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THE GENERA, SUBGENERA, AND SECTIONS OF THE HYMENOPHYLLACEAE

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ERRATA

Page 182, line 21: delete "T. cellulosum Kl."

Page 1%, line 16: read "...includes only the three species <u>T</u>. <u>arbuscula</u> Desv., <u>T</u>. <u>bicorne</u> Hook., and <u>T</u>. <u>cellulosum</u> Kl...."

Page 211: under "T. cellulosum," delete 182, add 196.

THE GENERA, SUBGENERA, AND SECTIONS OF THE HYMENOPHYLLACEAE

C. V. MORTON

Pteridologists have been attracted to the filmy-fern family Hymenophyllaceae for many years because of the variety and beauty of its species and its peculiar morphological structure. Presl, van den Bosch, Mettenius, Prantl, and Giesenhagen were all interested in the group and each contributed many important observations. Most of these workers recognized two large traditional genera, Trichomanes L. and Hymenophyllum J. E. Smith, although Presl and Prantl did segregate some additional genera, in Presl's case sometimes by faulty observations. The oriental species were revised some 30 years ago by the late E. B. Copeland; no real monograph has ever been produced, although one is needed since these are among the commonest plants of the tropical forests at middle elevations in both the Old and the New Worlds.

Christensen in the "Index Filicum" gave two classifications of Trichomanes that are contradictory in part. On page 634 of the Index (issued July 2, 1906) he named seven subgenera and arranged the species by means of symbols, following Prantl's classification. In the introductory pages of the Index (pp. XIV, XV, after Sept. 15, 1906) he gave a different and better classification, which has, however, been less known. Here he recognized eight subgenera with many sections, almost all with a lectotype indicated, although this was wrongly chosen in some instances according to our present International Code of Botanical Nomenclature.

The late E. B. Copeland published in 1933 a revision of the Old World species of Trichomanes 1 and a similar treatment of the Old World Hymenophyllum in 1937,2 both beautifully illustrated with line drawings. In Trichomanes he recognized a number of groups called Pyxidifera, Scandentia, Grandia, Apiifolia, Rigida, etc., but these cannot be considered as validly published names, since "group" is not a recognized taxonomic category. In Hymenophyllum, however, he

¹ Phil. Journ. Sci. 51: 119–280, pls. 1–61.

² Op. cit. 64: 1-188, pls. 1-89.

recognized a number of groups definitely called subgenera. In 1938, Copeland in his "Genera Hymenophyllacearum" raised most of the previously recognized groups and subgenera to generic rank, a total of 33 genera being recognized. A few years later, I published a review critical of this work and questioned the necessity of recognizing so many genera, some of which were separated by characters hardly more than specific it would seem, such as "fronds harsh in texture" opposed to "fronds soft in texture," or "fronds once-pinnate" opposed to "fronds more divided," or "margin naked" opposed to "margin hairy," and so forth. Essentially the same treatment of the family was presented by Copeland in his "Genera Filicum" (1947), but during continued work in the last 25 years I have seen no reason for changing my previous opinion.

Due to the prestige of Copeland, his system has been accepted by many workers without a truly critical examination of the basis of this system; however, the most eminent students, such as Christensen, Alston, Madame Tardieu-Blot, E.A.C.L.E. Schelpe, W. A. Sledge, R. M. Tryon, and R. E. Holttum have not accepted it. Copeland's defense of his system is that the traditional character of distinction, a 2-valved, only partly immersed involucre in Hymenophyllum and a tubular, almost wholly immersed involucre in Trichomanes, is a variable and unreliable character. Nevertheless, he uses only this character of "involucre valvate" as opposed to "involucre tubular or obconic" to separate his groups of genera in the keys both in the "Genera Hymenophyllacearum" and the "Genera Filicum" without seeming to realize that he is contradicting himself. If a multitude of genera can be separated by this character then the two traditional ones can be also. As a matter of fact, about 98 percent of the species fall easily into one group or the other without difficulty. The presence of a few species that are somewhat equivocal in this character need not invalidate the genuine unity of the traditional genera Trichomanes and Hymenophyllum, which are not separated solely by this character, as Copeland would seem to imply. There are other differences, as one would expect between good genera, and a fern specialist with some experience with the family can almost always place sterile specimens in one genus or the other correctly and without difficulty. The differences are a little subtle perhaps. Hymenophyllum usually has a more elastic frond, which often curls up on the sheet when dried; the fronds are usually a red-brown when dry, whereas those of Trichomanes are more usually persistently green. Hymenophyllum is always epiphytic or rupicolous, whereas Trichomanes is not infrequently terrestrial. The rhizones of Hymenophyllum are always widely creeping and the

³ Op. cit. 67: 1-110, pls. 1-11.

⁴ Amer. Fern Journ. 32: 30, 31. 1942.

fronds scattered, and they are always relatively slender and with pale rhizome hairs. Trichomanes often has thicker rhizomes, and in some groups these are contracted so that the fronds are clustered; they often have dark, blackish rhizome hairs. The stipes, too, tend to be thicker. The fronds of Hymenophyllum are usually more divided and simple blades do not occur, except in the aberrant H. marginatum. The cells of the fronds of Trichomanes often are larger and coarser, with thicker walls, these sometimes pitted. A number of species of Trichomanes are characterized also by the presence of false veins, which do not occur in Hymenophyllum. The segment margins are sometimes toothed in Hymenophyllum, never in Trichomanes. Stalked, stellate hairs occur in many Hymenophyllum (although there are many glabrous species also), and such hairs are perhaps not found in Trichomanes, although a few species do have sessile, stellate hairs. The venation pattern in Hymenophyllum is always anadromous and the soriation "paratact" (see p. 158), as Prantl termed it, but in Trichomanes many species are catadromous and "epitact," a character that seems to me to be fundamental but which Copeland essentially ignored. As pointed out by Bower, Stokey, and others, important gametophytic differences also occur between the two genera, although relatively few species have been investigated in this regard. Trichomanes and Hymenophyllum seem to differ in a great many more characters than merely the form of the involucre, important as that is. Therefore, it seems right that the traditional division into two major genera be maintained, and that the convenience of the general botanist and taxonomist will be better served by this treatment. It is clear that by the characters noted above the general botanist can recognize the traditional genera rather readily, but that only a specialist could recognize and remember the 33 genera of Copeland.

A word as to Copeland's general philosophy may well point up our basic difference in views. Although he would have vigorously disclaimed it, Copeland was an old-fashioned botanist in his general ideas, having been brought up under the influence of L. M. Underwood and N. L. Britton in the "New York" school of taxonomy back at the turn of the century. In general, he kept to the ideas of this school of thought that a plant was either a good species or it was nothing at all, a mere synonym. In his later years, at least, he never recognized any subspecies or varieties (cf. his treatments of the ferns of New Guinea, the "Fern Flora of the Philippines" and his "monographs" of Grammitis and Ctenopteris). Similarly, his larger groups were either full-fledged genera or else synonyms, with never or seldom any subgenera, sections, or subsections; instead all the species were massed together with no grouping. Similarly at the family level, Copeland split up the traditional Polypodiaceae into a number of

families, but he never recognized any subfamilies, tribes, or subtribes within them. There was no classification of the genera. He was thus essentially destroying the classification that had been carefully built up by Diels, Christensen, and previous workers. It was a flattening and leveling out process whereby only essentially three categories, family, genus, and species, were recognized. With such a philosophy it is understandable that he would find smaller families and smaller genera more "convenient."

However, this is not the traditional conception that has come down to us from the botanical masters of the past, who recognized that there are such things as subfamilies and tribes, that subgenera and sections do exist, and that species are not uniform but are divisible into subspecies and varieties. It is true that one can go to an extreme in subdividing ad infinitum, as was the case with some of the workers of the Englerian school, but this is preferable to an absence of classification, provided of course that the subdivisions are reasonably homogeneous and natural, as they are apt to be if subdivided finely enough. A middle course is certainly preferable. Just how much segregation into named groups is desirable depends largely on the size and variability of the group concerned. In the case of the Polypodiaceae, no one has shown that it is necessary to recognize a large number of segregate families (or even a smaller number), when the recognition of these groups as subfamilies is equally convenient. The only justification would be on theoretical grounds that these "families" had a different origin, i.e., that the family Polypodiaceae sens. lat. is polyphyletic. This has been claimed but not proved and is logically unlikely considering the relative uniformity of the Polypodiaceae sens. lat. in fundamental characters. Certain subfamilies like Adiantoideae show some similarities to the more primitive family Schizaeaceae, for instance, but in their sporangia, annulus, stomium, spores, embryos, gametophytes, and sex organs the Adiantoideae are similar to the Dryopteridoideae, Asplenioideae, and other subfamilies of Polypodiaceae, and a great gap exists between all of these and the Schizaeaceae. If there are relationships with the Schizaeaceae it would be with the whole family Polypodiaceae and not just with the subfamily Adiantoideae.

The situation is quite different in the Hymenophyllaceae, a very natural group and an obvious family it would seem; however, an extreme splitter like G. Kunkel instead of minimizing the differences between *Trichomanes* and *Hymenophyllum* has overvalued them and proposed to separate them into two different families, the Hymenophyllaceae and Trichomanaeaceae, without having brought out any

⁵ Repert. Sp. Nov. Fedde 70: 155. 1965.

new characters of family importance, or indeed without an adequate discussion of the existing characters. Several workers have divided the family into subfamilies, one for each of the traditional genera, but this too seems unnecessary, for the fineness of subdivision should depend on the size of the groups concerned. In their inclusive sense, both Hymenophyllum and Trichomanes are large enough genera that a classification of the species is surely needed, and therefore a division into several subgenera, some of them with several sections, seems to

be a logical and usable procedure.

The system set forth below is not in any sense original. It has not been expressed in exactly this way before but is adapted from the work of my predecessors. I have tried to pick out the best ideas of Presl, van den Bosch, Prantl, Christensen, and Copeland, and to unite them into a system. It is based in part on general knowledge of the family, acquired over about 38 years of study, but not on a really intensive study of all the species, as it ideally should. A number of species are almost unknown to me, and these are some of the most critical ones so far as their placing in the system is concerned. For this reason I leave some groups in an uncertain position, pending further study, by me or others. No doubt their relationships can be determined definitely when proper material is available and is studied completely. Unfortunately, some of these critical species are extremely rare and hard to come by in good condition.

The trickiest and in a sense one of the most difficult problems has been to typify properly the various names that have been proposed. Our present Code rightly requires that names be typified, or otherwise their application is indefinite and subject to change. Types were suggested for many names by Christensen in the preliminary pages of the "Index Filicum" (after Sept. 15, 1906) and by Copeland, but the choices have not always been in accord with the current rules set down in the Code. In particular, Christensen often designated as type a species that was not one of the original species of the genus, but which he thought, rightly or wrongly, to be a taxonomic synonym. Copeland's chief idea in choosing a type was to take the first species cited, but this arbitrary system is not only unacceptable but is specifically condemned in the Code, which indicates that all the species cited must be taken into account, and in particular that the designation of a lectotype by a previous author must stand unless it can be shown that is does not agree with the original description or was selected by some sort of erroneous conception. However, this study of typification has shown that almost all the groups I accept already have available acceptable names.

It might be thought that chromosome numbers would give some useful information as to the proper subgeneric and sectional distri-

bution, and it is likely that they will ultimately. However, only relatively few species have been counted and hundreds of additional counts of properly identified material will have to be taken before any definite statements can be made. At the present time the information is extremely indecisive and inconclusive. The Hymenophyllaceae have relatively low chromosome numbers, compared to the ferns in general, and so it would appear that counts would be made more easily, but this does not seem to be the case. It appears that several basic numbers are in the family (x=7, 9, 11, 13, or 17), but different basic numbers appear in closely allied species that obviously belong in the same section, the group known as "Meringium" having basic numbers of 7, 11, 13, and 21 reported. Indeed within the typical and small section Hymenophyllum itself there is no agreement: The type species of the genus H. tunbridgense is reported by Manton as n=13; Brownlie reported that H. peltatum has n=11, and yet Manton reported n=18 in H. unilaterale, which is not only close to H. peltatum but is generally regarded and probably correctly as a complete synonym. It is likely that the species counted by Manton was really H. wilsonii Hook., generally considered another synonym of H. peltatum, and may not differ other than in chromosome count. In all events they are closely allied and belong in the same section. So far as known, the species of Copeland's groups "Mecodium" and "Sphaerocionium" are more uniform, often having n=36, which is assumed to be from a base of x=9.

The genus Trichomanes gives an indication of different base numbers from Hymenophyllum, although x=9 does occur too. Trevor Walker has given a most interesting and valuable summary 6 of the results of his counts of 19 Jamaican species, which seems to show that base numbers of x=7 and x=8 are operative, although x=11 and x=17 also occur. It appears from the data available that subg. Didymoglossum is uniform with n=34 or 68 (presumably x=17), subg. Achomanes often at least has n=32 or 64 (presumably x=8), and subg. Trichomanes (as I recognize it) at least in part as x=9 (although other numbers such as x=17 also occur). The study of chromosome numbers in the future will be fascinating and will certainly shed new light on relationships and appropriate taxonomic groupings. However, some of the reported counts should be regarded with great discretion, for the numerous discrepancies may indicate errors in counting or errors in identification, or both.

A word should be said about the key characters used as primary ones. The terms "paratactic" or "paratact" and "epitactic" or "epitact" were invented by Prantl ⁷ to describe the positioning of the sori in

⁶ Trans. Roy. Soc. Edinburgh 66: 169-237, pls. 1-5. 1966.

⁷ Untersuch. Morph. Gefässkrypt. 1: 3-14. 1875.

the Hymenophyllaceae, and this positioning is correlated with the venation type. In anadromous venation, the first vein of a primary pinna or the first veinlet of a secondary pinnule points toward the apex of the blade or the pinna, respectively. The sorus is borne on the tip of a proximal veinlet, so that a distal vein or veinlet is free to continue growth and branch further; in other words there is at least the possibility of indeterminate growth. This is the paratactic type. Catadromous venation, in which the first vein faces downward, toward the base of the frond is accompanied by sori that terminate distal veins or veinlets. A proximal veinlet may or may not also be terminated by a sorus. The result is that such fronds with epitactic soriation are determinate, both in the growth of the fronds themselves and the individual pinnae, at least theoretically. After a pinna or a frond apex becomes fertile no more growth is possible since the distal veins that could have continued growth have been stopped by the production of a sorus. Of course, some fronds do continue to grow at the apex because they have not become fertile, and so this character is best shown by the lateral pinnae, and especially by the positioning of the sorus on a distal branch of a veinlet rather than a proximal. Although Copeland knew of this character from Prantl's exposition, he minimized its importance and did not truly employ it in his classification. It is probably a fundamental character, although sometimes it may be difficult to interpret, especially in plants where the fronds have become very dwarfed or even simple (as in some species of subg. Didymoglossum), when the character of catadromous venation can hardly be made out, for this is a character, like rhachis structure, that always is more determinable in compound fronds. Occasionally, especially in simple-bladed types like Hymenoglossum and Cardiomanes, all the veinlets may be fertile, a type of soriation called "pantotactic" by Prantl, an advanced type obviously correlated with simplicity.

The lists of species belonging to the various sections given in this paper do not represent in many cases my own personal study. I do know many of the American species, but the Old World ones are largely placed following the list given by Copeland in his "Genera Hymenophyllacearum." This list is in turn partly the result of Copeland's own studies and partly taken from Christensen's "Index Filicum." And so, although most species will be properly placed, some errors may need to be corrected by future studies. There are many more names than are mentioned here. Most of these are synonyms, the disposition of which can be found from the "Index Filicum" and from Copeland's papers. Some others have not been studied and

are of doubtful disposition at present.

Key to the Genera of Hymenophyllaceae

Involucre bivalved throughout or at least to the middle, the immersed part, if any, cuplike or conic and not tubular; fronds usually brown or red when dried, glabrous or often hairy, generally elastic, the margins entire or toothed; rhizomes always epiphytic or rupicolous, long-creeping with scattered fronds, usually slender, with pale rhizoids; cells of blade often small, with smooth walls, but not always; false veins absent; venation anadromous; sori paratactic or pantotactic; receptacle typically included or only slightly exserted from involucre, typically sporangiiferous toward apex only.

Fronds not simple, large, long-stipitate, or subentire.

Fronds minute and mosslike, simply pinnate with entire, leaflike pinnae, the stipe bearing rhizoids and scarcely distinguishable from the rhizomes, the axis red-pilose. Antarctic South America II. Serpyllopsis

Fronds otherwise, the stipe not bearing rhizoids.

Ultimate segments without plural veins, always with a single vein, this not black (or in *H. heimii* the blade simply pinnatilobate).

IV. Hymenophyllum

Involucre tubular or conic throughout with a truncate apex, or with two lips less than half as long as the tube; fronds often green, mostly glabrous but sometimes hairy, but then usually without stellate hairs, generally not especially elastic, the margins entire; rhizomes terrestrial or epiphytic, often thicker than in Hymenophyllum, widely creeping or contracted or even erect, with scattered or approximate fronds; cells of blade often large, and sometimes with thickened walls; false veins in the position of veins or marginal false veins sometimes present; venation anadromous or catadromous; sori paratactic or epitactic, or rarely pantotactic; receptacle typically exserted, typically sporangiiferous to the base but not to the apex.

Fronds simple, reniform, large, long-stipitate, ca. 4 cells thick. New Zealand.

Fronds not simple, reniform and long-stipitate VI. Trichomanes

I. Hymenoglossum

Hymenoglossum Presl, Hymen. 35. 1843.

Hymenophyllum sect. Hymenoglossum (Presl) Moore, Ind. Fil. cxii. 1857. Type: Hymenophyllum cruentum Cav.=Hymenoglossum cruentum (Cav.) Presl.

Although in general characters this genus is not particularly different from Hymenophyllum, it is so peculiar and isolated that its affinities really are not known and it can rank as a monotypic genus. The 2-rowed, differentiated band of black marginal cells are unlike any other marginal cells in Hymenophyllum, although they may be somewhat comparable to those of Hymenophyllum subg. Craspedophyllum, in which the marginal cells are dark and thickened, but differently placed

and in only one row. This species appears to be quite common in certain parts of the western slopes of the Andes in Chile, but appears not to have been able to cross the Andes into the comparable region of Argentina on the eastern slopes.

II. Serpyllopsis

Serpyllopsis v. d. Bosch, Versl. Meded. Konink. Akad. Wetens. Afd. Natuurk. 11: 318. 1861.

Hymenophyllum subg. Cycloglossum Presl, Hymen. 32. 1843. Lectotype: There were six original species: H. caespitosum Gaud., H. cumingii Presl, H. semibivalve Hook. & Grev., H. decurrens (Jacq.) Swartz, H. kohautianum Presl, and H. schomburgkii Presl (ined.). Christensen bindicated the type as H. decurrens (Jacq.) Swartz, but inasmuch as this species has never been identified and presumably was as unknown to Presl as it has been to others, it is not a suitable choice of lectotype. Copeland indicated the type as H. caespitosum Gaud., probably on the basis that this was the first species listed by Presl, and this must be accepted as a choice of lectotype. It is in fact a desirable lectotype, for if another lectotype were to be chosen subg. Cycloglossum would have priority over and would have to replace subg. Mecodium, which is now a fairly well-known name due to Copeland's use. Trichomanes subg. Serpyllopsis (v.d. Bosch) Christ, Farnkr. Erde 23. 1897. Hymenophyllum subg. Euhymenophyllum sect. Cycloglossum (Presl) C. Chr. Ind. Fil. XV. 1906.

Type: Trichomanes caespitosum Gaud. = Serpyllopsis caespitosa (Gaud.) C. Chr.

This small, monotypic Antarctic genus is of uncertain relationship, showing characters of both *Hymenophyllum* and *Trichomanes*. In its general appearance it suggests a bryophyte rather than a member of the Hymenophyllaceae, although it is certainly of the family.

III. Rosenstockia

Rosenstockia Copel. Gen. Fil. 36. 1947.

Type: Hymenophyllum rolandi-principis Rosenst.=Rosenstockia rolandi-principis (Rosenst.) Copel.

This is one of the most peculiar and distinctive of all fern genera, and probably one of the rarest, known only from about three collections from New Caledonia. The structure of the dark, coarse veins has not been investigated anatomically, but it may very well be quite different from the normal vein structure of the Hymenophyllaceae. The alliance, by reason of the involucres, is surely with Hymenophyllum. The structurally somewhat similar group in Trichomanes with large segments with plural veins (subg. Phlebiophyllum) is less distinctive and more typical of its genus in other characters.

⁸ Ind. Fil. XV. 1906.

⁹ Phil. Journ. Sci. 67: 14. 1938.

IV. Hymenophyllum

Hymenophyllum is a large, common genus in the tropics of both hemispheres, and it is well known and usually recognized by the general botanist. It really is quite uniform and its segregation into small genera is not only inconvenient but unnecessary, since all the species are closely related. Several writers have remarked that Copeland's segregates from Hymenophyllum are less distinct than those from Trichomanes, as by Miss Tindale in her recent fine treatment of the species of New South Wales,10 where most of the segregates are kept within Hymenophyllum as subgenera but those from Trichomanes recognized as genera. This is possible and somewhat a matter of opinion. However, the easier recognizability of some of the segregates from Trichomanes (but not all, by any means) does not require that they be recognized as genera rather than subgenera. Trichomanes is the larger genus and has varied more, for instance by sometimes assuming a terrestrial habitat, which necessitates a change in the rhizomes and in frond disposition. In its general structure and especially in its involucres Trichomanes is rather uniform and readily separated from Hymenophyllum, with the exception of a few aberrant species. There is no reason to suspect a polyphyletic origin and thus no theoretical or practical need to recognize a large number of segregate genera. Convenience in identification work, in anatomical and cytological study, and in herbarium arrangement is equally well served by recognizing a suitable number of subgenera and sections.

Key to Hymenophyllum

Margins of the segments toothed, the teeth not tipped by hairs or if rarely so, the hairs several cells long; involucre often somewhat conic at base.

Margins of the segments entire, or if rarely apparently slightly denticulate, the teeth tipped by one-celled or stellate hairs; receptacle typically included within the involucre, but sometimes exserted, the involucre rounded, cuplike, or conic at base.

Blades variously hairy, at least on the margins or veins beneath.

Subg. 2. Sphaerocionium

Blades glabrous.

Blades with a conspicuous row of black, differentiated marginal cells, simple or forked, one-veined. Australia, Tasmania, and New Zealand.

Blades without a black margin or differentiated cells, pinnatifid to decompound.

Involucres immersed and urceolate and cuplike at base. Australia.

¹⁰ Contr. New South Wales Nat. Herb., Flora Ser. 201: 1-49, pls. 1-7. 1963.

Subg. 1. Hymenophyllum

Lamina with normal laminal surface, sometimes with accessory teeth. Sori directed in a plane more or less perpendicular to the plane of the lamina, arched at the base and somewhat pedunculate; receptacle clavate, almost covered with sporangia to the base, only slightly exserted. Sect. 1. Hymenophyllum Sori directed in the plane of the lamina, not arched at the base or pedunculate; receptacle cylindrical to globose, generally without sporangia at the base, often exserted. Teeth or wings present in planes perpendicular to the blade; receptacle globose to clavate. Peru and Ecuador Sect. 2. Buesia Teeth or wings absent in planes perpendicular to the blade; receptacle clavate to linear. Pinnae symmetrical, more or less equally developed on both sides; receptacle cylindric, thickened at base, exserted. . Sect. 3. Ptychophyllum Pinnae asymmetrical, with segments developed mostly or entirely on the acroscopic side; receptacle filiform, somewhat slender at the base, thickened at the middle, included. South America. Sect. 4. Eupectinum Lamina reduced mostly to discrete teeth spreading in various planes. New Guinea. Sect. 5. Myriodon Subg. 2. Sphaerocionium Blades essentially reduced to filiform processes bearing stellate marginal hairs. Blades with normal laminar surfaces Sect. 6. Sphaerocionium Blades with hairs borne only on the margins and veins (sometimes only on the veins beneath)............ Subsect. Ciliata Blades with the hairs borne on the leaf-surfaces as well as on the margins and veins. Veins with accessory wings not in the plane of the fronds. West Indies; Central and South America Subsect. Plumosa Veins lacking accessory wings not in the plane of the frond. Hairs, or at least some of them, stellate and stalked . . Subsect. Hirsuta Hairs all simple or basally paired. Southern South America. Subsect. Leptocionium Subg. 3. Craspedophyllum A single section. Australia, Tasmania, and New Zealand. Sect. 8. Craspedophyllum Subg. 4. Hemicyatheon A single section. Australia Sect. 9. Hemicyatheon

Subg. 5. Mecodium

Blades one cell thick throughout (except the veins) . . . Sect. 10. Mecodium Veins without accessory wings not in the plane of the lamina. Subsect. Mecodium

Veins with accessory wings not in the plane of the lamina. Java and New Guinea. Subsect. Amphipterum

Blades 2- or 3-celled thick at least in part. Australia and New Zealand.

Subsect. Diplophyllum

Subg. 1. Hymenophyllum

Hymenophyllum sect. 1. Hymenophyllum

Hymenophyllum J. E. Smith, Mem. Acad. Turin 5: 418. 1793. Lectotype: Hymenophyllum tunbridgense (L.) J. E. Smith, selected by Presl, Hymen. 31. 1843. Copeland in his revision of Hymenophyllum 11 indicated that H. tunbridgense was the type because it was the sole original species, which is not true; there were nine original species, of which Trichomanes tunbridgense L., the first named, was the logical choice for a type, since it was the oldest and best known.

Ptychomanes Hedwig, Fil. Gen. & Sp. in nota sub Trichomanes asplenioides. 1800. An illegitimate change of name of Hymenophyllum J. E. Smith on etymological grounds; it has therefore the same type species, Trichomanes tunbridgense L.

Hymenophyllum subg. Euhymenophyllum Presl, Hymen. 31. 1843.

Hymenophyllum subg. Sphaerodium Presl, Hymen. 31. 1843. Lectotype: Hymenophyllum wilsonii Hook., selected by Copeland, Phil. Journ. Sci. 67: 14. 1938. In the "Index Filicum" (p. XVI) the type is erroneously indicated as H. tunbridgense L., which was not one of the original species of this subgenus, and which in fact Presl was trying to distinguish from Euhymenophyllum, as typified by H. tunbridgense, but on what grounds is not entirely clear.

Hymenophyllum subg. Leptocionium sect. Sphaerodium (Presl) C. Chr. Ind. Fil. XVI. 1906 (lectotype T. tunbridgense incorrect, as indicated above).

Hymenophyllum subg. Euhymenophyllum [sect.] Serrulata Presl, Hymen. 32. 1843. Lectotype: H. tunbridgense L.

Hymenophyllum subg. Euhymenophyllum [sect.] Serrulata [subsect.] Evoluta Presl, Hymen. 32. 1843. Lectotype: H. tunbridgense L.

Hymenophyllum subg. Euhymenophyllum [sect.] Serrulata [subsect.] Dimidiata Presl, Hymen. 32. 1843. Lectotype: H. unilaterale Bory.

The section Hymenophyllum contains according to Copeland the following presumed species: H. alveolatum C. Chr., H. antarcticum Presl, H. asperulum Kunze, H. barbatum Baker, H. brachypus Sodiro, H. ceratophylloides Christ?, H. cupressiforme Labill., H. dentatum Cav., H. falklandicum Baker, H. gracilescens Domin, H. herzogii Rosenst., H. moorei Baker, H. nahuelhuapiense Diem & Lichtenstein, H. nanum Sodiro, H. peltatum (Poir.) Desv. (incl. presumably H. wilsonii Hook.), H. perfissum Copel., H. pumilum C. Moore, H. revolutum Colenso, H. rugosum C. Chr. & Skottsb., H. secundum Hook. & Grev., H. simonsianum Hook., H. spicatum Christ, H. torquescens v.d. Bosch, H. tunbridgense (L.) J. E. Smith, and H. uncinatum Sim.

Hymenophyllum sect. 2. Buesia (Morton) Morton, comb. nov.

Hymenophyllum subg. Buesia Morton, Bot. Gaz. 93: 336. 1932. Type: Hymenophyllum mirificum Morton.

Buesia (Morton) Copel. Phil. Journ. Sci. 67: 47. 1938.

¹¹ Phil. Journ. Sci. 64: 77. 1937.

When I described this as a subgenus back in 1932 I really knew very little about the Hymenophyllaceae in general. The type species, H. mirificum, was so strange that it seemed to be subgenerically distinguishable from Meringium (or Leptocionium, as it was called at that time). The species is peculiar and still known only from the original material, but relatives are now known that are less distinctive. I am now uncertain that it even needs to be distinguished as a section, but it can perhaps separate a small group of species characterized by having some accessory wings not in the plane of the frond. The subglobose receptacle found in the type species is not uniformly present in others. The additional species referred here are: H. cristatum Hook. & Grev., H. jamesonii Hook., H. megistocarpum (Copel.) Morton, comb. nov. (Buesia megistocarpa Copel. Univ. Calif. Publ. Bot. 19: 295: 1941), H. sodiroi C. Chr., and possibly one or two additional undescribed ones.

Hymenophyllum sect. 3. Ptychophyllum (Presl) C. Chr. Ind. Fil. XVI. 1906.

Didymoglossum subg. Chilodium Presl, Hymen. 23. 1843. Lectotype: Trichomanes neesii Blume. The subgenus originally consisted of two unrelated
species, T. neesii Blume and Didymoglossum longisetum Presl; the first
is a Hymenophyllum and the second a Trichomanes of the section Pachychaetum. The first to typify the group was Christensen in the "Index
Filicum" (p. XVI), who chose the Hymenophyllum element, citing as
type H. denticulatum Swartz, which he considered the correct name,
taxonomically, for Trichomanes neesii Blume. This fixes the lectotype as
T. neesii.

Meringium Presl, Hymen. 24, pl. 8. f. B. 1843. Type: Meringium meyenianum Presl=Hymenophyllum meyenianum (Presl) Copel. There were two original species, but the second, M. blumeanum (Spreng.) Presl, was referred to the genus only with a query, and so M. meyenianum is unquestionably the type.

Myrmecostylum Presl, Hymen. 27, pl. 10, f. A. 1843. Lectotype: Myrmecostylum tortuosum (Hook. & Grev.) Presl=Hymenophyllum tortuosum Hook. & Grev. (chosen by C. Chr. Ind. Fil. XVI. 1906). There were two other original species, M. dichotomum (Cav.) Presl and M. clavatum (Swartz) Presl; the former was referred to the genus only with a query and the latter disagrees with the description, so Christensen's choice was the only possible one.

Ptychophyllum Presl, Hymen. 28, pl. 11, f. E. 1843. Type: Ptychophyllum plicatum (Kaulf.) Presl=Hymenophyllum plicatum Kaulf., the only original species. In the "Index Filicum" (p. XVI. 1906) Christensen indicated the type as H. dichotomum Cav., but this is an obvious error, since it was not

one of the original species.

Tetralasma Philippi, Linnaea 30: 208. 1860. An invalidly published provisional name, proposed in case the character of a 4-parted indusium should prove of generic significance. Copeland indicated (Phil. Journ. Sci. 67: 45. 1938) that this indusial character is probably teratological. Based on Hymenophyllum quadrifidum Philippi, considered by Diem & Lichtenstein 12 as a synonym of Hymenophyllum plicatum Kaulf.

¹² Darwiniana 11: 675. 1959.

Hymenophyllum subg. Leptocionium sect. Chilodium (Presl) C. Chr. Ind. Fil. XVI. 1906.

Hymenophyllum subg. Leptocionium sect. Myrmecostylum (Presl) C. Chr. Ind. Fil. XVI. 1906.

Hymenophyllum sect. Acanthotheca Nakai, Bot. Mag. Tokyo 40: 242. 1926. Type: Didymoglossum acanthoides v. d. Bosch=Hymenophyllum acanthoides (v. d. Bosch) Rosenst.

Hymenophyllum subg. Meringium (Presl) Copel. Phil. Journ. Sci. 64: 14. 1937. Illegitimate, because superfluous, the earlier subgeneric name Chilodium Presl being available for the same concept.

Hymenophyllum sect. Meringium (Presl) Diem & Lichtenstein, Darwiniana 11: 666. 1959. Illegitimate, because superfluous, the earlier sectional names Chilodium, Ptychophyllum, Myrmecostylum, and Acanthotheca all being legitimate and available.

As a generic name, Meringium Presl would be correct for this group, although Copeland might better have chosen Ptychophyllum or Myrmecostylum, both of the same date as Meringium, better described, and based on better known species. However, as a subgenus or as a section Meringium may not be used, since an earlier subgeneric name (Chilodium, which has not however been transferred to Hymenophyllum as a subgenus) is available, and several sectional names (Chilodium, Ptychophyllum, Myrmecostylum, and Acanthotheca) are earlier than Meringium and available. I choose Ptychophyllum, which is clearcut in its application. The competing sectional names, sect. Chilodium (Presl) C. Chr. and sect. Myrmecostylum (Presl) C. Chr. are of the same date (1906) as sect. Ptychophyllum (Presl) C. Chr., and no one has previously made a choice between them.

Copeland included within Meringium four species that were said to be anomalous in having entire-margined segments. ¹³ Hymenophyllum edentulum (v. d. Bosch) C. Chr. is not really "edentate" but has obvious although sparse teeth, and H. holochilum (v. d. Bosch) C. Chr. has obviously toothed segements typical of Ptychophyllum. The other two species H. macroglossum v. d. Bosch and H. pachydermicum Cesati really do have entire segments; they were placed in Meringium on presumed affinities, but these were not demonstrated, and in fact absolutely nothing is known regarding their phylogeny or real relationships. They could have arisen as hybrids between two sections or they could be the result of parallel or convergent evolution. However, they probably can be accommodated in subg. Sphaerocionium subsect. Ciliata without undue strain. In this way it is possible to define Ptychophyllum more accurately, even if conceivably more artificially.

Aside from the common Hymenophyllum fucoides (Swartz) Swartz, which may be an aggregate species as currently recognized, the American species of sect. Ptychophyllum are little known; they include

¹³ Phil. Journ. Sci. 67: 40. 1938.

H. calodictyon v. d. Bosch, H. durandii Christ, H. ectocarpon Fée, and H. peruvianum Hook. & Grev. The following four species of southern South America have been carefully studied and accurately defined in a recent study by Diem and Lichtenstein: H. krauseanum Philippi, H. magellanicum (Klotzsch) Willd. ex Kunze, H. plicatum Kaulf., and H. tortuosum Hook. & Grev.

The Old World species are much more numerous; they include: H. acanthoides (v. d. Bosch) Rosenst., H. affine Brack., H. archboldii (Copel.) Morton, comb. nov. (Meringium archboldii Copel. Phil. Journ. Sci. 73: 462, fig. 3. 1941), H. bakeri Copel., H. bartlettii (Copel.) Morton, comb. nov. (Meringium bartlettii Copel. Phil. Journ. Sci. 73: 464. 1941), H. batuense Rosenst., H. bicolanum Copel., H. bivalve Copel., H. blandum Raciborski, H. bontocense Copel., H. brachyglossum A. Braun, H. brevidens van Alderw. van Rosenb., H. bryophilum C. Chr., H. campanulatum Christ, H. cardunculus C. Chr., H. cincinnatum Gepp, H. denticulatum Swartz, H. dimidiatum Mett., H. edentulum (v. d. Bosch) C. Chr., H. elbertii Rosenst., H. ellipticosorum van Alderw. van Rosenb., H. feejeense Brack., H. firmum van Alderw. van Rosenb., H. foersteri Rosenst., H. gorgoneum Copel., H. hallieri Rosenst., H. hieronymii C. Chr., H. holochilum (v. d. Bosch) C. Chr., H. hosei Copel., H. howense Brownlie, H. johorense Holttum, H. kerianum Watts, H. klabatense Christ, H. latifolium (Copel.) Morton, comb. nov. (Meringium latifolium Copel. Phil. Journ. Sci. 73: 461. 1941), H. laxum (Copel.) Morton, comb. nov. (Meringium laxum Copel. Univ. Calif. Publ. Bot. 18: 217. 1942), H. lobbii Moore, H. macrosorum van Alderw. van Rosenb., H. melanosorum (Copel.) Morton, comb. nov. (Meringium melanosorum Copel. Phil. Journ. Sci. 73: 462. 1941), H. merrillii Christ, H. meyenianum (Presl) Copel., H. minimum A. Rich., H. multifidum (Forst.) Swartz, H. nutantifolium van Alderw. van Rosenb., H. ovatum Copel., H. penangianum Matthew & Christ, H. pediculariifolium Cesati, H. piliferum C. Chr., H. perparvulum van Alderw. van Rosenb., H. poilanei Tardieu, H. pollenianum Rosenst., H. praetervisum Christ, H. pseudotunbridgense Watts, H. pulchrum Copel., H. pumilio Rosenst., H. ramosii Copel., H. reductum Copel., H. reinwardtii v. d. Bosch, H. ricciifolium Bory, H. rosenstockii Brause, H. rubellum Rosenst., H. rufifolium van Alderw. van Rosenb., H. rufifrons van Alderw. van Rosenb., H. samoense Baker, H. subdimidiatum Rosenst., H. taiwanense (Tagawa) Morton, comb. nov. (Mecodium taiwanense Tagawa, Acta Phytotax. Geobot. 9: 141. 1940), H. tenellum Kuhn. H. thuidium Harrington, H. torricellianum van Alderw. van Rosenb., H. triangulare Baker, and H. vittatum Copel.

Hymenophyllum sect. 4. Eupectinum Diem & Lichtenstein

Hymenophyllum sect. Eupectinum Diem & Lichtenstein, Darwiniana 11: 635, 1959.

Type: Hymenophyllum pectinatum Cav.

This small group of South American species, distinguished by having one-sided pinnae, contains only *H. pectinatum*, *H. quetri-huense* Diem & Lichtenstein, and *H. umbratile* Diem & Lichtenstein.

Hymenophyllum sect. 5. Myriodon (Copel.) Morton, comb. nov.

Hymenophyllum subg. Myriodon Copel. Phil. Journ. Sci. 64: 73. 1937.

Type: Hymenophyllum odontophyllum Copel.

Myriodon (Copel.) Copel. Phil. Journ. Sci. 67: 47. 1938.

A small aberrant group of New Guinea, perhaps monotypic, containing H. brassii C. Chr., of which H. odontophyllum Copel. may be a variant.

Subg. 2. Sphaerocionium

Hymenophyllum subg. 2. Sphaerocionium (Presl) C. Chr.

Sphaerocionium Presl, Hymen. 33, pl. 4, f. B, pl. 10, f. B, C. 1843. Lectotype: Sphaerocionium hirsutum (L.) Presl=Hymenophyllum hirsutum (L.) Swartz, chosen by Copeland, Phil. Journ. Sci. 64: 10. 1937. A large number of species were referred to the genus originally. Copeland chose the first named, a suitable choice for maintaining the application of the name in its current sense. Christensen had refused to indicate a type in the "Index Filicum."

Hymenophyllum subg. Euhymenophyllum [sect.] Pilosa Presl, Hymen. 32. 1843. Lectotype: Hymenophyllum valvatum Hook. & Grev. Presl used the sectional name "Pilosa" twice, once in Hymenophyllum and once in his genus Sphaerocionium, both for essentially the same kind of plant. The first species cited, H. valvatum, agrees with the diagnosis better than the second, H. blepharodes Presl.

Sphaerocionium sect. Pilosa Presl, Hymen. 34. 1843. Lectotype: Sphaerocionium schiedeanum Presl=Hymenophyllum crispum H. B. K. (ex char.). Presl distinguished his section by the simple rather than stellate marginal hairs. No lectotype has been designated previously.

Hymenophyllum subg. Charitophyllum v. d. Bosch, in Junghuhn, Plant. Junghuhn. 562. 1856, nom. nud. Based on Hymenophyllum lineare Swartz.

Hymenophyllum subg. Euhymenophyllum sect. Sphaerocionium (Presl) C. Chr. Ind. Fil. XV. 1906.

Hymenophyllum subg. Sphaerocionium (Presl) C. Chr. Ind. Fil. Suppl. 3: 5. 1934.

This subgenus is divisible into two sections, Sphaerocionium and Apteropteris.

Hymenophyllum sect. 6. Sphaerocionium

The section Sphaerocionium is divisible into four subsections, as follows:

Hymenophyllum sect. Spaerocionium subsect. Ciliata Prantl

Hymenophyllum subsect. Ciliata Prantl, Untersuch. Morph. Gefässkrypt. 1:55. 1875. Lectotype: Hymenophyllum lineare Swartz, the first species mentioned by Prantl and which agrees with the characterization. This

group contains the species that are hairy on the margins or veins only and not on the surfaces.

Hymenophyllum sect. Sphaerocionium subsect. Ciliata Morton, Contr. U.S. Nat. Herb. 29: 144. 1947. Invalidly proposed without Latin diagnosis. No type indicated, but assumed to be H. ciliatum (Swartz) Swartz.

The subsection Ciliata includes the following American species: Hymenophyllum adiantoides v. d. Bosch, H. caparavense Brade, H. consanguineum Morton, H. crispum H. B. K., H. delicatulum Sehnem, H. dimorphum Christ, H. elegans Spreng., H. glaziovii Baker, H. hirsutum (L.) Swartz (incl. H. ciliatum Swartz), H. hirtellum Swartz, H. lineare (Swartz) Swartz, H. maxonii Christ ex Morton, H. microcarpum Desv., H. molle Morton, H. prionema Kunze, H. pulchellum Schlecht. & Cham., H. roraimense Morton, H. ruizianum (Klotzsch) Kunze, H. sampaioanum Brade & Rosenst., H. semiglabrum Rosenst., H. silvaticum Morton, H. silveirae Christ, H. subrigidum Christ, H. tenerrimum v. d. Bosch, H. trapezoidale Liebm., H. trichophyllum H. B. K., H. urbanii Brause, and H. valvatum Hook. & Grev. Among the Old World species are: H. aeruginosum (Poir.) Carm., H. capillare Desv., H. hygrometricum (Poir.) Desv., H. ivohibense Tardieu, H. lanceolatum Hook. & Arn., H. macroglossum v. d. Bosch, H. marlothii Brause, H. obtusum Hook & Arn., H. pachydermicum Cesati, H. poolii Baker, H. subobtusum Rosenst., and H. viguieri Tardieu.

Hymenophyllum sect. Sphaerocionium subsect. Plumosa Prantl

Dermatophlebium Presl, Epim. Bot. 17, 258. 1849 [1851], nom. nud.

Hymenophyllum [subsect.] Plumosa Prantl, Untersuch. Morph. Gefässkrypt.

1:55. 1875. Lectotype: Hymenophyllum plumosum Kaulf.

Hymenophyllum sect. Dermatophlebium C. Chr. Ind. Fil. XV. 1906, nom. nud.

In the "Index Filicum," Christensen indicated the type of the unpublished section Dermatophlebium as H. sericeum (Swartz) Swartz, which does belong in this group, but was not the original species listed by Presl. Copeland ¹⁴ indicated several species as belonging to a group Dermatophlebium, but without a Latin diagnosis or any indication of the rank of the group intended. In my revision of the American species of Sphaerocionium I did not assign any special rank to this group of species (my nos. 45–52), H. sericeum (Swartz) Swartz, H. horizontale Morton, H. lobato-alatum Klotzsch, H. pyramidatum Desv., H. plumosum Kaulf., H. multialatum Morton, and H. tomentosum Kunze, of which a synonym is H. fusugasugense Karst. (taken up as a correct name in my revision), but they do deserve some nomenclatural distinction.

Hymenophyllum sect. Sphaerocionium subsect. Hirsuta Prantl Sphaerocionium sect. Stellata Presl, Hymen. 34. 1843. Lectotype: Hymenophyllum interruptum Kunze.

¹⁴ Phil. Journ. Sci. 67: 30. 1938.

Hymenophyllum sect. Pilosa Prantl, Untersuch. Morph. Gefässkrypt. 1: 55. 1875. Lectotype: Hymenophyllum raddianum C. Muell.

Hymenophyllum [subsect.] Hirsuta Prantl, Untersuch. Morph. Gefässkrypt. 1:55. 1875. Lectotype: Hymenophyllum raddianum C. Muell. Prantl listed also H. hirsutum (L.) Swartz, but since this species was misinterpreted and does not agree with the characterization, H. raddianum must be the lectotype. This species is a synonym of H. fragile (Hedw.) Morton.

Hymenophyllum sect. Sphaerocionium subsect. Lanata Morton, Contr. U.S. Nat. Herb. 29: 144. 1947. Invalidly published without a Latin diagnosis.

No type was indicated, but H. lanatum Fée assumed typical.

The American species of subsect. Hirsuta are: Hymenophyllum amabile Morton, H. angustum v. d. Bosch, H. antillense (Jenm.) Jenm., H. dependens Morton, H. elegantulum v. d. Bosch, H. ferrugineum Colla, H. fragile (Hedw.) Morton, H. hemipteron Rosenst., H. interruptum Kunze, H. karstenianum Sturm, H. lanatum Fée, H. latifrons v. d. Bosch, H. lindenii Hook., H. plumieri Hook. & Grev., H. rufum Fée, H. sieberi (Presl) v. d. Bosch, H. simplex Morton, H. speciosum v. d. Bosch, and H. superbum Morton. The only Old World species are perhaps H. pilosissimum C. Chr., and H. splendidum van den Bosch.

Hymenophyllum sect. Sphaerocionium subsect. Leptocionium (Presl) Morton, comb. nov.

Leptocionium Presl, Hymen. 26, pl. 11, f. D. 1843: Type: Leptocionium dicranotrichum Presl. A second species was referred to the genus, L. fucoides (Swartz) Presl, but since this was indicated only with a query it may not be considered the type.

Hymenophyllum sect. Leptocionium (Presl) Prantl, Untersuch. Morph. Gefässkrypt. 1: 54. 1875 (as to type, not concept).

Hymenophyllum subg. Leptocionium (Presl) Christ, Farnkr. Erde 20. 1897.

This subsection includes only the southern South American H. dicranotrichum. Christensen misunderstood it and misapplied the name Leptocionium as a subgenus to include all the species of subg. Hymenophyllum and "Meringium" in the "Index Filicum," Supplement III.

Hymenophyllum sect. 7. Apteropteris (Copel.) Morton, comb. nov.

Hymenophyllum subg. Apteropteris Copel. Phil. Journ. Sci. 64: 176. 1937.

Type: Hymenophyllum malingii (Hook.) Mett.

Apteropteris (Copel.) Copel. Phil. Journ. Sci. 67: 34. 1938.

The single species of this group, *H. malingii*, is so peculiar in its vegetative structure that it can perhaps be regarded as representing a monotypic section. The structure was well described by Holloway.¹⁵

Subg. 3. Craspedophyllum

Hymenophyllum subg. Craspedophyllum Presl

Hymenophyllum subg. Craspedophyllum Presl, Hymen. 33. 1843. Type: Hymenophyllum marginatum Hook. & Grev.

¹⁵ Trans. New Zeal. Inst. 54: 596, pls. 66, 76. 1923.

Pachyloma v. d. Bosch, Versl. Meded. Konink. Akad. Wetens. Afd. Natuurk. 11: 318. 1861, non DC., 1828. Type: Hymenophyllum marginatum Hook. & Grev.

Hymenophyllum sect. Pachyloma (v. d. Bosch) Christ, Farnkr. Erde 15. 1897. Hymenophyllum sect. Craspedophyllum (Presl) C. Chr. Ind. Fil. XV. 1906. Craspedophyllum (Presl) Copel. Phil. Journ. Sci. 67: 27. 1938.

Hymenophyllum sect. 8. Craspedophyllum

Only two species are in this subgenus, *H. marginatum* Hook. & Grev., of Australia and Tasmania, and *H. armstrongii* Baker, of New Zealand.

Subg. 4. Hemicyatheon

Hymenophyllum subg. Hemicyatheon Domin

Hymenophyllum subg. Hemicyatheon Domin, Bibl. Bot. 20, Heft. 85. 20. 1913. Lectotype: Hymenophyllum baileyanum Domin, chosen by Christensen, Ind. Fil. Suppl. 3: 5. 1934.

Hemicyatheon (Domin) Copel. Phil. Journ. Sci. 67: 27. 1938.

Hymenophyllum sect. 9. Hemicyatheon

I do not feel confident that this entity deserves subgeneric rank. Copeland's reasons for maintaining it are: "Unless the group be recognized as such, either its two members must be widely separated contrary to nature, or it must be included in Meringium where H. baileyanum would be very much out of place, or in Mecodium, where H. deplanchei would be altogether misplaced. I have already shown that the occurrence of such a group as this is explicable by assuming hybridization between members of the two great groups the characters of which are here combined." Copeland's argument will hold only if it is true that H. baileyanum and H. deplanchei, the first with entire margins and the second with toothed margins, are really more closely allied to each other than to any other species, but this has not actually been demonstrated. It could be that they do really belong to different subgenera and are similar by reason of convergent evolution rather than by reason of a common origin, which is by no means impossible on a priori grounds. No doubt H. baileyanum, the type of Hemicyatheon, is very close to Mecodium, and frankly the only reason that I don't actually refer it to that subgenus is that as a subgenus Hemicyatheon has priority, and thus the great group of species known as Mecodium would all have to become Hemicyatheon, an argument that could be defended more on the grounds of practicality than theory. For the present I refer H. deplanchei to subg. Hymenophyllum.

Subg. 5. Mecodium

Hymenophyllum subg. Mecodium Copel.

Mecodium Presl, Epim. Bot. 258. 1849 [1851], nom. nud.

Hymenophyllum subg. Euhymenophyllum sect. Integra Presl, Hymen. 32. 1843. Lectotype: Trichomanes asplenioides Swartz=Hymenophyllum asplenioides (Swartz) Swartz. Presl described essentially the same group of species twice, once under Hymenophyllum as sect. Integra, and once under his genus Sphaerocionium as sect. Glabra.

Sphaerocionium sect. Glabra Presl, Hymen. 34. 1843. Lectotype: Hymeno-

phyllum caudiculatum Mart.

Hymenophyllum subg. Euphorophyllum v. d. Bosch in Junghuhn, Plant. Junghuhn. 563. 1856, nom. nud. Based on Hymenophyllum polyanthos (Swartz) Swartz.

Hymenophyllum subg. Hapalophyllum v. d. Bosch, in Junghuhn, Plant. Junghuhn. 566. 1856, nom. nud. Based on Hymenophyllum javanicum Spreng.

Hymenophyllum sect. Glabra Prantl, Untersuch. Morph. Gefässkrypt. 1: 54.

1875. Lectotype: Hymenophyllum polyanthos (Swartz) Swartz.

Hymenophyllum sect. Globosa Prantl, Untersuch. Morph Gefässkrypt. 1: 55. 1875. Lectotype: Hymenophyllum junghuhnii v. d. Bosch. A group distinguished by having the tip of the receptacle enlarged. Its significance is unknown, but eventually it might turn out to be of sectional importance.

Hymenophyllum subg. Euhymenophyllum sect. Mecodium C. Chr. Ind. Fil. XV. 1906, nom. nud.

Hymenophyllum subg. Mecodium Copel. Phil. Journ. Sci. 64: 93. 1937. Mecodium (Copel.) Copel. Phil. Journ. Sci. 67: 17. 1938.

Hymenophyllum sect. Mecodium (Copel.) Diem & Lichtenstein, Darwiniana 11: 637. 1959.

Lectotype: Hymenophyllum polyanthos (Swartz) Swartz, selected by Copeland, Phil. Journ. Sci. 64: 10. 1937. Later, Copeland (Phil. Journ. Sci. 67: 14. 1938) stated the type to be H. sanguinolentum Forst., which would have been the most logical original choice, since it was the species that Presl mentioned in proposing Mecodium as a nomen nudum, but nevertheless, Copeland's first choice may not be rejected.

Hymenophyllum sect. 10. Mecodium (Copel.) Diem & Lichtenstein.

Divisible into the three subsections:

Hymenophyllum sect. Mecodium subsect. Mecodium

Copeland (Phil. Journ. Sci. 67: 19. 1938) included within Mecodium three species (H. reinwardtii v. d. Bosch, H. thuidium Harrington, and H. samoense Baker) with toothed-margined segments. This destroys the unity of the group and is really unnecessary, since it was done on a priori assumptions regarding the relationships of these species, concerning which nothing is really known. As mentioned previously in discussing the inclusion by Copeland of two entire-margined species in Meringium, the origin of these few aberrant species ought not to be allowed to confuse the classification. It is possible that they represent ancient (or recent) hybrids or are the result of a kind of convergent evolution. Therefore I do not find it unnatural to in-

clude the three species mentioned above in "Meringium." In this way a reasonable and workable classification can be produced and these aberrant species placed where they fit best so far as our present knowledge goes, leaving the question of their ultimate relationships to be decided later by detailed anatomical, morphological, and cytological evidence. Copeland had no such evidence, only intuition.

The subsect. Mecodium is the largest group of the genus, at least so far as accepted names is concerned. It is also the most difficult group, for lacking characters of toothing and pubescence many of the species look quite alike, and many really are perhaps only variations of the common and worldwide H. polyanthos. They include: Hymenophyllum abruptum Hook., H. alfredii Ros., H. andinum v. d. B., H. angulosum Chr., H. apiculatum Mett., H. asplenioides Sw., H. atrovirens Col., H. axillare Sw., H. badium Hook, & Grev., H. balansae Fourn., H. bamlerianum Rosenst., H. bismarckianum Christ, H. botryoides v. d. Bosch, H. breve Rosenst., H. brevistipes Liebm., H. carnosum Christ, H. caudiculatum Mart., H. constrictum Christ, H. contextum Rosenst., H. contiguum (D. A. Smith) Morton, comb. nov. (Mecodium contiguum D. A. Smith, N. Queensl. Nat. 14: 4, f. 1. 1946), H. contortum v. d. Bosch, H. copelandii Morton, nom. nov. (Mecodium archboldii Copel. Phil. Journ. Sci. 73:458. 1941, non H. archboldii (Copel.) Morton, a species of sect. Ptychophyllum), H. corrugatum Christ, H. costaricanum v. d. Bosch, H. crispato-alatum Hayata, H. crispatum Wall., H. cuneatum Kunze, H. darwinii Hook. f., H. dendritis Rosenst., H. diversilabium (Copel.) Morton, comb. nov. (Mecodium diversilabium Copel. Occas. Pap. Bern. Bish. Mus. 14: 49, pl. 2. 1938), H. edanoi (Copel.) Morton, comb. nov. (Mecodium edanoi Copel. Phil. Journ. Sci. 81: 2. 1952), H. emarginatum Swartz, H. endiviifolium Desv., H. exsertum Wall., H. farallonense Hieron., H. fecundum v. d. Bosch, H. fendlerianum Sturm, H. ferax v. d. Bosch, H. fimbriatum J. Smith, H. flabellatum Labill., H. flexile Makino, H. flexuosum A. Cunn., H. fumarioides Willd., H. funckii v. d. Bosch, H. gardneri v. d. Bosch, H. gollmeri v. d. Bosch, H. heimii Tardieu (of Madagascar, one of the most peculiar species, with a simple blade with pinnate veins and a deeply pinnatilobate margin), H. helicoideum Sod., H. humbertii C. Chr., H. imbricatum Blume, H. inaequale Desv., H. intricatum v. d. Bosch, H. involucratum Copel., H. javanicum Spreng., H. junghuhnii v. d. Bosch, H. kuhnii C. Chr., H. laciniosum Christ, H. lehmannii Hieron., H. leratii Rosenst., H. levingii C. B. Clarke, H. longifolium van Alderw. van Rosenb., H. macrothecum Fée, H. mexiae (Copel.) Morton, comb. nov. (Mecodium mexiae Copel. Univ. Calif. Publ. Bot. 19: 294, pl. 48. 1941), H. micans Christ, H. microphyllum Mett., H. microsorum v. d. Bosch, H. mnioides Baker, H. montanum Kirk, H. myriocarpum Hook., H. nigrescens Liebm., H. nitiduloides Copel., H. oligosorum Makino, H. ooides Muell. & Bak., H. opacum Copel., H. osmundoides v. d. Bosch, H. paniculiflorum Presl, H. parvulum C. Chr., H. paucicarpum Jenm., H. polyanthos (Swartz) Swartz, H. productoides J. W. Moore, H. productum Kunze, H. protrusum Hook., H. pulcherrimum Col., H. rarum R. Brown, H. recurvum Gaud., H. remotipinna Bonap., H. reniforme Hook., H. retusilobum Hayata, H. rimbachii Sod., H. riukiuense Christ, H. rufescens Kirk, H. salakense Racib., H. sanguinolentum Swartz, H. siliquosum Christ, H. skottsbergii C. Chr., H. streptophyllum Fourn., H. tablaziense Christ, H. tenerum v. d. Bosch, H. todjambuense Kjellb., H. treubii Racib., H. trianae Hieron., H. trichomanoides v. d. Bosch, H. undulatum Swartz, H. veronicoides C. Chr., H. walleri Maiden & Betche, H. whitei Goy, and H. wrightii v. d. Bosch.

Hymenophyllum sect. Mecodium subsect. Amphipterum (Copel.) Morton, comb. nov.

Amphipterum Presl, Epim. Bot. 258. 1849 [1851], nom. nud.

Hymenophyllum sect. Amphipterum C. Chr. Ind. Fil. XV. 1906, nom. nud. Based on Amphipterum Presl.

Hymenophyllum subg. Amphipterum Copel. Phil. Journ. Sci. 64: 68. 1937. Type: Trichomanes fuscum Blume=Hymenophyllum fuscum (Blume) v. d. Bosch.

Amphipterum (Copel.) Copel. Phil. Journ. Sci. 67: 14. 1938.

This small group perhaps contains only Hymenophyllum fuscum and H. ledermannii Brause. The other two species referred here by Copeland, H. geluense Rosenst. and H. laminatum Copel., are probably referable to subg. Hymenophyllum on the basis of their toothed segments. The sect. Amphipterum is hardly worth recognizing, except perhaps for consistency, since it differs only in the presence of accessory wings not in the plane of the frond. Since I assign names to such groups in the subgenera Hymenophyllum and Sphaerocionium, a similar group can be distinguished here although it is perhaps not really necessary. I do not undertake to place Amphipterum humatoides Copel., which is unknown to me.

Hymenophyllum sect. Mecodium subsect. Diplophyllum (v. d. Bosch) Morton, comb. nov.

Hymenophyllum subg. Platynophyllum v. d. Bosch, in Junghuhn, Plant. Junghuhn. 569. 1856, nom. nud. Based on Hymenophyllum dilatatum (Forst.) Swartz.

Diplophyllum v. d. Bosch, Versl. Meded. Konink. Akad. Wetens. Afd. Natuurk. 11: 322. 1861, non Diplophyllum Lehm., 1814. Lectotype: Trichomanes dilatatum Forst. = Hymenophyllum dilatatum (Forst.) Swartz, chosen by C. Chr. Ind. Fil. XV. 1906 (as "Diploophyllum").

Hymenophyllum sect. Diplophyllum (v. d. Bosch) C. Chr. Ind. Fil. XV. 1906.

Hymenophyllum dilatatum and the related H. scabrum A. Richard, of New Zealand, are peculiar among the species of Hymenophyllum

in having the fronds three cells, rather than one cell, thick. This would seem to be a fundamental and important difference, but two other species, *H. australe* Willd. and *H. demissum* (Forst.) Swartz, are said to be sometimes partly two cells thick, and these would therefore perhaps go into the subsect. *Diplophyllum* technically. The matter needs to be investigated further.

V. Cardiomanes

Cardiomanes Presl, Hymen. 12. 1843.

Trichomanes subg. Cardiomanes (Presl) Christ, Farnkr. Erde 33. 1897 (erroneously attributed to Presl).

Trichomanes sect. Eutrichomanes [subsect.] Cardiomanes (Presl) van Alderw. van Rosenb. Malay. Ferns 83. 1908.

Type: Trichomanes reniforme Forst.=Cardiomanes reniforme (Forst.) Presl.

This peculiar plant, endemic in New Zealand, has always excited interest by its strange shape for a member of the filmy-fern family. In its indusial structure it is typical of *Trichomanes*, and the pantotactic sori are, of course, correlated with the simple blade with forked veins. The only character that might really be distinctive is that the blades are four cells in thickness, and this too doubtless is correlated with the blade shape. A blade of this size would be almost too delicate and flaccid if it were only one cell thick, although this is not necessarily the case, for in the comparable Chilean *Hymenoglossum* an equally large blade is still only one cell thick except at the very margin. Still, for convenience and because its near affinities are unknown, *Cardiomanes* can be recognized as a monotypic genus, as has been the tendency by those who otherwise do not favor splitting up the large genus *Trichomanes*.

VI. Trichomanes

Trichomanes L. Sp. Pl. 1097. 1753.

Type: There has been some uncertainty as to the correct lectotype for Trichomanes L. The 11 original species, arranged as was usual in the time of Linnaeus in the order of division of the frond, with the simplest first were: T. membranaceum, T. crispum, T. polypodioides, T. hirsutum, T. pyxidiferum, T. tunbridgense, T. adiantoides, T. scandens, T. chinense, T. canariense, and T. capillaceum. Obviously Linnaeus did not really understand Trichomanes because he included several species with somewhat similar involucres but which do not belong to the family Hymenophyllaceae. The first species removed were: adiantoides, an Asplenium; chinense, Adiantum chinense (L.) Burm.; ¹⁶ and canariense, Davallia canariensis (L.) J. E.

¹⁶ Now Sphenomeris chinensis (L.) Maxon.

Smith. J. E. Smith also removed tunbridgense as the type of Hymenophyllum, and Swartz later transferred hirsutum to Hymenophyllum.
The remaining species have all been left in Trichomanes, except by
Copeland, and I consider them congeneric. Christensen in the "Index
Filicum" (XV. 1906) did not indicate the type of his subg. Eutrichomanes, but his concept is shown by the species he included, namely
only T. pyxidiferum, scandens, and capillaceum. In this he was following the practice of previous specialists like Presl, van den Bosch, and
Prantl.

Copeland upset this concept completely in his "Genera Hymenophyllacearum" (1938) and "Genera Filicum" (1947) by coining the new name Vandenboschia and calling Trichomanes what had been termed subg. Achomanes or subg. Ptilophyllum, typified by T. crispum L. Because of his prestige Copeland has been followed in his typification by most subsequent workers without a critical evaluation of his reasoning. However, in this case as in many others, Copeland's typifications are not to be trusted since they were made on a highly personal basis not in accord with the rules of the International Code of Botanical Nomenclature or with practices currently accepted in Copeland's own time.

Copeland's reasoning was given in the "Genera Hymenophyllacearum" (pp. 68, 69), as follows:

Although the era of our botanic nomenclature began with the publication of Linnaeus's Species Plantarum in 1753, genera are not defined in that work. For Linnaean generic definitions and, therefore, for the typification of his genera, we must go to earlier works of the same author. ¹⁷ In the case of *Trichomanes* it is defined in the Corollarium Genera Plantarum (and, teste Underwood, in Hortus Cliffortianus, also dated 1737): "Calyx turbinatus, solitarius, erectus, ex ipso margine follii. Stylus setaceus capsulam terminans." No species is mentioned, but reference is made to Plumier ¹⁸ for an illustration. This is *Trichomanes crispum*. As Linnaeus' generic concept finds its first expression here, and no other species is mentioned or referred to, this species must be accepted as the type species of the genus.

This idea of Copeland's that to typify Linnaean genera we must go back into "pre-Linnaean" (i.e., pre-1753) literature in order to interpret the first or original application of a generic name is entirely contrary to the Code and to current practice. It is the same idea that Otto Kuntze had back in 1891, when he adopted the 1737 edition of Linnaeus' Genera as the starting date, and consequently made his name anathema to most of the botanists of the 1890's and early 1900's. In fact even today Kuntze's application of names is suspect and rightly so. Linnaeus' generic concepts were much changed and amplified

^{17 &}quot;The latest rule sends us to the next subsequent edition of the 'Genera,' but, to interpret the definition found there, we must still go back to the first edition, where the same definition is amplified by references which fix its type."

18 "Fil. 86."

between 1737 and 1753, and to try to go back and find out his original concept would lead to wholesale changes in names, such as Kuntze actually proposed. For Copeland to try to revive and justify this discredited notion is almost inconceivable. Dr. R. E. Holttum in "Ferns of Malaya," 87. 1954, criticized Copeland's choice of type and indicated that it should be reconsidered, but he did not actually make any change himself.

The present rules regarding lectotypes and the "Guide for the Determination of Types" of the International Code for Botanical Nomenclature (1961 ed.) lead us in exactly the opposite direction, not backward to the maze of pre-Linnaean usages but forward to subsequent usage. The first subsequent author who has definitely or inferentially designated a suitable lectotype must be followed. The

pertinent sections of the Guide are sections 4e and 4f:

In cases when two or more elements were included in or cited with the original description, the reviewer should use his best judgment in the selection of a lectotype, but if another author has already segregated one or two elements as other taxa, the residue or part of it should be designated as the lectotype if its essential characters correspond with the original description. If it can be shown that the element best fitting the protologue has been removed, it should be restored and treated as the lectotype. Whenever the original material of a taxon is heterogeneous, the lectotype should be so selected as to preserve current usage unless another element agrees better with the protologue. The first choice of a lectotype must be followed by subsequent workers unless the original material is rediscovered, or unless it can be shown that the choice was based upon a misinterpretation of the protologue.

After the above-mentioned species were removed to other genera (Asplenium, Adiantum, Davallia, and Hymenophyllum) there remained in Trichomanes only T. membranaceum, T. crispum, T. polypodioides, T. pyxidiferum, T. scandens, and T. capillaceum. These were all retained unchanged in the genus without any designation of a type until Presl's "Hymenophyllaceae" (1843). He removed T. membranaceum to a distinct genus, Lecanium, and placed T. crispum in a different subgenus, Trichomanes subg. Achomanes, thus removing it from consideration as a possible lectotype. Trichomanes polypodioides and T. capillaceum were not mentioned by Presl. In his Trichomanes subg. Eutrichomanes Presl retained only T. pyxidiferum and T. scandens, thus limiting the choice of lectotype to one of these. The choice was definitely made by John Smith 19 by citing T. scandens L. as the type of Trichomanes. This is the eminently suitable choice: It agrees with the protologue as well as any other species, it was not misinterpreted by Presl or John Smith, and in fact is one of the wellknown West Indian species of the genus, and it maintains the usage of all authors up to the time of Copeland as to the true subg.

¹⁹ Hist. Fil. 347. 1875.

Eutrichomanes, or subg. Trichomanes as it must now be called. The generic name Vandenboschia Copeland thus proves to be a superfluous, illegitimate name for the true Trichomanes L. to be abandoned by those who wish to continue to split up the Hymenophyllaceae into smaller genera.

Key to the Subgenera of Trichomanes

Venation anadromous; sori paratactic; ²⁰ fronds mostly bipinnatifid to quadripinnatifid, rarely only pinnatifid, simple or merely lobed; segments not ciliate (except in *T. scandens*) or with stellate marginal hairs; false veins absent (except in sect. *Crepidomanes*).

Rhizomes erect or short-creeping, the fronds somewhat clustered; stipes often rather coarse; plants mostly terrestrial Subg. 2. Pachychaetum

Venation catadromous; sori epitactic; fronds not more than pinnate-pinnatifid, sometimes simple or merely lobed; segments often ciliate or with sessile stellate marginal hairs; false veins present or absent.

False veins absent (except in sect. Neurophyllum with dark cross veins perpendicular to the true veins); fronds never simple, mostly deeply pinnatifid to once-pinnate; often terrestrial Subg. 4. Achomanes

Subg. 1. Trichomanes

Stipes distinctly different from the rhizomes; rhachis not proliferous.

Blades one cell thick throughout, at least mostly not pilose.

Cells not perpendicular to the veins, the distal walls not thickened. Marginal cells not differentiated.

Blades bipinnatifid to quadripinnatifid, the ultimate segments with a single, unforked vein.

Blades ciliate, the hairs simple or forked at base. False veins absent.

West Indies Sect. 1. Trichomanes

Blades not ciliate.

Blades simply pinnate or pinnate-pinnatifid, the segments broad, with a continuous midrib and forked veinlets. Australia, Tasmania, and New Zealand Sect. 4. Phlebiophyllum

Marginal cells (one or two rows) slightly differentiated from the others, more elongate. Philippines and Sumatra to Tahiti and New Zealand.

Cells of the segments more or less perpendicular to the veins and elongate, the distal walls thickened and giving the appearance of false veins.

Philippines

²⁰ See the introduction (p. 158) for a definition of this term.

Fronds ciliate.

Cilia simple.

Cilia with a dark bulbous base; blades pinnate-pinnatifid. American tropics Sect. 24. Ragatelus

Cilia without a markedly bulbous dark base; blades simply-pinnate. American tropics and West Africa Sect. 17. Achomanes

Veins without accessory wings not in the plane of the lamina.

Subsect. Crispa

Veins with accessory wings not in the plane of the lamina.

Subsect. Lamellata

Cilia stellate or forked at base. Blades pinnatifid to pinnate-pinnatifid. American tropics Sect. 25. Acarpacrium

Subg. 1. Trichomanes

Trichomanes subg. Trichomanes

Pyxidaria Gleditsch, Syst. Plant. 291. 1764. Lectotype: Trichomanes scandens L. Copeland (Gen. Hymen. 13) dismisses this name with the statement "This name has no status at all," which is hardly comprehensible. There is no category of names "without status"; names are either valid or invalid, legitimate or illegitimate. Pyxidaria Gleditsch is validly published. It is illegitimate, since it was superfluous, being merely a change of name for Trichomanes L., because Gleditsch took up the name Trichomanes in the "pre-Linnaean" sense as used by Tournefort for Asplenium trichomanes L. It must be remembered that Gleditsch was writing only about 10 years after the publication of Linnaeus' "Species Plantarum" (1753) and "Genera Plantarum" (ed. 5, 1754) and did not know that botanical nomenclature was later to be accepted as beginning at that time. From his point of view it was quite proper to reestablish Tournefort's genus Trichomanes and to rename Linnaeus' Trichomanes as Pyxidaria. No species was indicated for Pyxidaria and since the diagnosis is essentially the same as the Linnaean diagnosis for Trichomanes, 21 Pyxidaria is to be considered as based on the same type as Trichomanes and to be an absolute nomenclatural synonym.22

Trichomanes subg. Eutrichomanes Presl, Hymen. 16. 1843. Lectotype: Trichomanes scandens L.

Trichomanes subg. Eutrichomanes [sect.] Pinnata Presl, Hymen. 16. 1843. Lectotype: Trichomanes scandens L. This section originally included many species, but since it included the lectotype species of Trichomanes it should be considered as a nomenclatural synonym of sect. Trichomanes, with the same lectotype.

Trichomanes sect. Eutrichomanes (Presl) Moore, Ind. Fil. cx. 1857.

Trichomanes [subg.] Minora Prantl, Untersuch. Morph. Gefässkrypt. 1:

²¹ Gen. Plant. ed. 5. 1754.

²² Incidentally, it might be mentioned that *Pteris* Gleditsch (Syst. Plant. 289. 1764), omitted from the "Index Filicum," is not the same genus as *Pteris* L. Gleditsch describes his *Pteris* as having a dorsal, centrally petiolate, peltate indusium, which indicates that he intended it to apply to the genus now called *Polystichum* (i.e., *P. lonchitis*). The Linnaean *Pteris* is renamed *Cincinalis* Gleditsch (Syst. Nat. 290. 1764); however, the species name *Cincinalis* aquilina Gleditsch does not occur here as it is indicated in the "Index Filicum."

51. 1875. Lectotype: Trichomanes intramarginale Hook. & Grev. Prantl divided his restricted Trichomanes into two groups, "Minora" and "Maiora," each with a description. Since these both contained sections so named they must be considered to be subgeneric names, although Prantl may have thought of them as merely descriptive. Both of them refer to subg. Trichomanes as I delimit that subgenus, and so they do not cause any nomenclatural complications. A lectotype has been arbitrarily selected, the type of the first section included by Prantl within his subg. Minora.

Trichomanes [subg.] Maiora Prantl, Untersuch. Morph. Gefässkrypt. 1: 52.1875. Lectotype: Trichomanes scandens L. See the remarks above under subg. Minora concerning this name. Since this subgenus included the type of Trichomanes, it follows that the lectotype must be the same, T. scandens L.

Trichomanes subg. Holophlebium Christ, Farnkr. Erde 27. 1897. Lectotype: Trichomanes scandens L. Christ recognized four subgenera, the monotypic Serpyllopsis and Cardiomanes, Hemiphlebium (with the sections Microgonium, Lecanium, and Euhemiphlebium) characterized by the presence of false veins, and Holophlebium, without false veins, which contained all the rest of the genus, including the section Eutrichomanes. Holophlebium was therefore another name for the typical subgenus, with the same type as subg. Trichomanes.

As I construe it, the subg. Trichomanes is divisible into eight sections.

Trichomanes sect. 1. Trichomanes

LECTOTYPE: Trichomanes scandens L. See the discussion above concerning the typification of Trichomanes.

This typical section may be monotypic, containing only the common West Indian T. scandens. This has always been grouped with and considered closely allied to T. radicans Swartz, but it does differ somewhat in habit, in the ciliate fronds, and also in chromosome number as indicated by T. Walker. In T. scandens the number is n=64, presumably a polyploid on the base number x=17, whereas T. radicans (and related species so far as known) has n=36 or 72 (i.e., with a base x=9).

Trichomanes sect. 2. Lacosteopsis Prantl.

Trichomanes sect. Lacosteopsis Prantl, Untersuch. Morph. Gefässkrypt. 1: 53. 1875. Lectotype: Trichomanes luschnathianum Presl. There were two original species, T. radicans Swartz and T. luschnathianum Presl. In the "Index Fllicum," Christensen selected as type T. rupestre (Raddi) v. d. Bosch, not one of the original species. He intended T. luschnathianum, which he considered a taxonomic synonym. Copeland (Gen. Hymen. 15 1938) wrongly picked the first cited species, which he indicates as "Trichomanes 'radicans' = T. rupestre(?)." This is a misinterpretation. The T. radicans cited by Prantl was the true radicans of Swartz, and not T. rupestre, as shown by the specimens cited. Copeland's typification must be rejected because of the prior typification of Christensen. The species T. rupestre is rather peculiar and isolated, but the relationship is evidently with T. radicans Swartz and not with the group of T. crispum L. where Copeland placed it.

Trichomanes sect. Eutrichomanes [subsect.] Lacostea [series] Trichomanopsis van Alderw. van Rosenb. Malay. Ferns 84. 1908. Lectotype: Trichomanes aphlebioides Christ. Although no definite rank was assigned by van Alderwerelt van Rosenburgh to his group Trichomanopsis, by working downward one can consider it to have been a series. Since no rank has been assigned, this rank will stand as indicated here, by Art. 35 of the Code (1961 ed.).

Vandenboschia Copel. Phil. Journ. Sci. 67: 51. 1938. Type: Vandenboschia radicans (Swartz) Copel. = Trichomanes radicans Swartz. A superfluous illegitimate name since the type of Trichomanes is cited as a synonym.

Trichomanes subg. Vandenboschia (Copel.) Allen, Fl. N. Zeal. 34. 1961.23

This section Lacosteopsis includes T. radicans Swartz and most of the species included by Copeland in his genus Vandenboschia, with the exception of T. scandens L. (which I refer to sect. Trichomanes) and T. pyxidiferum L. (which I refer to sect. Crepidomanes, although with some slight doubt). Among the additional species referable here, mostly following Copeland, are: T. abrotanifolium v. d. Bosch, T. amabile Nakai, T. angustatum Carm., T. aphlebioides Christ, T. auriculatum Blume, T. axillare Sodiro, T. beckeri Krause, T. birmanicum Bedd., T. boschianum Sturm, T. brachyblastos Mett., T. bradei Christ, T. capillaceum L., T. cellulosum Kl., T. clathratum Tag., T. cocos Chr., T. colensoi Hook. f., T. collariatum v. d. B., T. cyrtotheca Hillebr., T. cystoceiroides Christ, T. davallioides Gaud., T. debile v. d. Bosch., T. diaphanum H. B. K., T. draytonianum Brack., T. exsectum Kunze, T fallax Christ, T. fargesii Christ, T. giganteum Bory, T. goetzii Hieron., T. haughtii Morton, T. herzogii Rosenst., T. hymenophylloides v. d. Bosch, T. hypnoides Christ, T. ingae C. Chr., T. johnstonense Bailey, T. junceum Christ, T. latifrons v. d. Bosch, T. latisectum Christ, T. liukiuense Yabe, T. longifrons Nakai, T. maximum Blume, T. melanotrichum Schlecht., T. miyakei Yabe, T. naseanum Christ, T. nipponicum Nakai, T. orientale C. Chr., T. parvum Copel., T. philippianum Sturm, T. schmidianum Zenker, T. serratifolium Rosenst., T. sinuatum Bonap., T. somae Nakai, T. stenosiphon Christ, T. subclathratum (K. Iwatsuki) Morton, comb. nov. (Vandenboschia subclathrata K. Iwatsuki, Acta Phytotax. Geobot. 17: 70. 1958), T. tenerum Spreng., T. tenuissimum v. d. Bosch, T. titibuense (Ito) Morton, comb. nov. (Vandenboschia titibuensis Ito, Journ. Jap. Bot. 24: 125, f. 1. 1949), T. ulei Christ, T. virgatulum v. d. Bosch, and T. wildii Bailey (?).

Trichomanes sect. 3. Crepidomanes (Presl) Prantl.

Trichomanes subg. Crepidomanes Presl, Epim. Bot. 17. 1849 [1851]. Type: Trichomanes intramarginale Hook. & Grev., the sole original species. In his "Genera Hymenophyllacearum" (p. 14), Copeland correctly had the type

²³ Holttum, Ferns Malaya 105. 1954, has *Trichomanes* subg. *Vandenboschia*, but since the basionym was not indicated and since it was published after the date requiring the definite citation of basionyms for valid publication, Holttum's subgeneric name must be considered invalid.

as T. intramarginale, from Ceylon, but in the "Genera Filicum" he arbitrarily changed it to T. brevipes Presl, on the grounds that Presl's description was based largely on specimens of T. brevipes; this is a mere supposition on his part; Presl's description may have been based in part on this Philippine species but it was also based in part on the cited true type T. intramarginale Hook. & Grev.

Crepidomanes (Presl) Presl, Epim. Bot. 258. 1849 [1851]. A raising, in the Addenda et Corrigenda, of his subg. Crepidomanes to generic rank, with the

same single species.

Taschneria Presl, Epim. Bot. 258. 1849 [1851]. Type: This is a nomen nudum based on Trichomanes filicula Bory. No subsequent author took up the name Taschneria until Christensen's Trichomanes subg. Eutrichomanes sect. Taschneria.

Trichomanes sect. Crepidomanes (Presl) Prantl, Untersuch, Morph. Gefässkrypt. 1: 51. 1875.

Trichomanes sect. Didymoglossum sensu Prantl, Untersuch. Morph. Gefäss-

krypt. 1: 52. 1875, not Didymoglossum Desv. (1827).

Trichomanes sect. Taschneria C. Chr. Ind. Fil. XV. 1906. Type: Based on the description of Trichomanes sect. Didymoglossum sensu Prantl (1875), not Didymoglossum Desv. (1827). The type was wrongly indicated by Christensen as T. bipunctatum Poir., because he considered the true type T. filicula Bory as a taxonomic synonym of T. bipunctatum Poir. The type is T. filicula Bory, as Presl had it. Copeland, in his paper on Trichomanes (p. 174) recognized a Group Taschneria, but "group" is not a recognized taxonomic category. Later, Copeland considered Taschneria as a synonym of Crepidomanes, apparently correctly.

The small section Crepidomanes contains probably only one New World species, T. pyxidiferum L., somewhat doubtfully referable to the section, and the following Old World species: T. acutilobum Ching, T. acuto-obtusum Hayata, T. bilabiatum Nees & Blume, T. bilobatum van Alderw. van Rosenb., T. bipunctatum Poir., T. boninense Koidzumi, T. brevipes (Presl) Baker, T. clarenceanum Ballard, T. christii Copel., T. insigne Beddome, T. intramarginale Hook. & Grev., T. kurzii Bedd., T. latealatum (v. d. Bosch) Christ, T. latemarginale D. C. Eaton, T. majorae Watts, T. makinoi C. Chr., T. megistostomum Copel., T. nanophyllum (Tagawa) Morton, comb. nov. (Crepidomanes nanophyllum Tagawa, Acta Phytotax. Geobot. 9: 142. 1940), T. nymanii Christ, T. pervenulosum van Alderw. van Rosenb., T. plicatum (v. d. Bosch) Beddome, T. pseudocapillatum van Alderw. van Rosenb., T. pseudonymanii (Hosokawa) Morton, comb. nov. (Crepidomanes pseudonymanii Hosokawa, Trans. Nat. Hist. Soc. Formosa 31: 44. 1941), T. rothertii van Alderw. van Rosenb., T. rupicola Racib., T. tagawanum (K. Iwatsuki) Morton, comb. nov. (Crepidomanes tagawanum K. Iwatsuki, Acta Phytotax. Geobot. 17: 161, f. 1, 2. 1958), T. tosae Christ, T. venulosum (Rosenst.) Copel., and T. walleri Watts (?).

Trichomanes sect. 4. Phlebiophyllum (v. d. Bosch) Prantl.

Phlebodium v. d. Bosch, Ned. Kruid, Arch. 4: 377, 1859, 1

Phlebodium v. d. Bosch, Ned. Kruid. Arch. 4: 377. 1859, non J. Smith, 1841.

This name is cited by Copeland ²⁴ as a validly published name, but it appears at the place cited only in synonymy as *Phlebodium brownii* v. d. Bosch in sched., as a synonym of *Trichomanes venosum* R. Brown. Before he published on this plant in 1861 van den Bosch evidently realized that the name *Phlebodium* was preoccupied and chose to call it *Phlebiophyllum*, which also turned out to be a homonym, of *Phlebophyllum* Nees (1832).

Phlebiophyllum v. d. Bosch, Versl. Meded. Konik. Akad. Wetens. Afd. Natuurk. 11: 321. 1861. Type: Trichomanes venosum R. Brown, the sole original species.

Trichomanes sect. Phlebiophyllum (v. d. Bosch) Prantl, Untersuch. Morph Gefässkrypt. 1: 52. 1875 (erroneously attributed to v. d. Bosch).

Polyphlebium Copel. Phil. Journ. Sci. 67: 55. 1938. New name for Phlebio-phyllum v. d. Bosch (1861), non Phlebophyllum Nees (1832).

Trichomanes subg. Polyphlebium (Copel.) Allan, Flora New Zeal. 34. 1961.

This group was assigned sectional rank by Prantl and Christensen and formed Copeland's "group" *Phlebiophyllum*, which was later recognized as a genus *Polyphlebium* Copel. No doubt *T. venosum* is a peculiar, isolated species by reason of its broad pinnae with forked veinlets, but it does not seem necessary to recognize it as a genus or even subgenus. It can take its place as a section, as Prantl and Christensen had it. The fact that as a genus *Phlebiophyllum* is a later homonym does not invalidate the use of this name at the sectional level. As a subgenus the proper name would be subg. *Polyphlebium* (Copel.) Allan.

Trichomanes sect. 5. Crepidium (Presl) C. Chr.

Didymoglossum subg. Crepidium Presl, Hymen. 23. 1843. Type: The sole original species is Didymoglossum humile (Forst.) Presl=Trichomanes humile Forst. In his "Epimeliae," Presl suggested that Crepidium might be regarded as a genus but he did not actually adopt it. As a genus, the name would have been a later homonym of Crepidium Blume (1825), a genus of Orchidaceae. In his treatment of Trichomanes, Copeland treated this as one of his informal "groups," but in his "Genera Hymenophyllacearum" he raised it to a genus, as Crepidopteris Copel., a later homonym of Crepidopteris Sternb. (1838) and was therefore renamed Crepidophyllum C. F. Reed. As a genus Reed's name is correct, but I do not regard this group of species as sufficiently distinct to rank even as a subgenus. It can take its place as a section of subg. Trichomanes.

Trichomanes sect. Crepidium (Presl) C. Chr. Ind. Fil. XV. 1906.

Crepidopteris Copel. Phil. Journ. Sci. 67: 57. 1938, non Sternb. 1838. Based on Didymoglossum subg. Crepidium Presl.

Crepidophyllum C. F. Reed, Amer. Fern Journ. 38: 88. 1948. Based on Didymoglossum subg. Crepidium Presl.

Trichomanes subg. Crepidopteris (Copel.) Allen, Fl. N. Zeal. 35. 1961.26

The only species are probably: T. apiculare Fourn., T. endlicherianum Presl, T. gracillimum Copel., T. humile Forst. f., T. samoense

²⁴ Phil. Journ. Sci. 67: 14. 1938.

²⁵ Phil. Journ. Sci. 64: 131, 138. 1933.

²⁶ Holttum, Ferns Malaya 98. 1954, proposed subg. Crepidopteris, but invalidly without definite citation of basionym.

C. Chr., T. vaupelii Brause, T. vieillardii v. d. Bosch, and T. werneri Rosenst.

Trichomanes sect. 6. Abrodictyum (Presl) Moore.

Abrodictyum Presl, Hymen. 20, pl. 7. 1843. Type: Abrodictyum cumingii Presl, the only original species=Trichomanes cumingii (Presl) C. Chr. Trichomanes sect. Abrodictyum (Presl) Moore, Ind. Fil. cx. 1857.

Habrodictyon Presl ex v. d. Bosch, Versl. Meded. Konink. Akad. Wetens. Afd. Natuurk. 11: 321. 1861. This is an orthographic correction that probably ought not to be adopted, since it involves the first syllable of the name, although it is more correct orthographically. The case is similar to the general adoption of the original spelling Eleocharis (Cyperaceae) in preference to the orthographically more correct Heleocharis, or of Aplopappus rather than Haplopappus, although the latter has obtained some currency in the United States through its adoption by H. M. Hall in his monograph of the genus.

Trichomanes sect. Leptomanes Prantl, Untersuch. Morph. Gefässkrypt. 1: 52. 1875. Type: Five species were listed originally: T. tenerum Spreng., T. schiedeanum C. Muell., T. trichoideum Swartz, T. exsectum Kunze, and T. smithii Hook. Under the last-named species Prantl correctly listed Abrodictyum cumingii Presl as a synonym. Since Presl's genus Abrodictyum had been reduced to a section of Trichomanes by Moore and since there was no obstacle to its use as a sectional name, the name sect. Leptomanes Prantl was superfluous when published, since the prior and available name sect. Abrodictyum (Presl) Moore should have been adopted. It is therefore to be considered as merely an unacceptable change of name for Abrodictyum and therefore with the same type, Abrodictyum cumingii Presl. Christensen's choice 27 of T. capillaceum L. as type therefore has to be rejected; it was chosen because Christensen considered T. trichoideum Swartz as a taxonomic synonym of T. capillaceum L. Similarly, Copeland's choice 28 of T. tenerum on the basis that it was the first species listed by Prantl must be rejected also.

Trichomanes sect. Eutrichomanes [subsect.] Abrodictyum (Presl) van Alderw. van Rosenb. Malay. Ferns 83. 1908.

Trichomanes sect. 7. Pleuromanes Presl.

Trichomanes sect. Pleuromanes Presl, Epim. Bot. 17. 1849 [1851]. Type: Trichomanes acutum Presl, the sole original species.

Pleuromanes (Presl) Presl, Epim. Bot. 258. 1849 [1851]. A raising in the Addenda et Corrigenda of his sect. Pleuromanes to generic rank with the same species T. acutum and the addition of a second species, T. pallidum Blume. In the Index Filicum (XV. 1906), Christensen erroneously gave the type as T. pallidum.²⁹

Leucomanes Presl, Epim. Bot. 258. 1849 [1851]. A nomen nudum, based on Trichomanes album Blume; the name Leucomanes has never been used by any author either as a genus or section, because it represents the same

group as Presl's Pleuromanes.

²⁷ Ind. Fil. XV. 1906.

²⁸ Phil. Journ. Sci. 67: 15. 1908.

²⁹ Holttum (Ferns Malaya 97. 1954) proposed *Trichomanes* subg. *Pleuromanes*, but invalidly without specific citation of basionym.

Craspedoneuron v. d. Bosch, Versl. Meded. Konink. Akad. Wetens. Afd. Natuurk. 11: 322. 1861.³⁰ Lectotype: Trichomanes album Blume. The name Craspedoneuron first appeared in van den Bosch's treatment of the Hymenophyllaceae in Junghuhn's "Plantae Junghuhnianae" (p. 550. 1856), where it appeared as an accepted name, apparently as a subgenus, but without a description. It is indicated as containing "T. album etc.," which fixes the type as album. The name appeared later in van den Bosch's Synopsis ³¹ as a subgroup of Trichomanes but again without a description or stated rank. Copeland ³² also indicated the type as Trichomanes album Blume.

Trichomanes sect. Craspedoneuron (v. d. Bosch) Prantl, Untersuch. Morph. Gefässkrypt. 1: 52. 1875.

Although recognized by Copeland as a distinct genus, the group of Trichomanes acutum and T. pallidum does not appear to be very different from other groups of subg. Trichomanes. This section is distinguished by having the fronds more than one cell wide along the veins; although this character is well developed in T. pallidum, it is less evident in the type species T. acutum and seems to be absent in T. latifrons, which Copeland associated with the other two in his 1933 paper on Trichomanes. I recognize Pleuromanes as a section only with hesitation, awaiting further anatomical study. It will be limited to T. acutum and T. pallidum, the latter including T. album Blume, tentatively, and T. retusum (Copel.) Morton, comb. nov. (Pleuromanes retusum Copel. Phil. Journ. Sci. 73: 466. 1941). The whitish or bluish color of the fronds may be distinctive.

Trichomanes sect. 8. Gonocormus (v. d. Bosch) Christ.

Gonocormus v. d. Bosch, Versl. Meded. Konink. Akad. Wetens. Afd. Natuurk. 11: 321. 1861. Lectotype: Trichomanes proliferum Blume (selected by Christensen). Van den Bosch refers here species 1, 2, 9, and 10 of his "Synopsis," namely T. parvulum Poir., T. saxifragoides Presl, T. proliferum Blume, and T. minutum Blume, which W. A. Sledge (pers. comm.) considers a synonym of T. proliferum. Prantl (1875) accepted Gonocormus as a genus and listed four species in sect. Gonocormus, of which two are G. prolifer and G. minutus, thus limiting the choice of lectotype to one of these two species. In the Index Filicum (XIV. 1906) Christensen definitely selected T. proliferum as the type; therefore Copeland's selection (Gen. Hymen. 14. 1938) of T. minutum as type must be rejected. Copeland selected the first species listed by van den Bosch in his "Hymenophyllaceae Javanicae," G. minutus, but the first-named species is not automatically the type of course. This does not change the application of the name, since T. minutum and T. proliferum are not different specifically.

³⁰ Also published in Verhandl. K. Akad. Wetens. Amsterdam 9, Hym. Jav. 12. 1861, without description.

³¹ Ned. Kruid. Arch. 4: 361. 1859.

³² Phil. Journ. Sci. 67: 14. 1938.

³³ Also published Verhandl. K. Akad. Wetens. Amsterdam 9, Hym. Jav. 7. 1861, without description.

Gonocormus sect. Gonocormus Prantl, Untersuch. Morph. Gefässkrypt. 1:51. 1875.

Trichomanes sect. Gonocormus (v. d. Bosch) Christ, Farnkr. Erde 27. 1897 (erroneously attributed to v. d. Bosch).

Trichomanes subg. Gonocormus (v. d. Bosch) C. Chr. Ind. Fil. XIV, 634. 1906. Trichomanes sect. Eutrichomanes [subsect.] Gonocormus van Alderw. van Rosenb. Malay. Ferns 83. 1908.

This somewhat peculiar group, best distinguished by its "proliferous" fronds, can rank best merely as a section of subg. Trichomanes. The following are probably referable here: T. alagense Christ, T. assimile Mett., T. bonapartei C. Chr., T. boninicola Nakai, T. brooksii Copel., T. gracile v. d. Bosch, T. latilabiatum E. Brown, T. mannii Hook., T. matthewii Christ, T. novoguineense Brause (?), T. ruwenzoriense Taton, T. subtilissimum Brause, T. teysmannii v. d. Bosch, and T. trinerve Baker.

Subg. 2. Pachychaetum

Trichomanes subg. 2. Pachychaetum Presl

Trichomanes subg. Pachychaetum Presl, Hymen. 16. 1843. Lectotype: Six species were originally assigned to this subgenus: T. luschnathianum Presl, T. rigidum Swartz, T. firmulum Presl, T. pyramidale Wall., T. speciosum Willd., and T. brevisetum Spreng. Since these species do not really form a natural group, a type could be chosen only arbitrarily. In proposing Trichomanes subg. Eutrichomanes sect. Pachychaetum (Presl) C. Chr., Christensen 34 designated T. rigidum Swartz as the type, and this therefore must stand as the lectotype. Copeland's choice of T. luschnathianum Presl as lectotype (Gen. Hymen. 14. 1938) merely on the basis that this was the first-cited species cannot be upheld.

Trichomanes subg. Macroglena Presl, Abhandl. Boehm. Gesell. Wiss. V, 5: 333. 1848. Type: Five species were originally named: T. gemmatum J. Smith, T. cellulosum Klotzsch, T. foeniculaceum Bory ex Willd., T. angustissimum Presl, T. meifolium Bory ex Willd. Trichomanes meifolium was selected as lectotype by Christensen 36 and there is no reason to make any change. The group was distinguished by Copeland as a genus distinct from Selenodesmium by the "bristle-like segements," i.e., with the laminae only 1 or 2 cells wide on either side of the midveins, which is true of the

³⁴ Ind. Fil. XV. 1906.

³⁵ As noted elsewhere in this article, the groups in Presl's work denoted by the symbol § are not sections, as this sign usually denotes, but are subgenera, which Presl calls them several times. He also calls them "paragraphs" on occasion but this is not a recognized botanical category. Presl used the term "sectio" (or rather misused it, according to our present concepts) for a suprageneric group, as for instance in the "Epimeliae Botanicae," p. 103, where the family Blechnaceae is divided into sectio Blechneae and sect. Blechnopsideae, each with several genera. Therefore, the combination *Trichomanes* subg. *Macroglena* (Presl) Allan, Flora New Zeal. 36. 1961, is superfluous, since it is the same as the original publication of Presl.

³⁶ Ind. Fil. XV. 1906.

type species, T. meifolium, and some others, such as T. asa-grayi; some species referred to Macroglena by Copeland, as for instance the New Zealand T. strictum Menzies and T. caudatum Brack., definitely do not have setaceous segments and approach closely T. rigidum Swartz, the type species of Selenodesmium.

Trichomanes sect. Selenodesmium Prantl, Untersuch. Morph. Gefässkrypt. 1: 53. 1875.37 Type: There were three original species, T. rigidum Swartz, T. obscurum Blume, and T. elongatum Cunningham. By placing sect. Selenodesmium as a synonym of sect. Pachychaetum, Christensen 38 effectively chose T. rigidum Swartz as lectotype, also the lectotype of sect. Pachychaetum. Christensen was wrong in adopting sect. Pachychaetum as the correct sectional name under the subgeneric name Eutrichomanes, inasmuch as Selenodesmium had priority as a sectional name, Pachychaetum having been originally proposed as a subgeneric name. However, this has no bearing on the effectiveness of the choice of a lectotype. When, as here, Pachychaetum is recognized as a subgenus distinct from Trichomanes ["Eutrichomanes"] then the proper sectional name must be Pachychaetum, repeating the subgeneric name according to the Code.

Macroglena (Presl) Copel. Phil. Journ. Sci. 67: 82. 1938. Selenodesmium (Prantl) Copel. Phil. Journ. Sci. 67: 80. 1938.

The subgenus *Pachychaetum* is divisible into five sections, as follows.

Trichomanes sect. 9. Pachychaetum.

Among the species referable to sect. Pachychaetum are: T. angustimarginatum Bonap., T. asa-grayi v. d. Bosch, T. batrachoglossum Copel., T. caudatum Brack., T. compactum van Alderw. van Rosenb., T. cupressoides Desv., T. dentatum v. d. Bosch, T. elongatum A. Cunn., T. extravagans Copel., T. ferrugineum Fourn., T. flavofuscum v. d. Bosch, T. gemmatum J. Smith, T. laetum v. d. Bosch, T. longicollum v. d. Bosch, T. meifolium Bory ex Willd., T. obscurum Blume, T. obtusum (Copel.) Morton, comb. nov. (Macroglena obtusa Copel. Phil. Journ. Sci. 84: 163. 1955), T. parviflorum Poir., T. schlechteri Brause, T. schultzei Brause, T. setaceum v. d. Bosch, T. siamense Christ, T. strictum Menzies, T. stylosum Poir., T. tamarisciforme Jacq., T. tereticaulum Ching, T. trichophyllum Moore, T. truncatum (Copel.) Morton, comb. nov. (Macroglena truncata Copel. Occas. Pap. Bern. Bishop Mus. 14: 51, pl. 4. 1938), and T. warburgii Christ (?).

Trichomanes sect. 10. Davalliopsis (v. d. Bosch) Prantl.

Davalliopsis v. d. Bosch, Versl. Meded. Konink. Akad. Wetens. Afd. Natuurk. 11: 323. 1861. Type: Copeland (Gen. Hymen. 82. 1938) commented that "Van den Bosch established this genus imperfectly, publishing no specific name under it; but his name fortunately was retained for subgeneric or section use by Prantl and Christensen." He evidently believed that it was necessary to publish a specific name for a genus to be validly described, but there is no such provision in the nomenclature rules. It was not necessary for any

³⁷ Holttum, Ferns Malaya 108, 1954, proposed *Trichomanes* subg. *Selenodes-mium*, but invalidly without definite citation of the basionym.

³⁸ Ind. Fil. XV. 1906.

species to be named prior to the present requirement that types be indicated after Jan. 1, 1958. Although he did not make any combinations under the name Davalliopsis, van den Bosch did name two species as belonging to his genus: species 86 and 87 of his "Synopsis," T. prieurii Kunze and T. anceps Hook. (p.p.). In reducing this genus to a section of Trichomanes, Prantl listed only T. prieurii, thus effectively choosing this species as lectotype. Christensen (Ind. Fil. XV. 1906) wrongly stated the type to be T. elegans L. C. Richard, which is considered to be the same as T. prieurii.

Trichomanes sect. Davalliopsis (v. d. Bosch) Prantl, Untersuch. Morph. Gefässkrypt. 53. 1875.

Trichomanes sect. 11. Cephalomanes (Presl) Morton, comb. nov.

Cephalomanes Presl, Hymen. 17, pl. V. 1843. The type and sole original species is Cephalomanes atrovirens Presl=Trichomanes atrovirens (Presl) Kunze. The type stated by Christensen in Ind. Fil. XIV. 1906, Trichomanes javanicum, is impossible, since it was not mentioned by Presl in the original description. In 1848 Presl enlarged the genus to include five species, of which T. javanicum was one; 39 it was further enlarged to nine species by van den Bosch. 40 Prantl in 1875 made Cephalomanes a section of Lacostea v. d. Bosch (1861), which is nomenclaturally impossible, since Cephalomanes has priority. Cephalomanes may tentatively be regarded as a section, Trichomanes sect. Cephalomanes (Presl) Morton. The character by which Presl separated it, the globose-inflated tip of the receptacle, was either an illusion or an abnormality. Copeland in his key in "Genera Hymenophyllacearum" separates Cephalomanes from Trichomanes (as typified by T. crispum) merely by the former being "Oriental" and the latter "American," hardly a generic distinction, and Copeland's discussion does not really bring out any characters. However, Cephalomanes may be distinguished by having the venation anadromous and the sori paratact, whereas Trichomanes subg. Achomanes (as typified by T. crispum) has the venation catadromous and the sori epitact. However, I have not examined all species with regard to these characters, which may not hold.

Trichomanes [subg.] Schizophlebium v. d. Bosch in Junghuhn, Plant. Junghuhn. 551. 1856, nom. nud. Based on Trichomanes javanicum Blume. In his first paper on Hymenophyllaceae, in "Plantae Junghuhnianae" (1856), van den Bosch adopted several of Presl's subgenera, such as Crepidomanes, and indicated them with the same sign as Presl used; therefore I consider that the new names proposed here by van den Bosch were also subgenera. Since no rank has been assigned by any other author, my decision will stand under the Code. All of van den Bosch's own names were nomina nuda, which he later ignored, and so the matter is of little importance in that respect. But if van den Bosch's groups were to be considered sections, then the various Presl names adopted would all be new combinations as sections and this would cause some changes in the sectional nomenclature. Therefore, it seems best to consider all of these groups as subgenera.

Lacostea v. d. Bosch sect. Cephalomanes (Presl) Prantl, Untersuch. Morph.

Gefässkrypt. 1: 50. 1875.

Trichomanes sect. Eutrichomanes [subsect.] Lacostea [series] Cephalomanes (Presl) van Alderw. van Rosenb. Malay. Ferns 84. 1908.

Trichomanes subg. Cephalomanes (Presl) C. Chr. Ind. XIV. 1906.41

³⁹ Abhandl. Boehm. Gesell. V, 5: 334. 1848.

⁴⁰ Ned. Kruid. Arch. 4: 350-352. 1859.

⁴¹ Also proposed by Bonap. Notes Pterid. 8: 26. 1919.

Probably the only species of sect. Cephalomanes, all Old World, are: T. acranthum Ito, T. acrosorum Copel., T. atrovirens (Presl) Kunze, T. boryanum Kunze, T. crassum Copel., T. densinervium Copel, T. foersteri Rosenst., T. infundibulare van Alderw. van Rosenb., T. javanicum Blume, T. kingii Copel., T. ledermannii Brause, T. mada-gascariense Moore, T. maluense Brause, T. preslii Morton, nom. nov. (Trichomanes asplenioides Presl, Hymen. 37. 1843, non Swartz, 1788), T. singaporianum (v. d. Bosch) van Alderw. van Rosenb., T. suffrutex van Alderw. van Rosenb., and T. sumatranum van Alderw. van Rosenb.

Trichomanes sect. 12. Callistopteris (Copel.) Morton, comb. nov.

Callistopteris Copel. Phil. Journ. Sci. 67: 64. 1938. Type: Trichomanes apiifolium Presl, chosen by Copeland.

The only known species, all Old World, are: Trichomanes apiifolium Presl, T. bauerianum Endlicher, T. baldwinii D. C. Eaton,
T. calyculatum (Copel.) Morton, comb. nov. (Callistopteris calyculata
Copel. Occas. Pap. Bern. Bishop Mus. 14: 50, pl. 3. 1938), and
T. societense J. W. Moore (T. polyanthum Hook., non T. polyanthos
Swartz).

Trichomanes sect. 13. Nesopteris (Copel.) Morton, comb. nov.

Nesopteris Copel. Phil. Journ. Sci. 67: 65. 1938. Type: Trichomanes grande Copel., chosen by Copeland.⁴²

This and the preceding section are similar and perhaps should be united. However, for the present they should be left as separate sections, since they may not be truly allied. The only species, all Old World, are: T. blepharistomum Copel., T. grande Copel., T. intermedium v. d. Bosch, T. pseudoblepharistomum Tagawa, T. superbum Backhouse, and T. thysanostomum Makino.

Subg. 3. Didymoglossum

Trichomanes subg. 3. Didymoglossum (Desv.) C. Chr.

Didymoglossum Desv. Mém. Soc. Linn. Paris 6: 330. 1827. Lectotype: Eight species were originally included: D. muscoides, pusillum, punctatum, decipiens, alatum, lineare, filicula, and magellanicum (lineare and magellanicum are referable to Hymenophyllum rather than Trichomanes). The first subsequent author to recognize Didymoglossum was Presl (1843), who divided the tribe Trichomanoideae into two groups, Trichomaneae and Didymoglosseae, distinguished by having the limb of the involucre entire or 2-lipped, respectively. These groups are termed "sectio" by Presl, and so they must be considered invalid, since the category "sectio" was misused for a suprageneric rather than infrageneric group as required by the Code. Presl divided Didymoglossum into three subgenera—Eudidymoglossum, Chilodium, and Crepidium; in Eudidymoglossum he included D. muscoides, punctatum, alatum, decipiens, and filicula, made D. pusillum the type of a new genus, Hemiphlebium, and removed lineare and magella-

⁴² Holttum, Ferns Malaya 108, 1954, proposed *Trichomanes* subg. *Nesopteris*, but invalidly, without the definite citation of the basionym.

nicum from the group Didymoglosseae entirely. In his "Epimeliae Botanicae" (1851), Presl indicated that the species filicula should be removed from Didymoglossum as the genus Taschneria, thus effectively limiting the choice of lectotype to the four species remaining in the genus, D. muscoides, punctatum, alatum, and decipiens. Unfortunately, van den Bosch, followed by Prantl, limited Didymoglossum to D. filicula (now properly known as Trichomanes bipunctatum Poir.) and its allies, thus seeming to provide a lectotype. However, such a typification would upset current nomenclature and it can be rejected on the basis that Presl had excluded filicula from the genus, even though he failed to provide his segregate genus Taschneria with a validating description; in 1851 the publication of the combination Taschneria filicula could have been taken as sufficient for a monotypic new genus. No further treatment of Didymoglossum was published until Christensen 43 proposed Trichomanes subg. Didymoglossum with the type T. hymenoides Hedw., which Desvaux had listed as a synonym of his D. muscoides. This effectively chooses T. muscoides as lectotype, which fortunately does maintain the current application of the name.

Didymoglossum subg. Eudidymoglossum (Desv.) Presl, Hymen. 23. 1843.

Didymoglossum subg. Eudidymoglossum [sect.] Flabellata Presl, Hymen. 23. 1843. Lectotype: Didymoglossum sphenoides (Kunze) Presl = T. sphenoides Kunze.

Didymoglossum subg. Eudidymoglossum [sect.] Pinnata Presl, Hymen. 23. 1843. Lectotype: Didymoglossum muscoides (Swartz) Desv.=T. muscoides Swartz.

Trichomanes sect. Didymoglossum (Desv.) Moore, Ind. Fil. CX. 1857. Trichomanes subg. Didymoglossum (Desv.) C. Chr. Ind. Fil. XIV. 1906.

As I construe it, subg. Didymoglossum contains three sections, as follows.

Trichomanes sect. 14. Didymoglossum

The sect. Didymoglossum, the American species recently monographed by Wessels Boer, contains the following American species: Trichomanes angustifrons (Fée) W. Boer, T. curtii Rosenst., T. gourlianum Grev., T. hymenoides Hedw., T. krausii Hook. & Grev., T. lineolatum (v. d. Bosch) Hook., T. melanopus Baker, T. nummularium (v. d. Bosch) C. Chr., T. ovale (Fourn.) W. Boer, T. petersii A. Gray, T. pinnatinervium Jenm., T. punctatum Poir., T. pusillum Swartz, T. reptans Swartz, and T. rhipidophyllum Slosson. In addition, a very few Old World species are presumed to belong here, such as T. exiguum (Beddome) Baker, T. giesenhagenii C. Chr., T. liberiense Copel., and T. wallii Thwaites.

Trichomanes sect. 15. Microgonium (Presl) Christ.

Microgonium Presl, Hymen. 19, pl. 6, f. A, B. 1843. Type: Two species were originally assigned to the genus, M. cuspidatum (Willd.) Presl and M. berteroanum Presl. The first of these, Trichomanes cuspidatum Willd., was chosen lectotype by Christensen (Ind. Fil. XIV. 1906).

Hemiphlebium sect. Microgonium (Presl) Prantl, Untersuch. Morph. Gefässkrypt. 1: 46. 1875.

⁴³ Ind. Fil. XIV. 1906.

Trichomanes sect. Microgonium (Presl) Christ, Farnkr. Erde 24. 1897 (erroneously attributed to Presl).44

The four American species of sect. Microgonium were treated by Wessels Boer, 45 namely: Trichomanes ekmanii W. Boer, T. godmanii Hook., T. hookeri Presl, and T. kapplerianum Sturm. The Old World species are more numerous and include: Trichomanes ballardianum Alston, T. bimarginatum v. d. Bosch, T. chamaedrys Taton, T. craspedoneurum Copel., T. cultratum Baker, T. cuspidatum Willd., T. erosum Willd., T. falsivenulosum (Nishida) Morton, comb. nov. (Microgonium falsivenulosum Nishida, Journ. Jap. Bot. 32: 156. 1957), T. fulgens C. Chr., T. henzaianum Parish, T. mindorense Christ, T. motleyi v. d. Bosch, T. omphalodes (Vieillard) C. Chr., T. papuanum Brause, T. sayeri F. Muell. & Baker, and T. sublimbatum K. Muell.

Trichomanes sect. 16. Lecanium (Presl) Christ.

Lecanium Presl, Hymen. 11, pl. 1. 1843, non Reinw. 1825. Type: The only original species Lecanium membranaceum (L.) Presl=Trichomanes membranaceum L. Copeland stated that Lecanium Reinw. was not validly published because Reinwardt proposed both Lecanium and Lecanopteris as substitute names for his illegitimate genus Onychium Reinw. (1824) non Onychium Kaulf. (1820). However, according to the Code, 46 such alternative names are validly published if proposed prior to Jan. 1, 1953. The implication is that the genus Lecanopteris Reinw. was also validly published in 1825 by Reinwardt and not by Blume in 1828, as Copeland would have it. The species T. membranaceum L. is certainly peculiar but I do not think it represents a distinct genus, and therefore Lecanium Presl does not need to have a new generic name provided. It can conveniently rank as a section of subg. Didymoglossum, differing especially only in the strange marginal "scales." The fact that Lecanium is illegitimate as a genus does not mean that the name cannot properly be used at the sectional level.

Hemiphlebium sect. Lecanium (Presl) Prantl, Untersuch. Morph. Gefässkrypt. 1: 46. 1875.

Trichomanes sect. Lecanium (Presl) Christ, Farnkr. Erde 25. 1897 (erroneously attributed to Prantl).

Subg. 4. Achomanes

Trichomanes subg. Achomanes Presl

Trichomanes subg. Achomanes Presl, Hymen. 15. 1843. Lectotype: Presl adopted the name Achomanes from Necker (1790), whose "genus" Achomanes is cited by Presl as a synonym of Trichomanes on p. 13. However, since Necker's names are all invalid by the Code, Presl must be considered as the sole author of the subgenus, and Necker should not be cited as a parenthetical author, as has been done. The typification must be from Presl and not from Necker. The three groups into which Presl divided

⁴⁴ Holttum, Ferns Malaya 91. 1954, proposed *Trichomanes* subg. *Microgonium*, but invalidly without the definite citation of the basionym.

⁴⁵ Acta Bot. Neerl. 11: 277-330. 1962.

^{46 1961} ed., Art. 34.

Trichomanes are preceded by the sign §, which usually denotes a section. However, on p. 31, where Presl is speaking of the subdivision of Hymenophyllum into four groups, he terms these groups subgenera. These groups are preceded by the same sign as the groups in Trichomanes, and therefore must also be considered subgenera and not sections. The instance noted above in Hymenophyllum is not the only place where such groups are called subgenera by Presl. As noted elsewhere in this paper, Presl used the term "sectio" for a suprageneric rather than infrageneric group. The matter is of great importance when deciding on the priority of subgeneric and sectional names in the Hymenophyllaceae. Presl included 16 species in his subg. Achomanes, among them T. crispum L. When Presl removed T. crispum from Eutrichomanes, he effectively eliminated it from consideration as a possible lectotype for Trichomanes itself, that is for subg. Trichomanes. As a section, the name Achomanes dates from van den Bosch (1859), where the group is preceded by the sectional sign and also referred to in a footnote as a section. By following the name Achomanes with "T. crispum, etc." van den Bosch inferentially chose T. crispum as lectotype, a choice confirmed later by Christensen in citing T. crispum as the type of Trichomanes subg. Achomanes.47

Trichomanes sect. Achomanes (Presl) v.d. Bosch, Ned. Kruid. Arch. 4: 358.

1859.

Ptilophyllum sect. Achomanes (Presl) Prantl, Untersuch. Morph. Gefässkrypt. 1: 47. 1875.

Trichomanes sect. Euachomanes C. Chr. Ind. Fil. XIV. 1906.

To those who wish to continue to segregate many genera in the Hymenophyllaceae, the question of the proper generic name for this group will arise at once. It was called *Trichomanes* L. by Copeland, but as I have shown above it was due to an incorrect and unacceptable typification on *T. crispum* L. It was called *Ptilophyllum* by Prantl, but this name is illegitimate and unavailable. Neither is *Achomanes* Necker available as a generic name, since Necker's names are specifically outlawed by the Code. The name to be adopted will depend on how finely workers wish to split up the group. If they accept the circumscription of Copeland, the earliest available name is *Ragatelus* Presl (1843). However, if they regard the species with dimorphic fronds as coming within the group, then *Feea* Bory (1824) will be the oldest name for the whole group. Other generic names that I include within subg. *Achomanes* are *Hymenostachis* Bory (1824), *Odontomanes* Presl (1851), *Neuromanes* Trev. (1859), and *Lacostea* v.d. Bosch.

Trichomanes subg. Achomanes sect. 17. Achomanes

The section Achomanes may be divided into two subsections, as follows.

Trichomanes sect. Achomanes subsect. Crispa (Prantl) Morton, comb. nov. Ptilophyllum sect. Achomanes [subsect.] Crispa Prantl, Untersuch. Morph. Gefässkrypt. 1: 47. 1875.

LECTOTYPE: Trichomanes crispum L.

⁴⁷ Ind. Fil. XIV. 1906.

The species of sect. Achomanes, subsect. Crispa, are numerous but little known. This would be a fine group for monographic study for the plants are common and widely distributed and need to have reliable names. At the present time there are the following nominal species, but the actual number is probably much smaller: T. accedens Presl, T. adscendens Kunze, T. anadromum Rosenst. (?), T. aureovestitum Proctor, T. badium Fourn., T. corcovadense v. d. Bosch, T. crassipilis Weatherby, T. crispum L., T. cristatum Kaulf., T. dactylites Sodiro, T. daguense Weatherby, T. delicatum v. d. Bosch, T. eriophorum v. d. Bosch, T. furcatum v. d. Bosch, T. galeottii Fourn., T. gardneri v. d. Bosch, T. guianense Sturm, T. holopterum Kunze, T. imbricatum Sodiro, T. kalbreyeri Baker, T. killipii Weatherby, T. lambertianum Hook., T. laxum Klotzsch, T. lindigii Fourn., T. lucens Swartz, T. ludovicianum Rosenst., T. macilentum v. d. Bosch, T. micayense Hieron., T. opacum v. d. Bosch, T. ornatulum v. d. Bosch, T. pellucens Kunze, T. procerum Fée, T. robustum Fourn., T. sellowianum Presl, and T. sublabiatum v. d. Bosch. The above are all tropical American. One species is in western tropical Africa, T. crispiforme Alston.

Trichomanes sect. Achomanes subsect. Lamellata (Prantl) Morton, comb. nov. Ptilophyllum sect. Achomanes [subsect.] Lamellata Prantl, Untersuch. Morph. Gefässkrypt. 1: 48. 1875.

Type: Trichomanes martiusii Presl, the only original species (presumed to be a taxonomic synonym of T. pilosum Raddi).

Inasmuch as the presence of accessory wings on the veins not in the plane of the frond is recognized as of subsectional importance in Hymenophyllum subg. Sphaerocionium, it seems only logical to recognize a similar group here in Trichomanes, as Prantl did. The only known species are Trichomanes pilosum Raddi (probably an aggregate) and T. anomalum Maxon & Morton.

Trichomanes sect. 18. Neurophyllum (Presl) Moore.

Neurophyllum Presl, Hymen. 18, pl. 4, f.C. 1843, non Torr. & Gray (1840). Type: There were three original species: Neurophyllum vittaria (DC.) Presl, N. pinnatum (Hedw.) Presl, and N. pennatum (Kaulf.) Presl. Since Neurophyllum Presl was an illegitimate later homonym, van den Bosch in 1859 replaced it with Neuromanes Trevisan, which is thus to be considered as a renaming rather than a new genus and to be based on the same type. The original Neuromanes Trevisan 48 was based on different material and was not intended as a new name for Neurophyllum Presl, but it was a mere nomen nudum and therefore not validly published and need not be considered further. Christensen 49 chose T. pinnatum Hedw. as the type of his sect. Neuromanes, and placed sect. Neurophyllum as a synonym, and this effectively chose T. pinnatum as lectotype. Copeland's choice of T. vittaria DC. as lectotype must therefore be rejected; he evidently chose this

⁴⁸ Atti Ist. Veneto II, 2: 163. 1851.

⁴⁹ Ind. Fil. XIV. 1906.

species merely because it was the first one listed by Presl. This small group of species can be recognized as a distinct section. The fact that Neuro-phyllum is illegitimate as a generic name does not mean that it may not correctly be used as a sectional name, and since it has priority as a sectional name over Neuromanes it must be adopted.

Trichomanes sect. Neurophyllum (Presl) Moore, Ind. Fil. cx. 1857.

Neuromanes Trev. ex v. d. Bosch, Ned. Kruid. Arch. 4: 347. 1859. Based on Neurophyllum Presl (1843), not Torr. & Gray (1840).

Trichomanes sect. Neuromanes (Trev. ex v. d. Bosch) C. Chr. Ind. Fil. XIV. 1906. (Superfluous and illegitimate).

This small section contains only $Trichomanes\ pinnatum\ Hedw.,\ N.$ $pennatum\ Kaulf.$, if that is distinguishable, and the simple-bladed T. $vittaria\ DC.$ It is distinguished by the presence of dark false veins, perpendicular to the true veins.

Trichomanes sect. 19. Odontomanes (Presl) C. Chr.

Odontomanes Presl, Epim. Bot. 20. 1849 [1851]. Type: The only original species was Odontomanes hostmannianum (Klotzsch) Presl=Trichomanes hostmannianum (Klotzsch) Kunze.

Neuromanes Trevisan, Atti Ist. Veneto II, 2: 163. 1851, nom. nud. Trichomanes sect. Odontomanes (Presl) C. Chr. Ind. Fil. XIV. 1906.

This very small group is perhaps too close to sect. Neurophyllum, differing chiefly in the absence of false veins. In addition to T. host-mannianum it contains perhaps only T. huberi Christ and T. laciniosum Alston.

Trichomanes sect. 20. Lacostea (v. d. Bosch) Christ.

Lacostea v. d. Bosch, Versl. Meded. Konink. Akad. Wetens. Afd. Natuurk. 11: 320. 1861. Type: Van den Bosch based his genus Lacostea on species 81 and 82 of his "Synopsis Hymenophyllacearum," namely T. ankersii Parker ex Hook. & Grev. and T. brachypus Kunze. Prantl (1875) recognized this group as a genus and included both of these species. Christensen in his "Index Filicum" gave two treatments of the group. On p. 634 in the body of the text (this part published July 2, 1906) he followed Prantl more or less and recognized Lacostea as a subgenus. In the preliminary pages of the "Index Filicum," published last (with a preface dated Sept. 15, 1906), he gave his own ideas of a suitable arrangement and here he recognized Lacostea as a section of his subg. Cephalomanes, citing T. pedicellatum Desv. as the type species, which was not one of the original species. However, this was in line with Christensen's practice of citing recognized species as the types. In the body of the text he refers T. brachypus Kunze to the synonymy of T. pedicellatum, and therefore really intended the type to be T. brachypus Kunze, now correctly called T. pedicellatum, a taxonomic synonym. This fixes the lectotype as T. brachypus Kunze. Copeland's choice 50 of T. ankersii Parker as type must therefore be rejected.

Lacostea sect. Lacostea Prantl, Untersuch. Morph. Gefässkrypt. 1: 50. 1875. Trichomanes sect. Lacostea (v. d. Bosch) Christ, Farnkr. Erde 29. 1897 (erroneously attributed to v. d. Bosch).

Trichomanes subg. Lacostea (v. d. Bosch) C. Chr. Ind. Fil. 634. July 2, 1906.

⁵⁰ Phil. Journ. Sci. 67: 15. 1938.

Copeland did not recognize Lacostea either as a genus or section, but reduced it outright to his genus Trichomanes, my Trichomanes subg. Achomanes, but it seems to deserve recognition as a section. The species of Lacostea, all American, are probably only the following: Trichomanes ankersii Parker, T. pedicellatum Desv., T. tanaicum Baker, and T. tuerckheimii Christ.

Trichomanes sect. 21. Trigonophyllum (Prantl) C. Chr.

Ptilophyllum sect. Trigonophyllum Prantl, Untersuch. Morph. Gefässkrypt. 1: 48. 1875. Type: There were two original species, T. bancroftii Hook. & Grev. and T. bicorne Hook. In selecting a type, Christensen 51 chose T. arbuscula Desv., not one of the original species, but considered by Christensen to be an older taxonomic synonym of T. bancroftii Hook. & Grev., which he reduced to synonymy. This fixes the lectotype as T. bancroftii Hook. & Grev.

Trichomanes sect. Trigonophyllum (Prantl) C. Chr. Ind. Fil. XV. 1906.

This small group perhaps still includes only the two species T. arbuscula Desv. and T. bicorne Hook., which do not appear to be especially closely allied.

Trichomanes sect. 22. Homoeotes (Presl) C. Chr.

Homoeotes Presl, Abhandl. Boehm. Gesell. V, 5: 331. 1848. Type: Trichomanes heterophyllum Humb. & Bonpl. ex Willd., the sole original species.

Ptilophyllum sect. Homoeotes (Presl) Prantl, Untersuch. Morph. Gefässkrypt. 1: 48. 1875.

Trichomanes sect. Homoeotes (Presl) C. Chr. Ind. Fil. XIV. 1906.

This monotypic section differs from Feea and Hymenostachis primarily in having the rhizomes elongate and the fronds distichous. Two other species that have been considered allied are probably not referable here, T. amazonicum Christ and T. spruceanum Hook. Their proper position remains to be determined, perhaps as a subsection of Feea.

Trichomanes sect 23. Feea (Bory) Christ

Feea Bory, Dict. Class. d'Hist. Nat. 6: 446. 1824. Lectotype: Feea polypodina Bory=Trichomanes osmundoides DC., taxonomically. There were two original species, F. polypodina and F. nana Bory. The first to choose a lectotype was apparently J. Smith, 52 who chose Trichomanes spicatum Hedw.—not one of the original species but was considered, doubt less rightly, a taxonomic synonym of Feea polypodina Bory by Presl. This fixes the lectotype as F. polypodina. In the "Index Filicum" (XIV. 1906) Christensen indicated the type as Trichomanes botryoides Kaulf., an impossible choice and not one of the original species. Copeland 53 erroneously indicated F. nana Bory as the type. In the "Genera Filicum" (1947), Copeland corrected this to F. polypodina.

Trichomanes subg. Feea (Bory) Hook. Sp. Fil. 1: 114. 1844.

⁵¹ Ind. Fil. XV. 1906.

⁵² Hist. Fil. 349. 1875.

⁵³ Phil. Journ. Sci. 64: 13. 1937.

The section *Feea* is so close in its general morphology to the species of sect. *Achomanes* that is seems unnatural to segregate it as a distinct genus, as Copeland does solely on the basis of the dimorphism of the fronds. The section *Homoeotes* is perhaps a connecting link, for its leaves are only slightly dimorphic. The following two subsections may be recognized.

Trichomanes sect. Feea subsect. Feea.

Maschalosorus v. d. Bosch, Versl. Meded. Konink. Wetens. Afd. Natuurk. 11: 320. 1861. Type: T. mougeotii v. d. Bosch. =T. osmundoides DC., taxonomically.

Ptilophyllum sect. Feea (Bory) Prantl, Untersuch. Morph. Gefässkrypt. 1: 48. 1875. Prantl recognized Feea as a section and reduced Hymenostachis to a straight synonym; therefore, as sectional name Feea has priority. Trichomanes sect. Feea (Bory) Christ, Farnkr. Erde 29. 1897 (erroneously attributed to Bory).

Trichomanes sect. Maschalosorus (v. d. Bosch) C. Chr. Ind. Fil. XIV. 1906.

The only species of subsect. Feea, which has free, stalked involucres, are T. osmundoides DC. and T. botryoides Kaulf.

Trichomanes sect. Feea subsect. Hymenostachis (Bory) Morton, comb. nov.

Hymenostachis Bory, Dict. Class. d'Hist. Nat. 6:588. 1824. Type: Trichomanes elegans Rudge, the only original species = Trichomanes diversifrons (Bory) Mett.. The name T. elegans Rudge (1805) was a later homonym of T. elegans L. C. Rich. (1792). The name "Hymenostachis" has been altered by almost all later authors to "Hymenostachys" on orthographical grounds, but probably unjustifiably. Bory doubtless knew a good deal of Greek and deliberately chose to use the transliteration "-stachis."

Trichomanes subg. Hymenostachis (Bory) Hook. Sp. Fil. 1: 114. 1844. The first to unite Feea and Hymenostachys as subgenera was apparently Christensen,⁵⁴ who chose Feea and reduced Hymenostachis to a section, and therefore, for those who may wish to recognize Feea as a subgenus rather than a section, the correct name is subg. Feea (Bory) Hook.

In subsect. Feea the involucres are separated and somewhat stalked, and very little leaf-tissue is on the fertile fronds. The two known species of subsect. Hymenostachis, T. diversifrons (Bory) Mett. and T. trollii Bergd., have the fertile frond entire, about three cells thick, and with the involucres deeply and completely immersed in the leaf-tissue. The group has not been recognized as distinct recently but can conveniently be separated.

Trichomanes sect. 24, Ragatelus (Presl) C. Chr.

Ragatelus Presl, Hymen. 14. 1843. Type: The type and sole original species is Ragatelus crinitus (Swartz) Presl=Trichomanes crinitum Swartz.

Ptilophyllum v. d. Bosch, Versl. Meded. Konink. Akad. Wetens. Afd. Natuurk. 11: 321. 1861. Type: As originally proposed, this genus included a large number of species, nos. 17 to 24 and 26 to 43 of van den Bosch's "Synopsis." Inasmuch as species 43, Trichomanes crinitum Swartz, had already received the generic name Ragatelus Presl in 1843, the name

⁵⁴ Ind. Fil. XIV. 1906.

Ptilophyllum was superfluous, since van den Bosch could have and should have used the prior name Ragatelus. Moreover, Ptilophyllum was later homonym of Ptilophyllum Reichenb. (1841) and thus doubly illegitimate. Nevertheless, Prantl adopted Ptilophyllum, reducing to synonymy such validly published earlier names as Feea, Hymenostachis, Ragatelus, and Neuromanes. In fact, Prantl even created a suprageneric group, the Ptilophylleae, but since this was called a "family" and yet was subordinated to a "tribe" it is an invalid name, since the Code prohibits such changes in the relative order of categories, i.e., a family can be divided into tribes but a "tribe cannot be divided into families as Prantl tried to do. Since Ptilophyllum included the type of the previously published Ragatelus Presl, it must be considered as an illegitimate change of name for the latter and to have the same type, namely Trichomanes crinitum Swartz.

Trichomanes sect. Ptilophyllum (v. d. Bosch) Christ, Farnkr. Erde 27. 1897 (as to type, not as to concept).

Trichomanes subg. Ptilophyllum (v. d. Bosch) C. Chr. Ind. Fil. 634. 1906 (as to type, not as to concept).

Trichomanes sect. Ragatelus (Presl) C. Chr. Ind. Fil. XIV. 1906.

The genus Ragatelus was erected on the impression that the receptacle was bifid, which was an erroneous observation or else a casual teratological form. This does not, of course, invalidate the publication of the name. The species T. crinitum Swartz is rather distinctive and isolated and can tentatively be accepted as representing a monotypic section, as Christensen did. Copeland did not give it any recognition.

Trichomanes sect. 25. Acarpacrium (Prantl) C. Chr.

Trichomanes subg. Pseudachomanes Presl, Epim. Bot. 16. 1849 [1851]. Type: Five species were originally assigned to this subgenus by Presl: T. sinuosum L. C. Richard, T. cognatum Presl, T. holopterum Kunze, T. bancroftii Hook. & Grev., and T. alatum Swartz. In the "Index Filicum," Christensen chose T. polypodioides L. as the type, which was not one of the original species, but considered by Christensen as a taxonomic synonym and the correct name for T. sinuosum L. C. Richard; therefore, the latter must be considered as having been designated as lectotype. The matter is of some importance, for the species listed originally by Presl are not really closely allied.

Ptilophyllum sect. Achomanes [subsect.] Sinuosa Prantl, Untersuch. Morph. Gefässkrypt. 1: 47. 1875. Lectotype: Trichomanes sinuosum L. C. Richard.

Ptilophyllum sect. Acarpacrium Prantl, Untersuch. Morph. Gefässkrypt. 1: 48. 1875. Type: There were six species referred originally to the section. Christensen in the "Index Filicum" chose T. alatum Swartz as the type, an impossible choice since this was not one of the original species, but this inferentially selects as lectotype Trichomanes ptilodes v. d. Bosch, the first named of the original species, which Christensen considered a taxonomic synonym of T. alatum.

Trichomanes sect. Acarpacrium (Prantl). C. Chr. Ind. Fil. XIV. 1906.
Trichomanes sect. Pseudachomanes (Presl) C. Chr. Ind. Fil. XIV. 1906.

This small group of species can be distinguished from sect. Achomanes by the presence of stellate (or at least bifid) hairs on the margins of the segments and also on the veins to some extent. It does not

appear necessary to distinguish between the merely pinnatifid species as sect. Pseudachomanes, such as T. polypodioides L. (syn. T. sinuosum L. C. Richard) and the more dissected species like T. alatum Swartz of sect. Acarpacrium, as Christensen did. The character of the rhizome hairs (termed "paleae" by Prantl) being straight in T. sinuosum and its allies and peltate in T. crispum L. and its allies of the section Achomanes needs further study; apparently this has received no attention since the time of Prantl. The number of species is uncertain; they include Trichomanes adscendens Kunze, T. alatum Swartz, T. attenuatum Hook., T. curranii Weath., T. fimbriatum Backh., T. pinnatifidum v. d. Bosch, T. polypodioides L., T. ptilodes v. d. Bosch, and T. trigonum Desv.

Unplaced Sectional Name

Trichomanes sect. Flabellata Presl, Hymen. 16. 1843.

Gonocormus sect. Microtrichomanes Mett. ex Prantl, Untersuch. Morph. Gefässkrypt. 1: 51. 1875. Lectotype: T. digitatum Swartz (chosen by Christensen).

Trichomanes sect. Microtrichomanes (Mett. ex Prantl) C. Chr. Ind. Fil. XIV 1906.

Microtrichomanes (Mett. ex Prantl) Copel. Phil Journ. Sci. 67: 35. 1938. Lectotype: Trichomanes digitatum Swartz.

This group "Microtrichomanes" has been one of the stumbling blocks in the recent classification of the family, because in some ways it seems to bridge the gap between Trichomanes and Hymenophyllum and does not fit into either comfortably; but this fact ought not influence our classification unduly. If it were a homogeneous group as delimited by Copeland, the species obviously more closely related to each other than to any others and to have had a common ancestry, then one would have some hope of placing it definitely in a system, in Trichomanes, in Hymenophyllum, or in a distinct genus intermediate between them. But this is not the case. It is decidedly heterogeneous and would seem to be polyphyletic. It may have arisen anciently from hybridization between various species of Trichomanes and Hymenophyllum, perhaps belonging to quite different groups, in which case it

⁵⁶ Holttum, Ferns Malaya 94. 1954, proposed Trichomanes subg. Microtricho-

manes, but invalidly without the definite citation of the basionym.

Mettenius proposed this previously (Abhandl. Math.-Phys. Class. König. Sächs. Gesell. Wiss. 7: 413. 1864) as "gruppe" Micro-trichomanes, but this cannot be considered a valid publication; since "gruppe" is not a recognized taxonomic category, it must be considered only an informal grouping. As members of the group Mettenius listed T. digitatum Swartz, T. palmatifidum C. Muell., and T. dichotomum Kunze; these same species were listed by Prantl when he recognized the section, along with two others, T. nitidulum v. d. Bosch and T. flabellatum v. d. Bosch. In recognizing this group as a section Christensen chose T. digitatum as lectotype.

would have little or no unity as a "hybrid genus," and would not really deserve separate generic status. Apparently most of the species can be accommodated in existing *Trichomanes* sections without undue problems, but they are too little known to me for me to make the attempt. The nine species referred here by Copeland are distributed from the East African Islands through Malaya, Malesia, and Polynesia to Australia, but they are everywhere rare. They should each be investigated morphologically from good fresh material and each one placed according to its merits, which is not something that is likely to be done in the near future.

The somewhat doubtful species (generically) referred here are: T. aswijkii Racib., T. dichotomum Kunze, T. digitatum Swartz, T. flabellatum v. d. Bosch, T. francii Christ, T. lyallii (Hook. f.) Hook., T. nitidulum v. d. Bosch, T. palmatifidum K. Muell. (Hymenophyllum borneense Hook.), T. parvulum Poir., T. piliferum van Alderw. van Rosenb., T. ridleyi Copel., T. taeniatum Copel., T. vitiense Baker, and Microtrichomanes zamboanganum Copel.

Rejected Names

Achomanes Necker, Elem. Bot. 3: 313. 1790.

Although often cited as a synonym of *Trichomanes* L., this name must be rejected as invalid, as are all of Necker's names according to Art. 20, Note 2, of the International Code of Botanical Nomenclature (1961 ed.).

Adiantopsis v. d. Bosch.

Christensen ⁵⁷ and Copeland ⁵⁸ cite this name as a synonym of *Davalliopsis* v. d. Bosch, but both without citing any place of publication. I have been unable to locate such a name among van den Bosch's works. If the name were published, it would be an illegitimate later homonym of *Adiantopsis* Fée (1852).

Boschia Copel. Phil. Journ. Sci. 64: 11. 1937.

A name not otherwise mentioned by Copeland, probably a provisional name that he intended to use (perhaps for *Mecodium*?) and later abandoned but overlooked here.

Hemiphlebium Presl, Hymen. 25, pl. 9. 1843. Type (the only original species): Hemiphlebium pusillum (Swartz) Presl = Trichomanes pusillum Swartz. Presl did have authentic type material of T. pusillum Swartz in hand. However, evidently one or more fronds of a different species were intermixed, which in Jamaica could only have been T. hookeri Presl, since Presl described and illustrated an intramarginal false vein, such as occurs in T. hookeri but not in T. pusillum. That the drawing was partly made from the true T. pusillum

⁵⁷ Ind. Fil. XV. 1906.

⁵⁸ Gen. Hymen. 14. 1938.

is shown by the marginal stellate hairs, which occur in pusillum and not in hookeri. Since Presl's differentiation of this genus Hemiphlebium from Didymoglossum was primarily on the presence of this false vein and since such a false vein does not occur in the cited type, it seems that there is no alternative but to abandon Hemiphlebium as a nomen confusum. This seems to be the position taken by J. G. Wessels Boer in his recent "The New World Species of Trichomanes sect. Didymoglossum and Microgonium." 59

Trichomanes sect. Hemiphlebium (Presl) Moore, Ind. Fil. cx. 1857.

Trichomanes subg. Hemiphlebium (Presl) Christ, Farnkr. Erde 23. 1897.

Trichomanes sect. Euhemiphlebium (Presl) Christ, Farnkr. Erde 23. 1897.

Trichomanes sect. Eutrichomanes [subsect.] Hemiphlebium (Presl) van Alderw. van Rosenb. Malay. Ferns 83. 1908.

The following names appear in Christ's "Farnkraüter der Erde" (1897) apparently intended as sections, but they are all nomina nuda, without descriptions: Hymenophyllum sect. Ciliata, Crispata, Elastica, Exserta, Flabellata, Fuciformia, Pendula, Pilosa, Pinnatifida, and Polyantha. In those instances where Christ has indicated that these names are adopted from Presl, Prantl, or van den Bosch, I have considered that these are validly proposed new combinations, where they differ from the original combination.

Some names, none original, appear in Sadebeck's treatment of the Hymenophyllaceae in Engler and Prantl's "Die Natürlichen Pflanzenfamilien," (1899) but without any indication of rank or any consistency in usage, some groups receiving names and others of coordinate rank without names. I have ignored these, since Sadebeck obviously did not intend to present a complete classification into subgenera, sections, and subsections but merely applied names to groups that had already received names by Presl or other previous authors, without designating or deciding on any rank.

Copeland in his paper on Trichomanes (Phil. Journ. Sci. 51: 131. 1933) used several new names: Pyxidifera, Taschneria, Scandentia, Grandia, Apiifolia, and Rigida; these were not considered either as subgenera or sections but were merely called "groups," which is not a recognized botanical category. I consider them as merely informal groupings and unpublished. Some of these same groups were indicated as sections by Alston in his key in the "Ferns and Fern-allies of West Tropical Africa" (1959) but without validating Latin descriptions or references to previously published descriptions, and these too are unpublished.

⁵⁹ Acta Bot. Neerl. 11: 277-330. 1962.

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