularum parietibus crassis conspicue reticulatis. Pinnae anadromicae. Rachis juvenis omnino alata trichomata ferens. Nervatio aperta sed paucis venis liberis distaliter convergentibus. Radices stipitis lateribus singulatim basaliter enatae. Sorus terminalis in lobo basali vel subbasali in pinnulae latere acroscopico. Involucrum campanulatum, ore integrum constrictum, basi contractum, plerumque 0.8 mm × 1 mm. Receptaculum longe exsertum.

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Sporangia numerosa, plerumque $200\ \mu\text{m}$ lata, 32 sporas triletas foveatas plerumque $21 \times 36\ \mu\text{m}$ capientia. Annuli cellulae 12–14.

TYPE: Along trail from Dumbea Dam to Montagne des Sources, ca 300 m alt, New Caledonia, *Bierhorst NC460* (to be deposited at GH).

OBSERVATIONS AND DISCUSSION

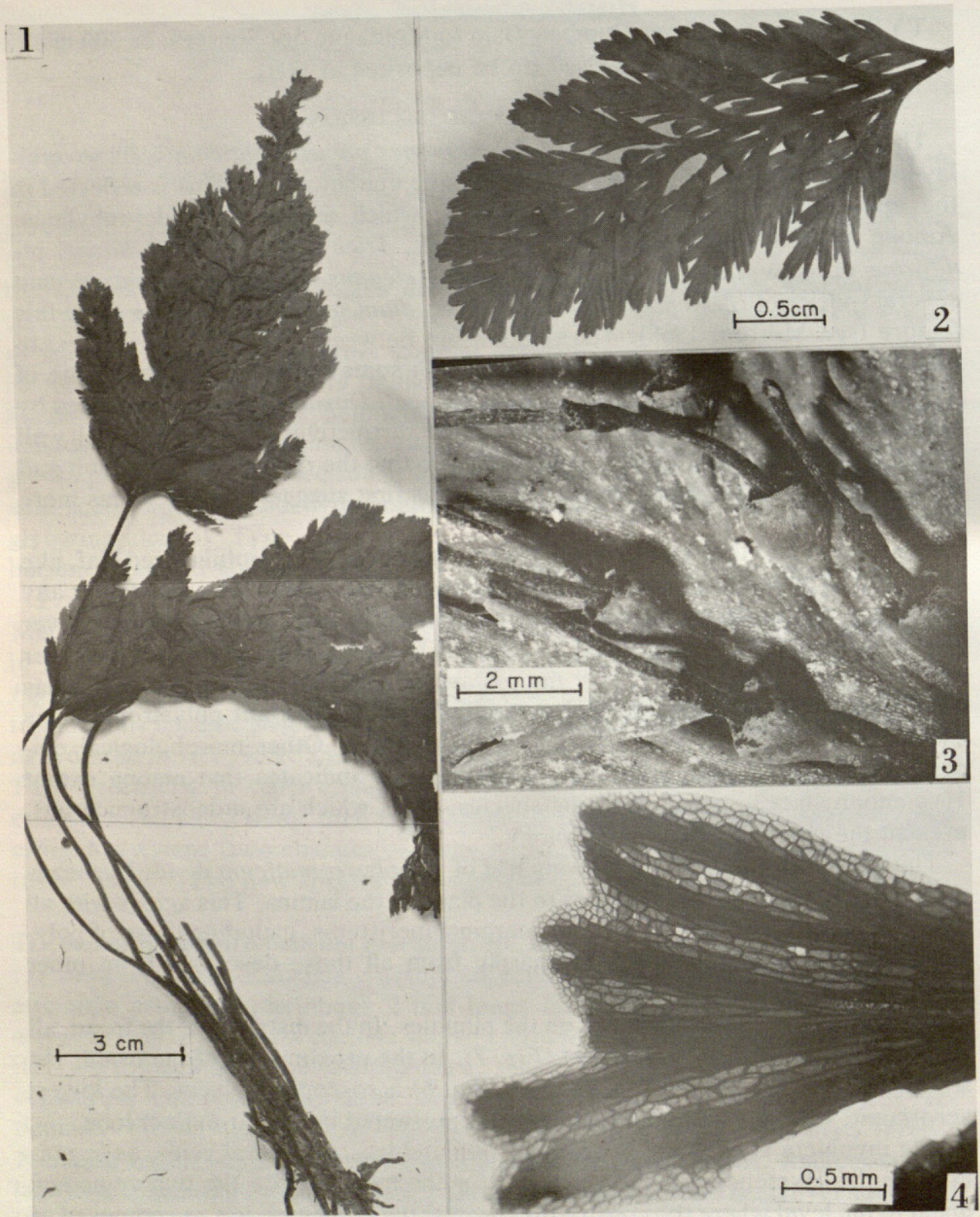
The most conspicuous feature of *Trichomanes polystromaticum* is its several-layered lamina (Fig. 11), to which the specific epithet refers. This is reflected in the appearance and texture of the frond, which approaches sclerophyllous. Among other described species of the family, *Trichomanes* (*Cardiomanes*) *reniforme* of New Zealand, *T. (Davalliopsis) elegans* of tropical America, and several species of *Hymenophyllum* subg. *Mecodium* sect. *Diplophyllum* share this feature (see Morton, 1968). The relationship between sect. *Selenodesmium*, to which *T. polystromaticum* belongs along with some ten other species, some of which are poorly defined, and the monotypic sect. *Davalliopsis* was suggested by Copeland (1938). He, however, emphasized distinctiveness of epidermal wall structure to the point of further suggesting also that the resemblance (in habit and frond and soral form) might be superficial. His first suggestion now seems more plausible.

Despite the fact that *Trichomanes polystromaticum* has a multilayered leaf, like other polystromaticous species of Hymenophyllaceae it bears no stomata nor any significant intercellular spaces within the lamina. In fact, no stomata have ever been reported in this family. This, in addition to the fact that several of the other multilayered species exhibit only the unilayered condition on young plants, has been interpreted (Holloway, 1923) to indicate that the extant polystromaticous species were derived from monostromaticous ones. Other morphological evidence (Copeland, 1938; Bierhorst, 1974) strongly indicates that among extant Hymenophyllaceae, small creeping species, all of which are monostromaticous, present the most primitive morphology.

The marginal initials in the growing leaf of *T. polystromaticum* divide by means of new walls formed at right angles to the plane of the lamina. This agrees with all other described hymenophyllaceous marginal meristems, including those of polystromaticous species, but differs sharply from all those described from other fern families (see Bower, 1923).

The position of the sorus varies on the pinnules. In the distal 2/3 of the frond, all are inserted on the lowest segment (Fig. 7). In the proximal 1/3 of the frond, the sori are on the second (Fig. 5) or third (Fig. 6) acroscopic segment. The lowest acroscopic segment when sterile is often represented by a near-extinct lobe.

The involucre is elliptical in cross-section and has two lateral veins, as is general for the Hymenophyllaceae. Except for the end between the two veins and distal to the level where the constriction begins, the involucre, too, is composed of several cell layers (center of the distal part of the involucre, Fig. 8). The mouth of the involucre is elliptical with angular edges. The receptacle with its collection of sporangia tends to force it into a circular outline (Fig. 6), but when sporangia fall away, the opening reassumes its original, bilateral form.



Holotype of *Trichomanes polystromaticum*. FIG. 1. Holotype plant. FIG. 2. A pinna. FIG. 3. Sori. FIG. 4. A cleared ultimate segment.

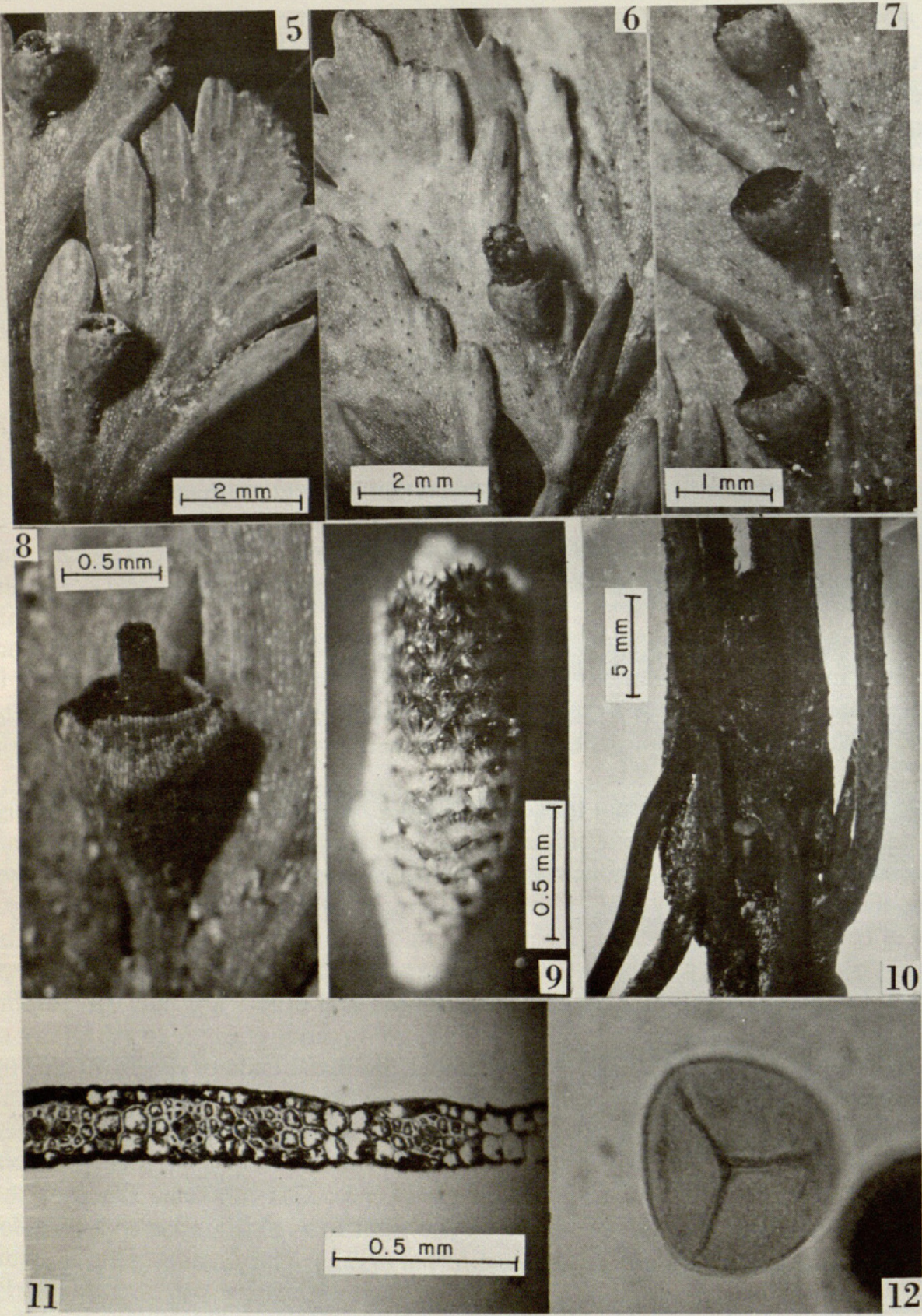
The receptacle is long-exserted and typical for its type. After the sporangia are produced in their characteristically basipetal-gradate sequence, no extended, sterile portion of the receptacle is produced. The absence of this feature, which is one of the major features of the Hymenophyllopsidaceae, makes it futile to compare *T. polystromaticum* with that family, despite some similarity in leaf structure.

Sporangium size, spore number per sporangium, high sporangium number per receptacle, and gametophytes one-celled when shed all appear relatively uniform among species of *Trichomanes* considered to be in sect. *Selenodesmium*. The new species is no exception. Preserved material of five other species collected by the author in Fiji, New Caledonia, and New Guinea, as well as dried herbarium material in the Gray Herbarium were available for comparison.

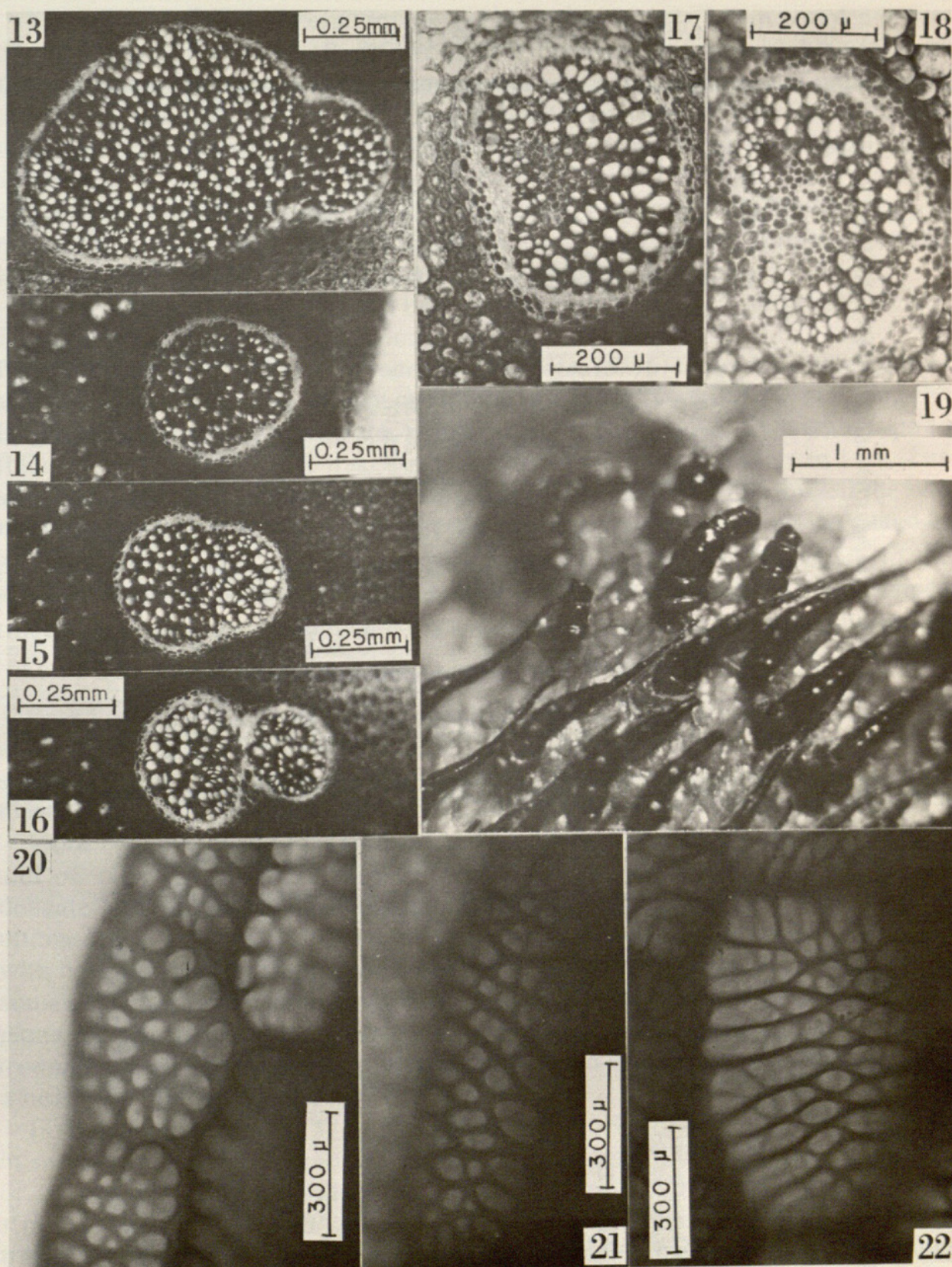
Patterns of outer epidermal wall thickening (Figs. 20–22), especially of the marginal cells, are reasonably diagnostic in sect. *Selenodesmium*. The manner in which the material is prepared, however, seems critical. The cells illustrated in Figs. 20–22 were stained with an acid stain. When material was unstained or stained with a basic stain such as Safranin or Methyl Green, areas of the wall which are not significantly thicker than elsewhere do not show up, and hence the fainter bars of the reticulum are not visible. The more or less rounded areas within this wall pattern have generally been termed “pits.” This has led to no misconceptions insofar as the author is aware, but anatomically the term is applied in error. There are no areas of the outer wall where secondary layers are absent. The continuous secondary wall is peculiarly differentially deposited to yield a reticulate or pseudo-pitted appearance.

Occasional convergent vein tips (e.g., the upper two in Fig. 4) are interesting, but seem quite unrelated to areole origin in fern leaves with fully or partly anastomosing venation. Throughout the Hymenophyllaceae, as well as in most other ferns with dichotomous venation, marginal initials of the lamina produce distinct files of cells in which cellular differentiation and maturation progresses toward the margin (see figures of Goebel, 1930; Hagemann, 1965). Within the marginal meristem certain cells are initials of the procambium and others are not. The lamina shown in Fig. 4 was in no way different. The convergence was due to the failure of cells within three cell lineages to enlarge near the distal ends of the two veins on either side, but the three files of cells were in no other way disturbed.

The stem anatomy of *T. polystromaticum* is consistent with that of all described *Trichomanes* species with upright, relatively robust stems. A highly parenchymatized (“vitalized”) central mass of xylem (Fig. 13) is present. Traces to the phyllophores (one is shown departing at the right in Fig. 13) arise in a pseudo-spiral, reflecting the attachment of the external organs. The pseudo-spiral is made up of subopposite pairs of phyllophores, with each successive pair rotated nearly 180° from the pair above or below. This type of attachment in *Trichomanes* grades into a true spiral when the sub-paired arrangement is lost and into a distichous arrangement in which the rotation of successive pairs is 0°. This latter condition is considered to represent the most primitive condition within the family and is found in groups of species with thin, creeping stems, like *Trichomanes* sect. *Gonocormus* and sect. *Crepidomanes* (Bierhorst, 1973, 1974).



Holotype of *Trichomanes polystromaticum*. FIGS. 5-7. A sorus on the second, one on the third, and one on the first (center of three) acropetal segment of a pinnule. FIG. 8. A single sorus. FIG. 9. Excised receptacle with sporangia. FIG. 10. The stem with petiole bases and roots. FIG. 11. Lamina cross-section. FIG. 12. A spore.



Holotype of *Trichomanes polystromaticum*. FIG. 13. The stem stele with departing phyllophore trace at right. FIG. 14. Phyllophore trace. FIGS. 15, 16. Phyllophore trace dividing to produce a leaf trace (left) and a pseudoaxillary bud trace (right). FIGS. 17, 18. The leaf trace ca 0.5 cm and ca 1.5 cm above the level of Fig. 16. FIG. 19. Stem trichomes. FIGS. 20-22. Outer lamina epidermal cell wall thickenings on a marginal cell, submarginal cell, and an intervenal cell, respectively.

TABLE I. SELECTED CHARACTERISTICS OF *Trichomanes dentatum*, *T. polystromaticum*, AND THEIR HYBRIDS.

Source	Collector	A ¹	B	C	D	E	F	F _c	G	H
<i>Trichomanes dentatum</i>										
New Caled.	Franc 1407	3-3.5	1	5-9	—	—	25.5(25-26)	27		0
Fiji	Smith 6013	3-4	1	5-8	+	—	25(21.5-28)	26.5		0
Society Is.	de La Rue	3-4	1	5-9	+	—	26.5(25-31)	28		0
Fiji	Degener 14137	3-4	1	5-9	+	—	25(23-28)	26.5		0
Samoa	Reinecke 86b	1.5-2	1	5-9	+	—	25.5(25-28)	27		0
Fiji	Smith 1349	2.5-3.5	1	6-12	+	—	26(25-28)	27.5		0
Tahiti	Wilkes 22 ²	2.5-3.5	1	5-9	+	—	25.5(23-26)	27		0
New Caled.	Franc 366	2.5-3.5	1	6-8	—	—	25(21.5-26.5)	26.5		0
Cook Is.	Parks 22034	2-3	1	6-9	+	—	26.5(23-28)	28		0
Fiji	Bierhorst Fx1	3-4	1	5-9	+	—	27(23-29)	—		0
<i>Trichomanes dentatum</i> × <i>polystromaticum</i>										
New Caled.	Vieillard 1663 ²	3-3.5	2-3	3-5	—	—	25.5(23-31)	27		0
New Caled.	McKee 4438	2.5-3	2	5-9	—	—	28.5(24-30)	30.5	29 × 22	23
New Caled.	Buchholz 1209	3-3.5	2	5-8	—	—	30(26-33)	32	32 × 22	37
New Hebr.	Morrison 20VII1896	2-3	1	5-9	+	—	29(28-30)	31	32 × 16.5	31
New Hebr.	Morrison 16VII1896	2.5-3.5	2	8-13	+	—	28(23-32)	30	30 × 21	61
<i>Trichomanes polystromaticum</i>										
New Caled.	Bierhorst NC460	ca. 1	2-3	2-4	—	+	36(33-38)	—		0

¹ A = Involucre, L:W. B = Lamina thickness, number of cells. C = Maximum number of cells between free vein endings. D = Involucre mouth, apical flaring. E = Involucre, subapical constriction. F = Average diameter of tetrad spores in μm , the range in parentheses. F_c = F × shrinkage correction factor of 1.065. G = Average dimensions of diad spores in μm . H = Percent diad spores.

² Isotype of *T. dentatum*.

³ Cited by Fournier as *T. platyderon* Fourn., who also later submerged it in *T. dentatum*.

The reference to the lateral organs as phyllophores rather than petioles is justified on several grounds (Bierhorst, 1974). In creeping forms such as in sect. *Gonocormus*, the apex of the phyllophore produces a lateral axis of appreciable extent. Its apex then dichotomizes and one of the two apices, after a transformation from radial growth to bilateral growth, produces a leaf, or occasionally both apices produce creeping stems. In some other forms, the phyllophore apex divides while still sessile upon the creeping stem, and thus a phyllophore axis is essentially absent. In upright forms such as the *Selenodesmium* species, the phyllophore apex divides to leave behind the so-called axillary bud.

Figure 14 shows the stele at the base of the phyllophore in *T. polystromaticum*. Its structure and symmetry is similar to that of the stem stele. Less than 1 mm from the stem the phyllophore trace divides (Figs. 15, 16) to produce two steles of still the same form. The smaller one (right in Fig. 16) supplies the bud, and the larger one is continuous with the petiolar strand. The change from stem-type to foliar-type symmetry in the trace is accomplished over a length of about 1 cm. The stele (left, Fig. 16) forms a pocket of parenchyma internally but toward the bud trace (Fig. 17) and at a slightly higher level those tracheids closing the island of parenchyma disappear (Fig. 18). Three protoxylem poles differentiate in the process, two becoming situated each near one of the two ends of the C-shaped trace and one, which is often indistinct, centrally located on the inside of the C.

HYBRIDS OF *T. DENTATUM* × *POLYSTROMATICUM*

Based on soral form and lamina structure, *Trichomanes polystromaticum* was not considered more closely related to *T. dentatum* v. d. Bosch than to other species of sect. *Selenodesmium*. But hybrids between the two species apparently exist.

More or less typical *T. dentatum* occurs from Fiji across Polynesia to Tahiti and on New Caledonia. It differs from *T. polystromaticum* in having a more delicate lamina which is but one cell thick, a greater number of cells between ultimate vein endings (Table 1), and an involucre considerably longer than wide with better developed, often somewhat flaring lips. In addition, *T. dentatum* has somewhat narrower pinnae and pinnules which overlap only slightly within the plane of the blade. The overlapping character is pronounced in *T. polystromaticum*, to the point where, although the blade is twice compounded, it forms a nearly complete shield (Figs. 1, 5).

Five specimens filed as *T. dentatum* in the U. S. National Herbarium suggested in some way *T. polystromaticum* (Table 1). All were collected in New Caledonia or the nearby New Hebrides. None bore the broad, short, and apically constricted involucre of *T. polystromaticum*. Four of the five collections had polystromaticous laminae. One (Buchholz 1209) exhibited epidermal wall thickenings on the adaxial surface only, a feature not previously reported for any *Trichomanes*. None exhibited the low number of cells between vein endings, a feature which adds appreciably to frond stiffness in *T. polystromaticum*.

An analysis of spore sizes and shapes proved to be more to the point. The spores were mounted directly in glycerine jelly without other treatment. From

slides so made, figures in *Table 1*, column F and G were derived. However, *Bierhorst Fx1* and *NC460* were liquid-preserved collections, and all others were dried. Another preparation of *Bierhorst Fx1* was made by first washing and drying the material. By comparison of the two types of preparations a correction factor of 1.065 was obtained. The average spore diameters of the dried collections were then multiplied by this factor to arrive at F_c in *Table 1*. If any of these measurements are to be compared to figures derived from preparations of spores which were dehydrated, cleared in xylene and mounted in resin, then they should be reduced by 16.7% to compensate for shrinkage by this treatment.

Of the five apparently aberrant collections, four produced some bilateral, diad spores which were often still attached in pairs, as well as normal, trilete, tetrad spores. The diameters of their tetrad spores were intermediate between those of *T. polystromaticum* and more or less typical *T. dentatum*.

The morphological and anatomical evidence allows one to suggest that the five aberrant collections are possible hybrids between *T. dentatum* and *T. polystromaticum*. The spore analysis results when superimposed (see Hickok & Klekowski, 1973) allows for a more positive conclusion of hybridization. The author is not prepared, however, to suggest which hybrids are F_1 and which are F_{1+n} , but he would speculate that there is backcrossing of F_1 hybrids to parental species and complete introgression. An extensive population study on New Caledonia should prove interesting.

Observations by the author on the gametophytes of *T. dentatum*, *T. obscurum*, and of another still unidentified species of sect. *Selenodesmium* allow the interpretation that physical opportunities for hybridization are particularly high. The filamentous gametophytes theoretically live forever, and they reproduce by gemmae in great abundance. Also, they appear sexually reproductive and not apogamous. The nature of the New Caledonian terrain is also pertinent. It appears to be a classic example of a highly dissected habitat resulting in a multitude of niches. This is reflected by especially high endemism and extremely limited specific ranges of ferns, conifers, and angiosperms.

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