

Studies in the Systematics of Filmy Ferns*
IV. Notes on the Species
with False Veinlets

By

Kunio IWATSUKI

Department of Botany, Faculty of Science, Kyoto University

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ABSTRACT The false veinlets found in the Hymenophyllaceae are described as consisting of one to several sclereids which are accompanied by stegmata covered with epidermis. In these morphological features, false veinlets are similar to true veins, differing only by the absence of a vascular bundle. Observations and discussion are made regarding various features indicative of the affinities of species and species groups having false veinlets. The marginal scales of *T. membranaceum* and the marginal hairs of *Didymoglossum* are compared and are interpreted as marginal emergences of the same nature. Morton's observation on the difference in venation between *Microgonium* and *Crepidomanes* is supported, and these two species can be better distinguished by removing *T. parvifolium* from *Microgonium* to *Crepidomanes*. The species of *Trichomanes* s. lat. bearing false veinlets are suggested to form three species groups, though the systematic positions of them are not elucidated pending further studies of *Trichomanes* s. lat. in general.

Trichomanes s. lat. is a heterogeneous assembly of species. From among these species, a number of genera, subgenera and sections have been established for definable groups, based on characters which include the occurrence of false veinlets, a feature found in some fifty species of filmy ferns belonging to *Trichomanes* s. lat. The species with false veinlets were placed by Copeland^{1,2)} in *Crepidomanes*, *Microgonium*, *Didymoglossum*, and *Lecanium*** , and by Morton³⁾ in *Trichomanes* subgen. *Trichomanes* sect. *Crepidomanes* and subgen. *Didymoglossum* sects. *Didymoglossum*, *Microgonium*, and *Lecanium*. Copeland suggested that *Crepidomanes* and *Microgonium* were close to each other and *Lecanium* was a near ally of *Didymoglossum*, though he

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** *Lecanium* is a name invalid at generic rank (Cf. Morton³⁾). It has been given the new name *Lecanolepis* Pic. Ser. *Webbia* 28 : 449. 1973.

separated these two pairs of genera among others having no false veinlets. On the other hand, Morton recognized a subgenus *Didymoglossum* with three sections, all having false veinlets, and separated *Crepidomanes* from these at the subgeneric level. The cytological evidence available at present is in accordance with the system of Morton (T. Walker⁴), Braithwaite^{5,6}). The occurrence of false veinlets is the only feature common to and unique in the four species groups in question.

In this article, the false veinlets are described in detail in an attempt to elucidate the systematic relationships among the species with this feature. Other features judged to be of systematic significance are also utilized.

False veinlets

The following observations are based on sections cut on a freezing microtome at a thickness of 25μ . Fresh materials were generally used, and when necessary dried materials were boiled a few minutes before sectioning. Bleaching of the fronds was done with bleaching powder.

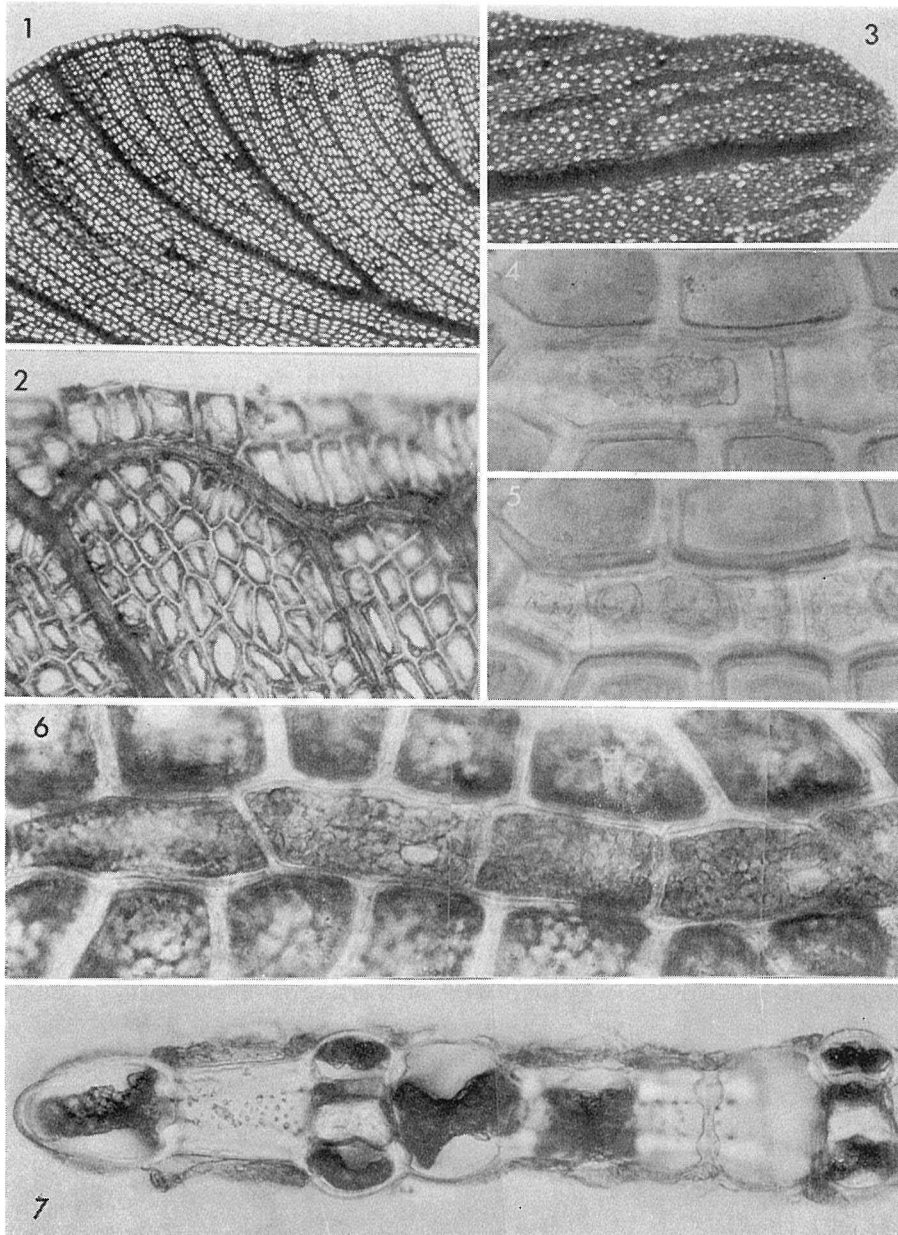
Morphology—The surface view of the false veinlets* is shown in Figs. 1-3 and 6 and reveals one or two rows of elongate cells. By making optical sections it is easily observed that the false veinlets are composed of more than one cell layer. Inner cells or sclereids are smaller than cover cells, usually one-third of the length of the latter (Figs. 4-5).

The fundamental construction of false veinlets was observed by Mettenius⁷) and by Giesenhagen⁸), and was appropriately drawn by Wessels Boer⁹), though few morphologists have studied this feature in spite of its importance as an indicative character in the groups treated here. Moreover, there can be no adequate comparison between true and false veinlets, except in the case where cross sections are comparatively illustrated. In cross view (Fig. 7), a false veinlet consists of one to several sclereids which are accompanied by stegmata** covered with epidermis. Except on veins and for some other portions in *T. membranaceum*, the laminae are unistratose without any differentiation of cells. In most cases, a false veinlet contains a single row of epidermal cells, but there are broader ones with two rows of epidermal cells.

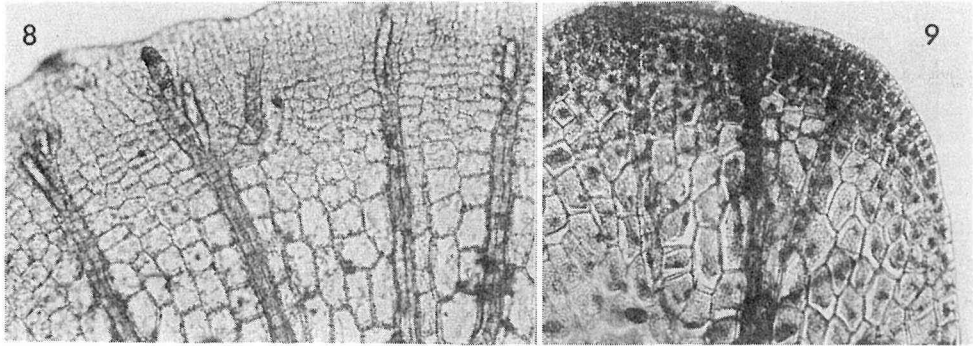
The frond of *T. tahitense* characteristically has continuous marginal growth. The false veinlets separate from the branches of true veins (Fig. 8) near the margin

* Copeland¹⁰) used the term 'false veinlets' for any strands not connected with the costa, whatever their composition, though Giesenhagen⁸) called any vein without vascular tissue 'false'. The term as used here is in accordance with the latter author.

** 'Stegmata' are the flat, tabular cells containing a mass of silica in contact with their inner wall (Cf. Wessels Boer⁹), p. 280).



Figs. 1-7 False veinlets. Figs. 1-3. Surface view of false veinlets; 1-2, *T. bimarginatum*, 1, $\times 16$, 2, $\times 300$, 3, *T. tosaе*, $\times 30$. Figs. 4-5. False veinlets of *T. tosaе*, cleared by bleaching powder, in different optical sections of the same material, $\times 800$. Fig. 6. Surface view of a false veinlet of *T. tosaе*, $\times 800$. Fig. 7. A cross view of an ultimate segment of *T. tosaе*, unistratose lamina with multilayered false veinlets, $\times 800$.



Figs. 8-9. Development of false veinlets in *T. tahitense* in: 8, margin of a leaf, $\times 200$, and 9, a first sporophytic leaf, $\times 200$.

of leaves, where actual connection may be observed. In the first several leaves of sporophyte development, the separation of false veinlets from the midrib is more easily recognizable (Fig. 9).

False and true veinlets—In *T. membranaceum*, the single species of *Lecanolepis*, the veins fork several times, having no vascular elements in some slender veins near the margin but only sclereids and stegmata. There are also false veinlets without any connection with true veins, and the construction of such false veinlets is similar to that of the veinlets having no vascular elements. In *T. bimarginatum*, a species of *Microgonium*, the midrib is a true vein which branches to bear several false veinlets of various thicknesses (Figs. 1, 2 and 10). There are also submarginal false veinlets, connecting the tips of the midrib and all its branches. *T. exiguum*, an Old World species of *Didymoglossum*, has no marginal veinlets, and the midrib branches to give off several simple or forked false veinlets (Fig. 11). In addition to the branches of the midrib, there are false veinlets having no actual connection with the midrib or its branches. In the species of *Crepidomanes*, the true veins form a pinnate pattern of branching, and there are many spurious veinlets arranged submarginally or obliquely (Figs. 3, 12), though no actual connection is observed between true veinlets and false ones. Illustrations given above concerning the four species each represent the species group in question, and the other species have fundamentally the same type of distribution of false veinlets as those species. Only in the species of *Crepidomanes* is there found no actual connection between true and false veinlets, even in the case of submarginal false veinlets.

Submarginal false veinlets—The submarginal false veinlets are not joined to the true veins in *T. (Crepidomanes) kurzii* even at the apices of young segments. At the apex of a young segment, a marginal row of cells is distinct and the submarginal false veinlet is situated just inside this row. The growing point of the veins is one

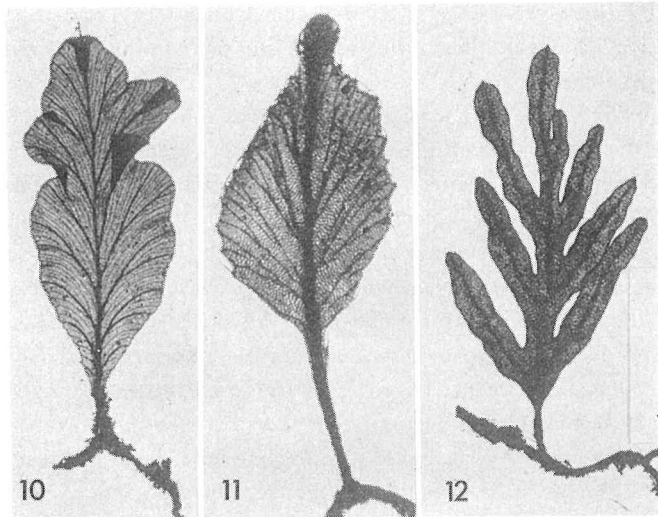


Fig. 10. *T. bimarginatum*, $\times 3$. Fig. 11. *T. exiguum*, $\times 8$. Fig. 12. *T. kurzii*, $\times 6$.

to three cells inside from the apical margin, and no connection is ever observed between submarginal false veinlets and veins. In contrast, the submarginal false veinlets have usually an actual connection with true veins in the species of *Microgonium* (as *T. bimarginatum* and *T. mindorensis*). In the marginal meristem in the young leaves of *T. bimarginatum*, submarginal false veinlets are inside of a row of marginal cells. The meristematic area is found still inside, the submarginal false veinlets maturing before the leaves.

No submarginal false veinlets were observed in any of the species referred to *Didymoglossum* and in *T. membranaceum*. In these species marginal emergences are peculiar, and these marginal 'scales' and 'setae' seem to be possible only if the marginal row of cells were active to produce them. In case they have a marginal row of predetermined cells outside the submarginal false veinlets, such marginal outgrowths could hardly be produced.

The submarginal false veinlets are a distinct specific character in some species of *Crepidomanes*. In *T. kurzii*, only one row of marginal cells are observed outside the false veinlets. In *T. latemarginale*, usually two rows of cells are seen outside of them, though it is not so rare to find only one row or even three rows of cells outside the false veinlets. In *T. bipunctatum*, the submarginal false veinlets are continuous, though there are depauperate leaves with occasional interruptions on the same rhizome as with the strictly continuous submarginal false veinlets. When interruption becomes more frequent, with additional oblique false veinlets, the leaves will be identified as *T. bilabiatum*. There are variations of interrupted submarginal false

veinlets, and it is hardly possible to draw a sharp boundary between *T. bilabiatum* and *T. latealatum* which is diagnosed as having no continuous submarginal false veinlets but only oblique ones.

Concluding remarks—Summarizing the above observations, it may safely be concluded that the false veinlets of these species are similar in construction to true veins, or in other words are veins without vascular bundles'. The false veinlets of some species of *Davallia* and *Angiopteris* are similar in appearance to true veinlets, though they resemble the margins of lobes in their histology (Iwatsuki & Kato¹¹⁾), and the spicular cells of *Vittaria* have no relation to veins and are sclerenchymatous cells placed in the epidermal tissue. The false veinlets of the filmy ferns are different from them in morphology. From these comparative observations, the false veinlets may be suggested to have been derived from true veinlets by the extinction of the vascular elements accompanying reduction in the total size of the plants in the course of their evolution to adapt to the moist gloomy habitat. This suggestion allows us to consider that the feature in question may have appeared in parallel along various phyletic courses.

Taxonomic features other than false veinlets

Besides the false veinlets, there are several characters of importance to diagnose the genera having false veinlets. A few observations will be added here concerning these features to elucidate the relationships among the species groups under consideration.

Roots and rhizoids—In most species now under consideration, roots are not present at least in the adult plants. In all the species of *Didymoglossum* and *Microgonium* examined, no roots were observed on any portion of rhizome. Giesenhagen⁸⁾ described for *T. membranaceum* a branching of the rhizome similar in appearance to roots and this observation was followed by later taxonomists including Copeland¹⁰⁾.

Roots are observed in mature plants in some species of *Crepidomanes* with large fronds. In most cases in *Microgonium* and *Didymoglossum* the fronds are simple to pinnatifid, usually adpressed to the substratum at least in their basal portion, bearing numerous rhizoids on stipe and rachis in addition to those on the rhizome. In *Crepidomanes*, on the contrary, the fronds are pinnate, larger, not adpressed to the substratum even in the basal portion, bearing no or few rhizoids on the fronds except for the base of the stipe. From these facts, it may be surmised that the roots of *Microgonium* and *Didymoglossum* have been lost in the course of their evolution to their present form, although the roots discussed here are in any case adventitious.

Pinnation—Most species of *Microgonium* and *Didymoglossum* have simple or pinnatifid fronds. The simplest form is a simple entire frond with a single midrib

or with a few lateral veins, either true or false. In some cases, the simple entire fronds are round-reniform in outline with no distinct midrib except in the basal portion. Even in such case, however, the pinnation of the main axis is not dichotomous, bearing lateral veins a few times dichotomously branched. In deeply pinatifid fronds, the main axis is distinct with a pinnately placed lateral axis in each lobe.

Among the species of *Microgonium*, the frond construction is unique in *T. tahitense*, previously known by the incorrect name *T. omphalodes*. This species has peltately attached simple fronds with a round and subentire outline. The whole frond margin is meristematic, and growth ends when the fronds become mature with sori at their edges. At the apex of a very short stalk at the place of peltate attachment, the main axis is divided radially, with each branch divided distally a few times in dichotomous fashion.

The larger fronds of *Crepidomanes* are pinnate in division ending in open dichotomy distally. There are several dwarf species of *Crepidomanes* having the frond seemingly digitate or only pinnatifid. Even in such cases, however, the axes are not simple but pinnately divided with additional spurious veins. The fronds are not adpressed to the substratum even in the basal portion, restricting the rhizoids to the rhizome and stipe bases.

T. parvifolium was included in *Microgonium* by Copeland¹⁰⁾ and followed by us¹²⁾ with a comment that this stood as an intermediate between *Crepidomanes* and *Microgonium*. In this species, the fronds are simple, bifurcate, trifurcate, or very rarely quadrifurcate. The branching is not dichotomous in the fronds with three or four lobes. The true veins are simple in each segment and no lateral branches of veins are found in any of the segments. False veinlets are oblique, having no actual connection to the veins. From these facts, I can not accept the suggestion of Copeland¹⁰⁾ that the species is merely a very small variant of *T. henzaianum*.

The venation is anadromous in the larger pinnate forms of *Crepidomanes*. Even in the dwarfed species of this genus, as in *T. rupicola*, *T. megistostomum*, *T. latemarginale*, and *T. kurzii*, the anterior branch of lateral veins is usually weaker than the posterior when the pinnae bear more than three segments. Contrary to this, the posterior branch is usually weaker in the species of *Microgonium* when the lateral veins are formed by more than three veinlets. This observation is not applicable to *T. membranaceum* and *T. tahitense* when no distinct midribs are formed in them, and to *T. craspedoneurum* and *T. beccarianum* when no lateral veins bear more than three veinlets.

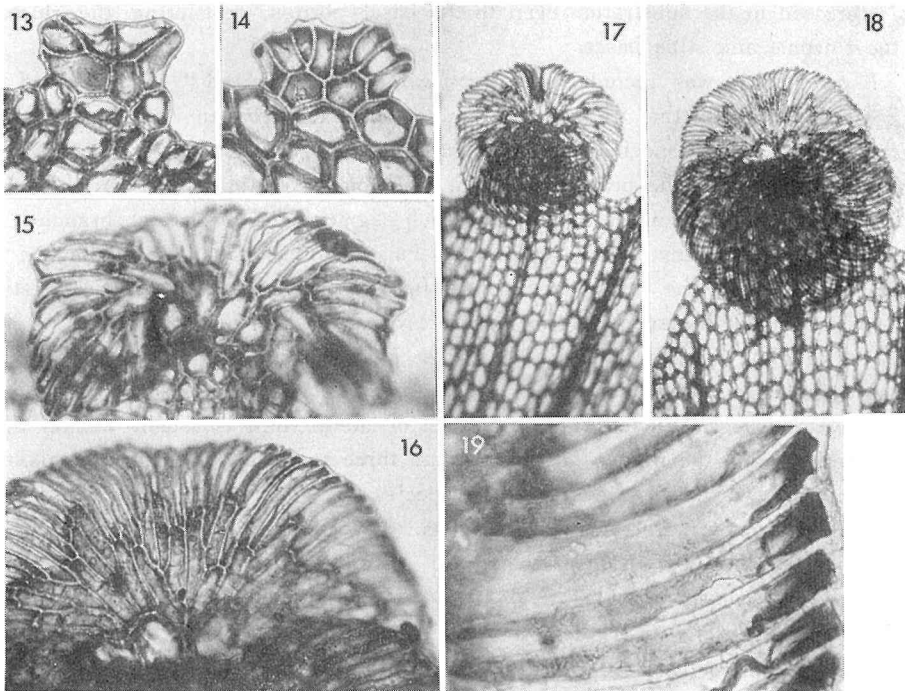
Laminar construction—Fronds of more than one layer of parenchyma were observed for *T. membranaceum* and *T. intramarginale*. Except for these two, the species now under consideration have generally unistratose laminae except in sori and veins, either true or false. Another exception is found at the base of fasciculate

setae in *Didymoglossum* where a few marginal cells are sometimes bistratose. There are no intercellular spaces developed even in the case of *T. membranaceum*.

Trichomes—The marginal 'scale' of *T. membranaceum* and marginal 'stellate' hairs of *Didymoglossum* are features characteristic of the respective taxa, and will be treated in separate paragraphs below.

Excluding the above features, no trichomes were observed for the species in question except for small bicellular glandular hairs on the veins underneath. These glandular hairs are small, 70–150 μ long, brownish, consisting of a small stalk cell and a larger cylindrical glandular cell.

Marginal scales of *T. membranaceum*. The presence of scales at the margin of the lamina of *T. membranaceum* is a unique feature among the filmy ferns, and was deemed by Copeland¹⁰⁾ a generic character. The morphology was observed in detail by K. Müller¹³⁾ with the conclusion that 'die Schuppe... ist... eine schneckenförmig gewundene Lamelle'. There are several descriptions and figures given afterwards, though my observations coincide most exactly with Müller's. Copeland¹⁰⁾ copied the



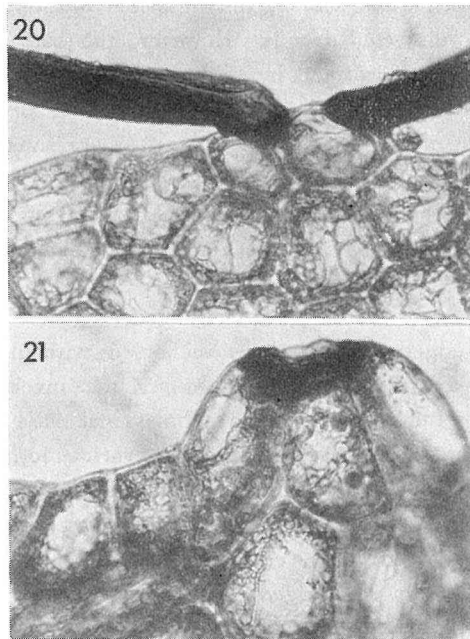
Figs. 13-18. Various developmental stages of marginal 'scales' of *T. membranaceum*, 13-16, $\times 200$, 17-18, $\times 80$. Fig. 19. Marginal row of cells in marginal 'scale' of *T. membranaceum*, $\times 800$.

description of the 'scales' by Maxon as 'a pair of concave cordate-orbicular sessile, opposed, membranous squamules, ...', although the marginal scales are actually spiral or snail-shaped as illustrated by Müller and Giesenhagen⁸⁾. The various developmental stages were figured by Müller in line drawings, and illustrated here by photographs (Figs. 13-17).

In very young developmental stages, the scales are placed at margin of laminae without any relationship with false veinlets. The bases of adult marginal scales, however, approach the apices of one to a few false veinlets. The adult marginal scales are composed of a few rows of longer cells at margins and of tetragonal cells near the center (Figs. 18-19). The marginal longer cells are thick-walled, with the walls tinted dark red to brown.

Marginal setae of *Didymoglossum*. *Didymoglossum* is distinguished from the other genera or sections having false veinlets by the presence of marginal setae. The other features cited by Wessels Boer⁹⁾ to distinguish *Didymoglossum* from *Microgonium* are not completely applicable to the Old World species.

The marginal setae in *Didymoglossum* are simple, geminate, or fasciculate with several unicellular arms (Fig. 20). The fasciculate setae are usually described as stellate, though there are no setae in *Didymoglossum* with a distinct stalk or with a



Figs. 20-21. Marginal 'setae' and their receptacles of *T. krausii*, $\times 800$.

basal cell in common. Each of the arms is thick-walled, dark brown to nearly black, acute at apex. Wessels Boer⁹⁾ observed that a simple seta may originate in a single marginal cell, and a geminate or 'stellate' hair in a cluster of marginal cells. The marginal cells are bistratose at bases of fasciculate setae (Fig. 21). In geminate setae, the two arms are either connected or separated at basal portion. In a separate form, the geminate setae may be composed of two simple setae placed together. If they have originated from a single cell, it would be difficult to have two arms separated from each other, for there is no sign of schizogenous separation found in these cells. In these respects, the fasciculate setae are morphologically similar to the marginal scales of *T. membranaceum*, which are long, falcate, thick-walled and often tinted red.

A similar type of seta is found in *Microtrichomanes* s. str. (Iwatsuki¹⁴⁾) and a few species of *Meringium* (Iwatsuki¹⁵⁾) among the filmy ferns, though the setae of these 'genera' are never geminate nor fasciculate. The stellate hairs of *Sphaerocionium* and the *T. palmatifidum* group are different from the 'stellate' setae of *Didymoglossum* in having stalks or a common basal cell.

Sorus—Morton³⁾ gave much importance to the paratactic position of sori in *Crepidomanes* to separate this from subgen. *Didymoglossum* including three sections with false veinlets. This feature is correlated with the pattern of venation, and *Crepidomanes* and *Didymoglossum* can be distinguished by this indicator at least for those with larger more dissected fronds. However, the sori of *T. membranaceum* and *Microgonium* are pantotactic, and it is difficult to interpret from which type this advanced feature has been derived. Some fronds of *Crepidomanes* bear sori pantotactically and most of the fronds of *Microgonium* are simple having pantotactic sori. It is difficult to separate *Crepidomanes* subgenerically by this feature alone, though it may be admissible to distinguish *Crepidomanes* from *Didymoglossum* by this feature in addition to some other characters such as in marginal setae, pinnation, connection between true and false veinlets, etc.

Wessels Boer⁹⁾ distinguished *Didymoglossum* and *Microgonium* by an involucre with two distinct dark-edged lips or wholly immersed without lips and not dark-edged. In many Old World species of *Microgonium*, the involucre is not wholly immersed, especially for the species without submarginal false veinlets. As to the construction of the mouth of the involucre, there are various forms observed according to the species: distinctly bilabiate to dilated and hardly bilabiate. The dark-edged lips of most species of *Didymoglossum* are peculiar and similar to the marginal 'scales' of *T. membranaceum* as to the coloration of the cells. None of the species of *Microgonium* has distinctly dark-edged lips, though some of *Didymoglossum* have the same construction of lips as *Microgonium*.

Comments on the relationships among species groups

As to the four 'genera' now under consideration, there are theoretically six combinations of two genera. Among them, three combinations may be excluded from the discussion: *Lecanolepis* has nothing comparable to *Crepidomanes* and *Microgonium*, and there is no sign of close affinity between *Didymoglossum* and *Crepidomanes*. The other three combinations will be briefly treated here.

1) *Didymoglossum* and *Lecanolepis*

Both Copeland and Morton recognized the close alliance of these two. Copeland¹⁰⁾ summarized the unique features of *Lecanolepis*, enumerating the plural cell layers of parenchyma, absence of roots substituted by metamorphosed shoots, and presence of marginal scales which were inaccurately described by Copeland¹⁰⁾ and Morton³⁾.

The marginal 'scales' of *T. membranaceum* and the marginal setae of *Didymoglossum* were suggested to be marginal emergences of lamina in the foregoing pages. If this speculation be correct, there is no important difference between the above two, for roots are also absent from the adult plants of *Didymoglossum* and plural cell layers of parenchyma are observed in the Hymenophyllaceae in various species groups. All of them grow in moist gloomy places in dense forests, usually epiphytic or on moss-covered rocks. Since the fronds expand considerably as compared with their tracheal elements, the marginal 'scales' and 'setae' seem to function to hold water or humidity. The thin and tender laminae seem to be less resistant to shortness of water supply.

2) *Didymoglossum* and *Microgonium*

Copeland and Morton differ as to the alliance of the above two. I can not understand the basis of Copeland's opinion from his imperfect key (Copeland^{2,10)}), and the statement that *Microgonium* is 'evidently derived, by reduction, from *Crepidomanes*'. Morton³⁾ adopted the conception of Wessels Boer⁹⁾ as to the treatment of *Microgonium* and *Didymoglossum*. Three characters were taken up by Wessels Boer in his key to distinguish them, i. e. the marginal hairs, submarginal false vein, and dark-edged lips of involucre. The last named feature is characteristic of most species of *Didymoglossum*, but is not observed for 3 (among 15 in all) New World species. Morton³⁾ did not utilize this feature in his key, probably for this reason. Submarginal false veinlets were here noted in all four New World species of *Microgonium* but in only about a half of the Old World species of *Microgonium* and *Crepidomanes*. It is impossible to distinguish *Microgonium* and *Didymoglossum* by this feature, though the species of *Didymoglossum* with marginal setae can hardly have submarginal false veinlets as noted above.

The difference between *Didymoglossum* and *Microgonium* may be summarized as the presence or absence of marginal setae. The species with submarginal false veinlets are not able to give off the marginal setae. However, there is doubt that any species of *Microgonium* were derived by loss of marginal setae.

3) *Microgonium* and *Crepidomanes*

Copeland considered *Microgonium* a dwarfed derivative of *Crepidomanes* but Morton separated them at subgeneric rank in his classification. The feature on which Morton distinguished them is the difference in pinnation and venation. As far as the venation is concerned, as noted in the section of laminar construction, the observation by Morton is acceptable if we consider *T. parvifolium* to be an extremely reduced species of *Crepidomanes*.

According to cytological observations, all the species of *Crepidomanes* observed have a chromosome number of $n=36$ or its multiples. In contrast to this, the species belonging to *Didymoglossum*, *Microgonium*, and *Lecanolepis* are represented by the figure $n=34$ or its multiples. Braithwaite^{5,6)} noted that the difference is not only in the numbers but also in the size of the chromosomes.

From the facts given above, we can not accept the view of Copeland in its entirety, though it is not quite satisfactory to treat *Microgonium* as a close ally of *Didymoglossum*, especially when the peltate construction of fronds in *T. tahitense* and the presence of submarginal false veinlets in *T. bimarginatum* and *T. craspedoneurum* are taken into account.

4) Comments on *T. pyxidiferum* and *T. latifrons*

T. pyxidiferum was referred to *Crepidomanes* by Morton³⁾ somewhat doubtfully. It is similar to some species of *Crepidomanes* in general appearance, but differs in having no trace of false veinlets and in the soral morphology: the involucre of this species is cup-shaped, with subtruncate mouth, hardly dilated nor bilabiate, with long-exserted receptacles. *T. pyxidiferum* is a species fairly variable in various features, although the soral morphology is distinct from that of *Crepidomanes* even if the variation in this feature is taken into account. By these two characteristic features, it may be safely concluded that *T. pyxidiferum* belongs 'Vandenboschia' or *Trichomanes* sect. *Lacosteopsis* but not to *Crepidomanes*.

T. latifrons is an Old World species often compared with the New World *T. pyxidiferum*. Copeland¹⁾ suggested the affinity of this species was with *T. pallidum* (*Pleuromanes*), but Ching¹⁶⁾ referred this to *Crepidomanes* without any special mention of the indicative features. Morton³⁾ supported Copeland's treatise of 1933, referring this to *Trichomanes* sect. *Lacosteopsis*. *T. latifrons* is distinct in having no trace of false veinlets and a cup-shaped involucre with subtruncate mouth. There is no special reason to regard this as close to *T. pallidum*, and *T. latifrons* may safely be referred to 'Vandenboschia' or *Trichomanes* sect. *Lacosteopsis*, probably next to *T.*

pyxidiferum.

Excluding *T. pyxidiferum* and *T. latifrons* from *Crepidomanes*, there is no species without false veinlets remaining in the four 'genera' defined by having false veinlets. The origin of these species groups, whether they are monophyletic or not, cannot be elucidated at present, except that there are three distinct groups. The correct status of these three groups, (1) *Didymoglossum* including *T. membranaceum*, (2) *Microgonium*, and (3) *Crepidomanes*, can be clarified when the other 'genera' of *Trichomanes* s. lat. are studied further.

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