Venation patterns, soral characteristics, and shape of the fronds of the microsorioid Polypodiaceae

By

W.L.A. Hetterscheid and E. Hennipman

With 14 figures in the text

Abstract

HETTERSCHEID, W. L. A. & HENNIPMAN, E.: Venation patterns, soral characteristics, and shape of the fronds of the microsorioid Polypodiaceae. — Bot. Jahrb. Syst. 105: 11—47. 1984. — ISSN 0006-8152.

The present paper deals with a detailed study of the venation, soral shape and distribution, and frondshape of the microsorioid Polypodiaceae, including taxa generally referred to the genera *Christiopteris, Colysis, Dendroconche, Dendroglossa, Diblemma, Lecanopteris, Leptochilus, Microsorium, Neocheiropteris, Neolepisorus, Paraleptochilus, Phymatodes,* and *Podosorus.* The fascinating diversity found in the characters studied is used to classify the taxa into 19 groups, which can be arranged into two main groups, using ontogenetic data of the venation.

The results suggest that the following genera can be united: *Colysis, Dendroglossa,* and *Paraleptochilus,* whereas *Dendroconche* and *Diblemma* should be merged with *Microsorium.* The latter genus is remarkably heterogeneous; a systematic study will be conducted in the near future.

1. Introduction

The present study deals with the gross morphology, venation pattern, and sorus shape and distribution of a number of genera selected from the family Polypodiaceae. The group includes in the first place the genera *Colysis, Dendroconche, Dendroglossa, Leptochilus, Microsorium* (incl. *Kaulinia*), *Paraleptochilus,* and *Podosorus,* which in our opinion may constitute a monophyletic group. This means that they are thought to be mutually more related to each other than one of them is to any other genus in the family. In the second place this paper deals with the group consisting of *Christiopteris, Lecanopteris, Neochei-*

0006-8152/84/0105-0011 $ 09.25

ropteris (incl. *Neolepisorus*), and *Phymatodes*, which are added, as present-day authors have suggested a possible relationship between these genera and those attributed to the first group. Most of the genera mentioned above are referred by CRABBE et al. (1975) to the subfamily Microsorioideae Nayar which also should include *Crypsinus* and related genera. This subfamily excludes *Neocheiropteris* which they referred to the Pleopeltoideae Nayar because of the presence of peltate paraphyses.

PICHI SERMOLLI (1977) subdivided the Polypodiaceae into 14 groups, one of these comprising the group of genera listed above with the exclusion of *Neocheiropteris*, *Lecanopteris*, and *Myrmecopteris* (syn.: *Myrmecophila* = *Lecanopteris*; see JERMY & WALKER 1975). PICHI SERMOLLI referred *Neocheiropteris* to a group of genera related to *Pleopeltis*. *Lecanopteris*, *Myrmecopteris*, and *Solanopteris* were taken together by this author as a separate group based on their myrmecophyly at the same time stating that *Myrmecopteris* and *Lecanopteris* are mutually more related than either of them is to *Solanopteris*. SEN & HENNIPMAN (1981) found that the first two taxa are characterized by the occurrence of cyclo- and cocyclocytic stomata.

The inclusion of the genus *Christiopteris* in this group results from the work of the senior author on the species formerly included in the genus *Leptochilus* by COPELAND (1928). The results suggest that the genus *Christiopteris*, described by COPELAND because of its acrostichoidy, frond shape, and diplodesmic venation of its fertile parts, is polyphyletic. Comments by COPELAND (1947) on the relative phylogenetic position of the species of this genus, pointed already to its heterogeneity. See for details HENNIPMAN & HETTERSCHEID (1984).

The genus *Podosorus* is listed in this group mainly because of the remarks made by the publishing author (HOLTTUM 1966), on its resemblance to *Microsorium tenuilore* (J. Smith) Copel. and/or *Diblemma*. SEN & HENNIPMAN (1981) found exclusively copolocytic stomata to occur in *P. angustatus* Holttum, hence an argument in favor of its grouping along with true microsorioids (the indication in SEN & HENNIPMAN, op. cit., p. 183, that only polocytic stomata occur in this species, is an error; compare their comments on p. 196).

The genus *Neocheiropteris* is usually placed in the alliance of *Pleopeltis* which includes the Polypodiaceae with peltate paraphyses. Recent investigations on the paraphyses of the Polypodiaceae revealed the existence of two major types of peltate paraphyses using morphological and ontogenetical criteria (pers. comm. R. P. BAAYEN). The type of peltate paraphyses found in *Neocheiropteris* is also present in the genera *Belvisia*, *Lemmaphyllum*, *Lepisorus*, *Paragramma*, and *Neolepisorus*. Investigations on the spores of these genera carried out by HENNIPMAN & SEN (in prep.) showed that the first four genera share a unique spore type which is absent in *Neocheiropteris* (see also HENNIPMAN & ROOS 1983). The latter genus finds its position in the group of microsorioids under study because of characteristics of its venation pattern as well as of its stomata (SEN & HENNIPMAN 1981).

Within the selection of microsorioids as delineated above, a character analysis is made of the venation pattern, shape of sterile and fertile fronds, including shape and distribution of the sori. Special attention is paid to the suggestion put forward by HENNIPMAN (1977, p. 38) to unite the genera *Microsorium*, *Colysis*, and *Leptochilus* (incl. *Dendroglossa* and *Paraleptochilus*) because of the profound instability of the soral characters on which these genera were originally based. Furthermore, we will discuss *Microsorium* into more detail as this genus appeared to be surprisingly heterogeneous.

This study is part of a research project on the phylogenetics of the family Polypodiaceae s.str. For details see HENNIPMAN (1984).

Thanks are due to the Directors of the British Museum (Natural History) (BM), the Paris herbarium (P), Royal Botanic Gardens, Kew (K), the Rijksherbarium (L), and the Utrecht herbarium (U) of which herbarium material was received on loan, as well as the authorities of the Botanical Gardens at Leiden and Utrecht for providing living specimens. The greater part of the material studied is present at L and U. The cooperation of Mr. J. GUBBELS, who prepared a significant number of projection photographs and of Miss G. P. VERDUYN, who assisted in preparing the plates, is much appreciated. Thanks are also due to Miss W. SLOOT for typing the manuscript.

2. Material and methods

2.1. Material

The enumeration of the material studied is given in Chapter 5. The taxonomy followed is largely that given by COPELAND (1947); a number of new genera described since are included.

2.2. Methods

2.2.1. Projection photography

Projection photographs of cleared material are prepared according to the method described by HENNIPMAN (1977). Duplicates of photographs are present in L. and U.

2.2.2. Terminology

2.2.2.1. Terminology of venation incl. areoles

The terminology used starts from the idea that the venation pattern of segments should be compared irrespective of whether the segments are primary or secondary segments. This practical procedure is suggested by the fact that the venation pattern of lobes and pinnae in the family Polypodiaceae is essentially the same compared to that of the undivided fronds. The same holds true if comparing lobes and/or pinnae with the apical lobe or pinna. Therefore, if an apical lobe or pinna is absent (e.g. *Drynaria* species) or ill-developed, the venation pattern in lateral lobes or pinnae can be extrapolated to the absent lobe or pinna. The following terms and definitions are used:

Vp: primary vein of a segment (Fig. 1a). The rhachis is the primary vein of S1 (= the lamina; definition see TRYON 1960).

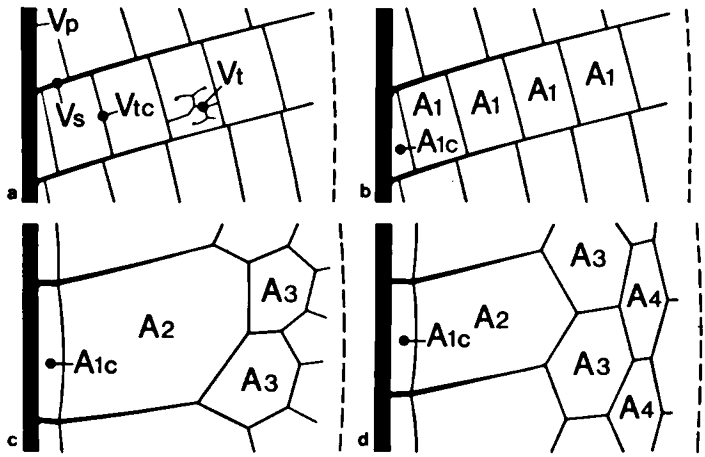

Fig. 1. Terminology of veins and areoles. — a, Terminology of veins. V_p = primary vein. V_s = secondary vein. V_t = tertiary vein. V_{tc} = connective. — b—d, Terminology of areoles. A_1 = primary areole. A_{1c} = costal areole. A_2, A_3, A_4 = main areoles.

Vs: secondary vein of a segment (Fig. 1a); a vein directly branching from a primary vein. If the segment is petiolate, this petiole is excluded from the definition.

Vt: tertiary vein of a segment (Fig. 1a); a vein branching directly from a secondary vein or from another tertiary vein.

Vtc: "connective" (Fig. 1a); those more or less straight tertiary veins that connect two adjacent secondary veins. Usually these veins are more prominent compared to the rest of the tertiary venation.

The tertiary venation is often copiously branched and anastomosed, thus forming areoles (with or without included veins). We distinguish:

— primary areoles (A1, Fig. 1b): areoles bounded by two adjacent secondary veins and two adjacent connectives. They are usually rectangular in outline, rarely quadrangular; their axis usually running parallel to the primary vein. When three or more primary areoles are present between adjacent secondary veins, the venation is called "areole-layered". The primary areole bordering the primary vein is called:

— costal areole (A1c, Fig. 1b): areoles usually narrower that the other primary ones with a less complex included venation. It is bounded by the primary vein, two adjacent secondary veins and their first connective.

— main areoles (A2, Fig. 1c, d): usually large areoles bounded by the primary vein, two adjacent secondary veins and one (not their first) connective. Usually the bordering venation is prominent, the areole outline dome-shaped and polygonal. It should be noted that a main areole includes by definition the costal areole (Fig. 1c, d). In species possessing main areoles, a second or third row of prominent areoles may develop in broad segments. As they are implicitly connected to the existence of main areoles, we have chosen to name them accordingly. However, it must be noted that they are only bounded by secondary and tertiary veins (Fig. 1c, d). Areoles in the first row are coded A3 and may be either regularly (Fig. 1d) or irregularly shaped (Fig. 1c). Areoles in a possible second row are coded A4 and are usually regularly shaped (Fig. 1d). The outline of A3 and A4 areoles is usually rounded and polygonal.

The above described five areole types are considered as primary order areoles. All areoles developed within them by anastomosing included venation, are considered secondary order areoles.

2.2.2.2. Terminology of soral characters

No special terms are used in describing soral shape.

2.2.2.3. Terminology of the frond shape

No special terms are used.

3. Results

The characters observed in the selected species have led to the recognition of a number of more or less distinct groups of species. Within each group, the species show a phenetic similarity to each other with regard to the characters studied.

3.1. Microsorium puncatatum-group (Fig. 2a—g)

Venation distinctly areole-layered, in broad fronds extensive (Fig. 2g), in narrow fronds reduced (Fig. 2d). A1 copiously subdivided into secondary order areoles, containing diffusely directed free included veinlets. Free veinlets in fertile frontparts shortened in length (Fig. 2e) or in number (Fig. 2c). A1c well-developed in narrow fronds (Fig. 2d) to irregularly deformed or absent in broad fronds (Fig. 2b, f).

Sori superficial, round to slightly elongate or irregular, curved, less than 1 mm, numerous to very numerous, scattered all over the frond or restricted to the upper two-thirds or less; situated all over the A1-lamina, on tertiary veins; terminal, subterminal on free veins or midway on anastomosing veins or on branching points of two to four veins. Also present in A1c.

Frondshape elongate, entire, base rarely dilated. Fronds monomorphous.

Representative species: *Microsorium punctatum, M. heterocarpum, M. musifolium* p.p. (see note 1), *M.* spec. *(Hennipman 5619).*

Note 1: Collections of *Microsorium musifolium* studied from L show a mixture of specimens belonging to two different species-groups as here defined. A number of specimens belong to the *M. punctatum*-group, whereas other specimens belong to the *M. zippelii*-group (see below). It is likely that they represent two different species. The decision awaits a taxonomic revision of the microsorioid ferns to be carried out at L during the coming years.

3.2 Microsorium zippelii-group (Fig. 3a—d)

Venation distinctly areole-layered. A1 copiously subdivided into secondary order areoles, containing largely excurrent-recurrent directed free included vein-

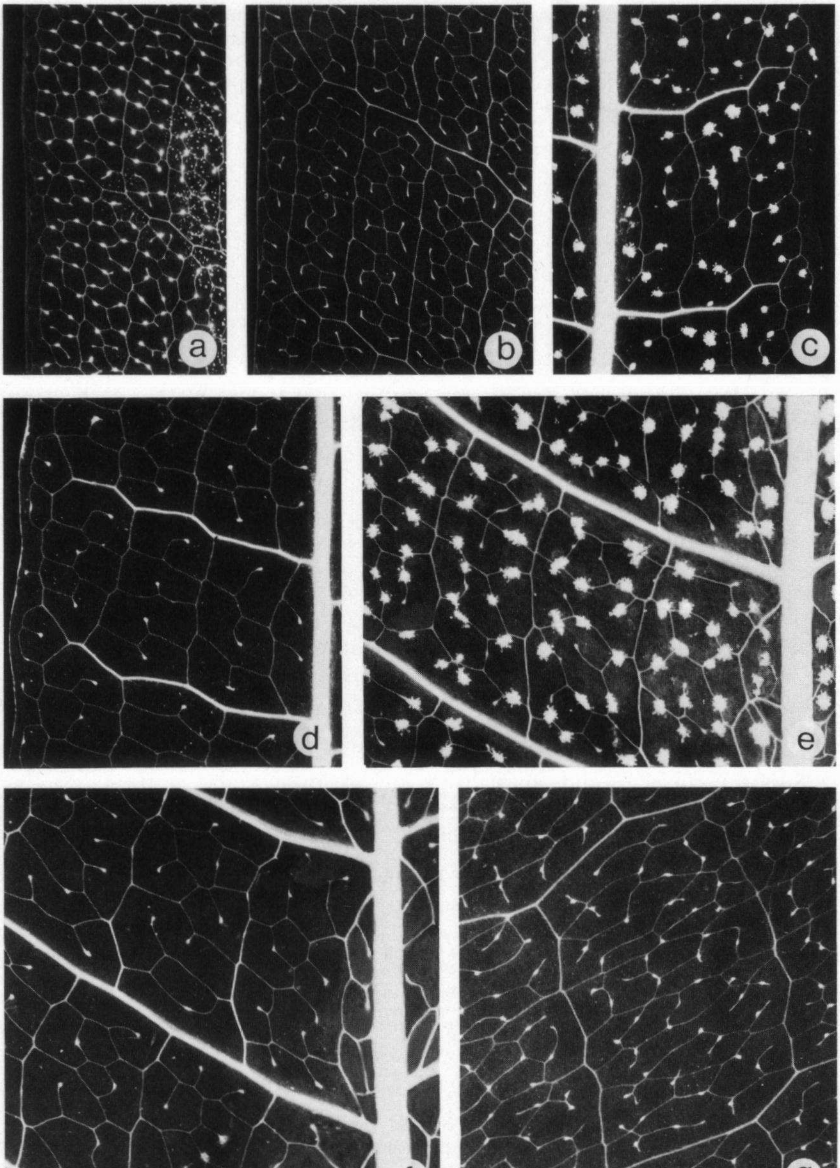

Fig. 2. Venation pattern of fronds. — a, b, *Microsorium punctatum*, a, fert., b, ster. — c, d, *Microsorium* spec., c, fert., d, ster. — e, f, *Microsorium heterocarpum*, e, fert., f, ster. — g, *Microsorium punctatum*, ster. (a, b, *Hennipman 3065*, L. — c, d, *id. 5619*, L. — e, f, *Samat b. Abdullah 257*, U. — g, *Lütjeharms 5151*, L.; all x 2, except g, x 3).

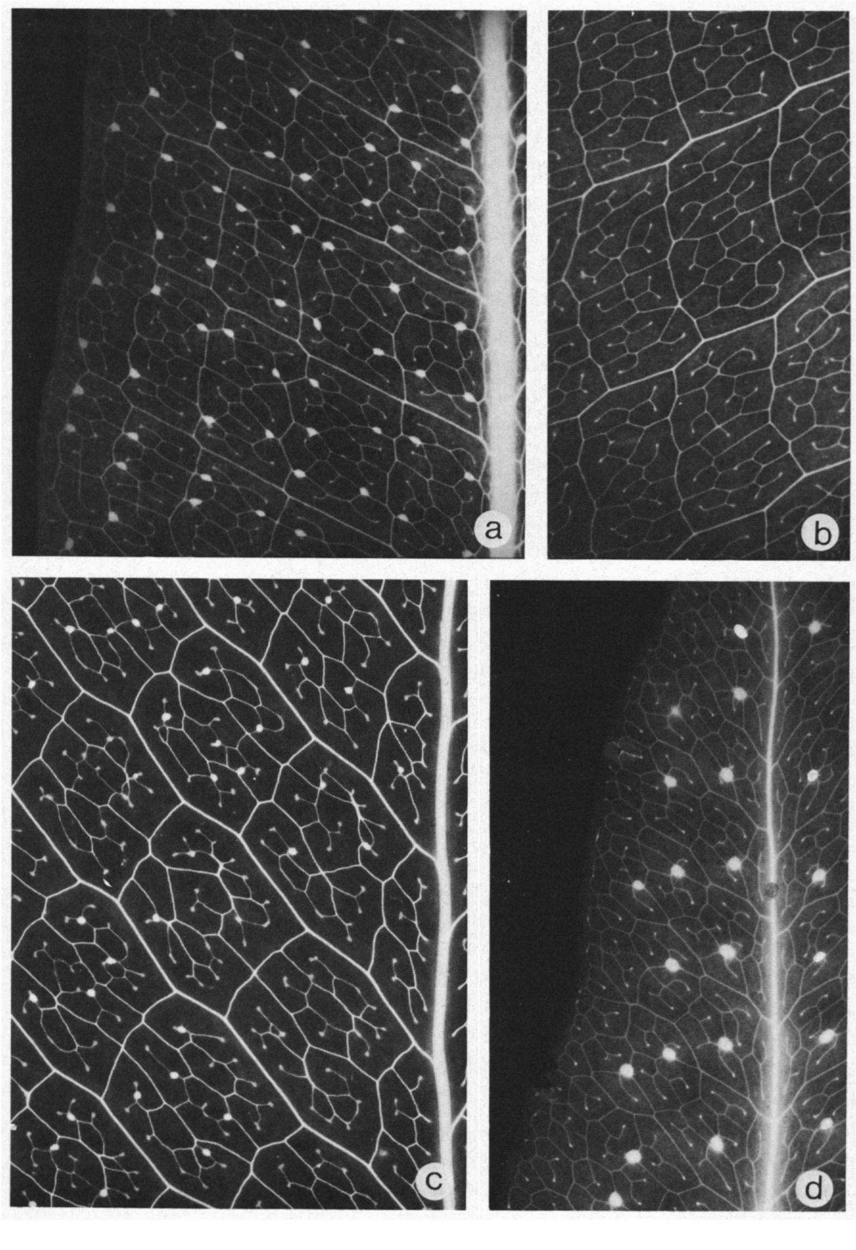

Fig. 3. Venation pattern of fronds. — a, b, *Microsorium* spec., a, fert., b, ster. — c, *Microsorium spectrum*, fert. — d, *Microsorium sarawakense*, fert. (a, b, *Foreman & Vinas, LAE 60249*, L. — c, *Lyon 1169*, L. — d, *Clemens 26943*, L.; all x 2).

lets (Fig. 3b). A1c either well-developed and with usually one recurrent vein, once or twice dichotomous, or irregularly developed or absent. Fertile and sterile venation isomorphous.

Sori superficial, round, relatively large, 1—3 mm, moderately in number to many, situated in the upper two thirds of the frond; situated on branching points in the tertiary venation of two to four veins or rarely midway on anastomosing veins; concentrated along the margins of A1, sometimes arranged in one row on each side of a Vs (Fig. 3a). One (rarely), two or more sori in each A1. A1c always sterile.

Frondshape elongate or ovate, entire, base rarely dilated. Fronds monomorphous.

Representative species: *Microsorium zippelii*, *M. musifolium* p.p. (see note 1 to the *M. punctatum*-group), *M. sarawakense* p.p. (see note 1).

Incertae sedis: *Microsorium spectrum* (see note 2).

Note 1. *Microsorium sarawakense* seems to be rather unstable regarding venation, sorus dimensions, and -distribution. Specimens either confirm to the description and drawing in HOLTTUM (1954: 175—176, fig. 84) and fit the description of the *M. zippelii*-group (these specimens actually look like dwarfed versions of *Microsorium zippelii*), or they fit the description of *Pleopeltis (Microsorium) forbesii* in VAN ALDERWERELT VAN ROSENBURGH (1908; 637). The latter has an irregular pattern of areole-layering with the sori reduced in number, and arranged in a different way (Fig. 3d).

Note 2. In contrast to the above mentioned characteristics of the *M. zippelii*-group, *Microsorium spectrum* has the sori placed subterminally on free veins as well; they are also located in A1c (Fig. 3c). Furthermore, this species has a different frondshape.

3.3. Microsorium membranaceum-group (Fig. 4a, b)

Venation distinctly areole-layered; A1 areoles often irregularly bounded or medially divided by a clearly raised Vt. A1c often irregularly developed with one or more included Vt, or absent; Vt free or anastomosed. Venation in fertile frondparts containing shortened tertiary veins.

Sori numerous superficial, round to slightly elongate or irregularly curved, small to relatively large, less than 1 mm to 2 mm, scattered all over the lower frondsurface or restricted to the upper half, sometimes in one row on each side of a Vs (Fig. 4b); situated midway on anastomosing tertiary veins or on branching points from two to four tertiary veins. A1c also containing sori.

Frondshape elongate or triangular, entire. Fronds monomorphous. Species of this group possess a very membranous frond texture, which is unique among microsorioids.

Representative species: *Microsorium membranaceum*, *M. leandrianum*, *M. (Neocheiropteris) lastii*.

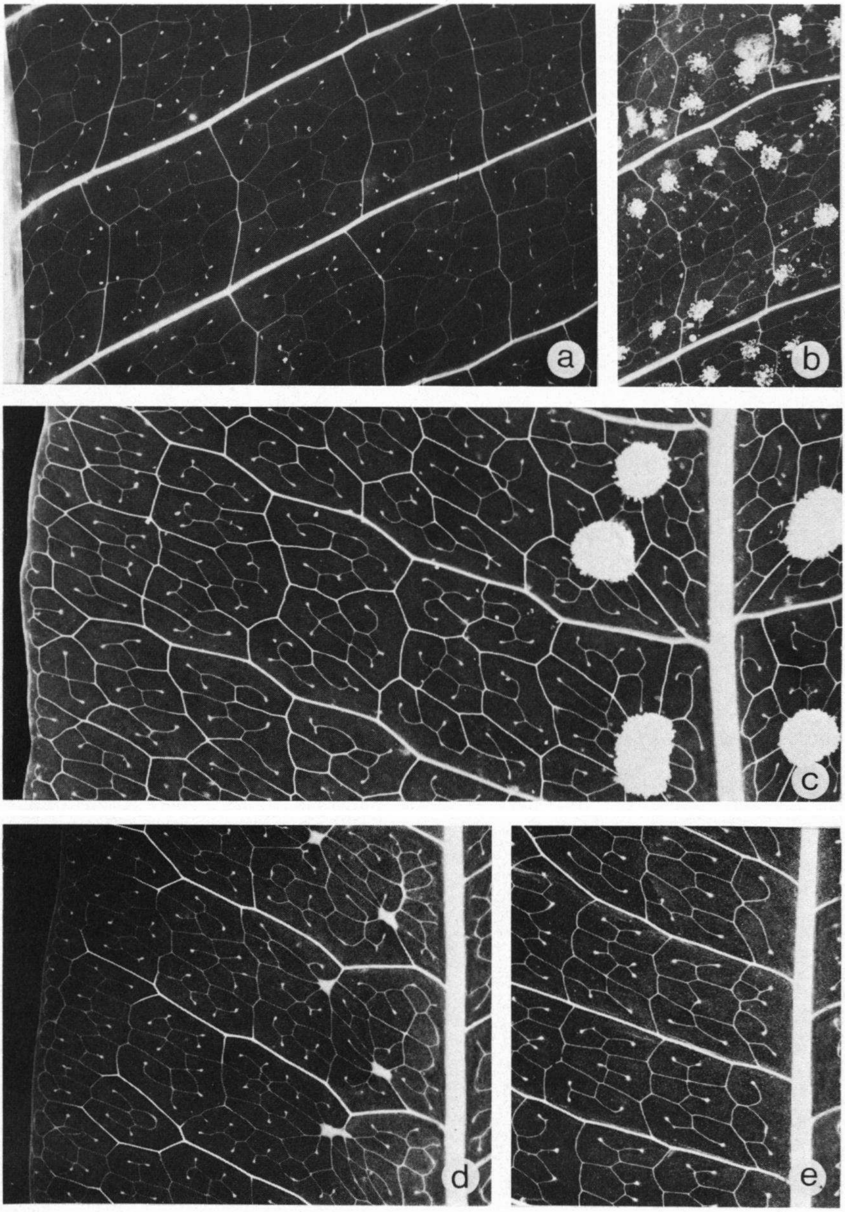

Fig. 4. Venation pattern of fronds. — a, b, *Microsorium membranaceum*, a, ster., b, fert. — c, d, e, *Neolepisorus ensatus*, c, d, fert., e, ster. (a, *Hooker s.n.*, U. — b, *Mridul s.n.*, U. — c, *Tagawa & Iwatsuki 539*, U. — d, e, *id. 3635*, L.; all x 2).

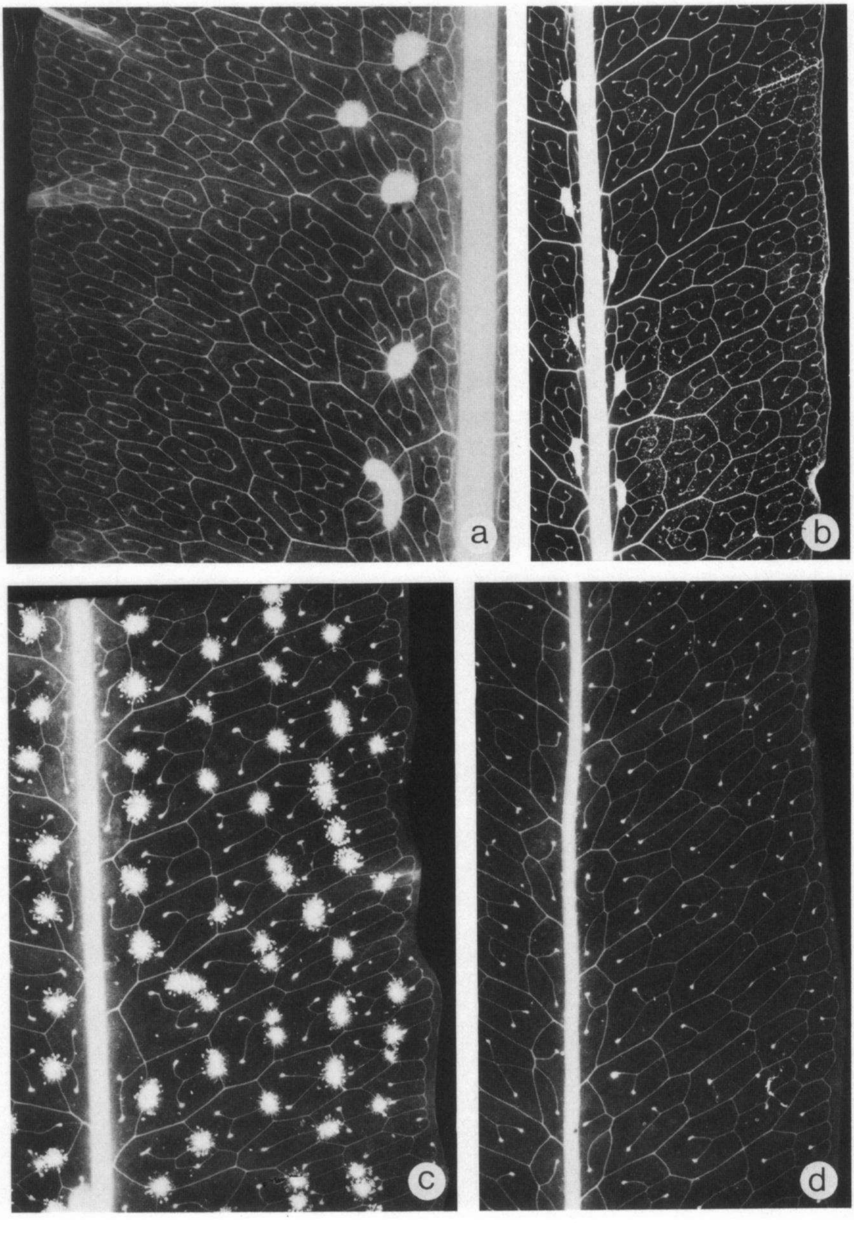

Fig. 5. Venation pattern of fronds. — a, *Microsorium fortunei*, fert. — b, *Neocheiropteris palmatopedata*, fert. — c, d, *Microsorium superficiale*, c, fert., d, ster. (a, *Linsley-Gressitt 348*, L. — b, *Anon. 4126*, L. — c, *Hooker & Thomson s.n.*, U. — d, *Simons s.n.*, U.; all x 2).

3.4. Neolepisorus-group (Fig. 4c—e; 5a)

Venation basically areole-layered. Vs either prominent to the margin or dichotomized anywhere between halfway their length and the margin (Fig. 4d), sometimes, however, becoming immersed near the Vp. A1c always present, containing one or more, simple or branched, free or anastomosed included veins. Tertiary veins in fertile areas directed to the sori.

Sori few to many in number, superficial (rarely slightly sunken), round to slightly elongate, curved, large to very large, 3 to more than 4 mm, inserted in one row on either side of the Vp, or spreading to the margin and arranged in one row on either side of secondary veins; situated on complex branching points in the tertiary venation, one or two (rarely more) sori in each A1; A1c always sterile.

Frondshape elongate or triangular, entire or irregularly lobate, basal lobes sometimes lobed as well. Fronds monomorphous.

Representative species: *Microsorium fortunei, M. pappei, Neolepisorus (Neocheiropteris) ensatus, N. (Neocheiropteris) ovatus.*

3.5. Neocheiropteris palmatopedata (Fig. 5b)

Venation basically areole-layered, but irregularly developed. Secondary veins usually immersed and near to the Vp dichotomous. A1-areoles subdivided in obliquely displaced secondary order areoles, the latter containing basically recurrent included veins. A1c irregularly developed or absent, very narrow containing one or more free, included veins. In fertile frondparts the venation is directed to the nearby sorus.

Sori superficial, elongate to linear, sometimes confluent, large; linear sori broad; restricted to the lower frond half or less; situated over the connectives of the costal areoles and their branching points with other veins (Fig. 5b).

Fronds palmatopedately lobed; basically monomorphous, but in the most basal parts of fertile fronds, the lamina may be reduced or absent (the latter specifically when the sori are confluent to linear).

Representative species: *Neocheiropteris palmatopedata.*

3.6. Microsorium buergerianum-group (Fig. 5c, d)

Venation usually areole-layered; in very narrow fronds the number of A1 areoles reduced; A1-areoles basically either undivided, with one or two recurrent, simple or once dichotomous included veins, or medially divided in two more or less equally shaped secondary order areoles, containing a free recurrent vein, simple or once dichotomous. The areole-dividing Vt-veins sometimes continuous, resembling secondary veins (Fig. 5c). The secondary order areoles sometimes obliquely displaced (Fig. 5d). In less complex venations, the A1-areoles are remarkably small and regularly shaped throughout the frond. A1c always present, regularly shaped throughout the frond, containing one or two simple or once dichotomously branched veins.

Sori scattered all over the frond, superficial, round to slightly elongate or irregular, 1—2 mm; almost exclusively on the connectives, either midway or on branching points, usually two on each connective; scattered all over the frond. A1 always sterile.

Frondshape elongate or triangular, entire. Fronds monomorphous.

Representative species: *Microsorium buergerianum, M. superficiale, M. (Neocheiropteris) subhastatum.*

3.7. Microsorium normalis-group (Fig. 6a, b)

Venation built up from primary areoles but very irregularly developed. The secondary order areoles are irregularly displaced, containing recurrent included free veins, which are either simple or once dichotomous. The secondary veins are dichotomized very near the Vp, immersed and because of this hardly discernable. A1c always present, either regularly or irregularly developed throughout a frond; containing one or a few, simple or once dichotomous, usually free veins. Venation near sori irregular. A1c always sterile.

Sori superficial, round or slightly elongate or irregular, 1—3 mm, concentrated in one row on either side of the Vp or spreading over the surface to marginally displaced; situated on branching points of two to four (rarely more) tertiary veins.

Frondshape elongate, entire. Fronds slightly dimorphous to dimorphous, fertile fronds narrowed.

Representative species: *Microsorium (Neocheiropteris, Tricholepidium) normale, M. hymenodes.*

3.8. Leptochilus axillaris (Fig. 6c—e)

Venation of sterile fronds: no veins prominent; basal part of secondary veins shortened, their first branching point retracted to the Vp. A1 divided in much the same way as in fertile fronds of a number of *Colysis* species (see below). The areole-dividing tertiary veins are continuous as to their longest axis, imitating secondary veins. Free included veins arranged in an excurrent-recurrent way. A1c asymmetrical as in *Colysis* species. Venation in fertile fronds: extremely reduced and hardly distinguishable, probably diplodesmic.

Sori acrostichoid, possibly marginally placed (Fig. 6e).

Frondshape of sterile fronds elongate, base sometimes a little dilated. Fertile fronds extremely narrowed, linear. Occasionally fronds are partly sterile, partly fertile.

Representative species: *Leptochilus axillaris.*

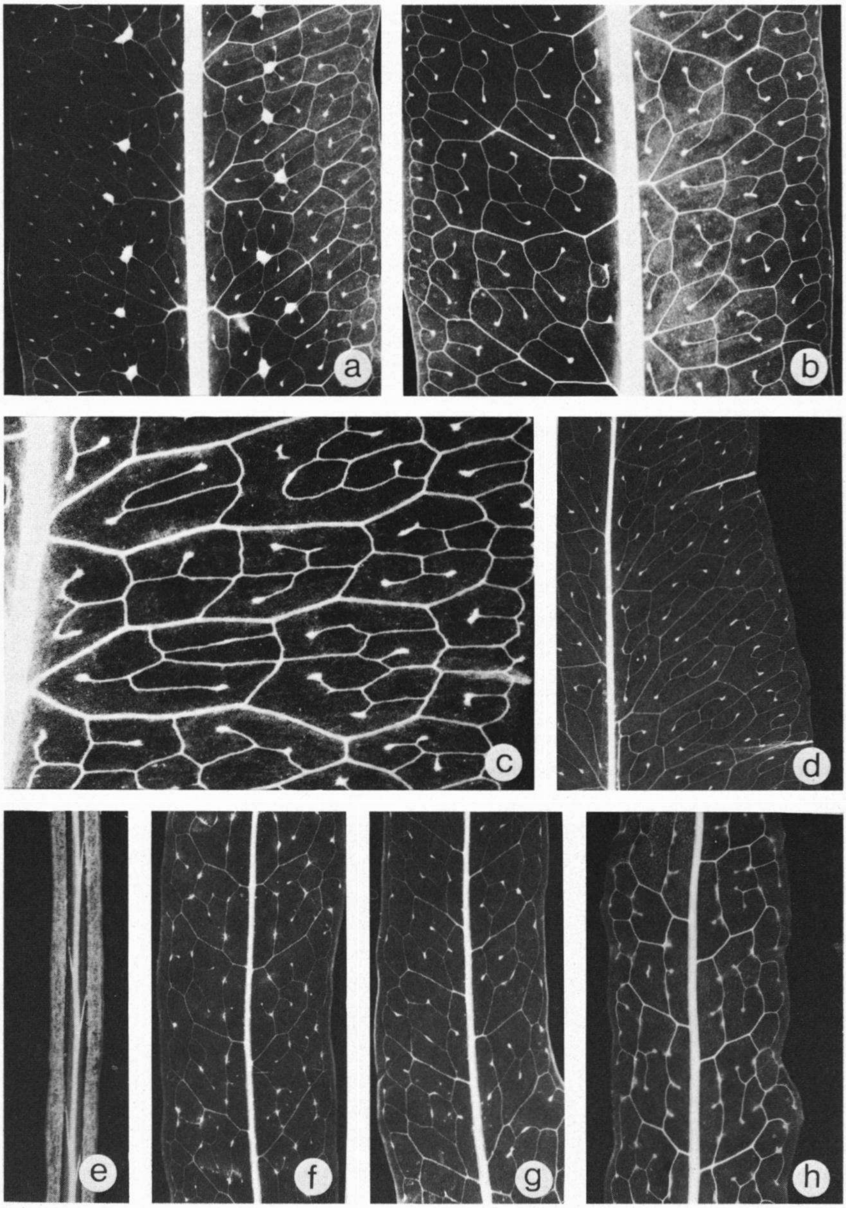

Fig. 6. Venation pattern of fronds. — a, b, *Microsorium (Neocheiropteris) normale*, a, fert., b, ster. — c, d, e, *Leptochilus axillaris*, c, d, ster., e, fert. — f, g, *Microsorium insigne*, f, fert., g, ster. — h, *Microsorium pentaphyllum*, fert. (a, b, *Hennipman 3393*, L. — c, *Sulit, PNH 8728*, L?. — d, e, *Kostermans 71*, L. — f, g, *Chew et al. 577*, L. — h, *Elmer 10768*, L.; all x 2, except c, x 3).

3.9. Microsorium pentaphyllum-group (Fig. 6f—h)

One or two primary areoles (rarely more) between adjacent secondary veins, containing usually one recurrent Vt which is often free, sometimes dividing the areole. A1c always present, with one recurrent, rarely branched, vein. The venation is immersed, soriferous Vt-veins shortened.

Sori round, slightly elongate or irregular; appr. 1 mm; numerous, scattered all over the frond. Situated on shortened Vt-veins or on the connectives, in the latter case always two per connective.

Fronds regularly lobate, monomorphous.
Representative species: *Microsorium pentaphyllum, M. insigne.*

3.10. Colysis-group (Fig. 7a—j; 8a—e)

Venation in sterile fronds: either with a few primary areoles situated between adjacent secondary veins, or areole-layered. A1 hardly to copiously subdivided by tertiary veins. Less complex venations with many recurrent free included veinlets, which are either simple or once dichotomous. A1c usually well-developed (except in a few very complex venations), often with the branching point of the bordering connective situated near the Vp (Fig. 7c). Venation in fertile fronds: slightly dimorphous species have the primary areoles divided by the Vt, carrying the coenosorus; as regards the two more or less equally-sized secondary order areoles, the apical one is situated closest to the margin (Fig. 7c); in species with more or less smaller individual sori, the venation is monomorphous. In distinctly dimorphous species the venation below the receptacle is diplodesmic; as a consequence of laminar reduction, the venation becomes reduced.

Sori superficial or slightly sunken, rarely round (Fig. 8a) or irregularly patch-like (Fig. 8c) slightly elongate (Fig. 8b) or linear (coenosorus Fig. 7c) to acrostichoid (Fig. 7h), narrow or broad; individual sori either irregularly arranged between adjacent secondary veins (Fig. 8a) or arranged in one row between them (Fig. 8b); coenosori also in between and parallel to adjacent secondary veins (Fig. 7c). Individual sori 1—2 mm. Sori situated midway on anastomosing tertiary veins or on simple branching points.

Fronds elongate, ovate, or obovate; entire, regularly lobate or digitately lobate. Slightly or strongly dimorphous, the fertile fronds linear in dimorphous species.

Representative species: *Colysis* spp., *Leptochilus* spp. (excluding *L. axillaris*), *Paraleptochilus decurrens, Dendroglossa minor.*

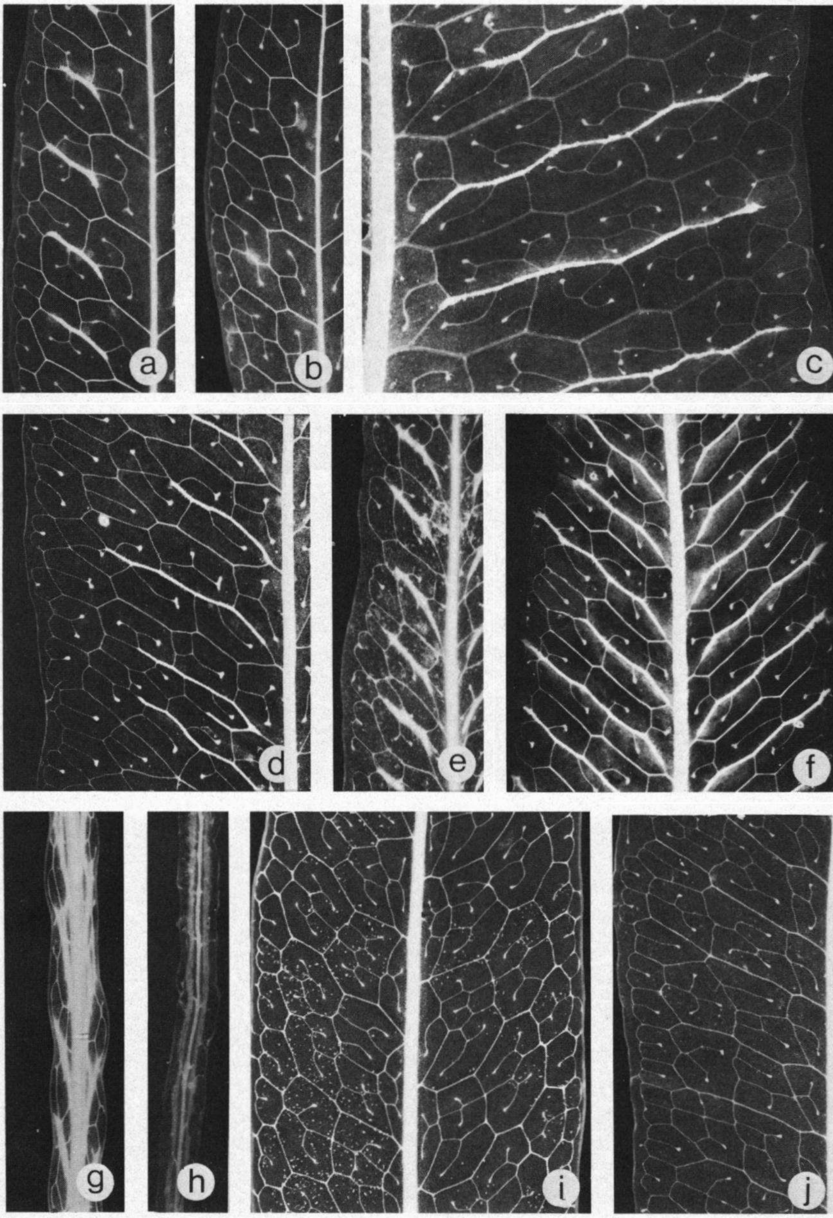

Fig. 7. Venation pattern of fronds. — a, b, *Colysis sayeri*, a, fert., b, ster. — c, f, *Colysis wrightii*, fert. — d, *Colysis elliptica*, fert. — e, j, *Colysis membranacea*, e, fert., j, ster. — g, i, *Leptochilus* spec. (*L. lanceolatus*?), g, fert., i, ster. — h, *Dendroglossa minor*, fert. (a, b, *v. Balgooy 1503*, L. — c, *Tagawa & Iwatsuki 4924*, L. — d, *Hennipman 3391*, L. — e, j, *Merrill 10493*, L. — f, *Walker 7617*, L. — g, i, *Kostermans 6031*, L. — h, *Ramos, BS 20400*, L.; all x 2).

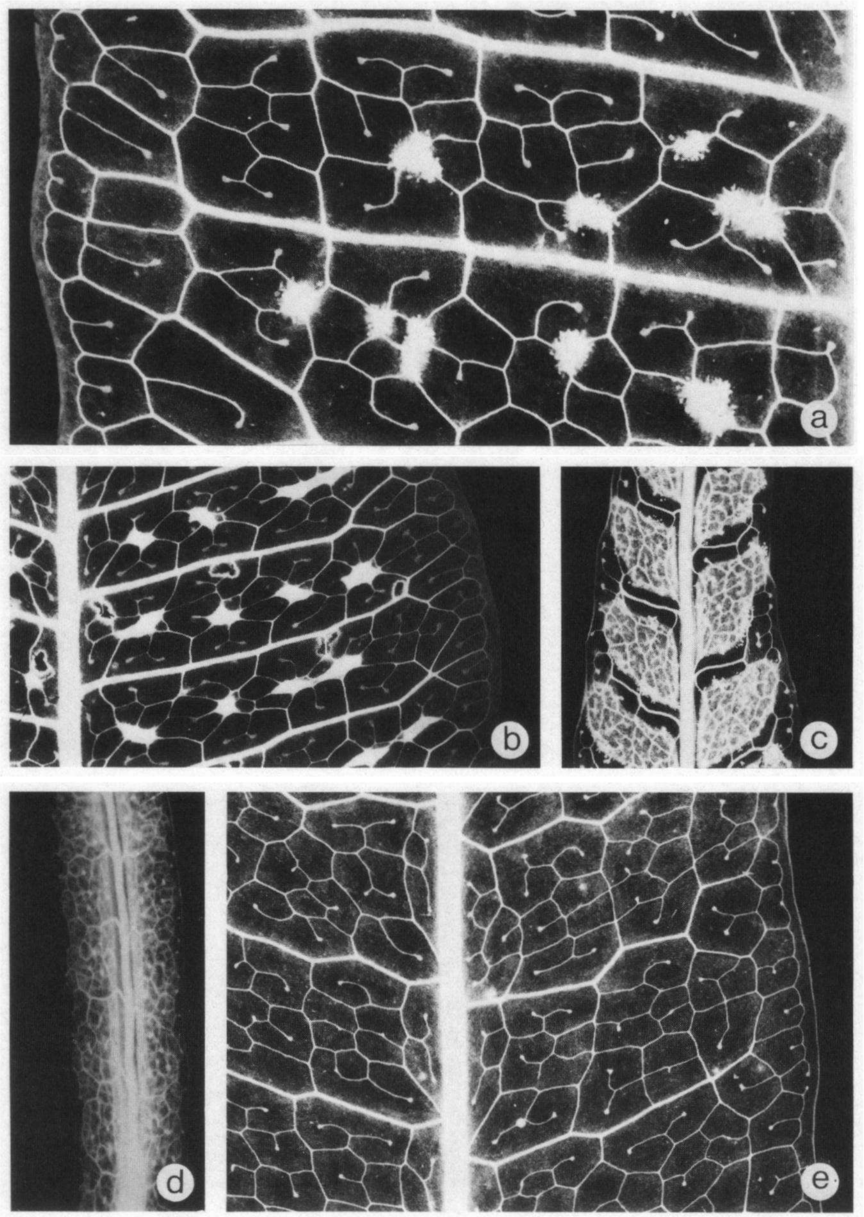

Fig. 8. Venation pattern of fronds. — a, b, *Colysis hemionitidea*, fert. — c, d, e, *Paraleptochilus decurrens*, c, d, fert., e, ster. (a, *Hennipman 3388*, L. — b, *Tagawa & Iwatsuki 3148*, L. — c, *v. Beusekom & Phengkhlai 202*, L. — d, e, *Hennipman 3836*, L.; all x 2, except a, x 3).

3.11. Microsorium scandens-group (Fig. 9a—e)

One or two A1-areoles between adjacent secondary veins, but in very narrow frondparts even absent. A1-areoles usually medially divided in two secondary order areoles, each containing one free included vein, either simple or once dichotomous. A1 always present, regularly shaped throughout the frond, containing one recurrent included vein, once dichotomous, sometimes the basiscopic branch again dichotomous. Venation near sori slightly directed towards it.

Sori pustulate, round, rarely slightly elongate, 1—3 mm, in one row on either side of the Vp or in one row along the margin. Situated on the branching point of the A1c-connective and the A1-dividing Vt, or sometimes marginally displaced at the end of the latter vein (Fig. 9e).

Fronds elongate, entire or regularly lobate. Fronds slightly dimorphous, fertile fronds narrower.

Representative species: *Microsorium scandens, M. diversifolium, M. vieillardii, M. novae-zealandiae.*

3.12. Microsorium powellii-group (Fig. 9f, g)

Venation consisting of immersed A2-areoles, sometimes also a row of A3-areoles present. Included venation of A2-areoles relatively simple but anastomosed, free included veins of secondary order areoles directed largely excurrent-recurrent. A1c always present, regularly shaped throughout the fronds, containing one recurrent free included vein, usually once dichotomous. Venation near sori slightly directed to it.

Sori sunken (usually slightly so), round, 1—3 mm, in one or two rows on either side of Vp; situated on the branching point of the A1c-bordering connective and its first off-branching Vt. This particular Vt is much reduced, and so its marginal branches are retracted to the sorus (compare this particular part of the venation in sterile and fertile parts). The soriferous branching point thus contains usually four veins. Sori in a second row situated on a branching point of a few veins in the A3-areoles. Always one sorus present in each A2 or A3-areole.

Fronds regularly lobate or once pinnate, slightly dimorphous, fertile frondparts narrower.

Representative species: *Microsorium (Phymatodes) lucidum, M. (Ph.) sibomense, M. (Ph.) powellii.*

3.13. Lecanopteris-group (Fig. 9h—j)

One or two primary areoles between adjacent secondary veins. A1-areoles either rectangular or divided into two slightly obliquely displaced secondary

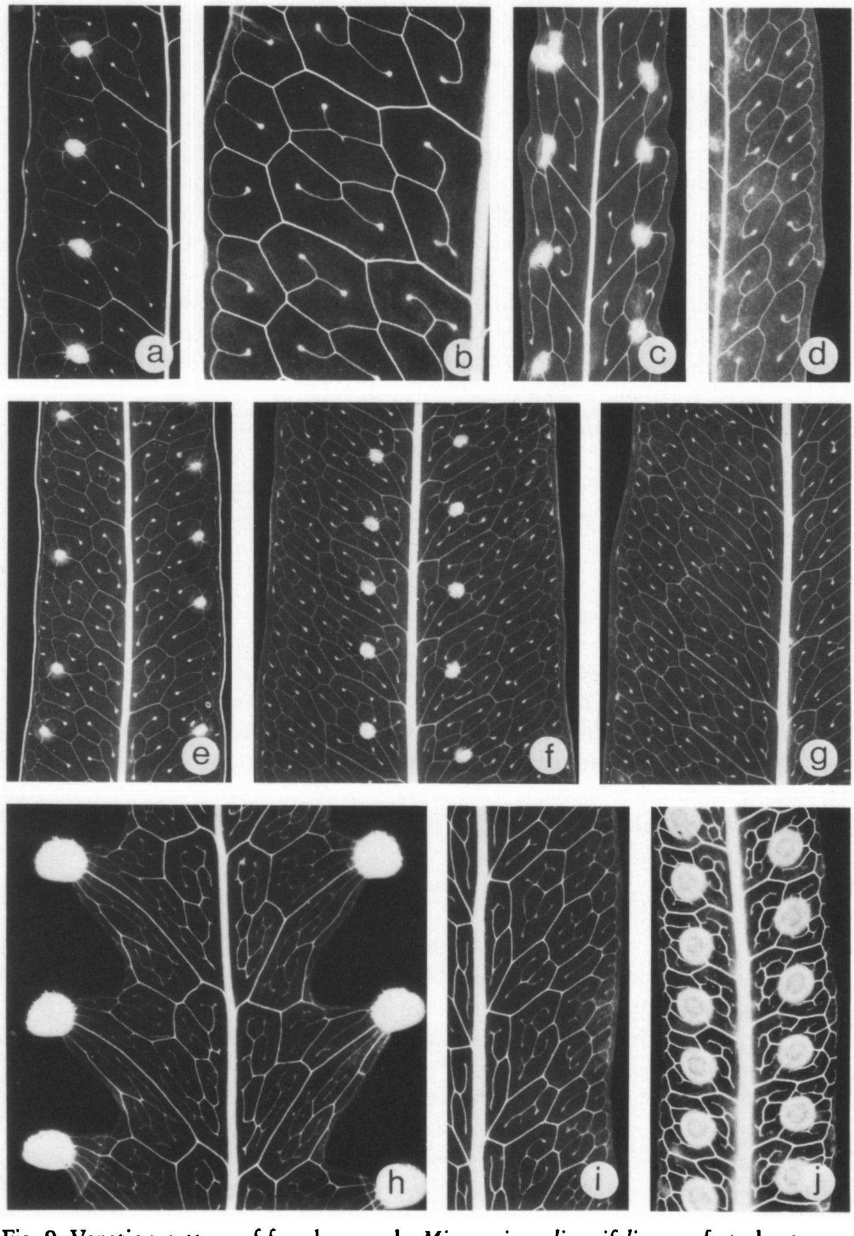

Fig. 9. Venation pattern of fronds. — a, b, *Microsorium diversifolium*, a, fert., b, ster. — c, d, *Microsorium scandens*, c, fert., d, ster. — e, *Microsorium vieillardii*, fert. — f, g, *Microsorium lucidum*, f, fert., g, ster. — h, i, *Lecanopteris* spec., h, fert., i, ster. — j, *Lecanopteris* aff. *L. crustacea*, fert. (a, b, *Varekamp 64*, L. — c, d, *Posthumus 3870*, L. — e, *Franc 340*, L. — f, g, *Bir. s.n.*, U. — h, i, *Hennipman 5993*, L. — *Pullen 7977*, L.; all x 2).

order areoles. Secondary order areoles containing one recurrent included vein, simple to copiously branched and anastomosed, free vein endings directed excurrent-recurrent. A1c always present and regularly shaped thoughout the frond, containing one recurrent included vein, usually copiously branched (rarely only once or twice dichotomous) and anastomosed. Venation in fertile parts either reduced (narrow lamina) or strongly directed to the sorus. Venation below the receptacle diplodesmic.

Sori pustulate, round or slightly elongate, in one row on either side of the Vp; situated either on the branching point at the A1c bordering connective and the first Vt (due to the large sori, a number of other tertiary veins are involved as well), or situated on the marginal end of the latter vein (also a complex branching point) and then extramarginal (Fig. 9h).

Fronds elongate, regularly lobate, partly lobate, partly pinnate or entirely pinnate. Fronds either partly (apically) or entirely fertile, fertile parts contracted.

Representative species: *Lecanopteris crustacea*, *L. lomarioides*, *L.* spec. (*Hennipman 5665* and *5993*, L).

3.14. Phymatodes scolopendria-group (Fig. 10a—d)

Venation consisting of A2-, A3- and A4-areoles, depending on the width of the frondpart. A2-areoles immersed or very prominent, dome-shaped or rarely much elongated perpendicularly to the Vp. Included venation copiously branched and anastomosed, developing a large number of secondary order areoles. Free included veins either directed excurrent-recurrent or diffuse. A1c always present, rarely irregularly developed, containing one or more, variously branched or anastomosed, included veins. A3-areoles regular or irregular throughout the frond. A4-areoles irregular. Venation near sori directed towards it, below the receptacle diplodesmic.

Sori pustulate, round or elongate, sometimes confluent, 2—4 mm or more, in one, two or three rows on either side of Vp, one in a main areole; situated on complex branching points of the tertiary venation in the centre of the areole, but basically as described in the *Lecanopteris* group (never extra-marginal).

Frondshape elongate, entire or regularly lobate. Fronds either partly (apically) or entirely fertile. Fertile fronds or frondparts slightly contracted.

Representative species: *Phymatodes scolopendria*, *P. nigrescens*, *P. papuana*, *P. cromwellii*, *Lecanopteris sinuosa*.

3.15. Microsorium commutatum-group (fig. 10e; 11a—c)

Venation either regularly consisting of A2- (plus A3- and A4)-areoles or regularly consisting of A1-areoles, or very unstable, developing patterns inter-

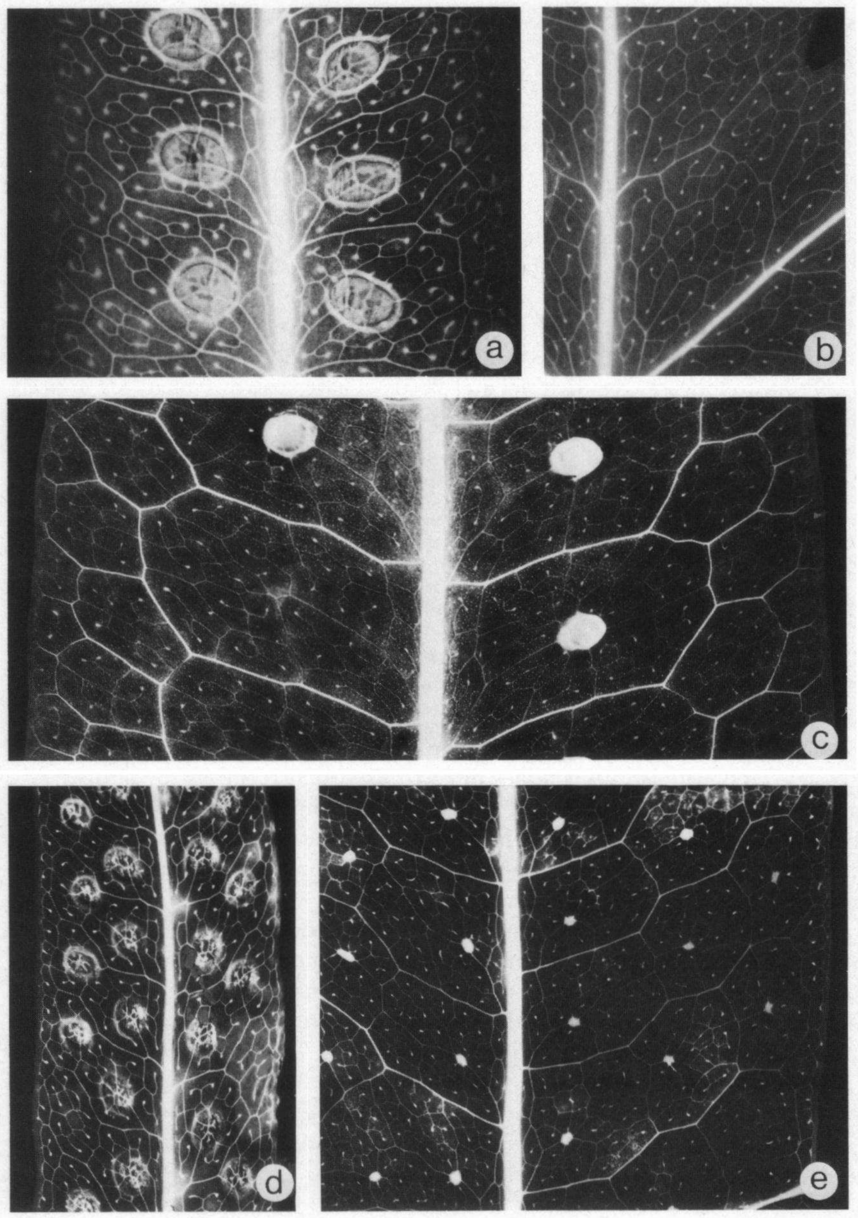

Fig. 10. Venation pattern of fronds. — a, *Phymatodes papuana*, fert. — b, d, *Phymatodes scolopendria*, b, ster., d, fert. — c, *Phymatodes nigrescens*, ster., fert. — e, *Microsorium commutatum*, fert. (a, *Kostermans & Soegeng 587*, L. — b, *Kalkman 4215*, L. — c, *Brass 23520*, L. — d, *Nedi & Idjan 164*, L. — e, *Croft, LAE 61152*, L.; all x 2).

mediate between both extremes mentioned. Main areoles in at least two rows (A2 and A3) often three (A4), either clearly separated from each other (Fig. 10e) or hardly so, because of immersed connectives (Fig. 11a). In the latter case, the main areoles are sometimes irregularly bounded (Fig. 11b) and tend to develop as A1-areoles (especially apparent because of a prominence of the secondary veins, which are arranged in a much more straight way). In the other extreme, a number of narrow A1-areoles is present between adjacent secondary veins in a very regular pattern.

A1c-areoles in the main areole patterns either present or absent, regularly or irregularly developed, containing one or more, simple or hardly branched, rarely anastomosed, included veins. In the other extreme the A1c is always present and regularly developed, containing one or two, simple or once dichotomous, included veins.

Included venation in A2-, A3- and A4-areoles complex, free veins directed diffusely; in A1-areoles relatively simple free veins directed excurrent-recurrent. Fertile venation similar to sterile parts, or very slightly directed to the sorus.

Sori superficial or slightly sunken, round, slightly elongate or confluent, 1—2 mm (rarely larger), in two or three regular rows on each side of the Vp, irregularly arranged, or in one row on each side of the secondary veins. Usually one sorus centrally in each main areole, sometimes two, irregularly placed in a main areole, or two in each A1-areole and over the entire frond regularly placed. Sori situated on not very complex branching points of the tertiary venation (3—5 veins) or midway on anastomosed tertiary veins.

Fronds regularly lobate, monomorphous, or slightly to rarely distinctly dimorphous; fertile fronds or frondparts contracted.

Representative species: *Microsorium commutatum, M. polynesicum, M. alatum.*

3.16. Microsorium varians-group (figures see HENNIPMAN & HETTERSCHEID 1984)

Venation basically consisting of main areoles (A2, A3, rarely A4). A2-areoles very large, prominent; included tertiary venation very complex, immersed or partly prominent, consisting of numerous secondary order areoles. With free included veins diffusely directed. A3-areoles accordingly, somewhat irregularly shaped. A1c always present, but highly irregularly developed throughout the fronds, containing one, simple or branched, free or anastomosed included vein. In narrower frondparts the venation is reduced accordingly, the main areoles disappearing. In the narrowest frondparts only secondary order areoles are present apart from the costal areoles. The costal areoles are then regularly shaped, containing one or two included veins, which are twice or more branched, free or anastomosed.

Venation in fertile parts much reduced, weakly diplodesmic.

Sori acrostichoid, covering the total frondsurface. Frondparts are rarely partly sterile, partly fertile.

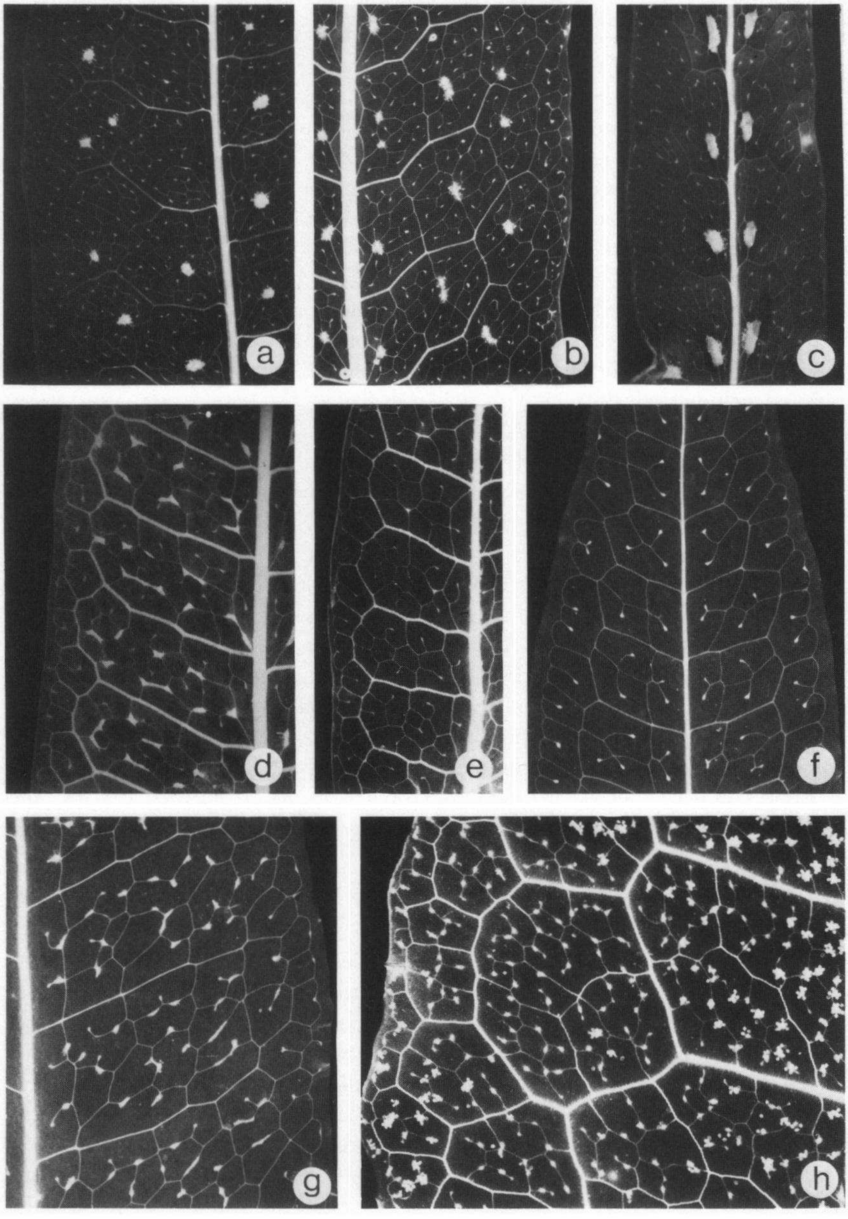

Fig. 11. Venation pattern of fronds. — a, *Microsorium commutatum*, fert. — b, *Microsorium polynesicum*, fert. — c, *Microsorium* aff. *M. commutatum*, fert. — d, e, *Microsorium pteropus*, d, fert., e, ster. — f, g, *Microsorium hancockii*, f, ster., g, fert. — h, *Microsorium sablanianum*, fert. (a, *Croft, LAE 65584*, L. — b, *Vaupel 40*, U. — c, *Croft, LAE 60581*, L. — d, e, *Hennipman 3955*, L. — f, *Anon. s.n.*, L. — g, *Linsley-Gressitt 271*, L. — h, *Sulit, PNH 20241*, L.; all x 2).

Fronds regularly lobate (both sterile and fertile), extremely dimorphous, fertile fronds much contracted.

Representative species: *Microsorium varians, M. latilobatum.*

3.17. Microsorium pteropus-group (Fig. 11d—g)

Venation basically consisting of main areoles, usually only of the A2-type which are extended almost to the margin. Sometimes the bordering connective becomes immersed and the tertiary venation arranged in A1-type areoles. Both states can be found in one frond. A2-areoles either prominent or partly immersed; included venation simple or complex and divided into numerous secondary order areoles. Free included veins directed diffusely. A1c always present, but often irregularly developed, with one or two, simple or once dichotomous, rarely anastomosed, included veins. In fertile frondparts the free tertiary veins are shortened.

Sori superficial, round or elongate, irregular, appr. 1 mm, scattered over the surface of A2-areoles (or their approximate equivalents in the more or less areole-layered types), but not beyond; either terminal on free veins (rarely), or subterminal, or running irregularly over anastomosed veins and their branching points. A1c also containing sori.

Frondshape elongate, entire, or regularly lobate. Fronds monomorphous.

Representative species: *Microsorium pteropus, M. hancockii.*

3.18. Microsorium sablanianum-group (Fig. 11h; 12a—e; 13a, b)

Venation basically consisting of main areoles, but in narrow fronds reduced to only secondary order areoles and the costal areoles. A2-, A3- and A4-areoles prominent, included venation rarely totally immersed but often partly prominent, highly complex and containing numerous secondary order areoles. A2-areoles rarely regularly shaped throughout the frond, A3- and A4-areoles always irregular. A1c often absent, but if present highly irregularly developed, only in very narrow fronds less irregular. Free tertiary veins in fertile parts shortened.

Sori superficial, round, slightly elongate or confluent to a coenosorus (marginal), less than 1 mm, scattered all over the frond, or partly or entirely marginal; situated terminally or subterminally on free veins or midway on anastomosed veins and their branching points. A1c also containing sori.

Frondshape broadly elongate to linear, entire or regularly to irregularly lobate. Fronds moderately dimorphous, fertile fronds narrowed.

Representative species: *Microsorium sablanianum, M. bamlerianum, M. longissimum, M. tenuilore, Diblemma samarensis.*

Incertae sedis: *Podosorus angustatus* (see note 1).

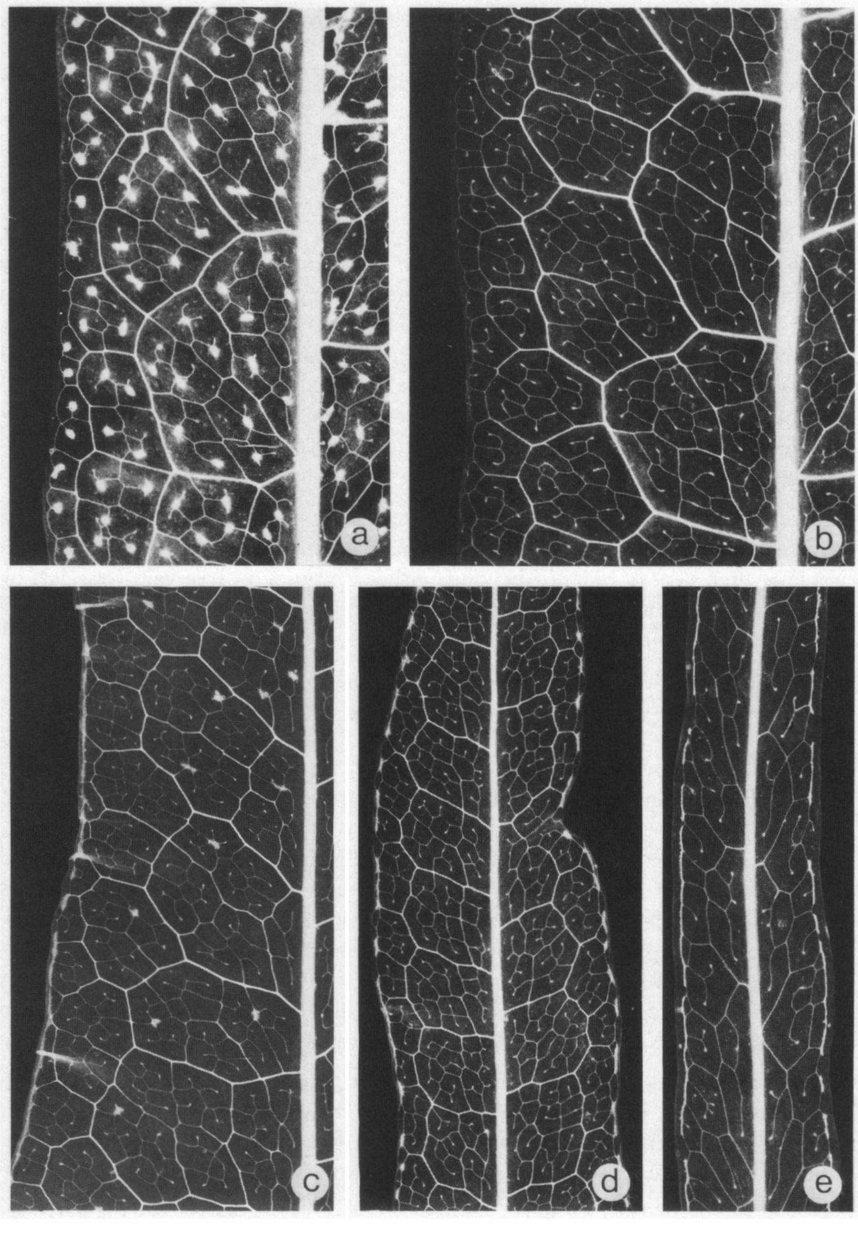

Fig. 12. Venation pattern of fronds. — a, b, *Microsorium longissimum*, a, fert., b, ster. — c, d, *Microsorium bamlerianum*, fert. — e, *Diblemma samarensis*, fert. (a, b, *Floyd 3517*, L. — c. d, *Craven & Schodde 1034*, L. — *Edaño, PNH 15133*, BO.; all x 2).

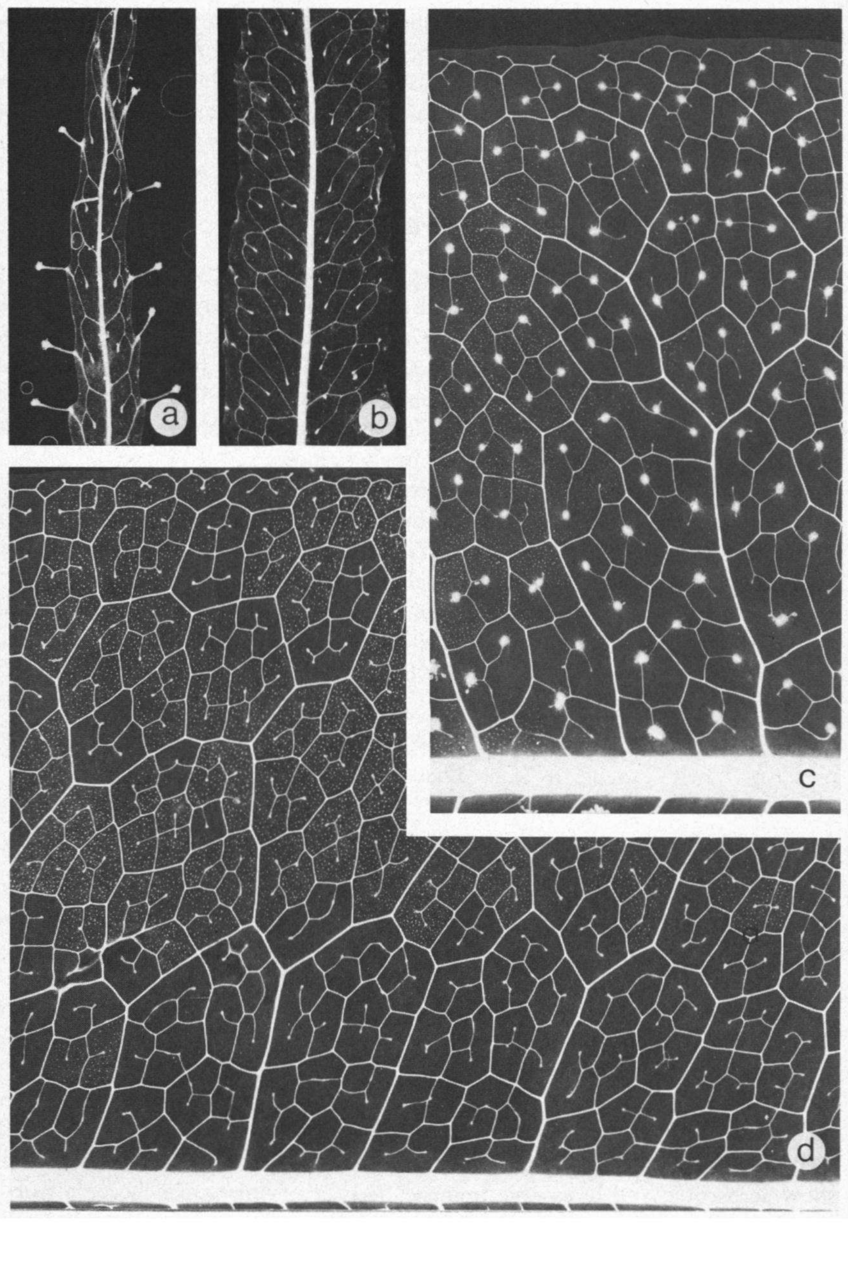

Fig. 13. Venation pattern of fronds. — a, b, *Podosorus angustatus*, a, fert., b, ster. — c, d, *Microsorium linguaeforme*, c, fert., d, ster. (a, b, *Gutierrez, PNH 78332*, L. — c, *Brass 27973*, L. — d, *id. 27434*, L.; all x 2).

Note 1. *Podosorus angustatus* shows a more regular venation than described above (Fig. 13a, b) and is placed here because of the similar linear fronds and the, basically marginally placed, minute sori. The publishing author (HOLTTUM 1966), also mentioned similarities to *Microsorium tenuilore* and *Diblemma.*

3.19. Microsorium linguaeforme-group (Fig. 13c, d)

Venation consisting of main areoles (A2, A3, A4). A2-areoles very large, usually prominent, but sometimes with an immersed bordering venation; the latter also holds true for A3- and A4-areoles. Included tertiary venation immersed or partly prominent, the latter specifically clear for that part of the tertiary venation in A2-areoles, dividing the latter perpendicularly to the Vp. A1c absent. Free tertiary veins in fertile parts shortened, in very dimorphous frondparts the total tertiary venation strongly reduced.

Sori superficial or slightly sunken, round or irregular patch-like, 1—2 mm; either scattered over the upper half of the frond or in one or two, more or less irregular rows, on either side of the Vp, situated terminally or subterminally on free tertiary veins, less often on branching points.

Frondshape either broadly elongate, with or without a dilated base; or almost perfectly round. Fronds with or without a thread-like, fertile apical part.

Representative species: *Microsorium linguaeforme, Dendroconche annabellae.*

4. Discussion

4.1. Venation

The venation in the mature fronds is preceded by usually much simpler patterns present in juvenile fronds. Ontogenetic data of the venation of the microsorioid ferns are far from complete. Those known concerning the group under study are partly collected from MITSUTA (1981, 1982) and partly the result of preliminary studies carried out by students in our research-group. From these data the following general picture of the ontogeny of the adult venation is drawn.

The first sporophytic fronds formed are provided with a single simple vein, i.e. the rhachis. In later formed fronds secondary veins are present. These are at first unbranched becoming apically forked in older fronds. Still older fronds show acroscopic and basiscopic branches (tertiary veins) which become fused, thus bounding the costal areoles (A1c); a single recurrent tertiary vein may develop from the point of fusion. In fronds formed subsequently excurrent veins develop from the outer margin of the costal areole. These are fused adjacently bounding the first row of primary areoles (A1). From this ontogenetical stage two main venation types develop in a characteristic way.

In the first main type of venation primary areoles are present in varying numbers whereas the branching of the tertiary venation shows considerable variation in different species; the A1 bordering venation is either prominent or immersed. This main type of venation is found in representatives of *Colysis, Dendroglossa, Diblemma, Leptochilus, Microsorium, Neocheiropteris, Neolepisorus, Paraleptochilus,* and *Podosorus.*

In the second type of venation there is a more or less prominent main areole formed by two adjacent secondary veins and a — not the first! — connective, and including the costal areole. Next to this main areole (A2) few increasingly smaller areoles may develop in broader fronds. These smaller areoles (A3, A4) may be surrounded by strongly developed parts of secondary and tertiary veins thus developing a second or even a third row of main areoles. The tertiary venation within the areoles is variously developed. This main type of venation is found in representatives of *Dendroconche, Lecanopteris, Microsorium,* and *Phymatodes.*

It should be noticed that in all venations found in the microsoroids studied, the first order areoles are all provided with included free veins showing a recurrent nature (distinctly present in at least the marginal frondparts). These included veins are always more or less curved, variously branched, and usually terminated by a hydathode.

Of the 19 groups of species listed above, the first 13 follow the first main type of venation ontogeny, whereas groups 14—19 follow the second one. These two larger groups of venation are, however, mutually connected by a number of intermediate venations of which the most striking ones are shortly discussed:

— In a number of specimens of *Microsorium heterocarpum* some marginal connectives are prominent suggesting a relatively large-sized marginally extended A2-areole. This, and other characteristics of the present species indicate a phenetic relationship to the *Microsorium sablanianum*-group or the *M. pteropus*-group. In *M. hancockii* (Fig. 11f, g) of the latter group the A2-areole is extended to the margin and includes A1-areoles.

— A different type of transition between A2- and A1-areoles is present in *Microsorium commutatum* and *M. alatum.* The unstable transitional venations found (Fig. 10e; 11a, b) show complete continuity between A2- and A1-areoles respectively. A transition is illustrated for *M. polynesicum.*

— In *Phymatodes scolopendria* the venation of relatively narrow fronds conforms well with A2- and A3-areoles (Fig. 10b, d) whereas in broad frondparts the A2-areoles are much elongated and situated perpendicularly to the Vp with the included veins more or less arranged in A1-like areoles; the A3-areoles are narrowed, rather resembling A1-areoles.

— Another type of transition is suggested after comparing venations with A2-areoles having a rather simple included venation (Fig. 9f, g) with A1-areoles in non areole-layered venations (e.g. Fig. 9a, b, i). In this case the suggestion is made that the only essential difference between these two types of venation, regards the prominence of the A2-bounding venation. The present transition further suggests an equivalence of an A2-areole to an A1c-areole together with the adjacent A1-areole. It is noticed that the location of the sori relative to the venation shows a striking similarity in the species having these different venations. A comparison of the venation of *Lecanopteris sinuosa* (with A2-areoles; *Phymatodes scolopendria* group) and other *Lecanopteris* species (e.g. Fig. 9i) with A1-areoles may suport the suggestions made.

Further studies on the venation of especially juvenile fronds are necessary to further elucidate the phenetical relationships between the venations described above.

4.2. The fertile fronds of Colysis, Dendroglossa, Leptochilus, Microsorium, and Paraleptochilus

4.2.1. Transitions between Colysis, Dendroglossa and Leptochilus p.p.

In atavistic fronds of a number of *Leptochilus* species (e.g. Fig. 7g) and *Dendroglossa minor*, the usually acrostichoid arranged sporangia are broken up into a number of coenosori arranged obliquely to the Vp at a very narrow angle. On the other hand, a number of species of *Colysis* (with linear sori) develop a profound dimorphism, the fertile fronds showing a condition exactly similar to that found in the atavistic fronds of *Leptochilus* and *Dendroglossa*. Transitions are illustrated in Fig. 7c—h. The photographs suggest that narrowing of the fertile fronds coincides with a reduction of the angle between the Vp and Vs, the sori finally fusing into a linear acrostichoid sorus situated on either side of the Vp. All intermediate venations have a rather simple tertiary venation and equally-wide (coeno)sori.

4.2.2. Transition between Colysis hemionitidea and Paraleptochilus

Colysis hemionitidea shows a marked plasticity regarding sorus- and frond-shape. The sori vary from round (Fig. 8a) to elongate, to partly (Fig. 8b) or completely confluent as is typical for the genus. Confluent sori express themselves sometimes as irregular large patches situated between adjacent secondary veins (BEDDOME 1868, Pl. 274) on constricted frondparts. Also, ± completely acrostichoid fertile fronds may be produced. The extremes as to sorus shape may be present on a single specimen! (Fig. 14). In still other species of *Colysis*, fertile fronds may bear broad sori with a wide angle between Vp and Vs. The latter condition is similar to that found in atavistic fronds of *Paraleptochilus decurrens* (Fig. 8c). These taxa further share a relatively complex included tertiary venation. The variation found can be arranged into a possible transforma-

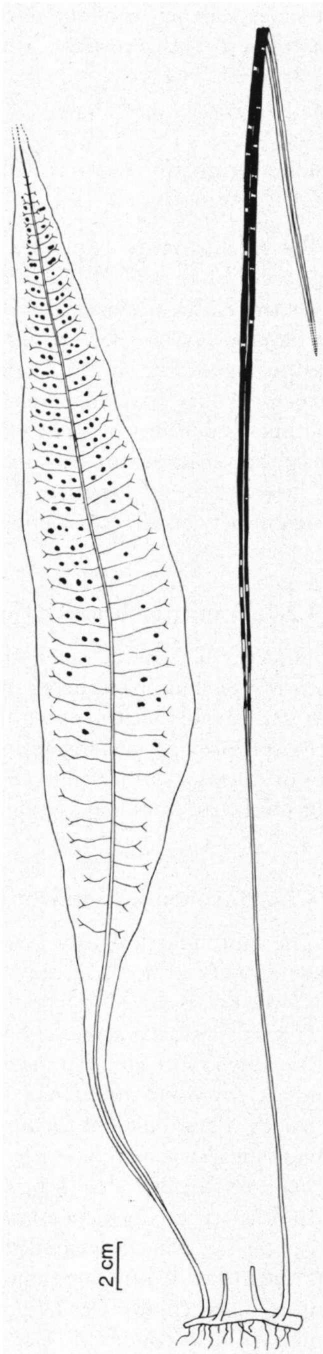

Fig. 14. Drawing of *Colysis hemionitidea* (*Sin 20337*, B), showing two fertile fronds on the same rhizome. The left frond with individual microsorioid sori, the right one almost entirely acrostichoid.

tion series starting from the microsorioid soral condition found in *Colysis hemionitidea* to the acrostichoid condition present in *Paraleptochilus decurrens* (Fig. 8a, c, d).

4.2.3. Transition between Colysis hemionitidea and Microsorium pteropus

The soral variation expressed by *Colysis hemionitidea* includes a soral shape reminiscent of that of *Microsorium pteropus*. In large-sized fronds of the latter species the A2-areoles extend to the margin whereas the included tertiary venation develops A1-areoles. A similar condition in *Colysis hemionitidea* is illustrated in Fig. 8a and in Fig. 14. Further, large-sized broad fronds of *Microsorium pteropus* may have their relatively broad sori arranged in a similar way as sometimes found in *Colysis hemionitidea*. The sori in both are confined to that part of the venation that is thought to be equivalent to the A2-areole as occurring in *Microsorium pteropus*. Therefore, a possible transformation series may be present between *Colysis hemionitidea* and *Microsorium pteropus*.

4.2.4. Transition between Colysis sayeri and Microsorium scandens

There is a striking similarity between *Colysis sayeri* and *Microsorium scandens* regarding frondshape, and characteristics of the sori and venation (Fig. 7a, b; 9a—d). In fact the only difference between the species regards the shape of the sorus which is elongate in *Colysis sayeri* and round (to somewhat elongate) in *Microsorium scandens*. The polarity of the possible transformation series of soral characters is as yet unsolved.

4.2.5. Taxonomic considerations

The morphological data given above strongly question the validity of the character state of acrostichoidy as a character to discriminate between genera within the microsorioid Polypodiaceae.

Nevertheless, the acrostichoid condition is the main criterion on which the genera *Leptochilus* and *Paraleptochilus* are based. The nature of the acrostichoidy in *Leptochilus axillaris* (type species) is as yet not solved, also as atavistic fronds are still, uninformative. Occasionally found broader fronds of this species, suggest a marginal insertion of the sporangia in possibly related taxa (Fig. 6e; see also PRICE 1974, p. 176).

In other species of *Leptochilus* the acrostichoid condition is highly unstable; the species showing this condition may be better merged in *Colysis* (see also HETTERSCHEID 1984). The same holds true for *Paraleptochilus decurrens*. Apart from its acrostichoidy *Dendroglossa* is sometimes also defined by its small-sized fronds. As such conditions also occur in *Colysis* species, e.g. *C. membranacea* from the Philippines, we understand PRICE (1974) who formally transferred *Dendroglossa minor* to *Colysis*.

The morphological similarities between *Microsorium pteropus*, *Paraleptochilus decurrens*, and *Colysis hemionitidea* cannot be used unambiguously for their taxonomy. Starting from the idea that *Colysis* is a monophyletic group with linear sori we may suppose that species with a soral condition as found in *Colysis hemionitidea* gave rise to species with narrow sori as found in other *Colysis* species and in part of *Leptochilus*. As a consequence the soral condition found in *Microsorium scandens* presents a derived condition. Consequently, this species should be transferred to *Colysis*. Following a similar reasoning, *Microsorium pteropus* should also be accommodated in *Colysis*.

Another alternative includes the possibility that the coenosorus as found in *Colysis hemionitidea* developed parallel to that found in other *Colysis* species. As *C. hemionitidea* is the type species of the genus this suggestion, if true, could have significant taxonomic implications. Which of the possible alternative should be followed depends of the results of a thorough systematic revision of all species.

4.3. Diblemma and Microsorium

In the *Microsorium sablanianum* group studied, it is possible to construct a morphological continuum between characterstates regarding the distribution of the sori, the soral shape, and the frondshape as present in *Microsorium* species and in *Diblemma samarensis*. Starting from sori distributed all over the lower surface, there is a tendency to restrict the sori to a marginal zone, being finally situated along the margin only. Associated with this is a gradual narrowing of the frond (Fig. 11h; 12a, c, d, e). In spite of the fact that the soral position in *Microsorium bamlerianum* may be marginal, this species has never been placed in *Diblemma*. This is fortunate as the morphological series produced here suggests *Diblemma* to be part of *Microsorium*.

4.4. Dendroconche and Microsorium

The uniquely shaped fertile fronds of *Dendroconche annabellae* are connected to those found in *Microsorium linguaeforme* through all possible intermediates, one of them represented by the type of *Dendroconche kingii* Copel. (COPELAND 1931, p. 407). From our studies on *Microsorium linguaeforme* it seems possible that *Dendroconche annabellae* is just a local variety of *Microsorium linguaeforme*.

4.5. Lecanopteris and Phymatodes

The phenetic similarity in venation between *Lecanopteris sinuosa* and other *Lecanopteris* species may suggest a relationship to *Phymatodes*. It are especially the species with entire fronds that share the same type of venation and soral characters. It should be remarked that this suggestion is not always supported by character analysis of different features.

4.6. Conclusions

The results presented in this paper illustrate the surprising heterogeneity in the characterstates of the features studied in a representative selection of microsorioid and possibly related Polypodiaceae. One of the main taxonomic questions that can be put forward is the position of the type species of *Microsorium*, *M. punctatum* of which the relationship to other microsorioids is not at all clear. A taxonomic study of this group to be executed in the near future at the Rijksherbarium, Leiden by Miss M.T.M. BOSMAN, will include a detailed morphological study of all species, including a final consideration of the unique morphological expressions of the characters studied.

5. Material studied

Colysis elliptica (Thunb.) Ching: Anon. (U 68391B); Bir s.n. (U 093050B); Devol 9012 (U); Elmer 11164 (U), 13929 (U); Hooker & Thomson 193 (U); Iwatsuki 3872 (U); Iwatsuki et al. T9641 (L); Kurata s.n. (U 205341B); Linsley-Gressit 77 (U); Masao Azuma s.n. (U 48563B); Shiu Ying Hu 9011 (U); Tagawa 2317 (U), 2594 (U), 6179 (U), 8531 (U); Wuyi exp. 1377 (U). — *Colysis hemionitidea* (Wall. ex Mett.) Presl: Anon. (U 68588B); Bir s.n. (U 093049B); Clemens 29624 (L); Fauri 209 (U), 476 (U); Hennipman 3388 (U); Hooker & Thomson s.n. (U 68586B), s.n. (U 68587B); Kurata 6177 (U); Masters s.n. (U 68590B); Ohba 662242 (U); Sin 20337 (B), Tagawa 1434 (L), 1938 (L); Tagawa & Iwatsuki 3148 (L, U). — *Colysis macrophylla* (Blume) Presl: Adelbert 249 (L); Bünnemeyer 4775a (U), 8501 (U); Surbeck 653 (L). — *Colysis membranacea* (Blume) Presl; Brass 8039 (L); Merrill 10493 (L). — *Colysis pedunculata* (Hock. & Grev.) Ching: Hennipman 3881 (L); Poilane 15814 (P); Tagawa et al. T6805 (L). — *Colysis poilanei* C. Chr. & Tard.: McClure 8552 (P); Poilane 5373 (P, type), 5488 (P), 6685 (P), 8455 (P). — *Colysis sayeri* (F. Muell. & Bak.) Copel.: v. Balgooy 1503 (L), 1603 (L). — *Colysis wrightii* (Hook.) Ching: DeVol 9070 (U); Fauri 206 (U), 207 (U); s.n. (U 317953B); Fosberg 37472 (L); Iwatsuki 4924 (U); Nakaike, Tamaki & Nakada 2901 (U); Tagawa & Iwatsuki 4924 (L); Togashi s.n. (U 174878B); Walker 7617 (L).

Dendroconche annabellae (Forbes) Copel.: Hartmann s.n. (BM); King s.n. (BM).

Dendroglossa minor (Fée) Copel.: Edano, PNH 35886 (L); Elmer 13244 (U, L), 16728 (U, L) 12473 (U); Mann s.n. (L 908.328—271); Merrill 616 (U); Ramos, BS 20400 (L).

Diblemma samarensis J. Smith: Cuming 238 (L); Edano, PNH 15133 (BO); Elmer 13259 (L).

Lecanopteris crustacea Copel.: Franken & Roos 341 (L). *Lecanopteris lomarioides* Copel.: Meijer 2511 (L). — *Lecanopteris sinuosa* Copel.: Anon. (U 68688B); Bakhuizen 2475 (U); Bakhuizen v. d. Brink Jr. 2129 (U); Docters v. Leeuwen-Reijnvaan 11579 (L), 12047 (L); Elmer 12065 (U), 18177 (U); Feuilletan & Bruyn 221 (L); Hennipman 3719 (U); Kornassi 58 (U); McGregor, BS 10306 (L); Price 2990 (L); Rutten 6 (U), 56 (U), 781 (U); Teysman 22 (U), 47 (U). — *Lecanopteris spec.*: Hennipman 5665 (L), 5993 (L); Jacobs 9148 (L).

Leptochilus axillaris (Cav.) Kaulf.: Anon. (L 908.315—401); Bloembergers, Kwai Noi Basin exp. 19 (L); Blume s.n. (L 908.286—747); Buysman 260 (U); Kostermans 71 (L); Mousset 901 (U), s.n. (Rosenstock Fil. Jav. Or. exsicc. 25) (L); Sulit, PNH 8728 (L?). — *Leptochilus lanceolatus* Fée: Anon. (U 61410B); v. Beusekom 396 (L); v. Hardeveld & v. d. Werff 324 (U); Kostermans 6031 (L); Perrottet s.n. (B); Stocks s.n. (U 61409B).

Microsorium alatum (Brack.) Copel.: Horne 331 (K); Parks 20248 (K); Seeman 731 (BM); Smith 8843 (K), 9001 (K). — *Microsorium bamlerianum* (Ros.) Copel.: Craven & Schodde 1034 (L); Pullen 7575 (L). — *Microsorium buergerianum* (Miq.) Ching: Anon. NTU 9026 (U); Buerger s.n. (L 908.298—240, type); Fauri 208 (U); Fosberg 37883 (L), 38080 (L); Kurata & Nakaike 706 (U); Tagawa 6162 (U), 7699 (U); Tagawa & Iwatsuki 764 (U); Yukio Ando 254 (U). — *Microsorium commutatum* (Blume) Copel.: Anon. (U 045189); Croft, LAE 60581 (L), LAE 65584 (L), 68119 (L); Croft et al., LAE 61152 (L). — *Microsorium diversifolium* (Willd.) Copel.: Boorman, NSW P3148 (L); Constable, NSW P8264 (L); Croft 601 (K); Davis, NSW P7876 (U); Docters v. Leeuwen-Reijnvaan 7374 (U); Orchard 3398 (U); Philipson 10073 (L); Pichi Sermolli 6187 (U); Varenkamp 64 (L). — *Microsorium fortunei* (Moore) Ching: Anon. 341 (K); Bartlett 6097 (L); Colani s.n., Herb. Ecole Sup. Hanoi 5212 (BM); Fauri 193 (U), 477 (U), 646 (U); Linsley-Gressitt 348 (U, L). — *Microsorium hancockii* (Bak.) Ching: Bautun 48/315 (BM); Fauri 201 (U), 204 (U) 474 (U); Hooker & Thomson s.n. (U55260B); Kramer & Nair 6019 (U); Linsley-Gressitt 271 (U); Tagawa 7696 (U), 7742 (U). — *Microsorium heterocarpum* (Blume) Ching: Brooks 221-s (BM); Elmer 20871 (U); Henderson 18588 (BM); Samat b. Abdullah 257 (U). — *Microsorium hymenodes* (Kuntze) Ching: Cavalerie 670 (K), 698 (BM); Copeland 281 (BM); Dickason 7754 (BM); Eberhardt S147 (BM); Esquirol 2031 (BM); 3124 (BM); Fang 2493 (K); 7503 (K), 8498 (K), 8494 (K), 8501 (K); Forrest 9453 (K); Hancock s.n. (K); Henry 1489 (K), 9265 (K), 13340 (BM); Linsley-Gressitt 156 (K), 1516 (BM); Ludlow, Sherriff & Elliot 12103 (BM), 12144 (BM); Maire s.n. (BM); Malhotra 124 (BM), McGregor 19810 (BM); Molesworth-Allen 2188 (BM); Petelot 1603 (BM), s.n. (BM); Poilane 3708 (BM); Rosenstock 112 (BM); Shiu Ying Hu 12555 (K); Tsiang 7646 (K). — *Microsorium insigne* (Blume) Ching: Chew et al. 577 (L); v. Steenis 12743 (L). — *Microsorium (Neocheiropteris) lastii* (Bak.) Tard.: Perrier de la Bathie 7493 (P), 7937 (P), 15621 (P). — *Microsorium lati-*

lobatum Hennipman & Hetterscheid: Balansa 799 (P); Baudouin 4 (P); Cribs 453 (P); Franc 656 (P), 686 (P), 1081 (P); Germain s.n. (P); Guillaume & Baumann-Bodenheim 10247 (P); 10415 (P); Mackee 4777 (P), 7953 (P), 8170 (P), 12043 (P), 12141 (P), 14420 (P); Montrouzier 250 (P); Vieillard 1525 (P, p.p.), 1526 (P, p.p.), 1528 (B). — *Microsorium leandrianum* Tard.: Capuron, Leandri & Razafindrakoto 1900 (P, type), Humbert 15565 (P); Leandri 810 (P), Leandri & Saboureau 2859 (P). — *Microsorium linguaeforme* (Mett.) Copel.: Brass 27434 (L); 27973 (L); Buwalda 5114 (L); Docters v. Leeuwen 9275 (L); Gjellerup 70 (U); Pulle 116 (U). — *Microsorium longissimum* (J. Smith) Fée: Cuming 66 (BM); Edano, PNH 4540 (L); Gutierrez 78328 (L); v. Steenis 17888 (L). —*Microsorium lucidum* (Roxb.) Copel.: Bir s.n. (U 093054B); Hooker s.n. (U 55227B); Simons s.n. (U 045174). — *Microsorium membranaceum* (Blume) Copel.: Elmer 8367 (U); Fauri 210 (U); Hennipman 3360 (L); Hooker s.n. (U 55228B); Hooker & Thomson s.n. (U 55225B); Iwatsuki et al. T9600 (L); Larsen, Santisuk & Warncke 2314 (L); Linsley-Gressitt 371 (U); Maas Geesteranus 14110 (L); Merrill 956 (U); Mridul s.n. (U 104763B); Murata et al. T15642 (L); Sabhaywal s.n. (U 176584B); Stocks s.n. (U 55223B). — *Microsorium monstrosum* Copel.: Elmer 8536 (U), 17761 (U); Merrill 955 (U). — *Microsorium musifolium* (Blume) Copel.: Anon. (U 045249); Docters v. Leeuwen 9853 (L); Foreman & Vinas, LAE 60249 (L); Jacobs 5070 (L); Lam 1108 (U). — *Microsorium aff. M. musifolium* (Blume) Copel.: Merrill 699 (U); Pulle 376 (U); Stone 4262 (U). — *Microsorium (Neocheiropteris) normale* (Don) Ching: Bünnemeijer 9552 (U); Hennipman 3393 (L); Hooker s.n. (U 55240B); Kramer & Nair 5990 (U); Lörzing 6785 (U); Tagawa et al. T2885 (L). — *Microsorium novae-zealandiae* (Bak.) Copel.: Hynes s.n. Plants of New Zealand 30265 (U). — *Microsorium pappei* (Mett. ex Kuhn) Tard.: Baron 3681 (P), 5310 (P); Capuron 3RC (P); Correard s.n. (P); Cours 822 (P); Decary 1743 (P), 17465 (P); Dümmer 472 (P); Forsyth Major 165 (P. p.p.); Perrier de la Bathie 15622 (P); Schelpe 5319 (P); Schlieben 2761 (P); Stolz 868 (P). — *Microsorium pentaphyllum* (Bak.) Copel.: Elmer 10768 (L), 17550 (U), 18211 (U). — *Microsorium polynesicum* (C. Chr.) ined.: Vaupel 40 (U). — *Microsorium pteropus* (Blume) Ching: Anon. 65 (U 55239B); Bakhuizen v.d. Brink jr. 559 (U), s.n. (U 25413A); Hennipman 3533 (U); 3955 (L); Samat b. Abdullah 438 (U); Sidney s.n. (U 204384B); Simons s.n. (U 55229B). — *Microsorium punctatum* (L.) Copel.: Anon. 11 (U 045243), (U 045455); Bakhuizen v.d. Brink jr. 2518 (U); Bünnemeijer 4315 (U), 12427 (U); Buysman 343 (U), Herb. Anal. 2746 (U); Dietrich 404 (U), 480 (U); Docters v. Leeuwen-Reijnvaan 1374 (U), 1534 (U); Elmer 7854 (U), 8263 (U); 16863 (U), 17511 (U); Fauri 198 (U); Geesink & Santisuk 5010 (L); Hennipman 3065 (L), 3531 (U); Huang & Kao, HNTU 7521 (U); Jacobson s.n. (U 20045A); Lam 843 (U), 1145 (U); Leeuwenberg 1785 (U), 2542 (U), 5032 (U), 6651 (U); Leeuwenberg & Voorhoeve 4689 (U); Lörzing 5652 (U); Merrill 665 (U), 698 (U); Rutten 141 (U); Samat b. Abdullah s.n., collection Turnau 904 (U); "Students" 9 (U 250760B); Taylor 1661 (U). — *Microsorium sablanianum* (Christ) Copel.: Alcasid et al., PNH s.n. (L.

951.97—458); Brooke, BAU 9869 (L); Brooks s.n. (BM); Gutierrez et al., PNH 117267 (L); Sulit. PNH 20241 (L). — *Microsorium sarawakense* (Bak.) Holttum: Bünnemeijer 8631 (L); Clemens 26943 (L); Holttum, SF 21502 (BM); Kiak, SF 23921 (BM); Nur 11053 (BM); Sinclair & Kiak, SF 38668 (BM). — *Microsorium scandens* (Forster f.) Tindale: Anon. (U 20267B), (U 20269B); Brownlie s.n. (U 127373B); Bukler s.n. (U 20271B); Constable, NSW P7073 (U); Hennipman 6280 (U); Hooker s.n. (U 20268B); Melville & Tindale, NSW P6410 (U); Muller 1861 (U); Posthumus 3870 (L); Smith 04771A (L); Varekamp 63 (L); Watts & Boorman, NSW P6118 (L). — *Microsorium sibomense* (Ros.) Copel.: Bamler 52 (BM); Carr 12929 (BM); Croft 386 (K); Gawi 9 (K); Hartmann 58 (BM); Hoogland 4395 (BM); Kimbag 004 (K); King 364 (BM); Kog 009 (K); Palis 2 (K); Streimann, NGF 45182 (K); Unkau 049 (K). — *Microsorium spectrum* (Kaulf.) Copel.: Lane 56—581 (U); H. & M. Lyon 1169 (L). — *Microsorium superficiale* (Blume) Ching: Bünnemeijer 4544 (U); Fauri 4878 (BM); Groenhart 228 (U); Hennipman 3283 (U); Hooker & Thomson s.n. (U 55248B); Mousset s.n. (U 029991); Pulle 3044 (U), s.n. (U 260584B); Simons s.n. (U 55249B); Wilford s.n. (BM). — *Microsorium tenuilore* (J. Smith) Copel.: Cachalian 126 (BM); Copeland 247 (BM); Cuming 287 (BM); Edano, BS 41703 (L); Elmer 16567 (U); Iwatsuki et al. P-1200 (L). — *Microsorium varians* (Fourn.) Hennipman & Hetterscheid: Balansa 1579 (P); Baudouin s.n. (P); Baumann-Bodenheim & Guillaumin 5441 (P), 8777 (P), 8788 (P), 8892 (P); Lécard s.n. (P); M. & Mme. Le Rat 63 (P), 958 (P); Mackee 5646 (P), 6558 (P); Mazagot s.n. (P); Schlechter 15612 (B, P); Vieillard 1525 (P, p.p.), 1526 (P, p.p.), 1528 (P). — *Microsorium vieillardii* (Mett.) Copel.: Crebs 503 (K); Deplanche 1 (K), 189 (K); Franc 340 (K); McGillivray 742 (K); Schlechter 14874 (K), 15493 (K). — *Microsorium zippelii* (Blume) Ching: Buysman 46 (U, p.p.), 2819 (U); Cockburn 94/95 (BM); Groenhart 23 (U); Hennipman 3706 (L); Holstvoogd 532 (L); Mann s.n. (L 3-1888); Pulle 3042 (U); Raciborsky s.n. (L 937. 232-61). — *Microsorium spec.*: Croft et al., NGF 12988 (L); Croft & Lelean LAE 65641 (L); Floyd 3517 (L); Foreman & Vinas, LAE 60249 (L); Hennipman 5618 (L); 5619 (L); Wormersley & Millar NGF 8519 (L).

Neocheiropteris palmatopedata (Bak.) Christ: Anon. 4162 (L 951.19-892); Beauvois 830 (P); Bodinier 25 (P), 2542 (P); Bodinier & Ducloux 25 (P); Cavalerie 4021 (P), 4162 (P); Delavay 1196 (P); Ducloux 25 (P), 2246 (P), 2419 (P), 5052 (P), 5489 (P), 7465 (P); Henry 9289 (P, type).

Neolepisorus ensatus (Thunb.) Ching: Azuma s.n. (U 47432B); Murata et al. 55 (U); Tagawa 2410 (U), 7465 (U), 7637 (U), 7650 (U); Tagawa & Iwatsuki 539 (U). — *Neolepisorus ovatus* (Bedd.) Ching: Balansa 1937 (P); Bon 3248 (P), 3291 (P); Colani 2835 (P), 2973 (P), 4915 (P); Eberhardt 5106 (P), 5111 (P); Poilane 18888 (P).

Paraleptochilus decurrens (Blume) Copel.: Anon. (U 045127), (L 908.206—57); Balansa 1893 (L); v. Beusekom & Phengkhlai 202 (L); Bir s.n. (U 09353B); Forbes 1226 (BM); v. Hardeveld & v.d. Werff 222 (U); Hennipman 3048 (L), 3737 (L), 3836a (U, L); Holttum SF 23506 (C, BM); Hooker & Thomson s.n. (U 61502B); Kostermans, Kwai Noi Basin exp. 832 (L); Mann s.n. (L 908.286-377); Phengkhlai 37 (L); Posthumus 3468 (L); Rawson 3278 (BM); Rock 2420 (C), 2722 (C); Winckel 1424b (U).

Phymatodes cromwellii (*Polypodium cromwellii* Ros.): Barker et al. LAE 67509 (L); Larivita, LAE 67128 (L). — *Phymatodes nigrescens* (Blume) J. Smith: Anon. 40 (L 908.357—101), Herb. Div. Bot. Java 201 (U), (U 045172), (U 045248); Bakhuizen v. d. Brink 2094 (U); Brass 23520 (L); Bünnemeijer 5374 (U); Buysman 47 (U), 2820 (U); Docters v. Leeuwen 9587 (U); Edeling 163 (U), 224 (U) 231 (U); Elmer 16282 (U), 18418 (U); Hoogland 4514 (L); Koopen 1023B (U), 1968 (U); Kramer & Nair 6153 (U); Lam 1139 (U); Nooteboom 1160 (L), 1210 (L); Pulle 449 (L), 3187 (U); Ramos, BS 1015 (U); Surbeck 574 (L). — *Phymatodes papuana* (*Polypodium papuanum* Bak.): Bamler 259 (BM); Kostermans & Soegeng 587 (L); v. Royen 3319 (BM). — *Phymatodes scolopendria* (Burm.) Ching: Bakhuizen v. d. Brink 696 (U); Brass 6345 (L); Buwalda 4828 (L); Edeling 194 (U), 208 (U), 218 (U); Elmer 16742 (U); Furuse et al. 646 (U), 1163 (U); Groenhart 29 (U); Hennipman 5972 (L); Iwatsuki et al. S. 1696 (L); Kalkman 4215 (L); Korthals s.n. (U 045234); Nedi & Idjan 164 (L); Schiffner s.n. (L 942.123—152); Teysman 5 (U), s.n. (U 24301B).

Podosorus angustatus Holttum: Guttierrez, PNH 78332 (K, type, L).

References

van Alderwerelt van Rosenburgh, C.R.W.K. 1908: Malayan Ferns. — Landsdrukkerij, Batavia.

Beddome, R. H. 1868: The ferns of British India. II. — Gantz Brothers, Madras.

Copeland, E. B. 1928: *Leptochilus* and genera confused with it. — Philipp. J. Sci. 37(4): 333—415.

— 1931: Miscellaneous oriental pteridophytes. — Univ. Calif. Publ. Bot. 12(5): 383—418.

— 1947: Genera Filicum. — Chronica Botanica Co., U.S.A.

Crabbe, J. A., Jermy, A. C. & Mickel, J. T. 1975: A new generic sequence for the pteridophyte herbarium. — Fern Gaz. 11: 141—162.

Hennipman, E. 1977: A monograph of the fern genus *Bolbitis* (Lomariopsidaceae). — Leiden Bot. Ser. 2.

— 1984: A new approach to the systematics of the Polypodiaceae (Filicales). — Taxon 33(1): 140—141.

Hennipman, E. & Hetterscheid, W. L. A. 1984: The emendation of the fern genus *Christiopteris*, including the transference of two taxa to the microsorioid Polypodiaceae. — Bot. Jahrb. Syst. 105: 1—10.

Hennipman, E. & Roos, M. C. 1983: Phylogenetic systematics of the Polypodiaceae (Filicales). — Verh. Naturwiss. Vereins Hamburg 26: 321—342.

Hetterscheid, W. L. A. 1984: Venation-pattern analysis, soral characters, and their bearing on the systematics of microsorioid Polypodiaceae. — Acta Bot. Neerl. 33 (2): 243 (abstract).

HOLTTUM, R. E. 1954: A revised flora of Malaya. II, Ferns of Malaya.
— 1966: New ferns from Malesia. — Kew Bull. 20(3): 455—460.
JERMY, A. C. & WALKER, T. G. 1975: *Lecanopteris spinosa* — A new ant fern from Indonesia. — Fern Gaz. 11:: 165—176.
MITSUTA, S. 1981: Venation of *Lepisorus* and *Pleopeltis* (Polypodiaceae). — Acta Phytotax. Geobot. 32(5—6): 147—164. (In Japanese with an English summ.).
— 1982: Studies in the venation and systematics of the Polypodiaceae. I—III. — Kyoto University (unpubl.)
PICHI SERMOLLI, R. E. G. 1977: Tentamen Pteridophytorum genera in taxonomicum ordinem redigendi. Webbia 31(2): 313—512.
PRICE, M. G. 1974: Nine new fern names. — Kalikasan, Philipp. J. Biol. 3: 173—178.
SEN, U. & HENNIPMAN, E. 1981: Structure and ontogeny of stomata in Polypodiaceae. — Blumea 27: 175—201.
TRYON, R. 1960: A glossary of some terms relating to the fern leaf. — Taxon 9: 104—109.

Accepted for publication May 11, 1984

Address of the authors:
W. L. A. HETTERSCHEID & E. HENNIPMAN, Institute of Systematic Botany, University of Utrecht, Heidelberglaan 2, NL-3508 TC Utrecht, The Netherlands.